The Liochelidae Fet & Bechly, 2001 (Scorpiones) of the Indo-Pacific Region

systematics and biogeography

by

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Volume I

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DISCLAIMER

All nomina followed by the acronym “n. sp.” designate new species that were discovered in the course of the present study but have not been formally described and named yet. These manuscript names will be made available in forthcoming publications.

ABSTRACT

THE LIOCHELIDAE FET & BECHLY, 2001 (SCORPIONES) OF THE INDO-PACIFIC REGION

SYSTEMATICS AND BIOGEOGRAPHY

by

Lionel Monod

Advisor: Doctor Lorenzo Prendini

The aim of the present project was to reassess the systematics, phylogeny and biogeography of the Indo-Pacific taxa of the scorpion family Liochelidae Fet & Bechly, 2001 based on morphology and molecules. The morphological matrix comprised of 85 terminal taxa and 263 characters was compiled based on the examination of more than 4000 specimens including most of the types and fresh material collected during several field surveys in Australia, Malaysia, New Caledonia, the Solomon Islands and Thailand. 101 DNA samples representing 42 taxa, half of the known diversity, were obtained for the molecular analysis. Three mitochondrial and two nuclear genes (approximately 4180 base-pairs) were sequenced from each sample. Cladistic analyses were then performed on the morphological, the molecular and the combined datasets respectively. Finally, dates of cladogenesis events estimated using molecular clocks were used to infer a plausible biogeographical hypothesis.

Results of the taxonomic revision lead to the following emendations: (1) the elevation of the subfamily Hormurinae Laurie, 1896 to family level, (2) the revalidation of *Hormiops* Fage, 1933 and *Hormurus* Thorell, 1876 that were placed into synonymy with *Liocheles* Sundevall, 1883, (3) the revalidation of 10 species placed into synonymy (eight *Hormurus* spp., two *Liocheles* spp.), (4) the discovery of 51 new species (1 *Hormiops*, 48 *Hormurus*, 1 *Liocheles*, 1 *Opisthacanthus* Peters, 1861 (*Monodopisthacanthus* Lourenço, 2001)), (6) the elevation of two subspecies to species rank, and (5) the synonymy of one genus (*Tibetiomachus* Lourenço & Qi, 2006), three species and one subspecies.

The biogeographical analysis indicates that vicariance, dispersal and vicariance are not mutually exclusive and that all three mechanisms played a significant role in the develop-

ment of the Indo-Pacific liochelids. The phylogeny and dating do not corroborate the “out-of-India” origin for the Southeast Asian taxa, but rather suggest that they may be part of an ancient Laurasian lineage. On the other hand, the colonisation of the Australo-Papuan Archipelago from Sundaland by liochelids is confirmed. However, the age estimate of divergence between Melanesian *Hormurus* and Asian *Liocheles* in the Paleocene contradicts the current geological model and suggests the existence of land connections between the two provinces well before the Eocene.

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INTRODUCTION
-
HISTORICAL CONTEXT

0.1 INTRODUCTION

Scorpions are among the oldest extant arthropods, with a fossil record dating to the mid Silurian, ca. 425–450 million years ago (Sissom, 1990). With more than 1700 scorpion species currently described (Fet & al., 2000), scorpions are widely distributed, occurring on all continents except Antarctica. They occur in every habitat, including deserts, savannas, grasslands, temperate forests, tropical forest, caves, and the intertidal and alpine zones with the exception of boreal ecosystems (Polis, 1990). Except for a few adaptable species, which exhibit a high degree of plasticity in habitat use, most scorpions are quite specific in microhabitat requirements (Polis, 1990). Because they are an old group phylogenetically, and exhibit high levels of endemism, they represent very interesting model organisms for biogeographical studies.

The family Liochelidae Fet & Bechly, 2001 represents a fascinating group with some of the most striking biological and morphological characteristics. The genus *Hadogenes* Kraepelin, 1894 is particularly remarkable and has sparked considerable interest among arachnologists. Besides including some of the largest living scorpions (Newlands, 1972A), it displays an extreme sexual dimorphism in metasoma length (fig. 1), with males up to 21 cm (Newlands, 1974). This unusual elongation of male metasoma is only reported in three closely related families, i.e. Hemiscorpionidae Pocock, 1893, Heteroscorpionidae Kraepelin, 1905 and Urodacidae Pocock, 1893 and is considered as an adaptation to live in narrow crevices of rocky environments (Newlands & Prendini, 1997; Prendini, 2001A, 2001C; Leeming, 2003; Lowe, 2010A). *Hadogenes* species, commonly known as flat rock scorpions, are obligate lithophiles and inhabit exclusively the narrow cracks, crevices and exfoliations of weathered rocky outcrops (Newlands, 1972A; Newlands & Prendini, 1997; Prendini, 2001A, 2001C, 2005, 2006). Furthermore, their potential longevity is exceptional for terrestrial arthropods. Some species may take 8-10 years to reach sexual maturity (Newlands & Cantrell, 1985) and live more than 30 years (Newlands, 1980). Unfortunately they are particularly vulnerable to habitat destruction because of their extremely specific ecological requirements and the restricted extent of their populations (Newlands, 1972B; Prendini, 2001A, 2001C, 2005, 2006). Moreover, their large size, peculiar appearance, docile temperament and mild venom make them particularly popular amongst amateur biologists and they are commonly kept in captivity. However, wild populations are slow

Fig. 1. *Hadogenes zumpti* Newlands & Cantrell, 1985. This species from the Northern Cape (South Africa) is a perfect example of the extreme sexual dimorphism in the metasoma elongation, characteristic of the genus. A, Male. B, Female. Photographs by R. Mercurio and L. Prendini.

A
B

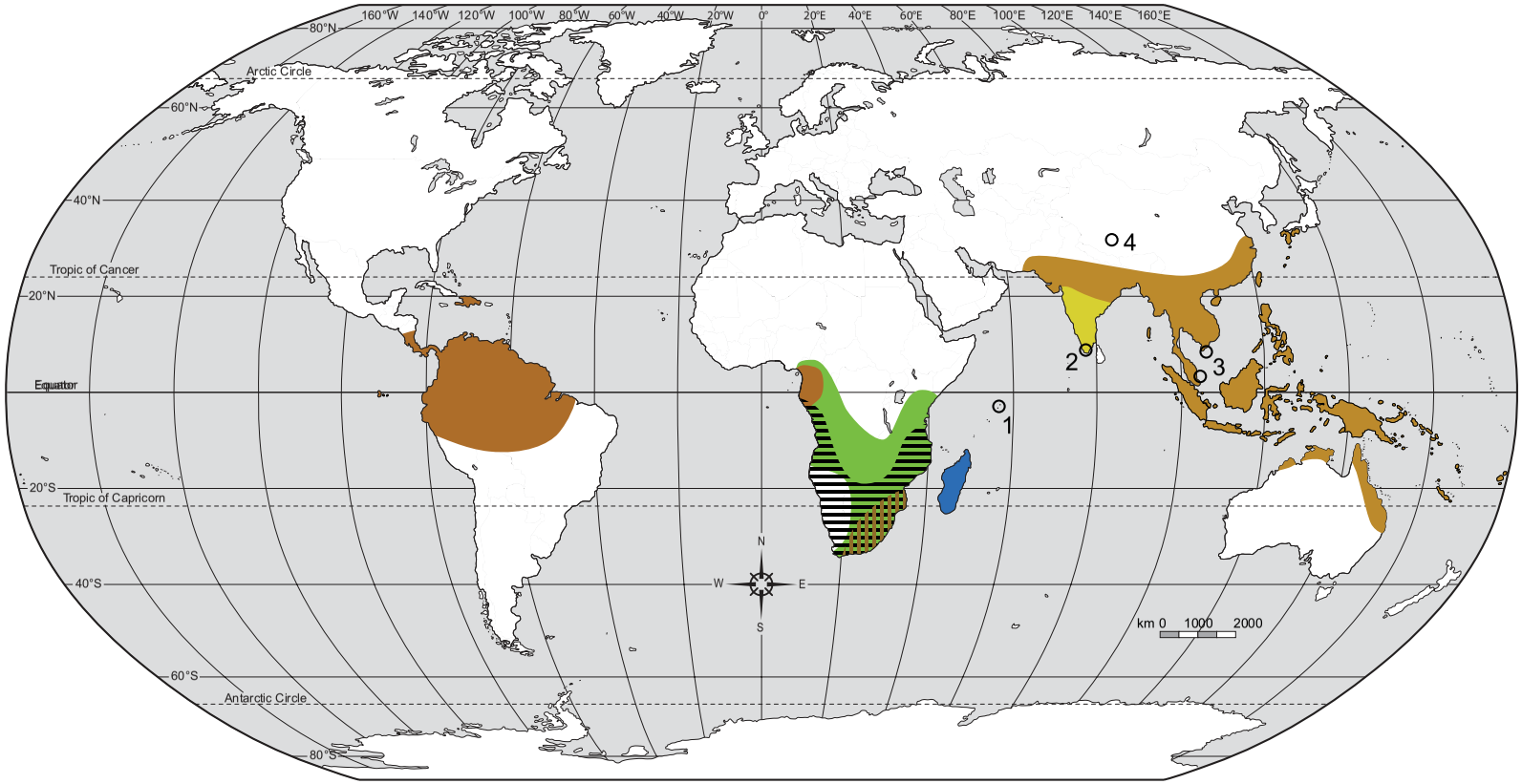
to repopulate and overharvesting for the international pet trade poses a major threat (Prendini, 2001A). Prendini (2001A, 2006) already recommended to assign several species to the IUCN Red List and many more for which data are currently insufficient should undoubtedly also be considered as threatened. Although not as marked as *Hadogenes*, the other liochelid genera also exhibit high specificity in their habitats use and ecology which make them vulnerable to the same threats but also good biogeographic models.

Liochelids are present in all southern continents (fig. 2). The family is thus regarded as a typical Gondwanan element and its evolution considered as intricately connected with the break-up and dispersion of the supercontinent Gondwana. The genus *Liocheles* Sundevall, 1883 which occurs from India to western Pacific islands, is particularly interesting in that respect. Its presence in Australia is not regarded as the result of vicariance events but rather as the result of secondary dispersal from India to Southeast Asia and then to Australia and Oceania during the Cenozoic (Koch, 1977; Sissom, 1990). A taxonomic and phylogenetic reappraisal of this poorly know genus and its close relatives in the Indo-Pacific region was conducted in the course of the present project in order to clarify the ambiguous biogeography of the group. Congruence between current liochelid distribution patterns and the complex geological history of the Indo-Pacific region (Whitmore, 1981, 1987; Besse & Courtillot, 1988; Patriat & Ségoufin, 1988; Ladiges & al., 1991; Plummer & Belle, 1995; Keast & Miller, 1996; Kroenke, 1996; Hall & Holloway, 1998; Metcalfe, 1999; Metcalfe & al., 2001; Hall, 1998, 2002) was used to test the different biogeographical theories.

0.2 SYSTEMATICS OF THE FAMILY LIOCHELIDAE

Fet *et al.* (2000) recognized 16 families in their catalogue of the scorpions of the world. The family Ischnuridae Simon, 1879 was first established by Simon (1879). Although once cited by Becker (1880), the name was not formerly recognised before Pocock (1893) who then considered it as a subfamily of Scorpionidae Latreille, 1802, i.e. the Ischnurini Simon, 1879. Thorell (1894) and Kraepelin (1894) followed Pocock's (1893) classification but Laurie (1896a) regarded Ischnuridae and Scorpionidae as separate families. However Laurie (1896b) subsequently embraced Pocock's nomenclature and downgraded the Ischnuridae to subfamilial rank

Fig. 2. Approximate distributional ranges of the genera belonging to the family Liochelidae Fet & Bechly, 2001.



Cheloctonus

1 *Chiromachus*

2 *Chiromachetes*

Hadogenes

3 *Hormiops*

Iomachus

Liocheles

Opisthacanthus (Monodopisthacanthus)

Opisthacanthus (Nepabellus)

Opisthacanthus (Opisthacanthus)

Paleocheloctonus

4 *Tibetiomachus*

within Scorpionidae. He also separated the genera *Hormurus* and *Iomachus* from the Ischnurini previously recognized by Pocock and placed them in their own subfamily, i.e. Hormurini Laurie, 1896 (type genus *Hormurus* Thorell, 1876). Kraepelin (1899) did not accept this division and combined both subfamilies into the initial Ischnurini. Pocock (1900) later assigned family level to Ischnurini but his decision was disregarded by Kraepelin (1901) and others. Kraepelin (1913) eventually acknowledged the subfamily Ischnurinae as a family. Birula (1917) provided a thorough review of previous classifications of scorpions and proposed his own revised version. He divided the family Scorpionidae into two tribes, i.e. Ischnuraria Simon, 1876 and Scorpionaria Latreille, 1802. Ischnurinae Simon, 1876 and Hormurinae Laurie, 1896 were among the four subfamilies assigned to Ischnuraria by the Russian taxonomist. All subsequent authors treated Ischnuridae as a subfamily of Scorpionidae except Fage (1933, 1946) who considered the group as a family. However, Fage was not able to convince his peers and his decisions were disregarded as well. Ischnuridae was finally re-elevated to family rank by Lourenço (1989). Lourenço (1999) later established a separate monotypic subfamily Hadogenidae Lourenço, 1999 based on the genus *Hadogenes* and placed under family Scorpionidae. Lourenço (2000) subsequently elevated this subfamily to family rank but this nomenclatural change was unanimously rejected (Prendini, 2001a; Soleglad *et al.*, 2003) and Hadogenidae was placed in synonymy with Ischnuridae. The name Liochelidae was proposed by Fet & Bechly (2001) to remove homonymy with Ischnurinae Fraser, 1957 (Insecta, Odonata) and approved by the ICZN (2003). The family Hemiscorpiidae Pocock, 1893 is considered to be the sister group of Liochelidae by Stockwell (1989) and Prendini (2000). In their revised classification of extant scorpions, Soleglad & Fet (2003) downgraded Hemiscorpiidae to a subfamily of Liochelidae. Soleglad *et al.* (2005) later proposed Hemiscorpiidae as a senior synonym of Liochelidae, and Hormurinae as a senior synonym of Liochelinae Fet & Bechly, 2001. However, Prendini & Wheeler (2005) rejected these changes and reinstated Liochelidae and Hemiscorpiidae.

Scorpions of the family Liochelidae are today well defined by several morphological characters, such as trichobothrial patterns and the shape of lateroapical lobes of the leg tarsi (Sissom, 1990), but phylogenetic relationships within the family remain poorly understood (Prendini, 2000) and the validity of some genera uncertain. This can be attributed in part to the

Table 1. Genera and sub-genera currently recognized in the family Liochelidae Fet & Bechly, 2001.

Genus ***Cheloctonus*** Pocock, 1892
TYPE SPECIES: *Cheloctonus jonesii* Pocock, 1892. 5 species, 6 subspecies.
DISTRIBUTION: AFRICA, Mozambique, Lesotho, South Africa, Swaziland.

Genus ***Chiromachetes*** Pocock, 1899
TYPE SPECIES: *Chiromachetes fergusoni* Pocock, 1899. 2 species.
DISTRIBUTION: ASIA, India.

Genus ***Chiromachus*** Pocock, 1893
TYPE SPECIES: *Chiromachus ochropus* (C.L.Koch, 1837). 1 species.
DISTRIBUTION: AFRICA, Mascarene Islands (Mauritius, Round Island), Seychelles, Tanzania (Zanzibar), Madagascar.

Genus ***Hadogenes*** Kraepelin, 1894
TYPE SPECIES: *Hadogenes trichiurus* (Gervais, 1843). 20 species, 12 subspecies.
DISTRIBUTION: AFRICA, Angola, Botswana, Democratic Republic of Congo, Mozambic, Namibia, South Africa, Swaziland, Tanzania, Zimbabwe.

Genus ***Iomachus*** Pocock, 1893
TYPE SPECIES: *Iomachus laeviceps* (Pocock, 1890. 6 species, 4 subspecies.
DISTRIBUTION: AFRICA, Ethiopia, Kenya, Mozambique, Tanzania, Uganda. ASIA, India.

Genus ***Liocheles*** Sundevall, 1833
TYPE SPECIES: *Liocheles australasiae* (Fabricius, 1775). 14 species.
DISTRIBUTION: ASIA, Aru Islands, Bangladesh, Cambodia, China, India, Indonesia, Japan, Korea, Laos, Malaysia, Myanmar, Papua New Guinea, Philippines, Thailand, Vietnam. AUSTRALIA, Australia, Christmas Island, Cocos Islands. OCEANIA, Federated States of Micronesia, Fiji, French Polynesia, Key Islands, Kiribati, Mariana Islands, Marshall Islands, New Caledonia, Palau, Ponape, Tuvalu, Samoa, Solomon Islands, Tonga, Vanuatu.

Genus ***Opisthacanthus*** Peters, 1861
Subgenus ***Opisthacanthus*** Peters, 1861
TYPE SPECIES: *Opisthacanthus elatus* (Gervais, 1844). 8 species.
DISTRIBUTION: AFRICA, Cameroon, Gabon. CENTRAL AMERICA & CARIBBEAN, Costa Rica, Haiti, Dominican Republic, Panama. SOUTH AMERICA, Brazil, Colombia, French Guiana, Peru, Venezuela.

Subgenus ***Monodopisthacanthus*** Lourenço, 2001
TYPE SPECIES: *Opisthacanthus madagascariensis* Kraepelin, 1894. 5 species.
DISTRIBUTION: AFRICA, Madagascar.

Subgenus ***Nepabellus*** Francke, 1974
TYPE SPECIES: *Opisthacanthus* (*Nepabellus*) *africanus* Simon, 1876. 11 species, 2 subspecies.
DISTRIBUTION: AFRICA, Angola, Botswana, ?Central African Republic, Cameroon, Congo, Democratic Republic of Congo, ?Equatorial Guinea, Gabon, Kenya, Lesotho, Malawi, Mozambique, South Africa, Swaziland, Tanzania, Zimbabwe.

Genus ***Palaeocheloctonus*** Lourenço, 1996
TYPE SPECIES: *Palaeocheloctonus pauliani* Lourenço, 1996. 1 species.
DISTRIBUTION: AFRICA, Madagascar.

† Genus ***Protoischnurus*** Carvalho & Lourenço, 2001
TYPE SPECIES: *Protoischnurus axelrodorum* Carvalho & Lourenço, 2001. 1 species.
GEOLOGICAL OCCURENCE: Lower Cretaceous (Aptian/Albian) of Brazil.

Genus ***Tibetiomachus*** Lourenço & Qi, 2006
TYPE SPECIES: *Tibetiomachus himalayensis* Lourenço & Qi, 2006. 1 species
DISTRIBUTION: ASIA, China (Tibet).

lack of recent global taxonomic revisions on and within the family. Few regional treatments provide keys for determination of liochelid scorpions. Lamoral (1979) revised the Namibian species of *Hadogenes*, while the Indian *Iomachus* Pocock, 1893 species were revised by Sreenivasa-Reddy (1968a, b, c, d) and Tikader & Bastawade (1983). The Australo-Papuan and Indian *Liocheles* were revised by Koch (1977) and Tikader & Bastawade (1983) respectively. *Opisthacanthus* Peters,1861 is the only genus for which a complete revision has thus far been published (Lourenço, 1988). A preliminary revision of *Liocheles* (Monod, 2000), demonstrated that species richness is much higher than previously expected and emphasized the taxonomic value of characters previously neglected. Hemispermatophores were particularly useful for species differentiation. Liochelidae currently includes 74 species and 24 subspecies in twelve genera and subgenera (see tab. 1), not all of which are recognized by all workers: i.e. *Cheloctonus* Pocock, 1892, *Chiromachetes* Pocock, 1899, *Chiromachus* Pocock, 1893, *Hadogenes* (fig. 1), *Iomachus*, *Liocheles* (fig. 3A), *Monodopisthacanthus* Lourenço, 2001, *Nepabellus* Francke, 1974 (fig. 3B), *Opisthacanthus*, *Palaeocheloctonus* Lourenço, 1996, and *Tibetiomachus* Lourenço & Qi, 2006. Additionally, a fossil genus *Protoischnurus* was described by Carvalho & Lourenço (2001) from the Crato formation of Brazil (lower Cretaceous, 110 Mya) and initially placed in a new extinct family Protoischnuridae. Menon (2007) recently synonymized Protoischnuridae with Liochelidae.

0.3 TAXONOMY OF THE GENUS *LIOCHELES*

Liocheles australasiae (Fabricius, 1775) was the first species of *Liocheles* to be described under the name *Scorpio australasiae* (Fabricius, 1775). Sundevall (1833) then proposed the name *Liocheles* as a subgenus for *Scorpio australasiae* but it is only mentioned in a footnote. Koch (1837) established a new genus, *Ischnurus* C. L. Koch, 1837, describing *Ischnurus complanatus* C. L. Koch, 1837 as the type species. Omitting the work of Sundevall, he (1838) transferred *S*. (*L.) australasiae* to this genus and described *Ischnurus ochropus* C. L. Koch, 1837 from the Seychelles Islands. *Ischnurus* was then accepted as a valid name and several species were subsequently described in this genus, i.e. *Scorpio* (*Ischnurus*) *waigiensis* Gervais, 1843, *Scorpio* (*Ischnurus*) *cumingii* Gervais, 1844, *Ischnurus caudicula* Koch, 1867,

Fig. 3. Liochelid genera. A, *Hormurus caudicula* (C.L.Koch, 1867) from Amamoor State Forest (Queensland, Australia), male. B, *Opisthacanthus* (*Nepabellus*) *capensis* Thorell, 1876 from Western Cape Province (South Africa), female, photograph by R. Mercurio and L. Prendini.

A
B

Ischnurus dechangei Becker, 1880, *Ischnurus neocaledonicus* Simon, 1877, *Ischnurus pistaceus* Simon, 1877. Thorell (1876a) wrongfully considered *Ischnurus trichiurus* (Gervais, 1843) (=*Hadogenes trichiurus*) as the type species of *Ischnurus*. The substantial morphological differences between *I. trichiurus* and *I. caudicula* evidently prompted him to separate the two species and to introduce a new genus, *Hormurus*, in order to accommodate the latter. Karsch (1879a, 1979b) was the first to acknowledge Thorell's new genus *Hormurus* but he (1880) eventually took note of Sundevall's work and synonymized it with *Liocheles*. Simon (1887) was the only author to follow this decision but he (1893, 1899, 1901) subsequently reverted to *Hormurus*. Other authors neglected Karsch's nomenclatural changes and continued to use Thorell's name *Hormurus*. Ten species and five subspecies were thus added to the genus. Kraepelin (1899) was aware of Sundevall's work but nonetheless placed *Liocheles* in synonymy with *Hormurus*; the citation was preceded by a question mark and no further justification given. Pocock (1902) formerly designated *Ischnurus complanatus* as the type species of *Ischnurus* and rightfully concluded that *Hormurus* should be synonymized with *Ischnurus* and that the genus *Chiromachus* Pocock, 1893 should be restored to accommodate *Ischnurus ochropus*. However, his correction was incomplete as he omitted Sundevall's contribution and the genus *Liocheles*. Taxonomists that subsequently worked on these genera did not take Pocock's decisions into consideration and *Hormurus* was still considered as a valid name.

As Karsch (1879a, 1879b) previously, Takashima (1941, 1942, 1945, 1948, 1949, 1950, 1952) noticed that *Liocheles* had priority over *Ischnurus* and *Hormurus* and that it should be used instead. However, as with his German predecessor, Takashima's conclusions were also disregarded or rather remained unknown by the scientific community. The validity of Sundevall's genus *Liocheles* was finally reinstated and endorsed unanimously more than twenty years later with Koch's (1977) taxonomic revision of Australian scorpions. Four species were recently described in *Liocheles* (Francke & Lourenço, 1991; Locket, 1997; Volschenk *et al.*, 2001; Monod & Volschenk, 2004). Besides the closely related genus *Hormiops* Fage, 1933 described from Vietnam by Fage (1933) was synonymized with *Liocheles* by Lourenço (1989). However, the single type species *Hormiops davydovi* Fage, 1933 was not synonymized or discussed. Fet (2000) thus putatively placed *H. davydovi* in synonymy with *L. australasiae*.

Table 2. Species and sub-species currently recognized in the genus *Liocheles* Sundevall, 1883. * : synonyms or subspecies recognized as valid species in Monod's (2000) unpublished Master thesis; (α): species belonging to the *australasiae* group (= *Liocheles* sensu stricto); (ω): species belonging to the *waigiensis* group (= *Hormurus* Thorell, 1876).

Liocheles australasiae (Fabricius, 1775) (α)
DISTRIBUTION: AFRICA, Egypt, Reunion (introduced). ASIA, Bangladesh, China, India, Indonesia, Japan, Korea, Malaysia, Myanmar, ?Nepal, Philippines, Thailand, Timor, Vietnam. AUSTRALIA, Australia, Christmas Island, Cocos Islands. OCEANIA, Federated States of Micronesia, Fiji, French Polynesia, Marianas, Marshall Islands, New Caledonia, Papua New Guinea, Palau, Ponape, Samoa, Solomon Islands, Tonga, Tuvalu, Vanuatu.

* ***Liocheles boholiensis*** (Kraepelin, 1914) (ω)
DISTRIBUTION: ASIA, Philippines.

* ***Liocheles caudicula*** (Koch, 1867) (ω)
DISTRIBUTION: AUSTRALIA (Queensland).

Liocheles davydovi (Fage, 1933) (α)
DISTRIBUTION: ASIA , Vietnam.

Liocheles extensus Locket, 1997 (ω)
DISTRIBUTION: AUSTRALIA (Northern Territory).

Liocheles karschii (Keyserling, 1885) (ω)
DISTRIBUTION: ASIA, Indonesia (West Papua). AUSTRALIA (Queensland). OCEANIA, Key Islands, Solomon Islands.

Liocheles litodactylus Monod & Volschenk, 2004 (ω)
DISTRIBUTION: AUSTRALIA (Queensland).

* ***Liocheles longimanus*** (Werner, 1939) (α)
DISTRIBUTION: ASIA, Indonesia (Sumatra).

* ***Liocheles neocaledonicus*** (Simon, 1877) (ω)
DISTRIBUTION: OCEANIA, New Caledonia.

Liocheles nigripes (Pocock, 1897) (α)
DISTRIBUTION: ASIA, India.

* ***Liocheles papuanus*** (Kraepelin, 1914) (ω)
DISTRIBUTION: OCEANIA, Papua New Guinea.

Liocheles penta Francke & Lourenco, 1991 (ω)
DISTRIBUTION: OCEANIA, Solomon Islands.

Liocheles polisorum Volschenk, Harvey & Locket, 2001 (ω)
DISTRIBUTION: AUSTRALIA, Christmas Island.

Liocheles waigiensis (Gervais, 1843) (ω)
DISTRIBUTION: ASIA, Aru Islands, Indonesia, Papua New Guinea, Philippines. AUSTRALIA. OCEANIA, Palau, Solomon Islands.

Lourenço and Monod (1999) reestablished the validity of the genus although without an empirical phylogenetic analysis to support their decision. Prendini (2000) considered the distinction between *Hormiops* and *Liocheles* unjustified and synonymized *Hormiops* with *Liocheles*. However contrary to Fet (2000), he recognized *Liocheles davydovi* (Fage, 1933) [= *Hormiops davydovi* Fage , 1933] as a valid species.

Currently, the genus *Liocheles* can be divided into two distinct species groups easily distinguishable by the trichobothrial pattern on the external side of the pedipalpal chela (fig. 4), i. e. the *waigiensis* species group (fig. 5A) that correspond to the genus *Hormurus* (presently in synonymy) and the *australasiae* species group (fig. 5B) which contains the type species *L. australasiae* (Monod, 2000; Monod & Volschenk, 2004). Four species are recognised within the *australasiae* species group (*Liocheles* sensu stricto) and ten species within the *waigiensis* species group (*Hormurus*) when considering Monod's (2000) unpublished revision of the genus (see Tab. 2). Over the years, the successive authors who attempted to revise the genus were unable to clearly assess the taxonomic status and position of most species. This can be attributed first to the paucity of diagnostic characters used, *Liocheles* species are indeed extremely similar morphologically. Furthermore the scarcity of material available in museum collections, especially mature males that are essential for specific diagnoses, prevented a thorough systematic revision of the genus, especially given the nature of the characters needed to differentiate species. For instance, assessing differences in density and size of granulation between different species pose major challenges without sufficient comparative material. Moreover describing these kinds of characters is virtually impossible given the subjectivity of the estimate and providing illustrations sufficiently precise to be used by others was also not possible at the time.

These difficulties to appropriately establish specific boundaries within the genus are illustrated by the indecision of the earlier authors regarding the specific status within *Liocheles*, especially species of the *waigiensis* group. Kraepelin (1894) first adopted a conservative approach and recognized only two species within *Hormurus*, i.e. *H. australasiae* and *H. caudicula*. He synonymized six species (*I. dechangei*, *I. neocaledonicus*, *I. waigiensis*, *H. insculptus* Thorell, 1888, *H. karschii* Keyserling, 1885, *H. weberi* Pocock, 1894) with *H. caudicula*,

Fig. 4. Trichobothriotaxic patterns of the external surface of the pedipalp chela in the genus *Liocheles* Sundevall, 1883 (= *Liocheles* sensu lato). A, in the *Liocheles australasiae* species group (= *Liocheles* sensu stricto); male of *Liocheles malaya* n. sp. from Bukit Larut (Malaysia) (MHNG). B, in the *Liocheles waigiensis* species group (= *Hormurus* Thorell, 1876); male of *Hormurus ischnoryctes* n. sp. from Mount Mulligan cattle station (Queensland, Australia) (to be deposited in the collection of the QM). The trichobothrium *Esb* is located approximately mid-palm, close to Est in species of the *waigiensis* group whereas it is basal, close to the *Eb* group in species of the *australasiae* group.

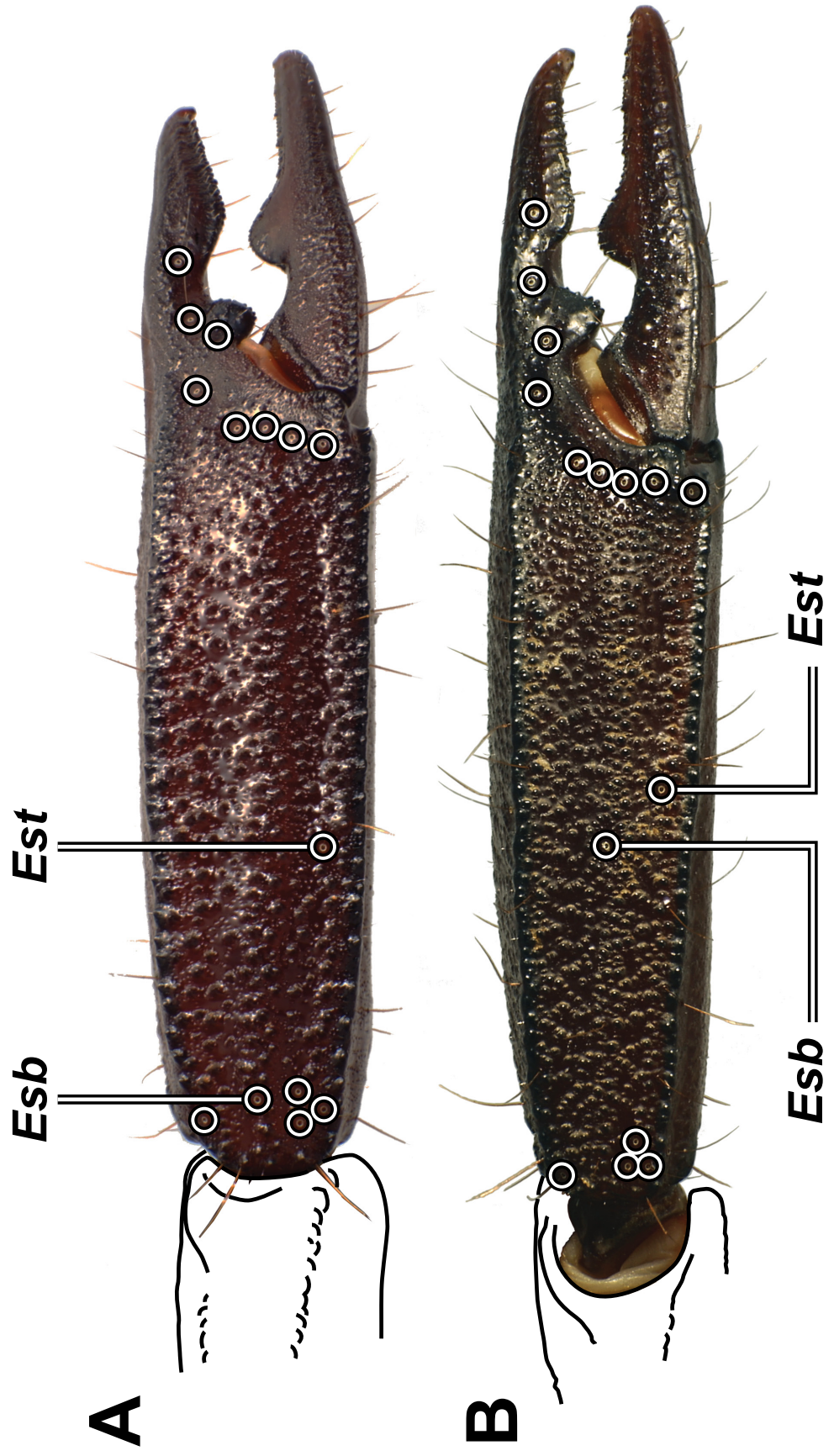

A
Est
Esb
B
Est
Esb

Fig. 5. A, Male of *Hormurus extensus* Locket, 1997 from Kakadu National Park (Northern Territory, Australia) [*waigiensis* species group]. B, Male of *Liocheles australasiae* (Fabricus, 1775) from Krabi Province (Thailand) [*australasiae* species group].

A
B

but treated three of them as distinct varieties (*H. insculptus*, *H. karschii*, *H. weberi*). Although he observed morphological differences between these three latter forms and *H. caudicula*, he considered the differences insufficient to warrant specific status. Kraepelin (1914) later described three new species (*H. boholiensis* Kraepelin, 1914, *H. papuanus* Kraepelin, 1914, *H. sarasini* Kraepelin, 1914), and one new sub-species (*H. karschii keyensis* Kraepelin, 1914) in *Hormurus* and reconsidered the status of several other 'forms': three species (*H. neocaledonicus*, *H. weberi*, *H. karschii*) he previously considered as synonyms were reinstated, three other species (*H. dechangei*, *H. insculptus* and *H. waigiensis*) were recognised as doubtful and left in synonymy with *H. caudicula.* Kopstein (1921) accepted Kraepelin's decision to split *H. caudicula* into several distinct species. Giltay (1931) cited Kraepelin's contribution of 1914 as the reference for taxonomic identification within *Hormurus* but contrary to Kopstein, he regarded the different species of the *waigiensis* group as subspecies of *H. caudicula*. More recently Koch (1977) treated *H. caudicula* and several species considered as valid by Kraepelin (*H. neocaledonicus*, *H. weberi, H. sarasini*) as junior synonyms of *Liocheles waigiensis* (Gervais, 1843). He also confirmed *Liocheles karschii* (Keyserling, 1885) as valid, with *H. papuanus* as a synonym. Although he noted a significant intraspecific morphological variation among the numerous *L. waigiensis* specimens he examined in the course of his revisionary work, he nonetheless did not judge appropriate to split the species into several distinct taxa. Lourenço (1983) was also undecided concerning the validity of the species *L. weberi* and did not exclude a possible synonymy with *L. waigiensis*. Thus *L. waigiensis* is regarded by contemporary authors as a widespread polymorphic species occurring from East Indonesia to the western Pacific islands. However two of its current synonyms are actually valid species (Monod, 2000), i. e. *Liocheles caudicula* (Koch, 1867) and *Liocheles neocaledonicus* (Simon, 1877), and it is probable that more of its synonyms should be given specific status. On the other hand, several species were also placed in synonymy with *L. australasiae* and subsequently considered as 'varieties' or subspecies. Their status was not as ambiguous and debated as for *L. waigiensis* 'forms'. However given the cosmopolitan distributional range of the species and the very complex geological history and biogeography of the Indo-Pacific region, it is very likely that the species actually represent a complex of cryptic species and that several of these 'forms' are also valid species.

A thorough reappraisal of the entire genus with an investigation of new morphological features and the use of new illustrative methods is thus warranted in order to properly clarify its taxonomic composition.

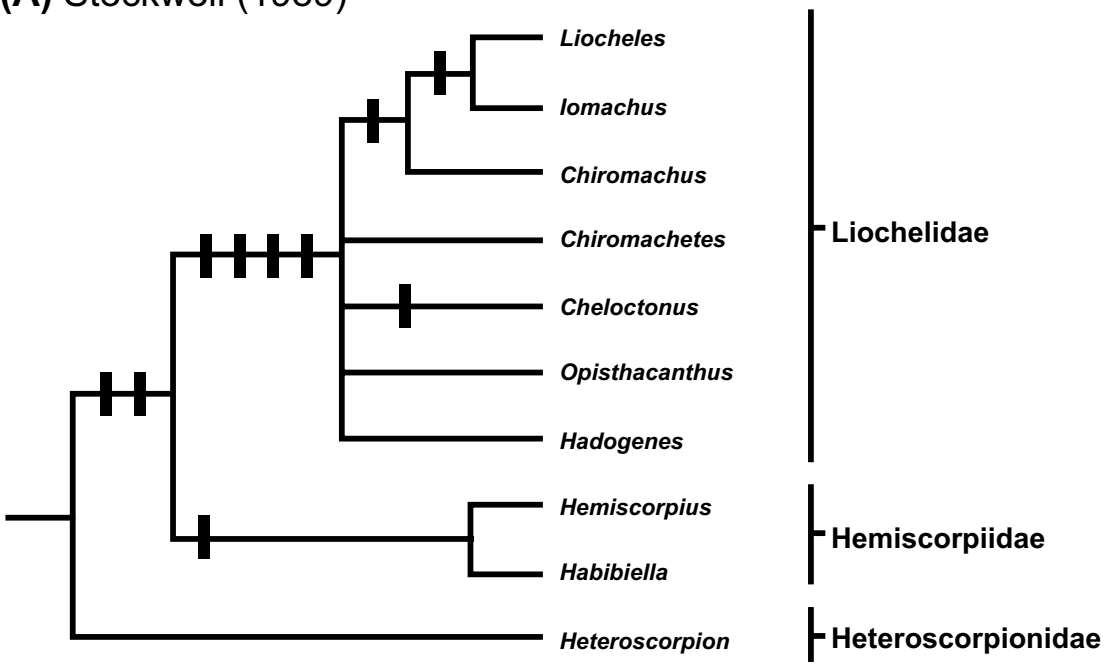
0.4 DISTRIBUTIONAL RANGES, PHYLOGENY, AND BIOGEOGRAPHY OF LIOCHELIDAE

The distributional range of Liochelidae is predominantly 'East Gondwanan' with species occurring in Africa, Australia, south and Southeast Asia (see fig. 2). However, *Opisthacanthus* is present in Africa, Madagascar but also in Central and South America. Three subgenera are currently recognized within *Opisthacanthus*: *Nepabellus* composed of Afrotropical species, *Monodopisthacanthus* with Malagasy species and *Opisthacanthus* Peters, 1961 with Neotropical and West African species. *Hadogenes* and *Cheloctonus* are Afrotropical. *Chiromachetes* occurs in southern India. *Iomachus* occurs in East Africa and India. *Liocheles* is distributed from India to the Pacific Islands (Fig. 9A). *Chiromachus* is only reported on the Mascarene Islands, Seychelles, and Zanzibar. *Palaeocheloctonus* and *Tibietiomachus* were recently described from Madagascar and from the Himalaya mountains of Tibet, respectively.

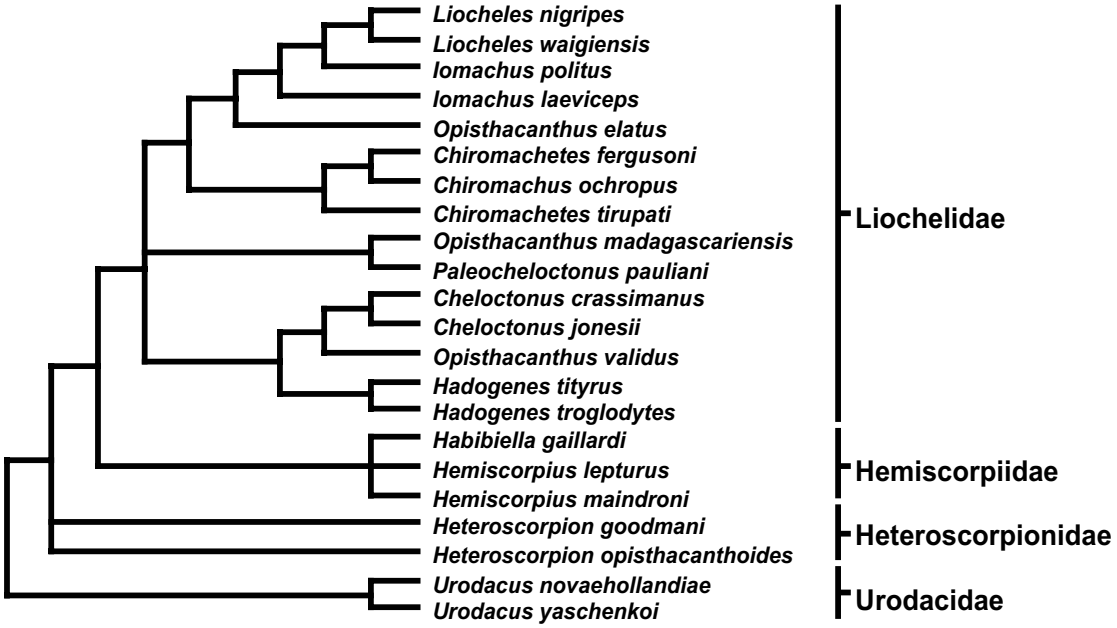
Liocheles appears to be the most derived genus of the family Liochelidae (fig. 6; Stockwell, 1989; Prendini, 2000) and *Iomachus*, which comprises four Indian and two African species, is currently considered its sister taxon. Prendini (2000) demonstrated that *Iomachus* is paraphyletic: the Afrotropical species, *Iomachus politus* Pocock, 1896, formed a monophyletic group with *Liocheles*, while the Indian species, *Iomachus laeviceps* (Pocock, 1890), was excluded from this clade. Hence he proposed to establish a separate genus for the two African *Iomachus*, the Indian species having nomenclatural priority. The taxonomic status of the other Indian liochelid genus, *Chiromachetes,* is also problematic and its validity is so far considered doubtful. This enigmatic genus is only known from two specimens. The type species, *Chiromachetes fergusoni* Pocock, 1899, was described from a single female specimen and a second species, *Chiromachetes tirupati* Lourenço, 1997 from a single male specimen. Stockwell's (1989) phylogenetic analysis placed *Chiromachetes* in a pectinate arrangement with *Cheloctonus*, *Hadogenes*, *Opisthacanthus* and the monophyletic grouping (*Chiromachus* (*Iomachus* + *Liocheles*)). On the other hand, *Chiromachetes* was found to be paraphyletic in Prendini's

Fig. 6. Hypotheses of phylogenetic relationships between liochelid, hemiscorpiid and heteroscorpionid genera derived from morphological analysis. (A) from Stockwell (1989), with synapomorphies indicated. (B) from Prendini (2000).

(A) Stockwell (1989)



(B) Prendini (2000)



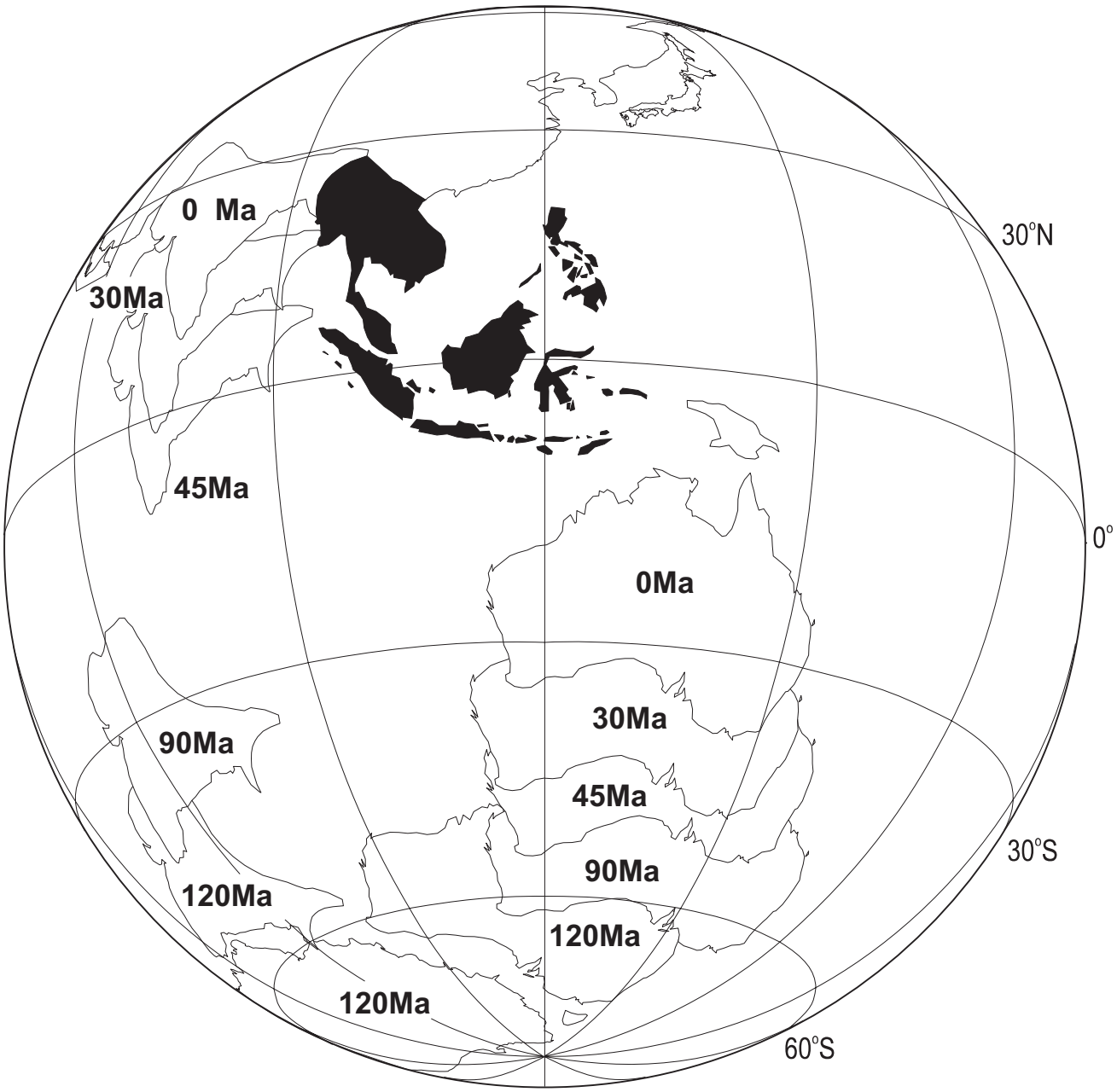
analysis (2000). In the cladogram obtained, *C. fergusoni* formed a monophyletic grouping with the Seychellian *C. ochropus*, while *C. tirupati* was the sister species to this clade. Besides the diagnostic characters that currently defined *Chiromachetes* as a genus are plesiomorphic. Prendini (2000) thus concluded that *Chiromachetes* is a potential synonymy of *Chiromachus* but that liochelid relationships needed to be more thoroughly investigated before a conclusive decision regarding the taxonomic status of the genus can be taken. Prendini (2000) also demonstrated that the largest liochelid genus, *Opisthacanthus*, is a polyphyletic assemblage: (1) The African *Opisthacanthus validus* Thorell, 1876 formed a monophyletic group with the genus *Cheloctonus*; (2) the Neotropical *Opisthacanthus elatus* (Gervais, 1844) was consistently placed as the sister taxon of the monophyletic group (*Iomachus* + *Liocheles*), (3) the African *Opisthacanthus lecomtei* (Lucas, 1858) is more closely related to the South American species, and (4) the Malagasy subgenus *Monodopisthcanthus* grouped with the other Malagasy genus *Palaeocheloctonus*. Hence, Prendini proposed to raise the subgenus *Nepabellus* as Francke (1974) originally stated and to exclude the Malagasy species from *Nepabellus* and placed them in *Palaeocheloctonus*. Neotropical species and the Afrotropical *Opisthacanthus lecomtei* would then be left in the genus *Opisthacanthus*. Lourenço (2001) subsequently erected a new subgenus, *Monodopisthacanthus*, to accommodate the Malagasy *Opisthacanthus* species rather than to place them into *Palaeocheloctonus* as suggested by Prendini.

Currently, the distribution range of the family is regarded as a consequence of vicariance induced by Gondwanaland fragmentation (Sissom, 1990; Lourenço, 1985, 1996A; Soleglad *et al.*, 2005). Common ancestors of the liochelids were widespread across the supercontinent before its breakup, genera subsequently survived on the different fragments (Africa, Madagascar, India and south America) evolving independently from one another. However, the biogeographical origin of Neotropical species of *Opisthacanthus* has been discussed extensively. Newlands (1973, 1978) argued that Neotropical and African lineages should have diverged more recently than *Opisthacanthus* and *Hadogenes* because of the greater morphological differences between the two African genera. Thus he doubted that *Opisthacanthus* presence in the New World was a result of vicariance induced by the fragmentation of the supercontinent Gondwana. He proposed that *Opisthacanthus* dispersed more recently from

Africa to the Neotropics by trans-Atlantic rafting, invoking favourable marine currents. On the other hand, Francke (1974) believed that *Opisthacanthus* species were rather Gondwanan relicts. His idea that liochelid ancestors were present in the Neotropics prior to its disjunction with Africa in the mid-late Cretaceous (119-105 Mya) (MacLoughlin, 2001), and subsequently evolved in isolation, became widely accepted (Lamoral, 1980; Lourenço, 1984, 1985, 1995, 1996a, 1998, 2001; Nenilin & Fet, 1992; Sissom, 1990). However, both hypotheses were based on the assumption that *Opisthacanthus* is monophyletic, which has been falsified by morphological evidence (Prendini, 2000). Several distinct lineages, that should be regarded as distinct genera, are currently grouped in the genus *Opisthacanthus* and clarifying their phylogenetic positions in the Liochelidae tree is necessary before accurate conclusions concerning their biogeography can be drawn (Prendini, 2005a). The recent discovery in Brazil of the fossil liochelid *Protoischnurus* (Carvalho & Lourenço, 2001; Menon, 2007) dated at about 110 Mya confirmed the presence of liochelids in South America before its split from Africa and favoured the vicariance hypothesis. Besides *Protoischnurus* is also the oldest liochelid known so far.

On the other hand there are no fossil data to confirm the presence of liochelids in Laurasia. Colonization of Southeast Asia by Indian liochelid ancestors during early the Paleocene is currently regarded as the most probable scenario to explain the origin of *Liocheles* on the Asian plate (Sissom, 1990; Soleglad *et al.*, 2005). The distribution of several other organisms in tropical Asia and peninsular India is congruent with a similar “out-of-India” hypothesis (Bossuyt & Milinkovitch, 2001; Gower *et al.*, 2002; Prendini *et al*., 2003; Praveen Karanth, 2006; Svenson & Whiting, 2009). This theory implies survival of ancient Gondwanan lineages on the Indian plate during its rapid northward drift (fig. 7) despite dramatic climatic changes and intense volcanism in the Late Cretaceous (Courtillot *et al.*, 1988; Duncan & Pyle, 1988; Cox, 1988). A rich and diverse biota was probably carried on this so called ‘Indian Ark’ and invaded SE Asia when the subcontinent finally collided with the Eurasian plate in the Late Cretaceous/Early Paleocene (65-55 Mya) (Beck *et al.*, 1995; Jaeger *et al.*, 1989). According to Prendini’s (2000) cladogram, the group (*Chiromachetes* + *Chiromachus*) was basal to (*Iomachus* + *Liocheles*). If these phylogenetic relationships are corroborated by the present investigation, the “out-of-India” origin of *Liocheles* would be confirmed. The (*Chiromachetes* + *Chiromachus*) clade potentially

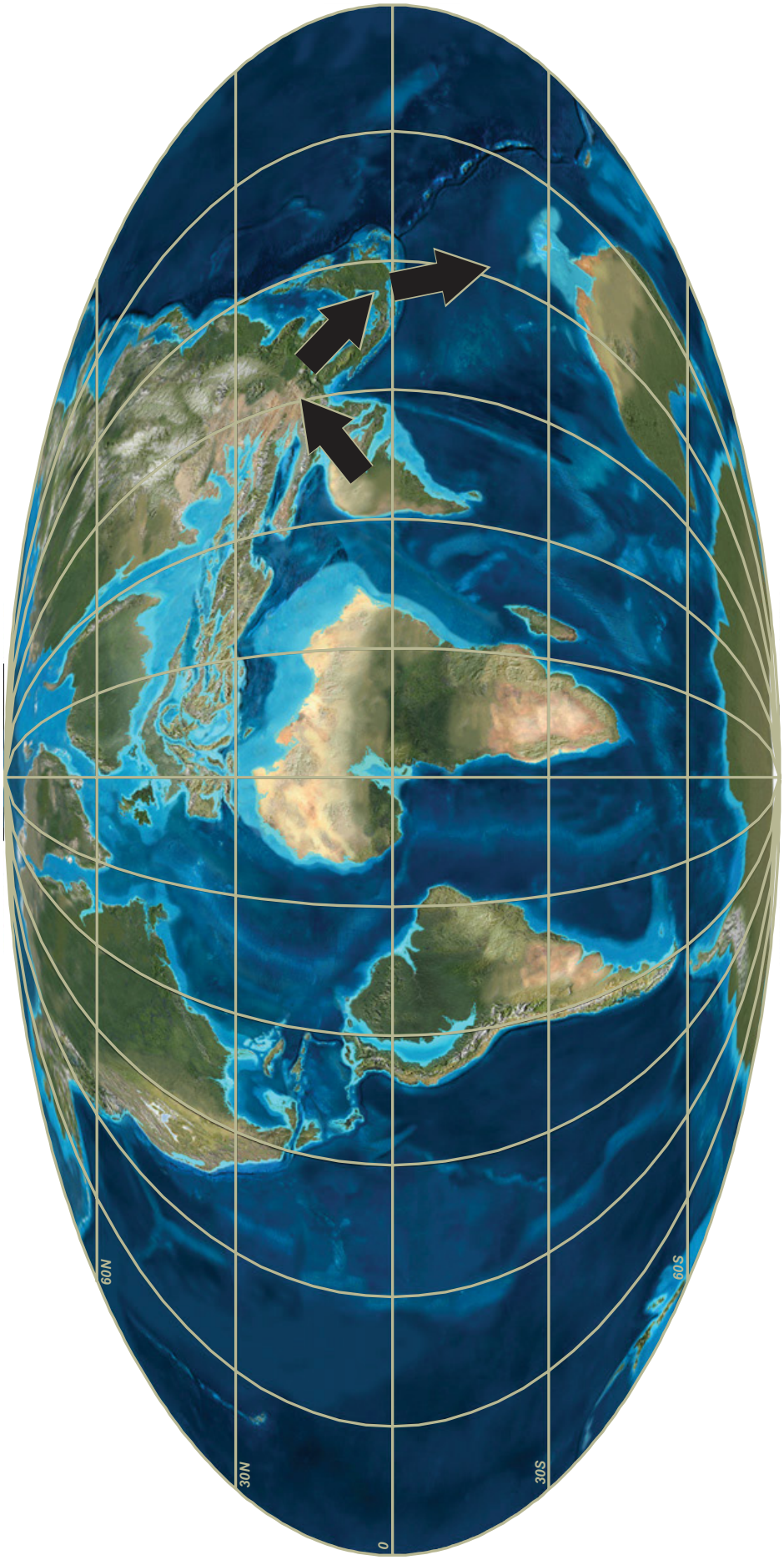
Fig. 7. India and Australia rifted from Gondwana in the Cretaceous. The map shows the late Cretaceous and Cenozoic movement of these two major continental fragments towards the Asia Asian plate (after Hall, 1998).


0 Ma
30Ma
45Ma
0Ma
30Ma
45Ma
90Ma
120Ma
120Ma
90Ma
120Ma
30°N
0°
30°S
60°S

represent a very ancient Gondwanan lineage the origin of which lies on the India-Seychelles plate (Central Gondwana). Such an ancient faunal linkage between Seychelles islands and the Western Ghats of India have been demonstrated for frogs (Dutta *et al.*, 2004; Biju & Bossuyt, 2003) and caecilians (Wilkinson *et al.*, 2002). Frog lineages from the Ghats mountains appear to be remnants of a unique ancient Gondwanan biota (Roelants *et al.*, 2004). Finally, the occurrence of *Liocheles* in Australasia and Melanesia has been suggested to be the result of dispersal, presumably over land bridges, from Southeast Asia during the Cenozoic (fig. 8; Sissom, 1990; Koch, 1977, 1981). However Monod & Volschenk (2004) disagreed and stated that *Liocheles* originated from eastern Gondwana and invaded SE Asia after the breakup of the supercontinent.

Liochelidae and Scorpionidae distributional ranges in Africa, India and Southeast Asia overlap for the most part. Liochelids do not occur in the Middle East, the Horn of Africa, Northern and Western Africa whereas scorpionids (i.e. the genus *Scorpio* Linnaeus, 1758) are commonly found throughout these regions. The same vicariance and/or dispersal events are also currently invoked to explained their respective geographical distributions. The scorpionid genera *Heterometrus* Ehrenberg, 1828 and *Pandinus* Thorell, 1876 are endemic to Africa and to India/Southeast Asia respectively. Several authors (Couzijn, 1981; Stockwell, 1989; Sissom, 1990) considered that the (*Pandinus* + *Heterometrus*) lineage predated the Mid-Jurassic (158-165 Mya) rifting of East Gondwana (comprising Antarctica–Madagascar–India–Australia) from east Africa (Plummer & Belle, 1995; Gnos *et al.*, 1997; McLoughlin, 2001), evolution of the two genera resulting from vicariance between Africa and India due to continental drift. Prendini *et al.* (2003) confirmed this hypothesis and the colonisation of Asia by scorpionids through secondary dispersal from India. However, contrary to Liochelidae, Scorpionidae are restricted to the Old World, they do not occur in South America and Australasia. This fundamental difference in the distributional ranges of the two families is regarded here as an important element to understand their respective biogeographies. One can hypothesized that scorpionids have more limited dispersal capabilities compared to some of the Liochelidae (see below) due to their burrowing habits and that this prevented the family from expanding its territory beyond East Gondwanan territories. Habitat requirement and ecological plasticity are probably important limiting factors

Fig. 8. Eocene paleogeographic reconstruction of the world (50 Mya). Dispersal of *Liocheles* Sundevall, 1883 from the Indian subcontinent to SE Asia and Australasia as suggested by Koch (1977) is indicated. Paleogeography and coastlines are from Blakey, 2011 (http://jan.ucc.nau.edu/~rcb7/globaltext2.html).

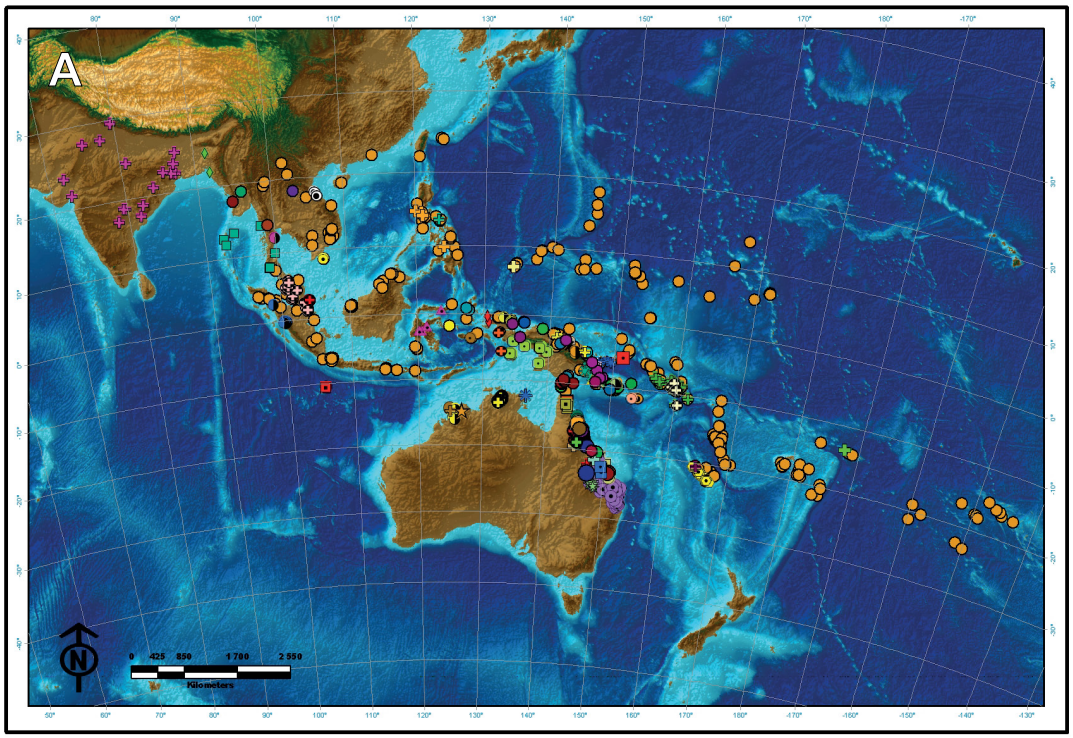

90N
30N
0
30S
60S

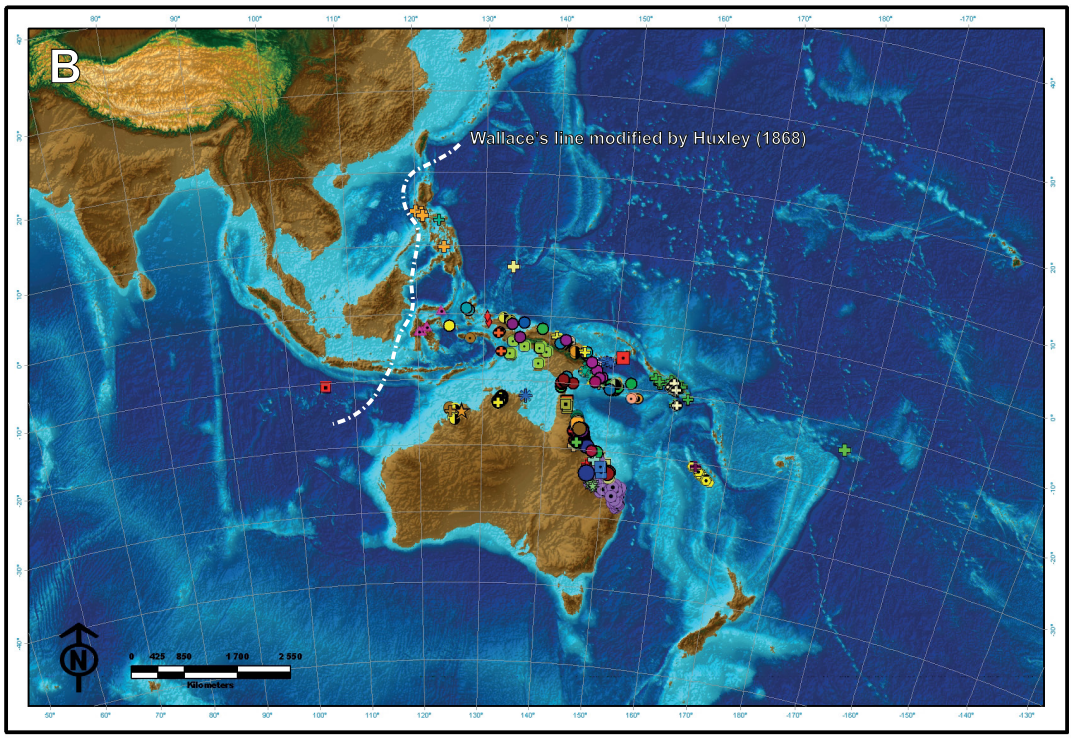
to the colonization of new environments and a good knowledge of the ecology of the different genera may provide valuable information to comprehend the biogeography the family.

0.5 DISTRIBUTIONAL RANGE AND BIOGEOGRAPHY OF THE GENUS *LIOCHELES*

Liocheles species inhabit humid tropical ecosystems (evergreen broadleaf forests) from India to the Pacific Islands. *Liocheles litodactylus* Monod & Volschenk, 2004 which is restricted to the Thornton Uplands, a small mountainous massif of the Queensland Wet Tropics (Monod & Volschenk, 2004), was the first species of the genus to be recognized as a short range endemic (Ponder, 1999; Harvey, 2002), that is a species with a natural distribution range of less than 10.000 km^2. However most species in this genus are at least semi-lithophilous (Prendini, 2001c) and have therefore very specific habitat requirements and limited distributions. The rate of narrowly endemic species within the genus is therefore very high and most *Liocheles* species discovered in the course of the present project can be unambiguously classified in this category. On the other hand *Liocheles australasiae* is a cosmopolitan species distributed from India to the western Pacific Islands and as far north as Japan. It is extremely successful at dispersing to remote islands and establishing new colonies if the areas colonized have appropriate habitats. This remarkable ability to disperse and colonize islands in the region has been documented by its presence on the remnant of the Krakatau Island, a volcano destroyed and fragmented during a massive eruption in 1883 (Dammerman, 1948; Vachon and Abe, 1988). The species was also observed far away from its traditional distribution range: Simon (1910) reported that it was extremely common on ships and in the wharves of Port-Said and Alexandria in Egypt and Lourenço (1996) mentioned specimens from Reunion Island in the Indian Ocean. However it is not known if populations of the species are actually permanently established in these areas. Goyffon (1992) and Lourenço & Cuellar (1994) suggested that the species was and is commonly dispersed as a stowaway in canoes and ships across the Pacific Ocean. Populations on small islands of the Western Pacific consist solely of females that produce female offspring asexually (Makioka & Koike, 1984, 1985; Williams, 1987; Makioka, 1992A, 1992B, 1993; Lourenço & Cuellar, 1994; Yamazaki & Makioka, 2001, 2004). Parthenogenesis probably facilitated successful colonization of small distant land masses and dispersal

Fig. 9. A, Distributional range of the genus *Liocheles* Sundevall, 1883 as currently recognized (= *Liocheles* sensu lato). B, Distributional range of the *waigiensis* group (= *Hormurus* Thorell, 1876); species belonging to this group occur only east of Huxley's line.

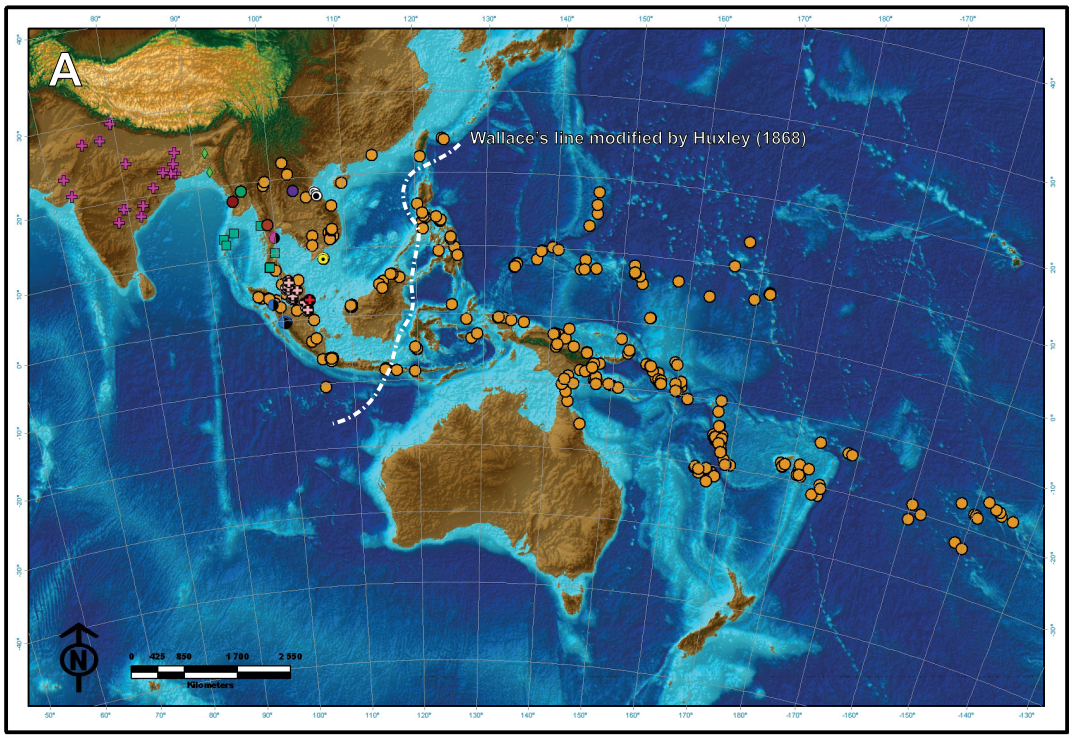

A
0 425 850 1 700 2 550
Kilometers

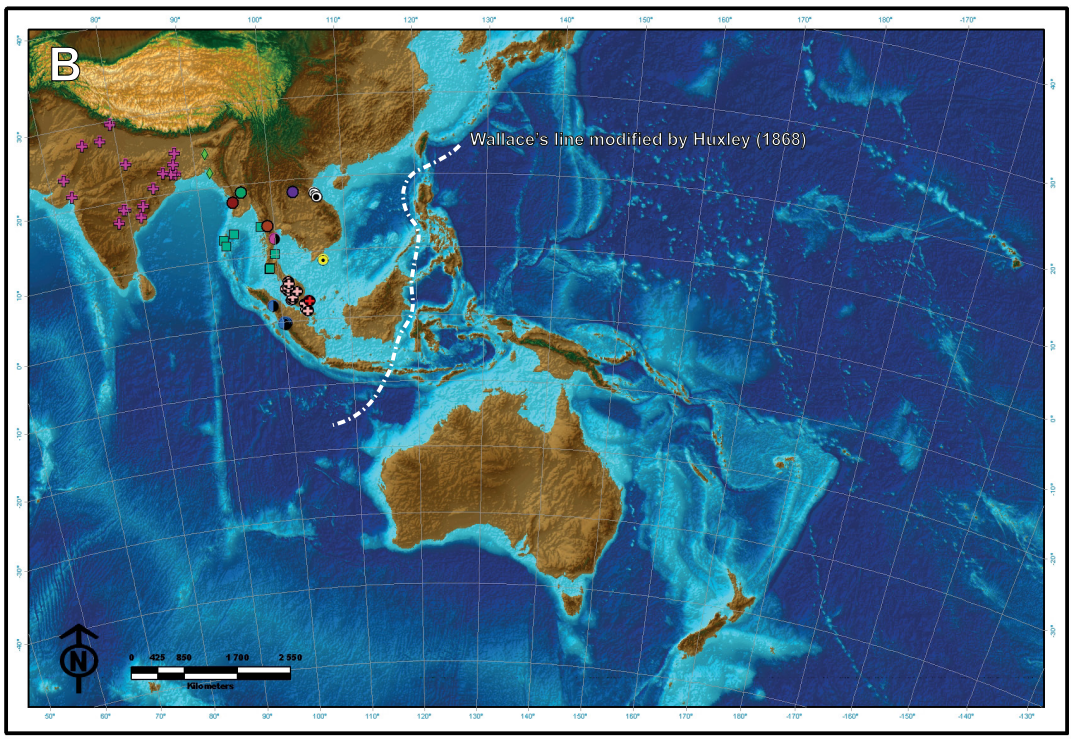

B
Wallace's line modified by Huxley (1868)
0 425 850 1 700 2 550
Kilometers

of the species. Parthenogenetic organisms tend to be better colonists and consequently their frequency on oceanic islands is high (Cuellar, 1977). A single female, drifting ashore on a floating log or dispersing in an islander's canoe, is sufficient to establish an entire new population.

The two species groups recognized within *Liocheles* occupy distinct biogeographic regions separated by Huxley's line (1868). Species of the *waigiensis* group are only recorded east of Huxley's line (Fig. 9B), i.e. in Australia, the Mollucas, New Guinea and surrounding islands, and the Philippines, whereas species of the *australasiae* group occur only west of Huxley's line (Fig. 10), i.e. in India, mainland Southeast Asia and the western part of Indonesia. The only exception is the widespread *L. australasiae*, which is present throughout the Indo-Pacific and consequently across all biogeographical lines of the region, an impressive distribution considering the relative low vagility of scorpions (Birula, 1917b; Harington, 1984; Prendini, 2001c). This clear biogeographic disjunction and the important morphological differences between the two lineages suggest that they probably evolved independently for an extensive period of time. Koch (1977) rejected the hypothesis that the genus originated on the Australian plate given its absence in the Southern part of the continent and its large occurrence outside the Australo-Papuan Region. Colonization by dispersal from Asia was thus regarded as the most probable scenario (Sissom, 1990). More recently Monod & Volschenk (2004) postulated that given its distribution and speciation pattern in Australia, *Liocheles* should have been present on the continent before the Neogene onset of aridification and contraction of rainforest habitats (Bowler, 1982; Kershaw *et al.*, 1994; White, 1998; Morley, 2000). Hence they considered more probable that the presence of the genus on the Australian plate predated Gondwana breakup and that dispersal occurred in the opposite direction, from Australia to SE Asia. However, presence of *Liocheles* in Australia before the Miocene does not necessarily imply a Gondwana origin. The Australian Craton drifted in close proximity of Southeast Asia as early as the late Eocene-Early Oligocene (35 Mya) (Hall, 1998, 2001, 2002) and biotic exchanges between the two geological provinces were probably possible at that time. Therefore if *Liocheles* ancestors originated in Asia, they could have potentially reached Australia from SE Asia before the Miocene. Besides the two landmasses may even have been connected before the Eocene by volcanic island arcs suitable for dispersal. In the Early Paleocene (61 Mya), north-south sea floor spreading began

Fig. 10. Distributional range of the *australasiae* species group (= *Liocheles* Sundevall, 1883 sensu stricto). A, when all known species are included. B, when the cosmopolitan parthenogenetic species *Liocheles australasiae* (Fabricus, 1775) is excluded.


A
Wallace's line modified by Huxley (1868)
0 425 850 1 700 2 550
Kilometers

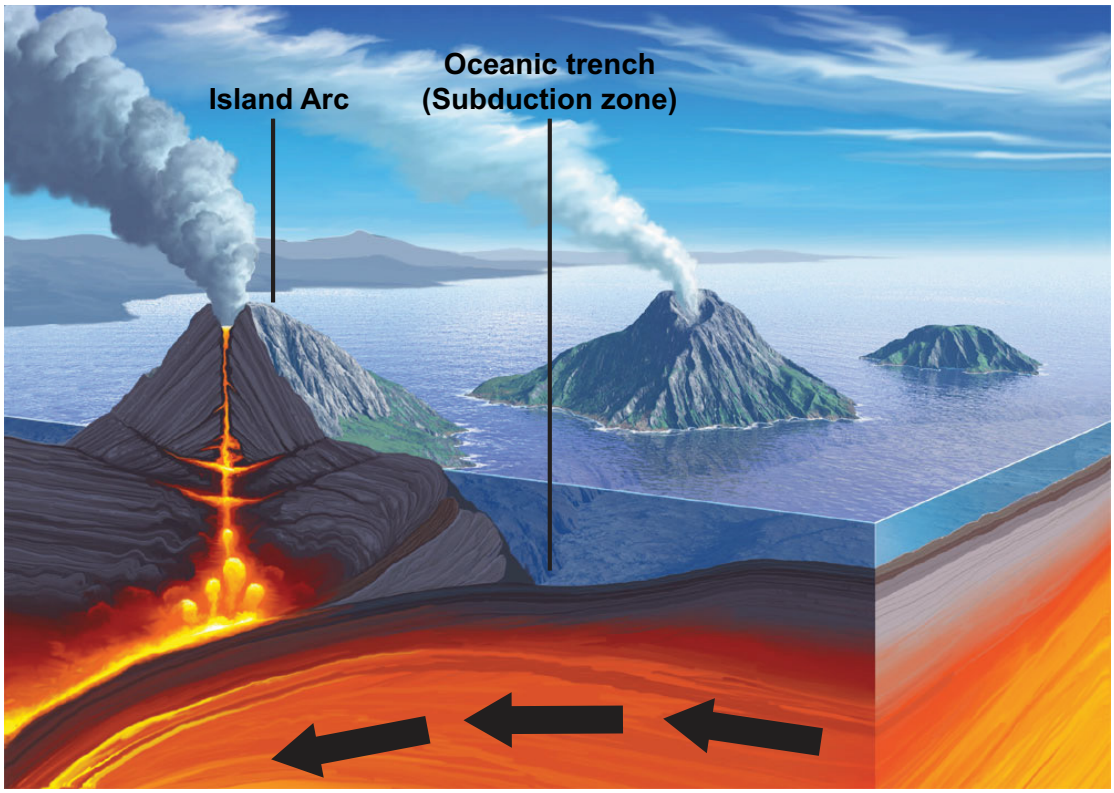

B
Wallace's line modified by Huxley (1868)
0 425 850 1 700 2 550
Kilometers

in the rift between Australia and Antarctica (Fig. 7; Kroenke, 1996; Hall, 1998; Müller *et al.*, 2000) inducing northward motion of the Australian plate and subduction of its northern margins beneath the Asian and Pacific plates (Fig. 11; Hamilton, 1988; Polhemus, 1996). Nowadays, the Indonesian Archipelago results from such subduction systems between the Asian, Australian and Pacific plates. It is currently not possible to unambiguously refute or confirm one of the two hypotheses about the distribution history of *Liocheles* because the phylogenetic relationships within the genus remain unknown. Clearly, deciphering the evolutionary history of the two *Liocheles* lineages is crucial to clarify their origin and draw some conclusions regarding their biogeographical history.

0.6 PROJECT OVERVIEW

Thorough phylogenetic analyses are crucial in order to clarify origins and monophyly of taxa. First, the more important characters systems and the associated terminologies used for diagnoses and scoring of the morphological matrix are presented. The second chapter consists of an investigation of the phylogenetic relationships of the Indo-Pacific genera and species groups of the family Liochelidae, based on morphological and molecular data. The methods and philosophical justifications are discussed first and the results of the three analyses (morphological, molecular and combined) are subsequently presented. Based on these conclusions, a revised taxonomy is proposed: the generic status of *Hormiops* and *Hormurus* [= *waigiensis* species group] is formally reinstated based on morphological and phylogenetic evidence, leaving only the species belonging to the *australasiae* group in the genus *Liocheles* (*sensu stricto*). Descriptions and diagnoses for all the valid described species and for several others selected among the newly discovered taxa are provided. The taxonomic revision is completed by a general identification key. The fourth and last part of the project is a reinterpretation of the biogeography of the family, wherein congruence between the distribution of the Liochelidae, their evolution in the Indo-Pacific Region, and geotectonic events that could have induced vicariance or allowed dispersal is assessed using relaxed molecular clocks.

Fig. 11. The formation of an island arc is induced by the subduction of an oceanic tectonic plate under another tectonic plate. The magma produced during this process at depth under the over-riding plate ascends to form a chain of volcanoes parallel to the subduction zone. Illustration by J. E. Kaufmann (http://jek2004.com/index.htm).


Island Arc
Oceanic trench
(Subduction zone)

CHAPTER I
-
COMPARATIVE MORPHOLOGY

1.1 MATERIAL & METHODS

Examination and imaging. The external morphology of approximately 4000 specimens was thoroughly examined in the course of the present work with two stereomicroscopes: a NIKON SMZ1500 and a ZEISS Stemi SV8. Morphological examination is sometimes hampered by mud and soil aggregates adhering to the tegument of specimens and that obscure fine characters. Ultrasonic treatment (sonication) was used to clean the specimens free of adherent particles (Nowak *et al.*, 2008). The specimens were placed for 15 to 90 seconds in a Digital ultrasonic cleaner filled with soapy water. This step was repeated until a satisfactory degree of cleanliness was achieved. For smaller and older specimens, more numerous but shorter rounds of sonication were carried out in order to avoid damage. Following sonication, the specimens were rinsed thoroughly with distilled water. High resolution images of the informative characters were taken using a Microptics ML 1000 digital imaging system (Microptics, USA) with normal light or with long-wave ultraviolet (see below). CombineZM (Hadley, 2005) was used to produce the final images. This “Focus Stacking” software allows to combine a series of photographs that were taken at different focal points into a single image with much greater depth of field than the original shots. The simultaneous comparison of high quality standard digital images facilitates the detection of informative characters unobservable with standard microscopy or previously overlooked. All photographs were edited in Photoshop CS5 (Adobe Systems, San Jose, CA, USA) (background removal, contrast and color adjustment) and plates prepared with Illustrator CS5 (Adobe Systems, San Jose, CA, USA).

Dissection and internal morphology. Mature male specimens were dissected using microsurgical scissors and forceps to study their hemispermatophores. Paraxial organs tissues were removed either manually with forceps or chemically with Proteinase K (Qiagen, Venlo, The Netherlands). Drawings of hemispermatophores and their internal structures were produced, using a stereomiscroscope (NIKON SMZ1500 or ZEISS Stemi SV8) mounted with a camera lucida. The sketches were subsequently inked with Koh-I-Noor Rapidograph pens and scanned for further processing and editing with digital tools. Scanning electron microscopy (SEM) was also utilized to explore the morphology of the fine structure of the hemispermatophore’s capsular region. Hemispermatophores were first immersed in Proteinase K or Trypsine

in order to dissolved membranous residues of the paraxial organs. They were then dehydrated in a graded alcohol series, and critical point dried with a Baltec critical point dryer 030. They were then mounted on standard aluminium Scanning Electron Microscopy stubs (diameter of 12 mm, height of 7 mm; Electron Microscopy Sciences) and sputter coated with gold/palladium in a Denton Vacuum Desktop II model. Samples were then examined with a Hitachi S4700 field emission scanning electron microscope at the American Museum of Natural History. Illustrations and photographs were finally edited in Photoshop CS3 and Illustrator CS3 (Adobe Systems, San Jose, CA, USA).

UV FLUORESCENCE IMAGING. The fluorescence of scorpion cuticle when exposed to long wavelength ultraviolet (366.3 nm) light was first reported in 1954. Lawrence (1954) tested various groups of arthropods, including scorpions, for cuticle photoluminescence. Pavan (1954a, 1954b, 1954c) and Pavan & Vachon (1954) demonstrated that photoluminescence of scorpions under blacklight is due to the presence of chemical compounds in the outermost layer of the cuticle, the epicuticle. Stahnke (1972) later noted that the intensity of emission depends on the age of the specimen and on the hardness of the cuticle: third and later instars fluoresce more brightly than first and second instars, and newly molted specimens do not fluoresce at all. Stachel *et al.* (1999) established that fluorescence occurs as a result of sclerotisation and isolated one of the fluorescent compounds of the epicuticle, the β-carboline. This enigmatic property of scorpion tegument provides a fantastic tool for observation, detection and capture of specimens (Stahnke, 1972). The use of a blacklight at night is nowadays the primary method to collect scorpions as it turned out to be much more efficient than daylight hunting by turning over rocks and logs. Besides improving research in the field, scorpion photoluminescence also proved to be extremely useful in the laboratory. Recently, Volschenk (2002, 2005) explained how it can be used to produce photographs that reveal characteristics such as the granulation and microscultptures of the cuticle. The technique is now widely used to illustrate taxonomic publications (Prendini, 2003A, 2003B, 2004, 2005a, 2005b, 2006; Prendini *et al*., 2003, 2006; Ojanguran-Affilastro *et al*., 2007A, 2009; Vignoli & Prendini, 2008; Navidpour & Lowe, 2009; Lowe, 2010A, 2010B).

The morphosculptures of the tegument surface is an important source of data for the

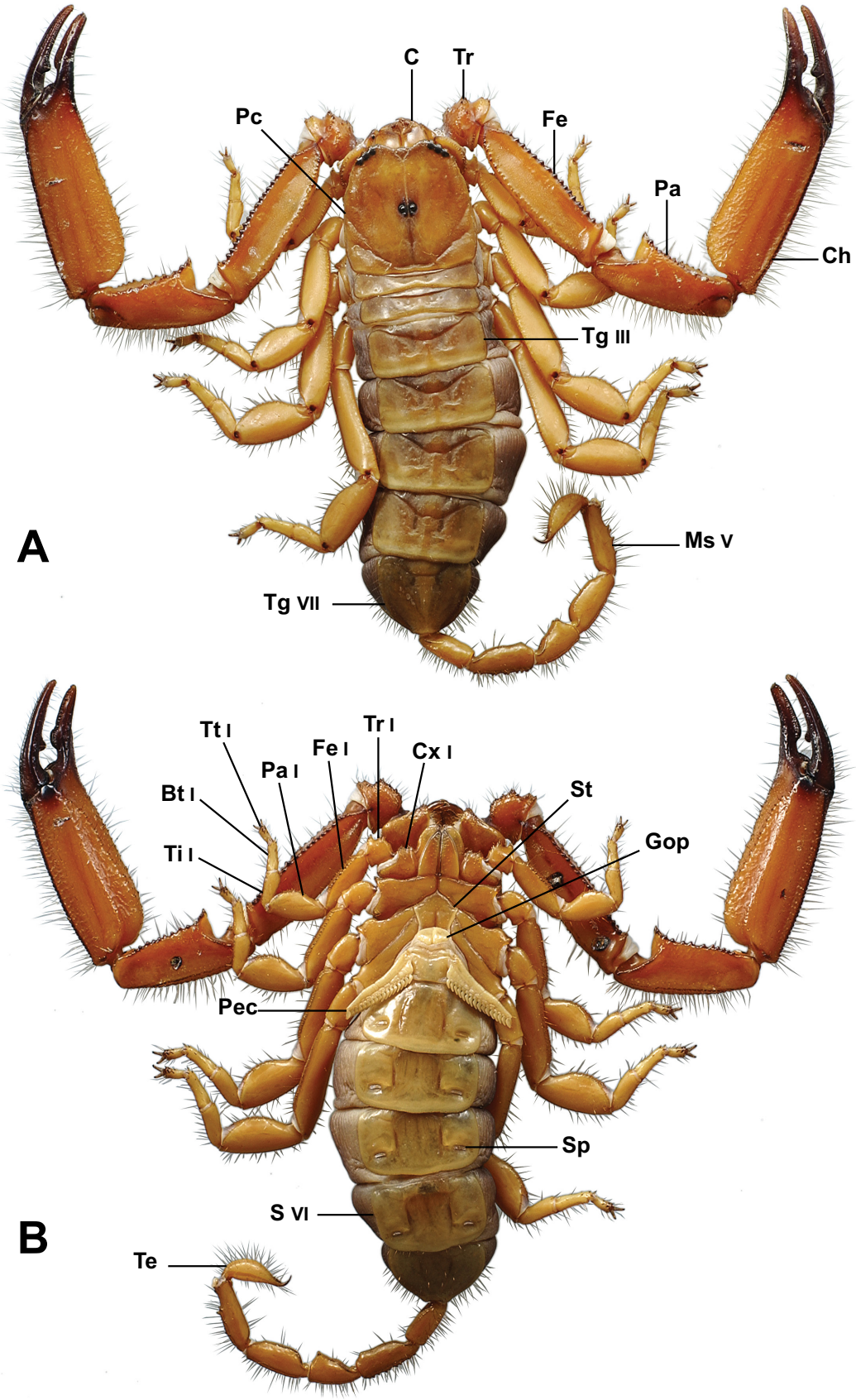
identification and phylogenetic study of scorpions, however it can be extremely difficult to examine and more so to photograph under normal light as it is often obscured by complex color patterns lying beneath the cuticle or reflexions on the shiny teguments. This technique overcomes these problems and allows the production of SEM-like photographs without the need for complex and destructive preparation of the specimens. The major shortcoming of this technique is the need of high sensitivity photograph settings due to the limited amount of light provided by UV flashes and therefore pictures produced when the method was first implemented had a grainy and unsharp appearance. However, with the recent technological advances made in digital SLR camera, the resolution of images taken under low light conditions has improved considerably. The use of UV lighting coupled with focus stacking allows the production of high quality images that facilitate the comparison between different taxa and reveal many characters previously unnoticed. It is so far the best tool available for the documentation of tegument sculpture of scorpion but it is also used in the present work to illustrate many other diagnostic characters, for instance chaetotaxy (basal areoles of bigger setae and trichobothria typically fluoresce more brightly than the surrounding surfaces; figs 17-18) and carinal pattern (figs 26-28).

Terminology follows Stahnke (1970), Stockwell (1989), Sissom (1990) and Hjelle (1990) for pedipalp segmentation (fig. 12), Prendini *et al.* (in prep) for pedipalp carinae, Vachon (1974) for trichobothrial patterns, Couzjin (1976) for leg segmentation (fig. 12), Prendini (2000) for metasomal carinae, and Lamoral (1979) and Monod & Volschenk (2004) for hemispermatophores.

1.2 CHARACTER LIST AND MAJOR MORPHOLOGICAL CHARACTERISTICS

Trichobothriotaxy, setation and/or spination of the ventral surface of leg tarsi and granulation of the cutting edge of the pedipalp movable finger are the main features currently used to distinguish liochelid genera. Pedipalps appear to be extremely informative for taxonomic and phylogenetic analysis with several important character systems derived from their morphology, i.e. carinae, morphosculptures of the pedipalp chela fingers dentate margins and trichobothrial pattern. Besides the granulation and texture of the prosoma and mesosoma as well as the

Fig. 12. Scorpion gross morphology and segmentation. *Hadogenes tityrus* (Simon, 1888), male from Gamsberg, Windhoek District, Namibia (AMNH). A, dorsal view. B, ventral view. Legend: Bt I= basitarsus I; C= chelicera; Ch= chela; Cx I= coxa I; Fe= femur; Fe I= femur I; Gop= genital operculum; Ms V= metasomal segment V; Pa= patella; Pa I= patella I; Pc= prosomal carapace; Pec= pectine; S VI= sternite VI; Sp= spiracle; St= sternum; Te= telson; Tg III= tergite III; Tg VII= tergite VII; Ti I= Tibia I; Tt I= telotarsus I; Tr= trochanter; Tr I= trochanter I.


C
Tr
Pc
Fe
Pa
Ch
Tg III
A
Ms V
Tg VII
Tt I
Tr I
Fe I
Cx I
Pa I
Bt I
St
Ti I
Gop
Pec
Sp
S VI
B
Te

granulation of the metasomal carinae also provide useful data to reconstruct the evolutionary tree of the Liochelidae. Contrary to the external morphology, the internal morphology was for the most part overlooked by previous authors, albeit being an important indicator of relationships at the generic and even specific level. Within Liochelidae, the male reproductive organs are particularly instructive in a taxonomic and phylogenetic perspective, especially the morphology of the capsular region of sclerotized hemispermatophores. However, current terminology of many of these characters systems are based on inappropriate homology hypotheses and are therefore not used to their full potential as a source of phylogenetic data. All characters used to compile to master morphological matrix of the present phylogenetic analysis are listed below. A review of the major characters systems investigated is provided and important and newly discovered characters are discussed with more emphasis and details.

Correspondence with characters discovered in previous publications are indicated with the following abbreviations (author + date/number): HWC81 = Couzijn (1981); G02 = Giribet *et al.* (2002); J94 = Jeram (1994); KP08 = Kamenz & Prendini (2008); BHL79 = Lamoral (1979); BHL80 = Lamoral (1980); WRL = Lourenço (1985); LP00 = Prendini (2000); LP01 = Prendini (2001E); LP03 = Prendini (2003B); LP unpublished = Prendini unpublished; PCW03 = Prendini, Crowe and Wheeler (2003); S&F03.5 = Soleglad & Fet (2003), table 5; SFK05 = Soleglad, Fet & Kovarik (2005); S&S01 = Soleglad & Sissom (2001); S89 = Stockwell (1989); VP08 = Volschenk & Prendini (2008). It is also mentioned if these characters were modified in the present analysis. Character states are scored 1, 2, 3, 4, 5, or - (inapplicable). 57 uninformative characters are indicated by †.

Continuous characters [Characters 0–9]

#0. Pectinal teeth, number, ♂ [WRL10].

#1. Pectinal teeth, number, ♀ [WRL10].

#2. Telotarsi I, prolateral row, number of spiniform macrosetae [PCW03/70] [split into eight characters, 2–9].

#3. Telotarsi I, retrolateral row, number of spiniform macrosetae [PCW03/70] [split

into eight characters, 2–9].

#4. Telotarsi II, prolateral row, number of spiniform macrosetae [PCW03/70] [split into eight characters, 2–9].

#5. Telotarsi II, retrolateral row, number of spiniform macrosetae [PCW03/70] [split into eight characters, 2–9].

#6. Telotarsi III, prolateral row, number of spiniform macrosetae [PCW03/70] [split into eight characters, 2–9].

#7. Telotarsi III, retrolateral row, number of spiniform macrosetae [PCW03/70] [split into eight characters, 2–9].

#8. Telotarsi IV, prolateral row, number of spiniform macrosetae [PCW03/70].

#9. Telotarsi IV, retrolateral row, number of spiniform macrosetae [PCW03/70].

Colouration [Characters 10–13]

#10. † Tergites, colouration: 1, uniform: 2, distal third noticeably paler [LP01/148].

#11. Chelicerae, colouration, dorsal surface: 1, pale or nearly so, fingers: may be very slightly infuscated (manus similar to or paler than carapace); 2, dark (manus as dark as or darker than carapace) [LP01/140].

#12. Legs, colouration: 1, pale (as pale as as or paler than tergites); 2, dark (as dark as tergites) [LP01/155].

#13. Telson, colouration: 1, pale (as pale as or paler than metasoma); 2, dark (as dark as metasoma) [LP01/151 (part)].

Tegument punctation [Character 14]

#14. Non granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp, punctation: 1, present; 2, absent [LP00/8].

Pedipalp meristics and setation [Characters 15–16]

#15. Femur, length, expressed as ratio of carapace length (fl/cl): 1, short (equal to or shorter); 2, long (longer than carapace, up to 2 times longer) [LP01/40, PCW03/21].

#16. Chela, macrosetal development [additive]: 1, virtually asetose; 2, sparsely setose; 3, densely setose [LP01/41, PCW03/22].

Pedipalp finger morphosculptures [Characters 17–36]

#17. Chela, movable finger, dentition, inner accessory denticles (IAD): 1, present; 2, absent [S&S01/33, S&F03.5/49 F, S&F03.5/52, SFK05/96].

#18. † Chela, movable finger, dentition, number of row of primary denticles: 1, multiple: 2, double, often fused at the base; 3, single [S89/45, LP00/33, LP03/07, VP08/12]

#19. † Chela, fixed finger, basal lobe extending from the base of the fixed finger onto the distal part of the retrolateral surface of the manus, partially covering the connecting membrane between the manus and the movable finger: 1, present; 2, absent.

#20. Chela, movable finger, supra-basal lobe, ♂ [additive]: 1, well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed); 2, weakly developed, low and long hump (from the base of finger to mid-finger) at the base of movable finger; 3, weakly developed, low hump; 4, absent, margin straight or nearly so, at most a low hump [LP00/35, LP01/45, PCW03/25, LP03/29, VP08/13] [modified] [split into three characters, 20–22].

#21. Chela, fixed finger, supra-basal notch, ♂ [additive]: 1, distinct and deep; 2, distinct but shallow; 3, absent [LP00/35, LP01/45, PCW03/25, LP03/29, VP08/13] [modified] [split into three characters, 20–22].

#22. Chela, movable finger, supra-basal lobe, shape, ♂: 1, gently rounded dorsally and lacking a sharp conical tooth; 2, unevenly pointed dorsally, due to the presence of a sharp conical tooth or at least with a larger tooth; -, inapplicable [LP00/35] [modified] [split into three characters, 20–22].

#23. Chela, movable finger, supra-basal lobe, shape, ♂: 1, wider than high (low); 2, conical, as high as wide or higher than wide; -, inapplicable.

#24. Chela, movable finger, supra-basal lobe and corresponding notch connectiv-

ity, ♂: 1, contiguous (adjoin) or with a small gap; 2, with a distinct posterior gap; 3, with a distinct upper gap/anterior gap; -, inapplicable.

#25. Chela, movable finger, supra-basal lobe, shape, ♂: 1, not overlapping with fixed finger; 2, overlapping with retrolateral surface of fixed finger (in front of notch); -, inapplicable.

#26. Chela, movable finger, supra-basal lobe, ♀ [additive]: 1, well-developed, almost midway along movable finger; 2, weakly developed, large low hump on proximal half of movable finger with a corresponding kink in the fixed finger; 3, absent or at most weakly developed, close to base of movable finger [LP00/37] [modified] [split into two characters, 26–27].

#27. Chela, fixed finger, supra-basal notch, ♀ [additive]; 1, distinct; 2, shallow ("kink"); 3, absent [LP00/37] [modified] [split into two characters, 26–27].

#28. Chela, movable finger, basal lobe and corresponding notch in fixed finger, shape, ♂ [additive]: 1, absent or at most 2–3 small spiniform granules; 2, low hump with 2–3 larger conical; 3, present and well developed [LP01/44] [modified].

#29. † Chela, movable finger, basal lobe, shape, ♂: 1, gently rounded dorsally, lacking a sharp conical tooth; 2, unevenly pointed dorsally, due to the presence of a sharp conical tooth; -, inapplicable [LP unpublished] [modified].

#30. Chela, movable finger, basal lobe and corresponding notch in fixed finger, ♀: 1, absent; 2, present [LP00/38] [modified].

#31. † Chela, movable finger, basal lobe, shape, ♀: 1, gently rounded dorsally, lacking a sharp conical tooth; 2, unevenly pointed dorsally, due to the presence of a sharp conical tooth; -, inapplicable [LP00/38] [modified].

#32. Chela, fixed finger, supra-basal lobe, projecting downward, ♂: 1, absent or at most weakly developed; 2, present and distinct [LP00/36].

#33. † Chela, fixed finger, basal lobe as 3–4 conical teeth, ♂: 1, absent; 2, present.

#34. Chela, fixed finger, supra-basal lobe, shape, ♂: 1, low/reduced; 2, conical/well developed; -, inapplicable.

#35. Chela, fixed finger, supra-basal lobe, projecting downward, ♀: 1, absent; 2,

present, at least weakly developed [LP00/36].

#36. Chela, fixed and movable fingers, cutting edge: 1, even distally, without enlarged granules; 2, uneven, with additional enlarged granules (lobes) distally [LP01/43].

Pedipalp chelae are extremely important during courtship and mating. The male grasps and kneads the female's pedipalp chelae with his own. Once his grip is firmly established, he leads her to a location suitable for spermatophore's deposition. Once the hemispermatophore has been deposited on the substrate, the male assists his partner in positioning her genital aperture over the spermatophore to allow sperm transfer. Once the sperm has been transferred, the male released his grasp over the female. This mating dance termed *promenade à deux* was first described by Maccary (1810) and Fabre (1923). It is therefore not surprising that pedipalpal sexual dimorphism is a common trend in scorpions. For instance, in males of the family Bothriuridae Simon, 1880 the inner surface of pedipalps can bear either an apophysis or a semicircular depression at the base of fixed finger (Maury, 1975a). Both these features are thought to help the male secure his grip over the female by holding the tip of her chela fingers during mating. A more common modification of the pedipalpal chela is the presence of a distinct lobe on the cutting edge of the movable finger and of a corresponding notch on the fixed finger. However it is currently not known if these sculpturings on finger denticulate margins serve some purposes during the courtship/mating, either as a "lock" or as a sexual recognition signal. Unlike the apophysis and depression of bothriurids, the lobe-notch combination is not strictly present in males. In some species, both males and females display the character, while in other it is absent in female or in both sexes (Newlands & Prendini, 1997; Monod & Volschenk, 2004). Besides finger morphosculptures are usually indicative of sexual maturity in both males and females, juveniles and subadults lacking the feature which appears only in the final instar.

The morphology of pedipalp chela fingers is recognized as an important diagnostic and phylogenetic character within the family Liochelidae and was used to discrimininate between species (Lamoral, 1979; Newlands, 1980; Newlands & Prendini, 1997; Prendini, 2001a, 2006; Monod & Volschenk, 2004) or to assess evolutionary relationships (Prendini, 2000). The pres-

ence of the lobe and notch in adult males and females is considered here to be plesiomorphic in Liochelidae. Subsequent loss of the structures in females occurred several times independently during the evolutionary history of the family; it is considered to be autapomorphic for some species of the *Hadogenes tityrus* (Simon, 1888) species group (Newlands & Prendini, 1997) and of the genus *Opisthacanthus* (*Nepabellus*), and synapomorphic for the genus *Liocheles* and for the monophyletic grouping (*Iomachus politus* + *Opisthacanthus* (*Opisthacanthus*)) (Prendini, 2000). On the other hand, the absence of the lobe and notch in males is deemed to be independently derived and autapomorphic for four liochelid species, i.e. *Hadogenes zumpti* Newlands & Prendini, 1997, *Hormiops infulcra* n. sp., *Hormurus orthodactylus* n. sp. and *Hormurus litodactylus* Monod & Volschenk, 2004 (figs 15G-H). The unusual shape of the lobe and notch in males and females of *Iomachus laeviceps* (Pocock, 1890), *Iomachus nitidus* Pocock, 1900 and *Iomachus punctulatus* Pocock, 1897 from India was not reported by previous authors; the lobe of these species evolved into a very low hump that extends from the base to the middle of the movable finger giving the cutting edge a distinct bend (figs 14E-F). This unique feature within the family is considered as a possible synapomorphy for the three *Iomachus* mentioned above. Conversely, *Iomachus malabarensis* Pocock, 1900, the remaining Indian species of this genus included in the study, displays the traditional lobe and notch (figs 14A-B) which is most likely a plesiomorphy.

Prendini (2000) recognized 1 lobe on the movable finger (characters 35 and 37; SbL_{mf} in fig. 13) and 1 lobe on the fixed finger (character 36; SbL_{ff} in fig. 13). He also mentioned the presence of a sharp conical tooth at the base of movable finger in females of *Iomachus politus* Pocock, 1896 and *Opisthacanthus* (*Opisthacanthus*) (character 38). This feature is regarded here as a second lobe for the movable finger, namely the basal lobe (BL_{mf} in fig. 13), and can be devoid of a distinct tooth at its apex, for instance in *Chiromachus ochropus* (C. L. Koch, 1837) (figs 14G-H). It is present in males and females of *C. ochropus* (Figs 14G-H), *Opistacanthus* (*Opisthacanthus*) *cayaporum* Vellard, 1932 (figs 13) and *O*. (*O*.) *elatus* (Gervais, 1844) but only in females of *I. politus* and *O*. (*O*.) *lecomtei* (Lucas, 1858) (figs 14C-D). The presence on the movable finger of a basal lobe in females and its absence in males are considered here as potential synapomorphies for (*I. politus* + *O*. (*O*.)) and (*I. politus* + *O*. (*O*.) *lecomtei*) respectively,

Fig. 13. *Opisthacanthus* (*Opisthacanthus*) *cayaporum* Vellard, 1932 from Campos de Cayapos, (Para State, Brazil), male (MHNG). Morphosculptures of the denticulate edges of pedipalpal chela fingers. The different lobes recognized are indicated. Trichobothries are indicated by small white circles. Abbreviations: BL_{mf} = basal lobe of movable finger; SbL_{ff} = supra-basal lobe of fixed finger; SbL_{mf} = supra-basal lobe of movable finger; SbN_{ff} = supra-basal notch of fixed finger.

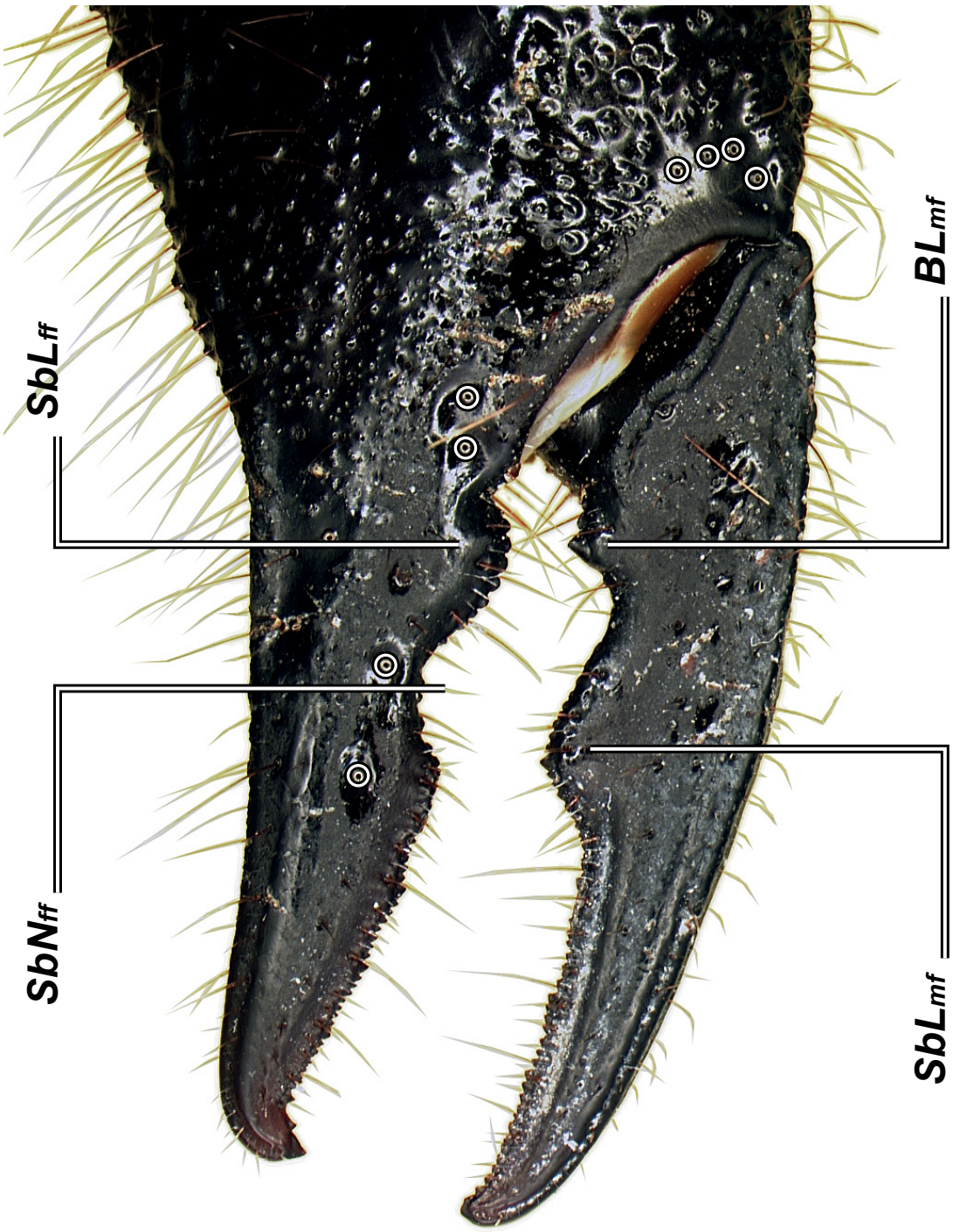

SbLff
SbNff
BLmf
SbLmf

Fig. 14. Morphosculptures of the denticulate edges of the pedipalp chela fingers in the family Liochelidae Fet & Bechly, 2001. *Iomachus malabarensis* Pocock, 1900 from Mangalore, Karnataka, India (NHML). A, Female. B, Male. *Opisthacanthus* (*Opisthacanthus*) *lecomtei* (Lucas, 1858). C, Female from Mount Cameroon, Cameroon, Africa (CAS). D, Male from Monts Doudou, Province Ogoone, Gabon, Africa (LP 1608). *Iomachus punctulatus* Pocock, 1897 from Coimbatore, Tamil Nadu, India (NHML). E, Female. F, Male. *Chiromachus ochropus* (C. L. Koch, 1837) from Fregate Island, Seychelles (USNM). G, Female. H, Male. Trichobothria of the external surface of fingers are also clearly visible.

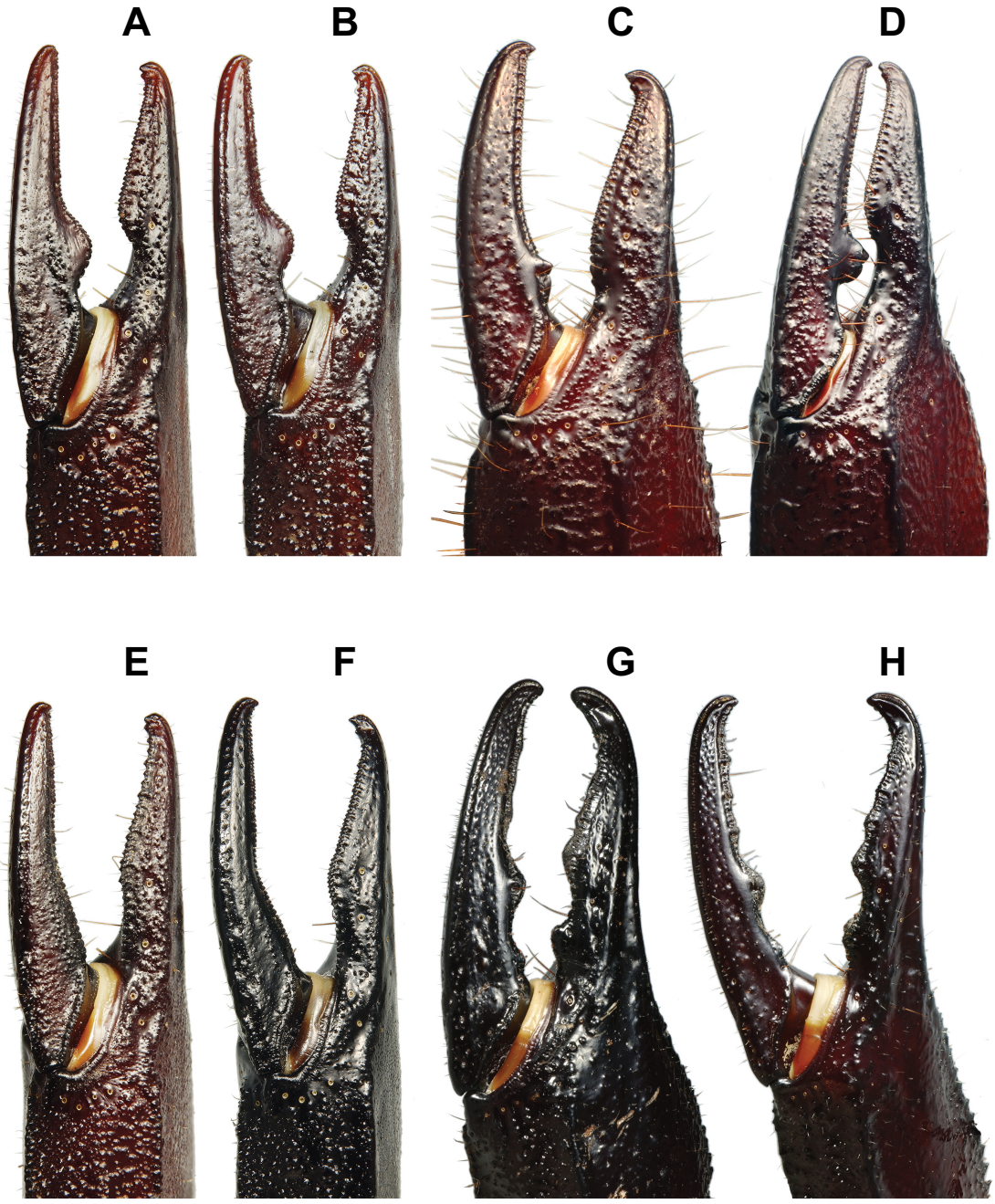

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Fig. 15. Morphosculptures of the denticulate edges of the pedipalp chela fingers in the genera *Hormurus* Thorell, 1876 and *Liocheles* Sundevall, 1883. *Liocheles nigripes* (Pocock, 1897) from Janida, West Bengal, India (CAS). A, Female (ASU 65-0332 #1). B, Male (ASU 65-0331 #1). *Hormurus karschii* (Keyserling, 1885) from Sekroe, West Papua, Indonesia (NNHM). C, Female. D, Male. *Hormurus aethes* n. sp. from Mount Obree, Central Province, Papua-New Guinea. E, Female (LP 3003). F, Male (LP 3001). *Hormurus litodactylus* (Monod & Volschenk, 2004) from Mount Sorrow, Queensland, Australia (LM). G, Female. H, Male. Trichobothria of the external surface of fingers are also clearly visible.

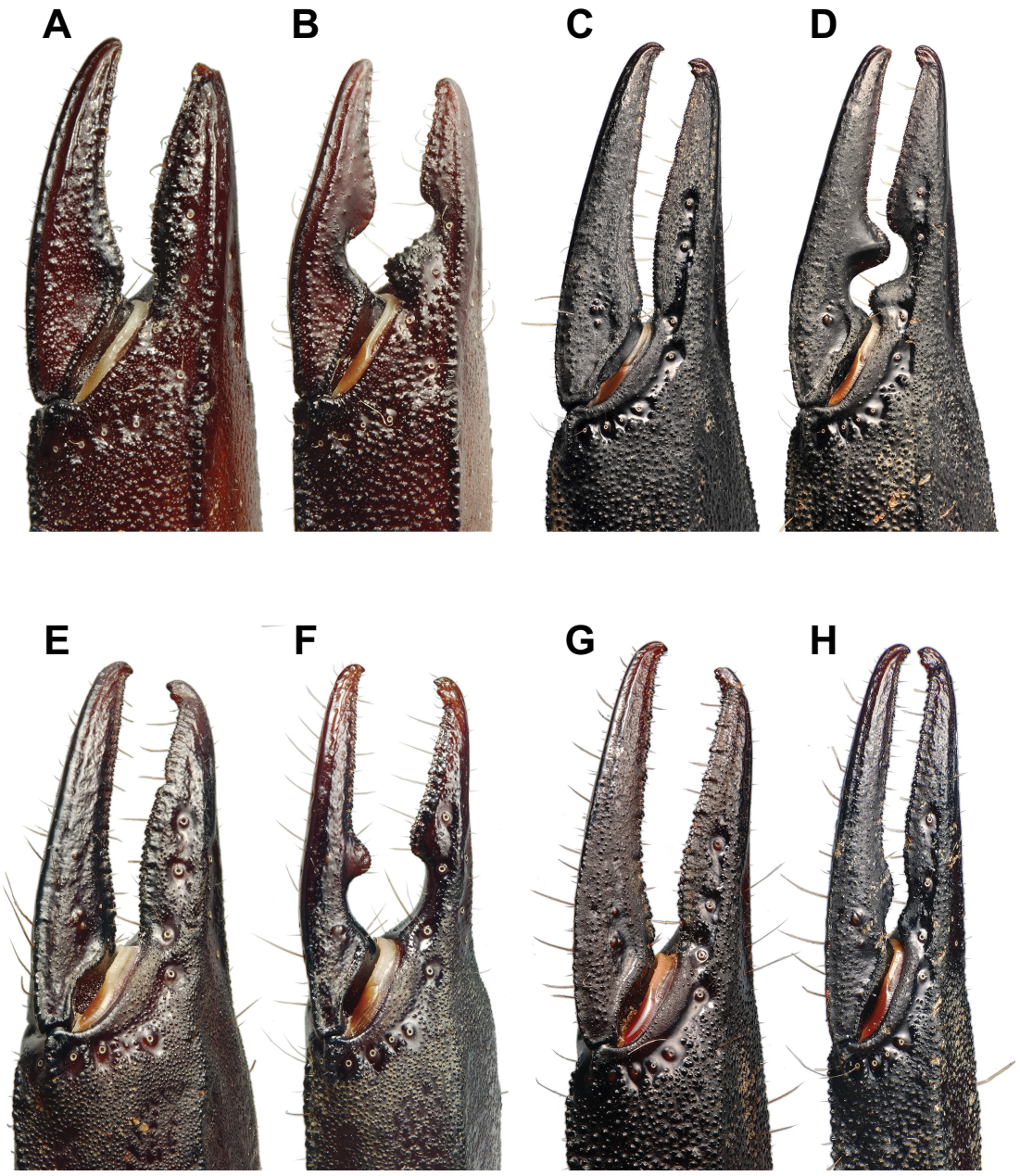
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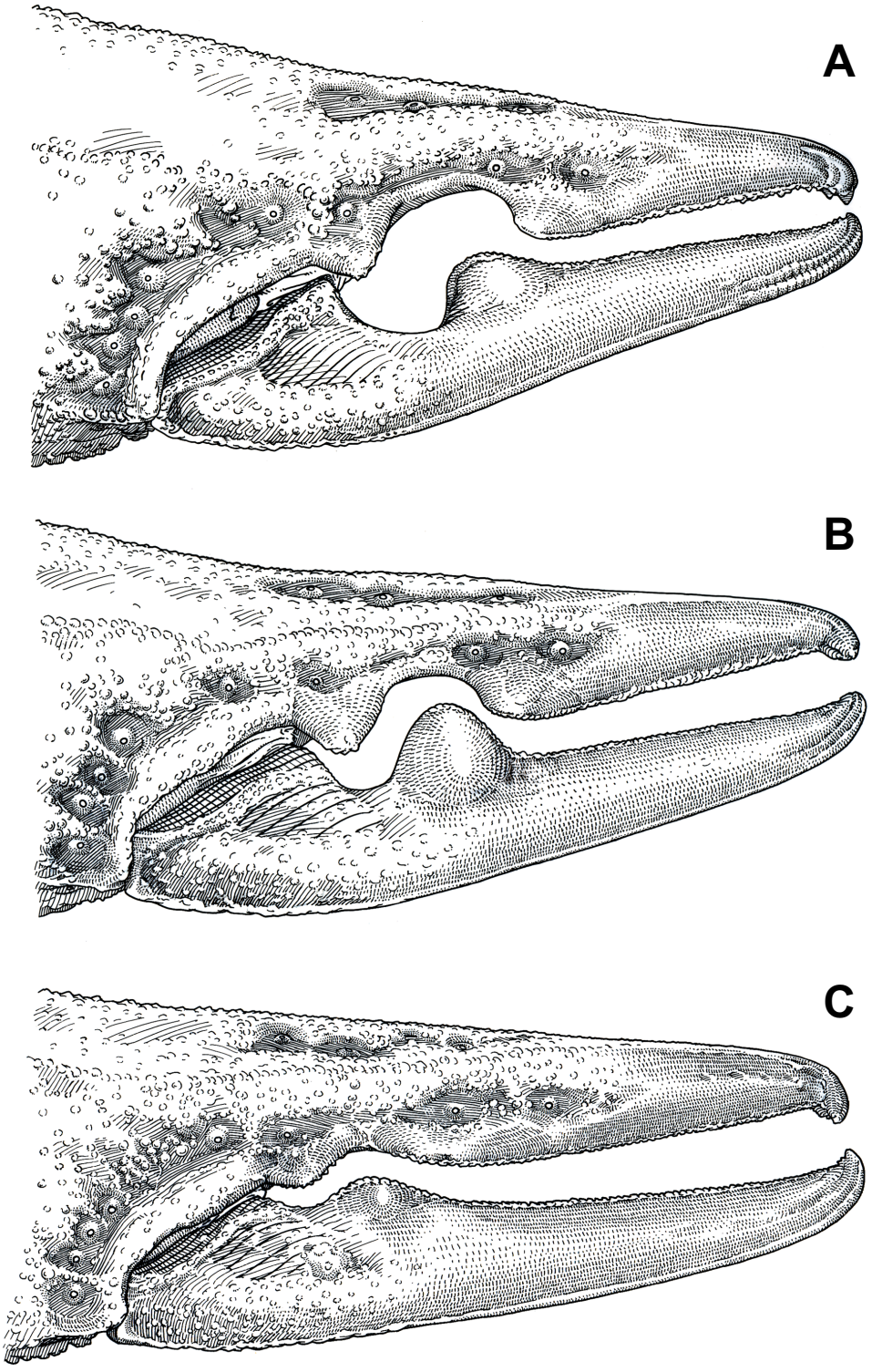
Fig. 16. Morphosculptures of the denticulate edges of the pedipalp chela fingers in mature males of three species of the genus *Hormurus* Thorell, 1876 from New Guinea and Maluku (Indonesia). A, *Hormurus* sp., Halmahera, North Maluku, Indonesia (NNHM). B, *Hormurus karschii* (Keyserling, 1885) from Sekroe, West Papua, Indonesia (NNHM). C, *Hormurus asychnachaena* n. sp. from Lae Botanical Garden, Morobe Province, Papua-New Guinea (AMNH).


A
B
C

and autapomorphic for *C. ochropus*. Besides, this lobe is also expressed as a low hump with few larger teeth (vestigial state) on the pedipalpal movable finger of *Hormurus neocaledonicus* (Simon, 1877), *Hormurus penta* (Francke & Lourenço, 1991), *Hormurus samoa* n. sp., and *Hormurus oreospyridus* n.sp, which represent a synapomorphic state for this group of species. As in Prendini (2000), a dorsally rounded basal lobe lacking a sharp apical tooth is treated as plesiomorphic whereas a lobe bearing a sharp conical tooth is treated as a derived character. Therefore the presence of an apical tooth on the basal lobe and supra-basal lobe of the movable finger are potentially synapomorphic for the group (*I.politus* + *O.*(*Opisthacanthus*)). Finally, a second notch is newly identified on the pedipalpal fixed finger of *Opisthacanthus* (*Nepabellus*) *laevipes* (Pocock, 1893). It extends from the proximal extremity of the fixed finger onto the distal part of the retrolateral surface of the manus, partially covering the connecting membrane between the manus and the movable finger. It is not present in any other taxa studied and constitute therefore a plesiomorphy for *O.*(*N.*) *laevipes*.

Except for *Hormiops infulcra* n. sp., *Hormurus orthodactylus* n. sp. and *Hormurus litodactylus* (Monod & Volschenk, 2004) (figs 15G-H), all males of *Hormurus* and *Liocheles* species possess the lobe-notch combination while the females are without this feature. The morphology of the different lobes and corresponding notches provide clear diagnostic characters that allow the distinction between species within the two genera. The supra-basal lobe of the movable finger can exhibit various degrees of development and shapes, from well developed (figs 15D, 16A-B) to almost absent (figs 15H, 16C), and from relatively narrow (fig. 15F) to much wider (fig. 15B). Besides this lobe and its corresponding notch are not contiguous in all the species and three different types of gaps were observed (character 22; figs 15F, 16A). However all these characteristics appear to be autapomorphic and are not very valuable in the context of a phylogenetic analysis. They are nevertheless included in the matrix in order to provide more accurate descriptions.

Pedipalp trichobothriotaxy [Characters 37–61]

#37. Chela manus, trichobothriotaxy, dorsal surface, position of *Dt* trichobothrium: 1, manus, on proximal half of manus: 2, manus, distal end (at least more than

midpalm); 3, fixed finger, proximal end [S89/81, S89/83-85, LP00/52, S&F03.5/19, LP03/43, VP08/24] [modified].

#38. Chela manus, trichobothriotaxy, dorsal surface, position of *Dt* trichobothrium (if on proximal half of manus): 1, midpalm or slightly less than midpalm; 2, on proximal 1/3 of manus; -, inapplicable.

#39. † Chela manus, trichobothriotaxy, ventral surface, number of *V* trichobothria: 1, 4; 2, 5 (3 distal, 2 proximal); 3, single row of 7–9; 4, single row of 12-15; 5, single row becoming multiple rows distally, more than 25 [LP00/49, LP01/80; PCW03/51, LP03/40, VP08/26] [modified].

#40. Chela manus, trichobothriotaxy, ventral surface, V_3–V_4 relative position: 1, close together, proximal part of manus; 2, apart from each other [HWC81/52, LP01/81; PCW03/52].

#41. † Chela manus, trichobothriotaxy, retrolateral surface, accessory trichobothria: 1, absent (orthobothriotaxic); 2, present, one (neobothriotaxic); 3, more than 20 (neobothriotaxic) [L80/14, P00/53, S&F03.5/33, P03/44] [modified].

#42. Chela manus, trichobothriotaxy, retrolateral surface, position of *Esb* trichobothrium [additive]: 1, more basal than *Eb* group; 2, basal, on the same line as *Eb* group; 3, more distal than *Eb* group, midway between *Eb* group and *Est*; 4. more distal than *Eb* group, close to *Est*, sometimes slightly more distal than *Est*.

#43. Chela manus, trichobothriotaxy, retrolateral surface, position of Eb_3 trichobothrium: 1, close to $Eb_{1–2}$; 2, distal to basal group $Eb_{1–2}$ [S89/88, LP00/54] [modified].

#44. † Chela manus, trichobothriotaxy, retrolateral surface, accessory trichobothria: 1, absent, orthobothriotaxic; 2, 1, neobothriotaxic; 3, more than 20, neobothriotaxic [BHL80/14, LP00/53, S&F03.5/33, LP03/44] [modified].

#45. Chela manus, trichobothriotaxy, retrolateral surface, position of *Est* trichobothium: 1, distal; 2, midpalm or nearly so; -, inapplicable [S89/86, LP00/55, LP03/45].

#46. Chela, fixed finger, trichobothriotaxy, position of *db* trichobothrium: 1, dorsal surface; 2, prolateral surface [LP00/59, LP03/49, VP08/21].

#47. Chela, fixed finger, trichobothriotaxy, position of *est* trichobothria: 1, *esb*, *eb*, *est* and *et* ca. equidistant from each other (distance *est–esb* similar to distance *esb–eb*) or *est* closer to *esb*; 2, *esb* closer to *eb* and *est* closer to *et* (distance *est–esb* greater than distance *esb–eb*) or *est* closer to *et* [BHL79/14, 15].

#48. Chela, fixed finger, trichobothriotaxy, position of *eb* trichobothrium: 1, above *esb–et* axis; 2, in line with *esb–et* axis [LP00/62, LP03/52, VP08/22].

#49. Chela, fixed finger, trichobothriotaxy, position of *esb* trichobothrium: 1, below *est–et* axis; 2, in line with *est–et* axis [LP00/62, S&F03.5/20, S&F03.5/21, LP03/52, VP08/22].

#50. Chela, fixed finger, trichobothriotaxy, position of *esb* trichobothrium: 1, midway along fixed finger; 2, in proximal region of fixed finger; 3, at base of finger, behind point of articulation between fixed and movable fingers [LP00/62, LP03/52, VP08/22].

#51. † Chela, fixed finger, trichobothriotaxy, position of *eb* trichobothrium: 1, proximal region of fixed finger; 2, base of finger, behind point of articulation between fixed and movable fingers; 3, manus, behind movable finger condyle [LP00/61, LP03/51].

#52. † Chela, fixed finger, trichobothriotaxy, number of *i* trichobothria: 1, 2; 2, >2 [PCW03/53].

#53. Patella, trichobothriotaxy, dorsal surface, position of d_2 trichobothrium: 1, more distal than patellal spur; 2, less than mid length (same level as patellal spur).

#54. † Patella, trichobothriotaxy, retrolateral surface, *et* series, number: 1, 3 (0 accessory); 2, 4 or more (1 or more accessory) [L80/17, S89/60-68, LP00/45, S&S01/51, 54–56, 59–65, S&F03.5/30, S&F03.5/36] [split into four characters, 54-57].

#55. † Patella, trichobothriotaxy, retrolateral surface, *est* series, number: 1, 1 (0 accessory); 2, 2 (1 accessory); 3, 3 or more (2 or more accessory) [L80/17, S89/60-68, LP00/45, S&S01/51, 54–56, 59–65, S&F03.5/30, S&F03.5/36] [split into four characters, 54–57].

#56. † Patella, trichobothriotaxy, retrolateral surface, *em* series, number: 1, 2 (0 ac-

cessory); 2, 3 (1 accessory); 3, 4 or more (2 or more accessory) [L80/17, S89/60-68, LP00/45, S&S01/51, 54–56, 59–65, S&F03.5/30, S&F03.5/36] [split into four characters, 54–57].

#57. Patella, trichobothriotaxy, retrolateral surface, *esb* series, number: 1, 2 (0 accessory); 2, 3 (1 accessory, between eb and esb series); 3, 3 (1 accessory, between esb and em series); 4, 5 (3 accessory); 5, 6 or more (4 or more accessory) [L80/17, S89/60–68, LP00/45, S&S01/51, 54–56, 59–65, S&F03.5/30, S&F03.5/36] [split into four characters, 54–57] [modified].

#58. † Patella, trichobothriotaxy, retrolateral surface, *eb* series, number: 1, 5 (0 accessory); 2, 6 or more (1 or more accessory) [S&S01/59].

#59. Patella, trichobothriotaxy, retrolateral surface, em-esb series, relative position: 1, 2 groups [esb_{1-2}][em_{1-2}]; 2, 1 group [esb_{1-2}/em_{1-2}] (esb_{1-2} close to em_{1-2}) or 2 groups [esb_2][esb_1/em_{1-2}] (esb_1 close to em_{1-2} or far away from esb_2).

#60. † Patella, trichobothriotaxy, retrolateral surface, organisation of *eb* series: 1, 2 groups [eb_1]/[eb_{2-5}] or 2 groups [eb_1/eb_{4-5}][eb_{2-3}]; 2, 3 groups [eb_1][eb_2/eb_{4-5}][eb_3] [LP unpublished] [modified].

#61. Patella, trichobothriotaxy, ventral surface, number of v trichobothria: 1, orthobothriotaxic, 3 trichobothria; 2, neobothriotaxic, 5 trichobothria [L80/1, L80/17 (part), S89/52, 56-59, LP00/42, 43, S&S01/52, 53, S&F03.5/35, LP03/34, PCW03/55, VP08/30] [modified].

Pedipalp trichobothriotaxy is considered as one of the major character systems for scorpion higher-level systematics. Stahnke (1970, 1974) and Vachon (1972, 1974) were the first to propose nomenclatural systems for trichobothrial patterns. The terminology proposed by Vachon was universally adopted over Stahnke's and other contemporary systems and is still the standard used in scorpion taxonomy because contrary to the other systems, it documented the similarities and differences among taxa and provided a comparative framework for the terms used. However, the hypotheses of homology on which it is based are not satisfactory. Positional differences between putatively homologous trichobothria were deemed by Stahnke

and Vachon to be the result of trichobothrial “migration”. This theory has been regularly and rightfully questioned by various authors (Francke & Soleglad, 1981; Francke, 1982; Prendini, 2000; Prendini & Wheeler, 2005). For instance, the trichobothrium *Esb*, as it is currently recognized in the genus *Liocheles*, is located either basally or midpalm on the retrolateral surface depending on the species group (fig. 4). It is very likely that *Est* trichobothria in the *australasiae* and *waigiensis* groups are actually not homologous and should be renamed as such. Prendini (2000) argued that trichobothrial migration can be explained to some extent by allometric variations resulting from the high plasticity in the shape of pedipalp observed across the order and that despite its shortcomings Vachon’s approach presented no difficulty to implement while still providing phylogenetic information, i.e. positional differences among “homologous” trichobothria. On the other hand, Soleglad & Sissom (2001) and Soleglad & Fet (2001) advocated that trichobothrial homology statements should be made at the level of individual trichobothria, rather than at the level of pedipal segments or surfaces. Prendini *et al.* (2006) endorsed this opinion but recognized the significant practical challenges inherent to such a task (see below). Prendini & Volschenk (2007) finally proposed an elegant new paradigm which they referred to as the “placeholder” approach and in which trichobothrial homology is determined strictly on topographical identity. A detailed mapping of setal distribution under ultraviolet light (see paragraph 1.4) is used for primary homology assessment of trichobothrial position or “placeholder”, each “placeholder” whether it is a trichobothrium, a macro- or microseta is then treated as a distinct character and is coded accordingly. The assumption behind this procedure is that each placeholder can be expressed as any kind of seta and that differences in trichobothrial patterns are the results of gains or losses rather than “migration” events. The method was successfully applied for the first time in a phylogenetic analysis of the troglomorphic family Typhlochactidae (Prendini *et al.*, 2010).

The *modus operandi* proposed by Prendini & Volschenk (2007) is promising, however it remains so far extremely difficult to apply when taxa with numerous setae and/or accessory trichobothria, such as the genus *Hadogenes* and some *Opisthacanthus* and *Monodopisthacanthus* species, are concerned. Accurately mapping and homologizing hundreds of placeholders is indeed a very challenging task. Whereas most liochelids are orthobothriotaxic (type C),

Fig. 17. Trichobothrial patterns of the external and ventral surfaces of the pedipalp chela in the family Liochelidae Fet & Bechly, 2001. *Hormurus ankistros* n. sp. from Sindik (Saudaun Province, Papua New Guinea), female (LP 4339), orthobothriotaxic. A, External surface with 15 trichobotrium. B, Ventral surface with 4 trichobotrium. *Opisthacanthus elatus* (Gervais,1844) from Santan der Simacota (Colombia), female (LP 2288), orthobotriotaxic. C, External surface with 15 trichobothria. D, Ventral surface with 4 trichobotria. *Hadogenes troglodytes* (Peters, 1861) from Kruger National Park (Limpopo Province, South Africa), female (AMNH), neobothriotaxic major. E, External surface with 43 trichobotria. F, Ventral surface with 54 trichobothria. *Opisthacanthus validus* Thorell, 1876 from Southeys Hoek (Free State, South Africa), female (AMNH), orthobothriotaxic. G, External surface with 15 trichobotrhia. H, Ventral surface with 4 trichobothria. The difference in density of setation between the different species, and especially between *H. troglodytes* and *Hormurus ankistros* n. sp. is clearly visible in the photographs.

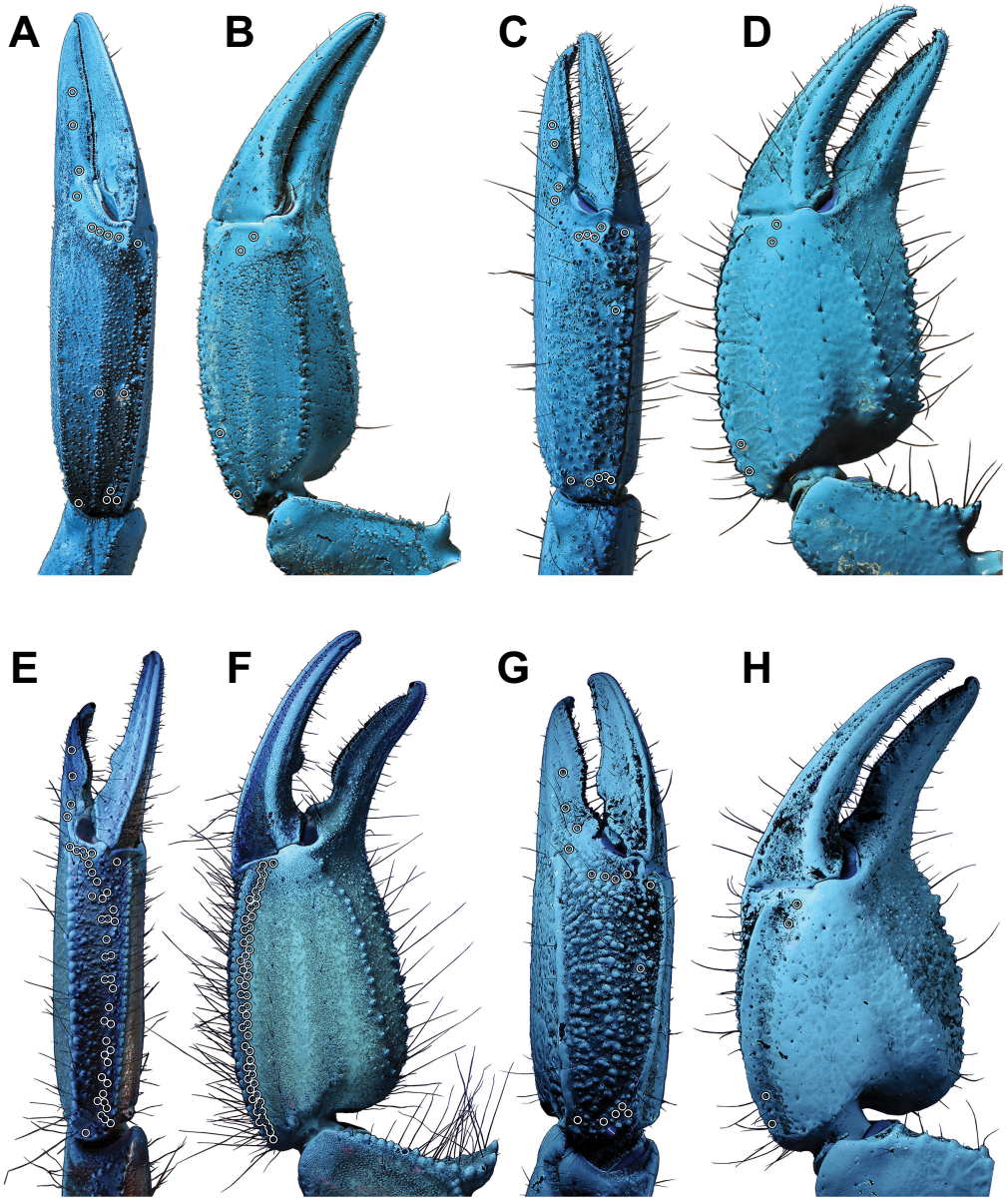

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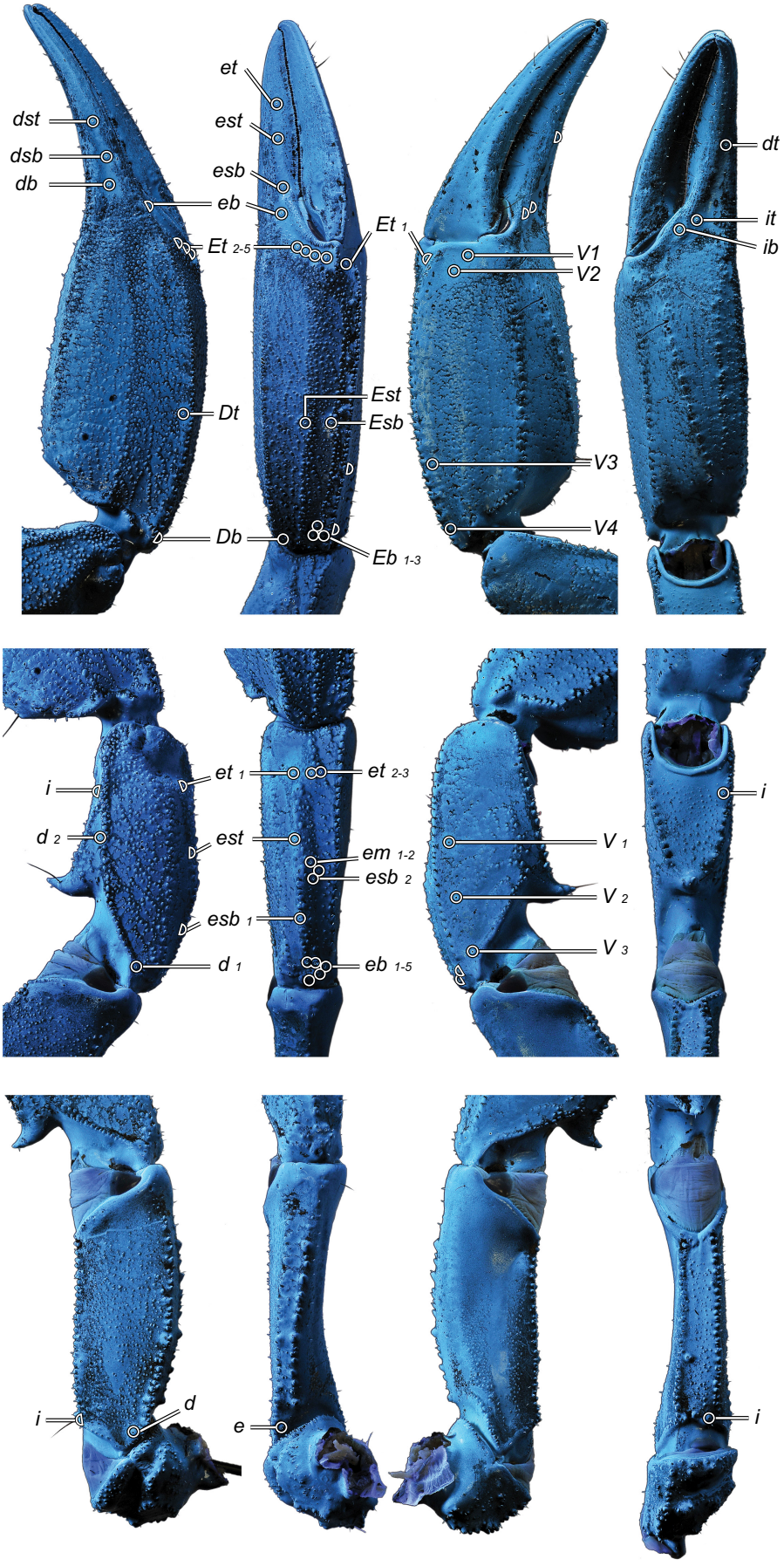
Fig. 18. *Hormurus ankistros* n. sp. from Sindik (Saudaun Province, Papua New Guinea), female (LP 4339). Trichobothrial pattern of the pedipalp. Each trichobothrium is indicated by a white circle and named after Vachon's terminology (1974).


dst
dsb
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Esb
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dt
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d 2
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et 1
et 2-3
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em 1-2
esb 2
esb 1
eb 1-5
V 1
V 2
V 3
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i

possessing a “fundamental” number of 48 trichobothria on the pedipalp (3 trichobothria on the femur, 19 on the patella and 26 on the chela; figs 17A-D/G-H, 18), *Hadogenes* species can have more than 200 (neobothriotaxy major; figs 17E-F; Prendini, 2001A, 2005). The numerous accessory trichobothria observed in the scorpionoid genera *Hadogenes* and *Heteroscorpion* are located for the most part on the external and ventral surfaces of the chela and patella (Lamoral, 1979; Newlands & Cantrell, 1985; Sissom, 1990; Prendini, 2000; Soleglad & Sissom, 2001; Lourenco & Goodman, 2002) and make the identification of the “fundamental” pattern impossible on these surfaces. Besides, *Hadogenes* species also possess numerous setae in addition to the trichobothria which further increase the number of placeholders. Several orthobothriotaxic species included in the present analysis, i.e. *Chiromachus ochropus* (C. L. Koch, 1837), *Iomachus punctulatus* Pocock, 1897, *Opisthacanthus* (*Monodopisthacanthus) piceus* Lourenço & Goodman, 2006, *Opisthacanthus* (*Opisthacanthus*) *cayaporum* Vellard, 1932 are also covered with hundreds of setae and determining the setal map proved to be as difficult as for *Hadogenes*. On the other hand, the rest of liochelids including the genus *Liocheles* are almost completely asetose and the number of “hairs” is consequently much lower than in the above-mentioned taxa. As the number of placeholders greatly differs between the “hairy” and the “bare” liochelids, it is currently not possible to correctly assess the positional congruence of setae between these taxa. This difference in the number of placeholders between the different taxa can potentially be attributed to an inaccurate inventory of the setae. Trichobothria and the bigger macrosetae arise from a distinct cup-shape areola and therefore can be relatively easily located on the cuticle. Besides trichobothria and macrosetae are easily differentiated; the areola is completely filled by the base of the macrosetae whereas it is not by the base of trichobothrium. However, unlike trichobothria and macrosetae, microsetae arise from a minute and poorly developed areolar cup that can be difficult to locate on the cuticle especially when the hair is absent. Setae are indeed extremely fragile and can be fallen or broken off in old collection specimens. No satisfactory consensus to address these issues was achieved at the time of writing. A way to produce reliable and exhaustive mapping of the setae may be to develop an imaging technology that will automatically analyse photographs of the pedipalps to locate setae. Vallotton & Thomas (2008) recently implemented a software that objectively and rapidly

count and measure hairs on different parts of the human body. The software was apparently able to detect hairs that people find hard to see. A similar approach could be applied to quickly produce standardized and accurate maps of the setation of scorpion pedipalps for the different taxa, comparisons would then be facilitated. However it is beyond the scope of the present study and is only mentioned here as a potential direction for future researches.

Vachon's (1974) trichobothrial nomenclature and "migration" interpretation, albeit inaccurate in regard to homology hypotheses, is used in the present study because (1) it remains the only practical alternative to Prendini & Volschenk's (2007) method and (2) it still diagnoses differences in trichobothrial patterns that provide phylogenetic information. The "migration" and the "placeholder" approaches differ in the way characters are coded, different states referring to different positions or to different setal identities respectively. Prendini & Volschenk's (2007) paradigm surpasses the old approach because it correctly assigns homology and will undoubtedly contribute to significant improvements of the phylogeny by revealing numerous additional characters from the chaetotaxy.

Most taxa included in the present study were orthobothriotaxic (Vachon, 1974), the few exceptions only have between one or two additional trichobothria. i.e. *Hormurus dodecatrichos* n. sp. possess one accessory trichobotrium on the retrolateral surface of the chela, *H. penta* and *H. samoa* n. sp. two on the ventral surface of the patella, *Hormurus tetrakaideca* n. sp., *O.* (*N.*) *laevipes* one on the ventral surface of chela and one on the retrolateral surface of the patella, and *O. (O.) cayaporum* one on the retrolateral surface of the patella. All these neobothriotaxies major are autapomorphies. On the contrary, many positional differences in orthobothriotaxic patterns are synapomorphic and indicative of monophyletic groups. The following were identified in the pedipalpal chela and patella:

(1) The *Dt* trichobothrium is located on the proximal half on the dorsal surface of the chela in all liochelids (figs 19 B, C) except *Palaeocheloctonus pauliani* Lourenco, 1996 and *Opisthacanthus* (*Monodopisthacanthus*) (fig. 19 A). The distal position of *Dt* is considered synapomorphic for the group (*P. pauliani* + *Opisthacanthus* (*Monodopisthacanthus*)). [Character 37]

(2) The *db* trichobothrium is on the dorsal surface of the chela in *Hormiops*, *Hormurus* (fig. 19C), *I. politus* (fig. 19B) and *Liocheles* whereas it is on the prolateral surface in all remain-

Fig. 19. Trichobothrial patterns of the dorsal surface of the pedipalp chela in the family Liocheli-dae Fet & Bechly, 2001. A, *Opisthacanthus* (*Monodopisthacanthus*) *madagascariensis* Kraepe-lin, 1894 from Parc National Tsingy de Bemahara (Majanga Province, Madagascar), male (LP 2805). B, *Iomachus politus* Pocock, 1896 fom Hadeni (Tanzania), male (AMNH). C, *Hormurus macrochela* n. sp. from Palm Island (Queensland, Australia), male (QM-S59212). Trichobothria differing in position compared to the pattern observed in the genus *Liocheles* are indicated with arrows.

A
B
C

ing taxa (fig. 19A). The dorsal position is considered synapomorphic for (*Hormiops* + *Hormurus* + *Liocheles*) and might be autapomorphic for *I. politus*. [Character 46]

(3) The *Est* trichobothrium is located distally on the retrolateral surface of the chela in most basal liochelids included in this study (figs 20A, B). A midpalm location for *Est* is therefore synapomorphic for (*Chiromachetes* + Indian *Iomachus*), (*Hormiops* + *Hormurus* + *Liocheles*) (Figs 20C-E), and potentially autapomorphic for *C. ochropus*. [Character 45]

(4) The distal position of the *Esb* trichobothrium (close to Est) on the retrolateral surface of the chela is considered synapomorphic for *Hormurus* (fig. 20D, E). When basal, *Esb* also provides some insight into phylogenetic relationships, depending on its placement compared to the *Eb* group. It is more basal than the *Eb* group or on the same line as the more basal trichobothria of the group (figs 20A, B) except in *Hormiops* and *Liocheles* (fig. 20C). In these two genera, *Esb* is more distal than the two basal *Eb*. This pattern is considered as more derived and synapomorphic. [Character 42]

(5) Trichobothria V_3 and V_4 of the ventral surface of the chela are close in *O*. (*N*.) *laevipes*, the Indian *Iomachus*, *Chiromachetes*, *Chiromachus*, *Opisthacanthus* (*Monodopisthacanthus*) and *Palaeocheloctonus* (fig. 21A) and some *Liocheles* whereas they are far apart in *Hormiops*, *Hormurus* (fig. 21D), *I. politus* (fig. 21B), some *Liocheles* (fig. 21C), and *O*. (*O*.) *lecomtei*. The closeness of V_3–V_4 is regarded as plesiomorphic and a greater distance between the two trichobothriotaxy as synapomorphic for (*I. politus* + (*O*.)(*Opisthacanthus*)) and (*Hormiops* + *Hormurus* + *Liocheles*) respectively. Some *Liocheles* species apparently reverted to the plesiomorphic state. [Character 40]

Trichobothrial patterns of the patella are extremely conserved across the genera studied with very few divergences from the fundamental scheme. Only three characters were deemed important for the phylogenetic analysis:

(1) The position of the trichobothrium d_2 on the dorsal surface diagnoses two distinct groups. It is located on the same line as the patellar spur apex or slightly more distally (fig. 22A) in the basal liochelids, i.e. *Chiromachetes*, Indian *Iomachus*, *Opisthacanthus* (*Monodopisthacanthus*), *Opisthacanthus* (*Nepabellus*), and *Palaeocheloctonus*. The more distal placement of d_2 (figs 22B, C) occurs in *C. ochropus*, *Hormiops*, *Hormurus*, *I. politus*, *Liocheles* and *Opistha-*

Fig. 20. Trichobothrial patterns of the external surface of the pedipalp chela in the family Liochelidae Fet & Bechly, 2001. A, *Opisthacanthus* (*Monodopisthacanthus*) *madagascariensis* Kraepelin, 1894 from Parc National Tsingy de Bemahara (Majanga Province, Madagascar), male (LP 2805). B, *Iomachus politus* Pocock, 1896 from Hadeni (Tanzania), male (AMNH). C, *Liocheles malaya* n. sp. from Bukit Larut (Perak, Malaysia), male (MHNG). D, *Hormurus ischnoryctes* n. sp. from Mount Mulligan Cattle Station (Queensland, Australia), male (to be deposited in the collection of the QM). E, *Hormurus penta* Francke & Lourenco, 1991 from Mount Austen (Guadalcanal, Solomon Islands), male (NHML). Trichobothria differing in position compared to the genus *Liocheles* Sundevall, 1883 are indicated with arrows.

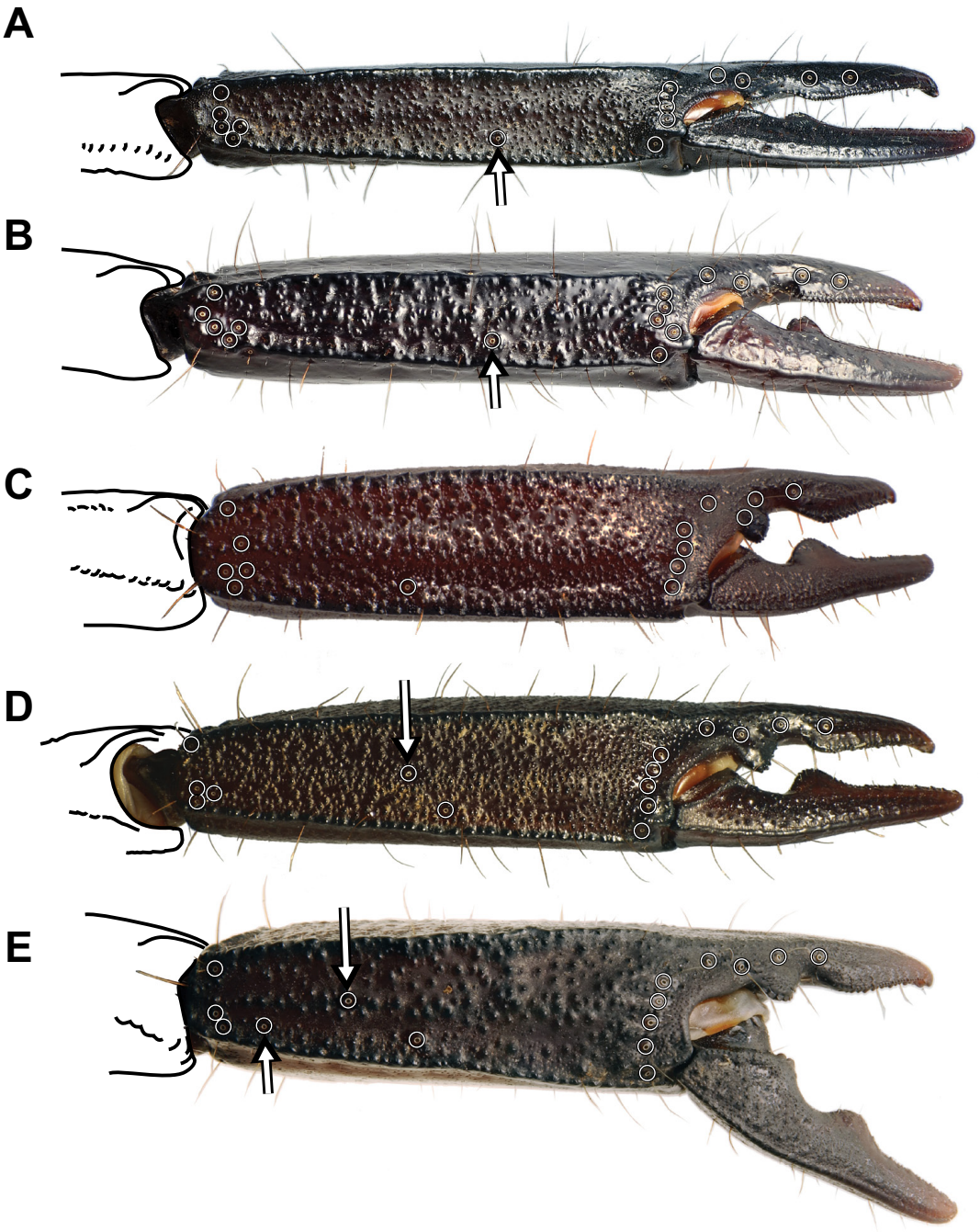

A
B
C
D
E

Fig. 21. Trichobothrial patterns of ventral the surface of the pedipalp chela in Liochelidae Fet & Bechly, 2001. A, *Opisthacanthus* (*Monodopisthacanthus*) *madagascariensis* Kraepelin, 1894 from Parc National Tsingy de Bemahara (Majanga Province, Madagascar), male (LP 2805). B, *Iomachus politus* Pocock, 1896 from Hadeni (Tanzania), male (AMNH). C, *Liocheles malaya* n. sp. from Bukit Larut (Perak, Malaysia), male (MHNG). D, *Hormurus ischnoryctes* n.sp from Mount Mulligan Cattle Station (Queensland, Australia), male (to be deposited in the collection of the QM). Trichobothria differing in position compared to the pattern observed in the genus *Liocheles* Sundevall, 1883 are indicated with arrows.

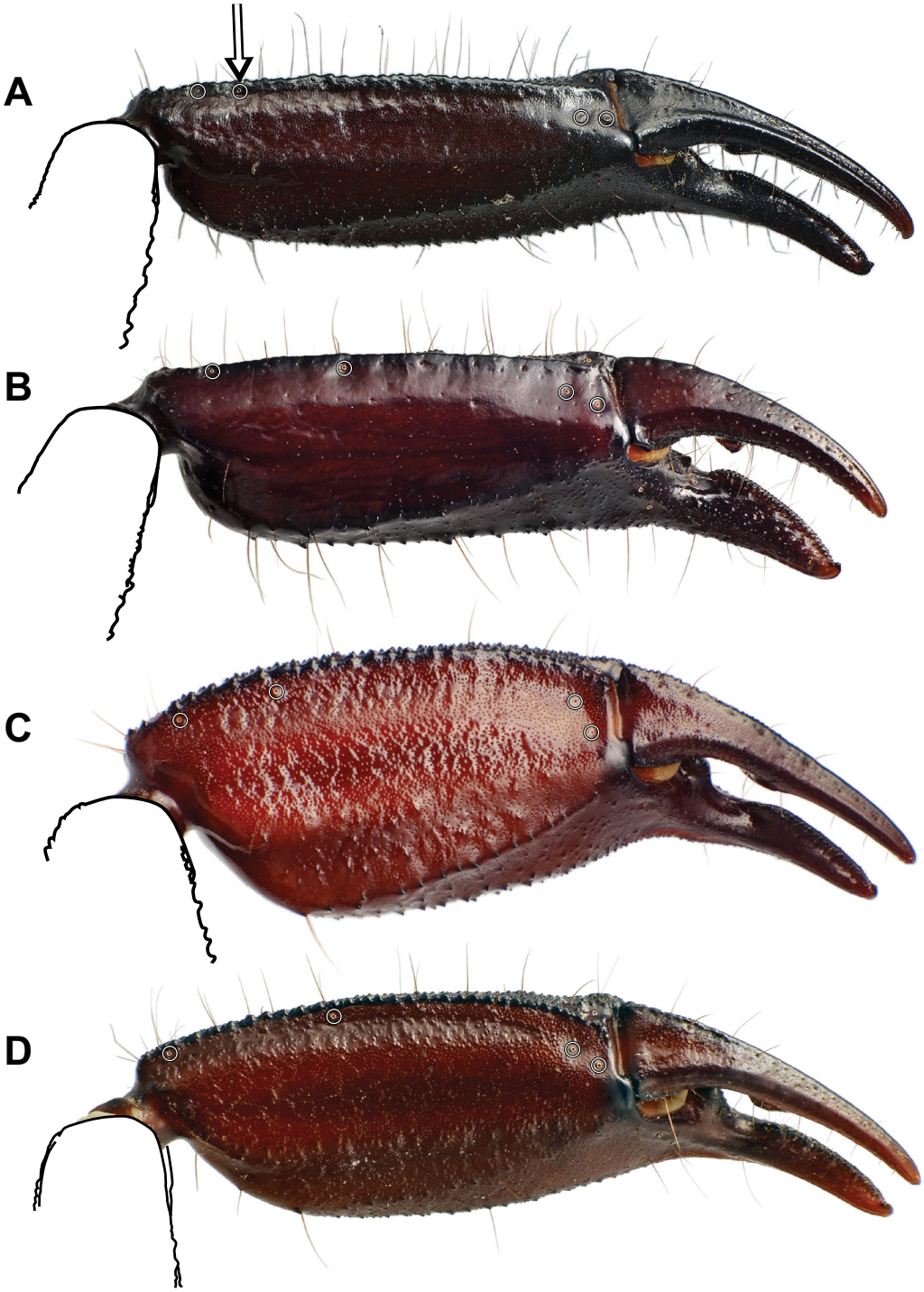
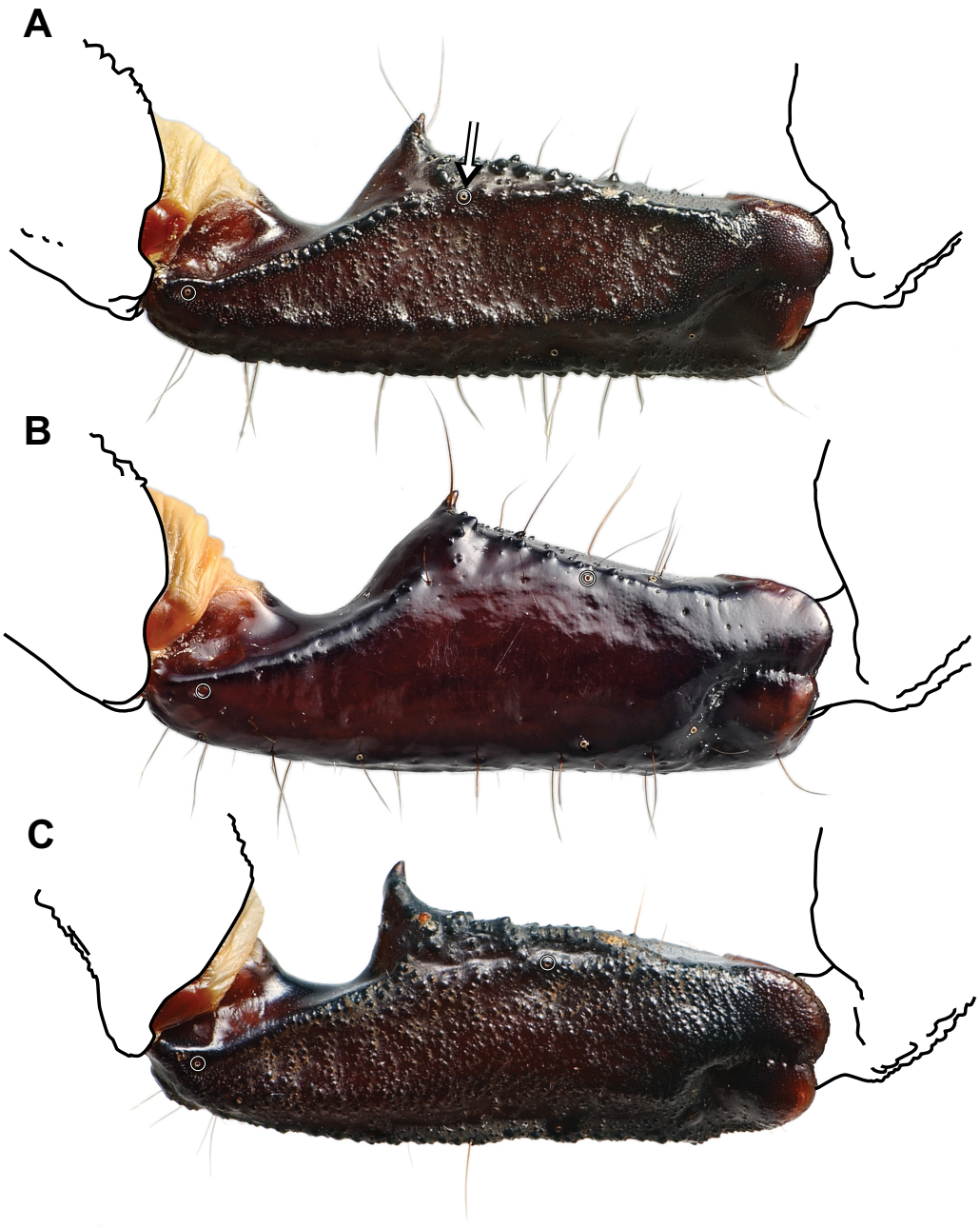

A
B
C
D

Fig. 22. Trichobothrial patterns of the dorsal surface of the pedipalp patella in the family Liochelidae Fet & Bechly, 2001. A, *Opisthacanthus* (*Monodopisthacanthus*) *madagascariensis* Kraepelin, 1894 from Parc National Tsingy de Bemahara (Majanga Province, Madagascar), male (LP 2805). B, *Iomachus politus* Pocock, 1896 from Hadeni (Tanzania), male (AMNH). C, *Hormurus macrochela* n. sp. from Palm Island (Queensland, Australia), male (QM-S59212). Trichobothria differing in position compared to the pattern observed in the genus *Liocheles* Sundevall, 1883 are indicated with arrows.


A
B
C

canthus (*Opisthacanthus*) is potentially synapomorphic. [Character 53]

(2) The esb_2 trichobothrium is placed more closely to the *em* group in the Neotropical *O. (*O.) *cayaporum* and *O.* (*O.*) *elatus*, and several *Hormurus* species (fig. 23D). Although it is a synapomorphy for the Neotropical *Opisthacanthus* (*Opisthacanthus*), it is probably not the case for the *Hormurus* species which will probably not all fall in the same phylogenetic cluster. However the character may represent a synapomorphy for smaller assemblages among these species. [Character 59]

(3) All liochelid species of the present analysis possess three trichobothria on the ventral surface of the patella except *H. penta* and *H. samoa* n. sp., which have five. The presence of two accessory trichobothria on the ventral surface of the patella is a synapomorphy for these two species. [Character 61]

All other variations of the trichobothrial pattern observed on the patella concern the retrolateral surface: (1) eb_3 trichobothrium is located distally from the other *eb* trichobothria in *I. politus* (fig. 23B) whereas it is close to eb_2 and $eb_{4–5}$ in all other taxa (figs 23A, C-D) [Character 60]; (2) neobothriotaxy major is reported in *Hormurus tetrakaideka* n. sp. (one accessory trichobothrium between *eb* and *esb* groups), in *O.* (*O.*) *cayaporum* (one accessory trichobothrium between *esb* and *em* groups) and *O.* (*N.*) *laevipes* (one accessory trichobothrium between *eb* and *esb* groups) [Character 57]. All of these alternative patterns are considered autapomorphic.

Pedipalp ornamentation, carinae [Characters 62–92]

#62. Chela manus, dorsal prosubmedian (*dps*) carina: 1, absent or obsolete; 2, present and distinct at least distally.

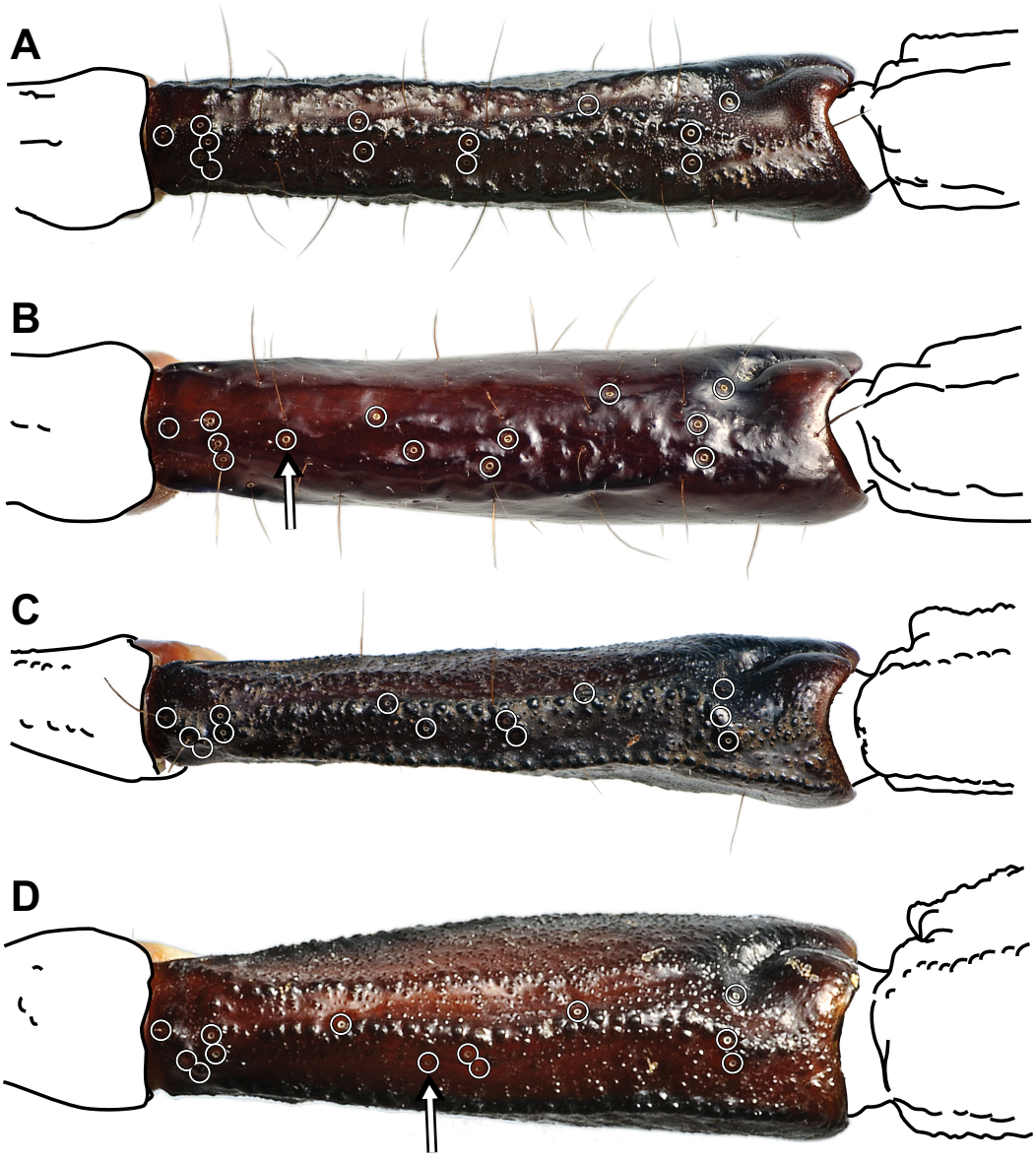
#63. † Chela manus, dorsal median *(dm*) carina: 1, distinct; 2, obsolete [LP00/20–22, LP03/16–18, PCW03/31 [part, Incorporates HWC81/61], VP08/14].

#64. † Chela manus, dorsal retrolateral (*drl*) carina: 1, distinct; 2, absent or obsolete [LP00/23, PCW03/31 [part], LP03/19].

#65. Chela manus, dorsal retrol*at*eral (*drl*) carina, macrosculpture: 1, as a smooth ridge or slightly costate; 2, costate or granular; -, inapplicable [LP01] [modified].

#66. † Chela manus, dorsal retrol*at*eral (*drl*) and [retrolateral median (*rlm*) + ret-

Fig. 23. Trichobothrial patterns of the external surface of the pedipalp patella in the family Liochelidae Fet & Bechly, 2001. A, *Opisthacanthus* (*Monodopisthacanthus*) *madagascariensis* Kraepelin, 1894 from Parc National Tsingy de Bemahara (Majanga Province, Madagascar), male (LP 2805). B, *Iomachus politus* Pocock, 1896 from Hadeni (Tanzania), male (AMNH). C, *Hormurus macrochela* n. sp. from Palm Island (Queensland, Australia), male (QM-S59212). D, *Hormurus asynaptodactylus* n. sp. from Bulolo Gorge (Morobe District, Papua New Guinea), male (CAS). Trichobothria differing in position compared to the pattern observed in the genus *Liocheles* Sundevall, 1883 are indicated with arrows.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rolateral ventrosubmedian (*rlvs*)] carinae, relative development: 1, *drl* carina stronger than [*rlm*+*rlvs*] carina; 2, *drl* and [*rlm*+*rlvs*] carinae equally developped; 3, [*rlm*+*rlvs*] carina stronger than *drl* carina [LP00/25] [modified].

#67. † Chela manus, [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae: 1, absent or obsolete; 2, distinct [LP01/57].

#68. Chela manus, ventral retrol*at*eral (*vrl*) carina: 1, as a smooth ridge; 2, costate; 3, granular or crenelate [BHL79/21; LP01/58] [modified].

#69. † Chela manus, ventral median (*vm*) carina: 1, absent or obsolete; 2, distinct [LP01/62].

#70. † Chela manus, ventral prolateral (*vpl*) and prolateral ventrosubmedian (*plvs*) carinae, relative development: 1, *vpl* carina more strongly developed than *plvs* carina, which may be obsolete; 2, *vpl* carina equally or less strongly developed than *plvs* carina [LP00/29, LP03/23, PCW03/36, VP08/16].

#71. Chela manus, ventral prolateral (*vpl*) carina: 1, absent or obsolete; 2, present at least as a faint ridge or a distinct row of granules.

#72. † Chela manus, ventral prolateral (*vpl*) carina: 1, granular (at least sparsely or faintly); 2, smooth; -, inapplicable.

#73. Chela manus, prolateral ventrosubmedian (*plvs*) carina: 1, present, granular (at least sparsely or faintly); 2, absent or obsolete [PCW03/35].

#74. Patella, prolateral process: 1, present (distinct); 2, weakly developed, reduced; 3, absent or vestigial [WRL5, LP00/18, LP03/14, VP08/17] [modified].

#75. Patella, prolateral process, development if present: 1, low; 2, strongly developped, high; -, inapplicable.

#76. Patella, prolateral process, shape: 1, forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; 2, forming a single large spine; -, inapplicable.

#77. Patella, dorsal prodorsal (*pd*) carina: 1, distinct; 2, absent or obsolete [LP unpublished].

#78. † Patella, dorsal prosubmedian (*dps*) carina: 1, distinct; 2, absent or obsolete

[PCW03/39].

#79. Patella, dorsal retrol*at*eral (*drl*) carina: 1, distinct, at least a low ridge or a row of granules; 2, absent or obsolete [LP00/16, LP03/12].

#80. † Patella, dorsal retrol*at*eral (*drl*) carina: 1, smooth or nearly so; 2, costate or granular; -, inapplicable [LP01/68].

#81. Patella, [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae: 1, granular or costate; 2, as a smooth ridge, at most faintly costate; 3, absent or obsolete [PCW03/43] [modified].

#82. Patella, ventral retrol*at*eral (*vrl*) carina: 1, obsolete/absent or only expressed in distal half; 2, present and distinct (sometimes not expressed on proximal and distal extremities).

#83. Patella, ventral retrol*at*eral (*vrl*) carina: 1, as a smooth ridge or faintly costate; 2, costate or granular; -, inapplicable [LP unpublished] [modified].

#84. † Femur, dorsal retrol*at*eral (*drl*) carina: 1, present and distinct, at least as a ridge usually more distinct in proximal half; 2, absent or obsolete [LP unpublished].

#85. Femur, dorsal retrol*at*eral (*drl*) carina: 1, less strongly developed than dorsal prosubmedian (*dps*) carina; 2, equally developed than *dps* carina; 3, more strongly developed than *dps* carina [HWC81/28, PCW03/44] [modified].

#86. † Femur, dorsal prosubmedian (*dps*) carina: 1, present and distinct; 2. absent or obsolete [PCW03/45].

#87. Femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae: 1, present and distinct, or at least vestigial marked by several larger granules; 2, absent or obsolete [LP unpublished].

#88. Femur, prolateral subdorsal (*pls*) carina [additive]: 1, vestigial with 3–4 large spines; 2, vestigial with 2 large spines; 3, absent without spines or granules (or with a single basal spine).

#89. Femur, prolateral median (*plm*) carina [additive]: 1, vestigial with 3–4 large spines; 2, vestigial with 2 large spines (one proximal and one midway); 3, absent

without spines or at most vestigial with a single spine at proximal extremity.

#90. Femur, prolateral subdorsal (*pls*) and prolateral median (*plm*) carina: 1, oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) carinae; 2, oriented diagonally across from *vpl* carina to *plvs* carinae; -, inapplicable [PCW03/46].

#91. Femur, ventral retrosubmedian (*vrs*) carina: 1, absent or obsolete; 2, partial, expressed only proximally; 3, present [LP01/75; PCW03/47] [modified].

#92. † Femur, ventral prolateral (*vpl*) carina: 1, present; 2, absent [LP unpublished].

The carinae or keels are raised sclerotized ridges on the surface of the cuticle, that indicate internal points of muscle attachment. They have long been recognized for their importance in scorpion systematics as diagnostic characters (Kraepelin, 1899; Werner, 1934; Hoffmann, 1931; Vachon, 1952; Stahnke, 1970; Soleglad, 1973; Francke, 1977; Sissom, 1985, 1989, 1991; Sissom & Francke, 1985; Sissom & Stockwell, 1991; Prendini, 2004) and more recently as phylogenetic characters (Lamoral, 1979, 1980; Stockwell, 1989; Prendini 2000, 2001b; Soleglad & Sissom, 2001; Prendini *et al.*, 2003; Soleglad & Fet, 2003; Ochoa, 2004a). The carinae on the pedipalp femur, patella and chela represents a significant source of characters to reconstruct the phylogeny of scorpions. However, as with trichobothriotaxy (see above) and most other character systems in scorpion systematics, the amount of phylogenetic data provided by the pedipalp carination is currently limited by an inadequate understanding of the patterns of homology both within and among taxa (Prendini *et al.*, in prep.).

Discrepancies in the primary homology assessment of pedipalp carinae are initially caused by the lack of an explicit criteria for the identification of the structure. The problem is further increased by the non recognition of a hierarchy in the information content of homologous structures by some authors. At a broad level, a carina may be considered as absent or present independently of its morphological expression. The same carina can indeed be present as a granular or a smooth ridge, as a row of setae or as a pigmented band depending on the taxa. These differences can then be applied at a lower, less inclusive level of the taxonomy. Disregarding the different “layers” of information has considerable implications on how the carina is defined, and scored in a phylogenetic matrix thereof and undoubtedly results in the misinterpre-

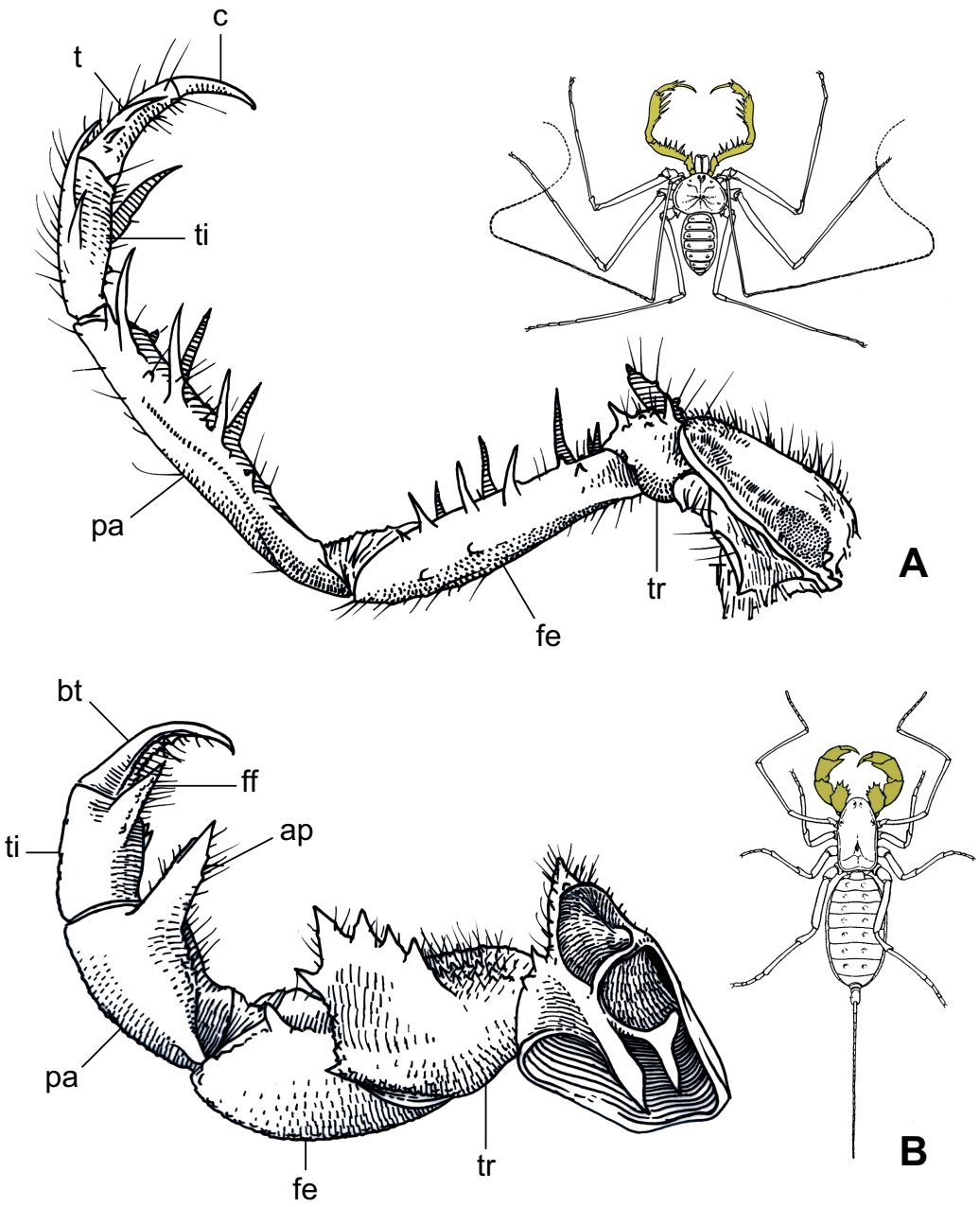
tation and sometimes omission of an important source of data. These deficiencies led to major disagreements between authors concerning the presence, absence, fundamental number and expression of carinae and numerous nomenclatural systems were eventually created to accommodate all the different opinions. In order to address these problems, L. Prendini initiated a group project the aims of which were (1) to provide explicit criteria for identifying pedipalp carinae and for evaluating and objectively describing their differential expression among taxa, (2) to determine the location of the “missing” carinae in order to establish the fundamental number of carinae on each segment, and finally (3) to implement a new terminology, reflecting homology among the taxa studied and across the segments. The system developed by L. Prendini and coworkers, i.e. L. Monod, L. Esposito, E. Gonzalez, C. I. Mattoni and E. S. Volschenk (in prep.) is adopted here.

Previous terminologies. Lawrence (1928), Hewitt (1918), Kraepelin (1899), Werner (1934), Hoffmann (1931, 1932), and Vachon (1952), each proposed their own nomenclature for the pedipalp carinae. Stahnke (1970) attempted to provide a standardized terminology but his consensus was not adopted universally and many scorpiologists subsequently continued to use one of the earlier systems or developed new alternative schemes (Gertsch & Soleglad, 1972; Soleglad, 1973; Francke, 1977; Williams & Savary, 1991). Most of these systems overlapping to various degrees were still in use by the late 90s. It is probably the different carinal patterns exhibited by different taxa that induced the development of many different systems of nomenclature for the pedipalp carination. The carinae are not expressed the same way in different taxa, some carinae are present in some while obsolete or absent in others, for instance the dorsal median carina of the patella observed in the Buthidae is absent in the Liochelidae. The systems of Vachon (1952), of Gertsch & Soleglad (1972) and Soleglad (1973), and of Francke (1977) were developed for Buthidae, Vaejovidae, and Diplocentridae respectively. Thus each of these systems reflects the carinal patterns observed in the group studied and was established without taking the variability across the whole order into consideration. Consequently there are little phylogenetic congruence among the different systems and it is frequent that homologous structures in different taxa are assigned different terms and/or that non-homologous structures

in different taxa are assigned the same term depending on the system used. This makes the use of literature to assess primary homology across diverse taxa for phylogenetic analysis extremely difficult. Recently, this problem was partially addressed by Prendini (2000) who proposed a standardized nomenclature for carination of the pedipalp chela that was based on an assessment of homology between 36 scorpionoid genera and that incorporates terminology from earlier systems (Stahnke, 1970; Francke, 1977; Stockwell, 1989). In a similar way, Soleglad & Fet (2003) presented a nomenclature for the carinal pattern of the patella based on an assessment of homology between sixteen scorpion genera and modified from the terminologies of Vachon (1952) and Stahnke (1970). However, unlike the chela and patella, the pedipalp femur has been neglected as a potential source of data and homology of its carinae between diverse scorpion taxa has not been recently reevaluated in the context of a global phylogenetic analysis.

Serial homology. Although it is not as conspicuous in scorpions as in other arachnid orders (see fig. 24), pedipalp femur, patella, chela and movable finger are arguably derived from the same original ground-plan structure and are therefore serially homologous. However, previous authors never considered the pedipalp carinae as serial homologue. Carination pattern is the external cuticular expression of the internal muscular and neural systems of the three segments and consequently should also reflect serial homology. It follows from this assumption that the same basic number of carinae must exist on the different segments regardless of their phenotypic expression. However, different numbers of carinae are currently identified on each segment, i.e. ten on the chela (Vachon, 1952; Prendini, 2000; Soleglad & Sissom, 2001; Soleglad & Fet, 2003), eight on the patella, and six on the femur (Vachon, 1952; Stahnke, 1970; Soleglad & Fet, 2003). Hence it is legitimate to assume that the fundamental number of carinae on the patella and femur has been underestimated. Secondary carinae are undoubtedly much more difficult to locate on these two segments than on the chela because of the smaller cuticular surface and were omitted by previous workers (“missing” carinae). It is especially true for the prolateral and retrolateral aspects where numerous carinae are crammed onto a very reduced tegument surface. Conversely, all carinae identified on the patella and femur should be present

Fig. 24. Pedipalp morphology in the arachnid orders Amblypygi and Uropygi. A, *Charinus milloti* Fage, 1939 (Amblypygi), *in toto* with pedipalps indicated in color and detail of the left pedipalp (dorsal aspect). B, *Mastigoproctus giganteus* (Lucas 1835) (Uropygi), *in toto* with pedipalps indicated in color and detail of the left pedipalp (dorsal aspect). Segments of the pedipalps of Amblypygids are the least modified with only a few large spines. The pedipalps of Uropygids are more derived but their morphology still remains close to the plesiomorphic state. The patella bears a large internal apophysis. The tibia possesses a similar process refered to as fixed finger and which is homologous to the fixed finger of the scorpion chela. The basitarsus is homologous to the movable finger of the scorpion chela. Abbreviations: ap = patellar apophysis; bt = basitarsus; c = claw; fe = femur; ff = fixed finger; pa = patella; t = tarsus; ti = tibia; tr = trochanter. Modified from Millot (1949a, 1949b).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B

on the chela and they should be given equivalent names on all three articles. However it is not the case and carinae assigned the same terms on different segments are not necessarily homologous. The discrepancy in the fundamental numbers of carinae across pedipalp segments and the inadequacy of the current terminology to accurately reflect serial homology between these units emphasizes the need for a complete reinterpretation of the carinal patterns and of a new terminology that is consistent across the segments (Prendini *et al.*, in prep.).

Semantics. A raised sclerotized cuticular ridge is the most conspicuous form of phenotypic expression of a carina on cuticular surfaces. However the absence of a ridge is not necessarily indicative of the absence of a carina. Carinae may indeed be expressed in various other ways. In many taxa, rows of macro- and/or microsetae, pigmented bands or combinations of several of these aspects are observed instead of raised ridges. Thus, a carina is considered as absent only when there is no evidence for any of the attributes mentioned above. If present, a cuticular ridge may be further characterized (1) by the strength of its sclerotization or vertical development and (2) by its macrosculpture or ornamentation. The following adjectives are currently employed to define and score the different characteristics of carinae in the phylogenetic matrix:

- “Prominent”, “well developed” or distinct” refers to a ridge that is strongly sclerotized, protruding well above the intercarinal surfaces, whereas “weakly developed”, “indistinct” or “obsolete” refers to a carina that is weakly sclerotized, protruding only slightly above the intercarinal surfaces or not at all but that remains discernible.

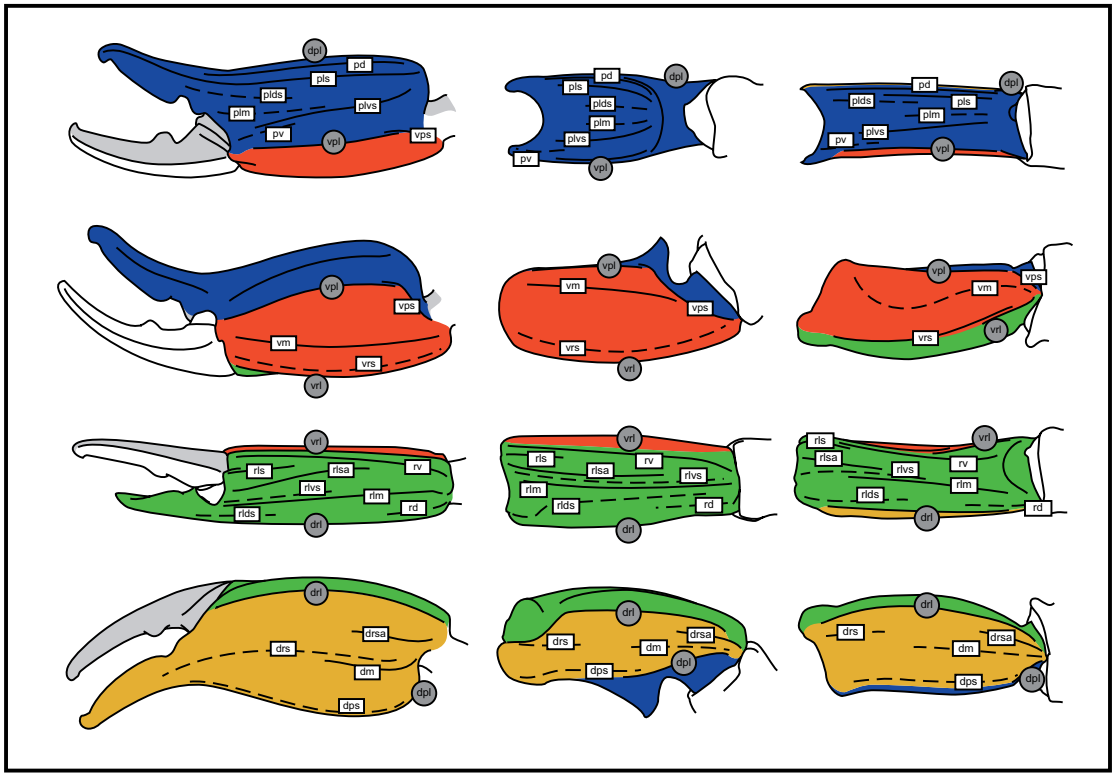
- “Vestigial” refers to a carina that is reduced to only one or a few granules (usually at one extremity of the segment).

- “Granular” refers to a discontinuous ridge comprising isolated granules, “costate-granular” to a continuous ridge comprising confluent granules that may be variably developed, e.g. serrate or crenulate and “costate” to a continuous, smooth ridge.

Besides, when referring to the pedipalps, “internal” and “external” are terms that are not anatomically correct, and should be replaced by “prolateral” and “retrolateral”, respectively (Acosta *et al.*, 2008).

Anatomical implications. 24 carinae per segments were necessary to satisfactorily accommodate homologies of the carinae among all scorpion families (see tabs. 3-5, figs 25-28) and the three pedipalp segments (Prendini *et al.*, in prep.). This represents a substantial increase from the fundamental number of 10 carinae previously recognized on the chela. Several carinae omitted by previous workers are identified in the new system and others from the earlier systems (see tabs. 3–5 for carinal synonymies between the different systems) are regarded here as resulting from the "fusion" of two carinae, i.e. one originating from the basal extremity of a segment and another originating from the distal extremity, and split accordingly. For instance, the ventral internal carina of the pedipalp chela of Stockwell (1989) and Prendini (2000) is divided into two distinct units, *vps* (ventral prosubmedian) located on the proximal extremity and *vpl* (ventral prolateral) extending from the distal extremity almost along the entire ventral surface and merging with *vi* proximally. This assumption is congruent with what was previously interpreted as differences in the longitudinal development of carinae between diverse taxa. A carinal ridge can extend continuously across a segment's surface from one extremity to the other in some taxa (complete carina) whereas the same ridge extends only partially across the surface from one extremity but terminates before reaching the other extremity (incomplete or partial carina) in other taxa. However as for the "migration" of trichobothria, the "extension" or "shortening" of carinae is difficult to advocate from an anatomical and evolutionary perspective given the nature of the carinae themselves and should therefore be rejected. As outlined before, carinae are points of attachment of the internal musculature and consequently their positions on the cuticle are determined by the intrinsic function of associated muscles, presently motions of the pedipalps. Hence, any evolutionary mechanism that accounts for carinal extension or shortening must also explain a modification of the related muscles and of their biomechanical function thereof. Pedipalp femur, patella and chela are articulated in the same horizontal plan, parallel to the ground in all scorpions. This entails that the organisation of the muscular system is extremely similar across the order and as a result there must be no major variation in the carinal pattern of the pedipalp. Each individual carina should occupies approximately the same position (proximal, distal or along the entire length of the surface) in all

Fig. 25. Carinal pattern of the pedipalp chela, patella and femur as proposed by Prendini *et al.* (in prep.). Primary carinae are indicated with plain lines and secondary carinae with dashed lined on the drawings, each surface is indicated with a different colour. The carinae and different surfaces are also represented on a simplified cross-section diagram.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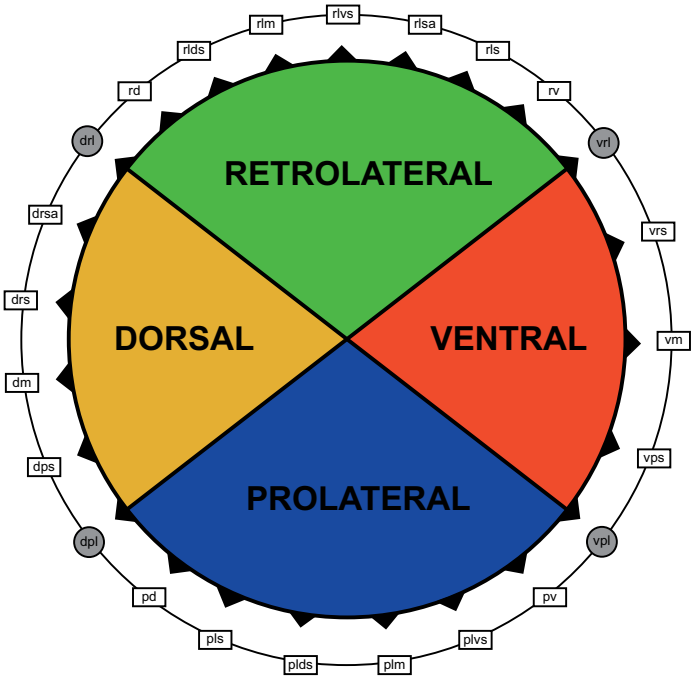
RETROLATERAL
DORSAL
VENTRAL
PROLATERAL
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rlvs
rlsa
rls
rlds
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vm
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pv
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plvs
pls
plds
plm

Table 3. Carinal terminology for the pedipalp chela according to Prendini *et al.* (in prep.). The names and acronyms of each carinae are provided. Synonymies with the most recent nomenclatural systems are summarized. The sign "—" indicates when carinae from earlier terminologies are divided into several distinct units in the present system.

	CARINA	ACRONYM	Stockwell, 1989	Prendini, 2000	Soleglad & Sissom, 2001	Soleglad & Fet, 2003
NUMBER RECOGNIZED	24		8	10	10	10
DORSAL	dorsal prolateral	*dpl*	dorsal marginal	dorsal marginal	D4	D4
	dorsal prosubmedian	*dps*				
	dorsal median	*dm*	dorsal secondary	dorsal secondary	D3	D3
	dorsal retrosubmedian	*drs*				
	dorsal retrosubmedian accessory	*drsa*		subdigital	D2	D2
	dorsal retrolateral	*drl*	digital	digital	D1	D1
RETROLATERAL	retrodorsal	*rd*				
	retrolateral dorsosubmedian	*rlds*				
	retrolateral median	*rlm*	external secondary	external secondary	E	E
	retrolateral ventrosubmedian	*rlvs*	—	—	—	—
	retrolateral subventral accessory	*rlsa*				
	retrolateral subventral	*rls*				
	retroventral	*rv*				
VENTRAL	ventral retrolateral	*vrl*	ventromedian	ventroexternal	V1	V1
	ventral retrosubmedian	*vrs*				
	ventral median	*vm*		ventromedian	V2	V2
	ventral prosubmedian	*vps*	ventrointernal	ventrointernal	V3	V3
	ventral prolateral	*vpl*	—	—	—	—
PROLATERAL	proventral	*pv*				
	prolateral ventrosubmedian	*plvs*	internomedian	internomedian	I	I
	prolateral median	*plm*	—	—	—	—
	prolateral dorsosubmedian	*plds*				
	prolateral subdorsal	*pls*	dorsointernal	dorsointernal	D5	D5
	prodorsal	*pd*				

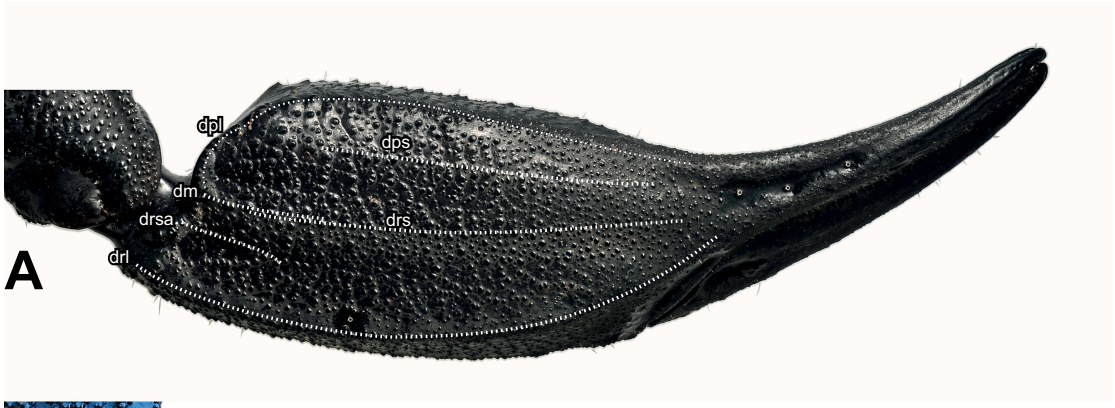
Table 4. Carinal terminology for the pedipalp patella according to Prendini *et al.* (in prep.). The names and acronyms of each carinae are provided. Synonymies with the most recent nomenclatural systems are summarized. The sign "—" indicates when carinae from earlier terminologies are divided into several distinct units in the present system.

	CARINA	ACRO-NYM	STOCKWELL, 1989	PRENDINI, 2000	SOLEGLAD & SISSOM, 2001	SOLEGLAD & FET, 2003
NUMBER RECOGNIZED	24		8	7	7	8
DORSAL	dorsal prolateral	*dpl*	dorsointernal	dorsomedian	dorsomedian	dorsointernal
	dorsal prosubmedian	*dps*	—	—	—	—
	dorsal median	*dm*	dorsomedian			dorsomedian
	dorsal retrosubmedian	*drs*	—			—
	dorsal retrosubmedian accessory	*drsa*				
	dorsal retrolateral	*drl*	dorsoexternal	dorsoexternal	dorsoexternal	dorsoexternal
RETROLATERAL	retrodorsal	*rd*				
	retrolateral dorsosubmedian	*rlds*				
	retrolateral median	*rlm*	externomedian	externomedian	externomedian	externomedian
	retrolateral ventrosubmedian	*rlvs*	—	—	—	—
	retrolateral subventral accessory	*rlsa*				
	retrolateral subventral	*rls*				
	retroventral	*rv*				
VENTRAL	ventral retrolateral	*vrl*	ventroexternal	ventroexternal	ventroexternal	ventroexternal
	ventral retrosubmedian	*vrs*				
	ventral median	*vm*				
	ventral prosubmedian	*vps*	ventrointernal	ventrointernal	ventrointernal	ventrointernal
	ventral prolateral	*vpl*	—	—	—	—
PROLATERAL	proventral	*pv*				
	prolateral ventrosubmedian	*plvs*	internomedian	internomedian	internomedian	VPS (ventral patellar spur)
	prolateral median	*plm*	—	—	—	—
	prolateral dorsosubmedian	*plds*				
	prolateral subdorsal	*pls*	internomedian	internodorsal	internodorsal	DPS (dorsal patellar spur)
	prodorsal	*pd*	—	—	—	—

Table 5. Carinal terminology for the pedipalp femur according to Prendini *et al.* (in prep.). The names and acronyms of each carinae are provided. Synonymies with the most recent nomenclatural systems are also summarized. The sign "—" indicates when carinae from earlier terminologies are divided into several distinct units in the present system.

	CARINA	ACRONYM	STOCKWELL, 1989	PRENDINI, 2000	SOLEGLAD & SISSOM, 2001	SOLEGLAD & FET, 2003
NUMBER RECOGNIZED	24		6	6	6	6
DORSAL	dorsal prolateral	*dpl*				
	dorsal prosubmedian	*dps*				
	dorsal median	*dm*				
	dorsal retrosubmedian	*drs*				
	dorsal retrosubmedian accessory	*drsa*				
	dorsal retrolateral	*drl*	dorsoexternal	dorsoexternal	dorsoexternal	dorsoexternal
RETROLATERAL	retrodorsal	*rd*				
	retrolateral dorsosubmedian	*rlds*				
	retrolateral median	*rlm*	ventroexternal	ventroexternal	ventroexternal	ventroexternal
	retrolateral ventrosubmedian	*rlvs*				
	retrolateral subventral accessory	*rlsa*				
	retrolateral subventral	*rls*				
	retroventral	*rv*				
VENTRAL	ventral retrolateral	*vrl*	ventromedian	ventromedian	ventromedian	ventromedian
	ventral retrosubmedian	*vrs*	—	—	—	—
	ventral median	*vm*				
	ventral prosubmedian	*vps*				
	ventral prolateral	*vpl*				
PROLATERAL	proventral	*pv*				
	prolateral ventrosubmedian	*plvs*	ventrointernal	ventrointernal	ventrointernal	ventrointernal
	prolateral median	*plm*	internomedian	internomedian	internomedian	internomedian
	prolateral dorsosubmedian	*plds*				
	prolateral subdorsal	*pls*				
	prodorsal	*pd*	dorsointernal	dorsointernal	dorsointernal	dorsointernal

Fig. 26. *Hormurus ankistros* n. sp. from Sindik (Saudaun Province, Papua New Guinea), female (LP 4339). Carinal pattern of the pedipalpal chela, according to the terminology proposed by Prendini *et al.* (in prep). A, dorsal aspect under normal light. B, dorsal aspect under UV light. C, external aspect under UV light. D, ventral aspect under UV light. E, internal aspect under UV light.


dpl
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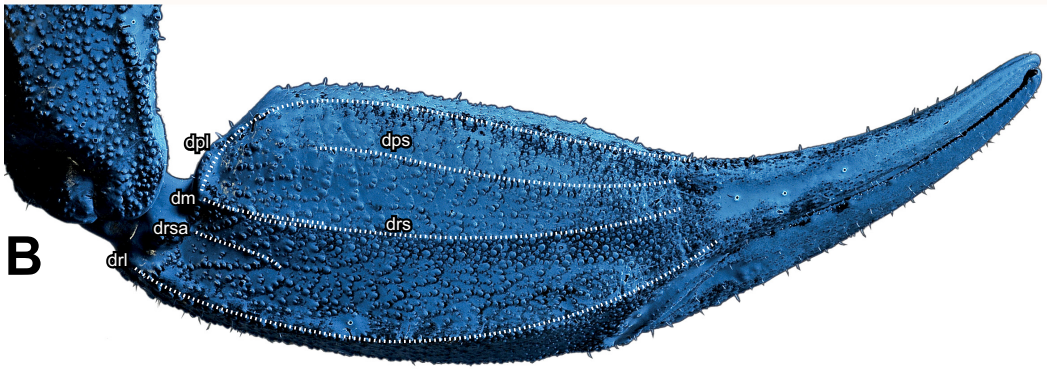
drl

A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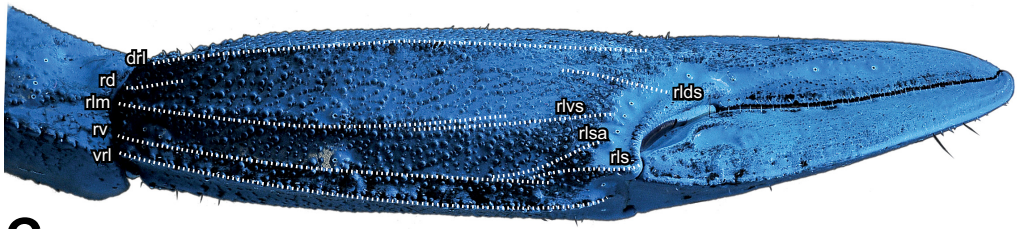
drl
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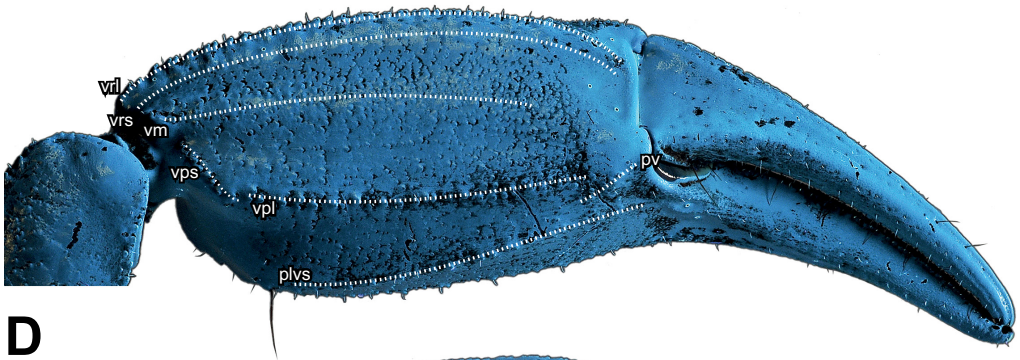
C


vrl
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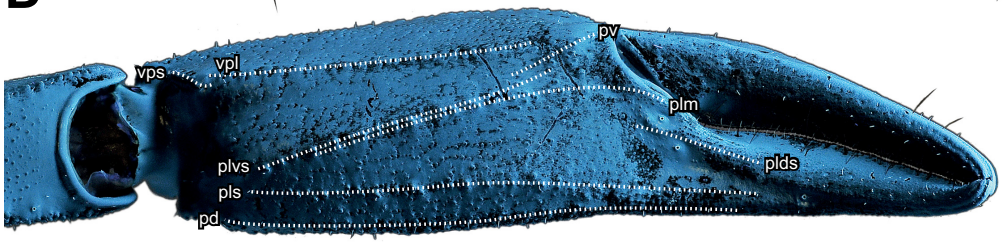
plvs
pv

D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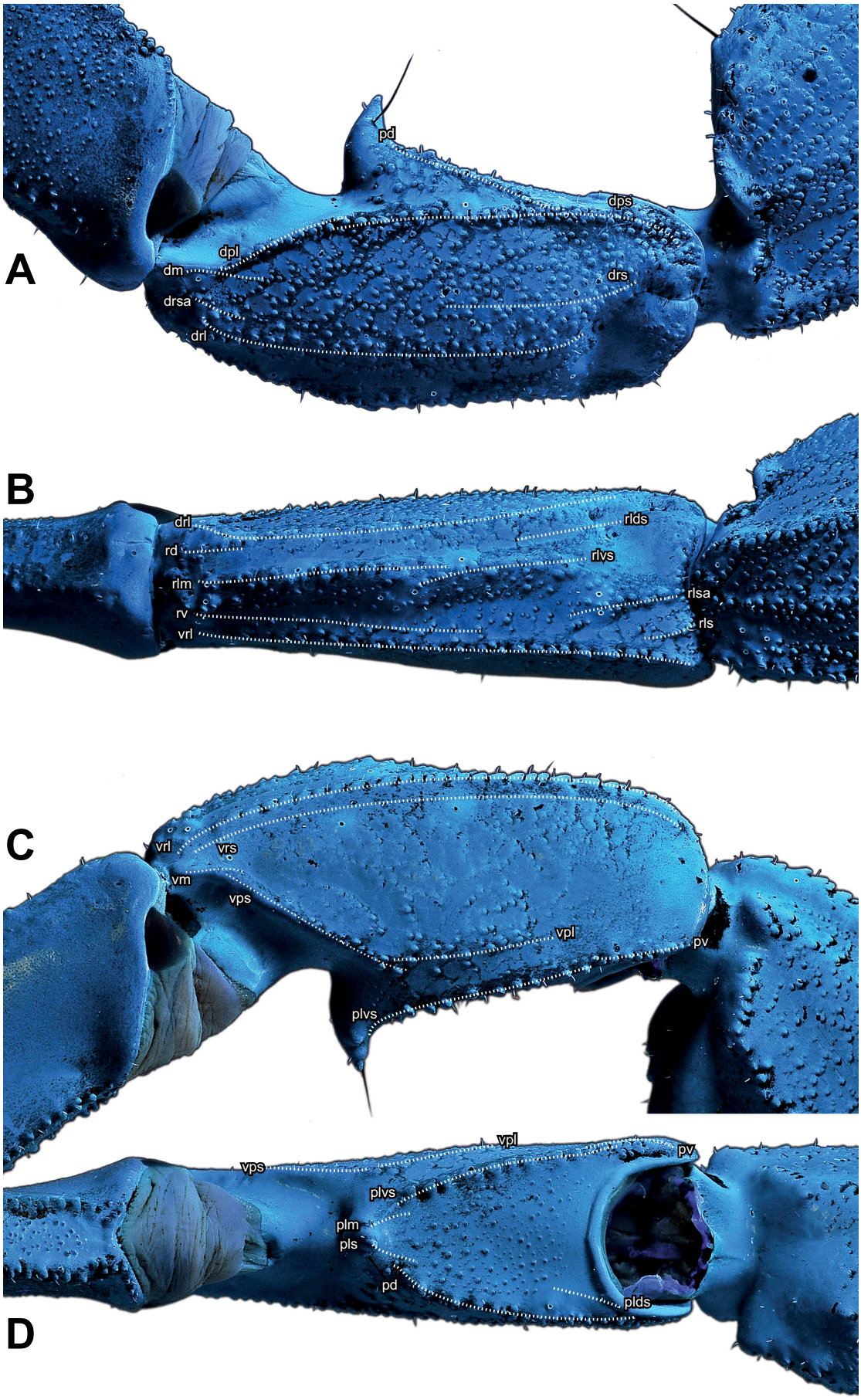
pd

F

Fig. 27. *Hormurus ankistros* n. sp. from Sindik (Saudaun Province, Papua New Guinea), female (LP 4339). Carinal pattern of the pedipalpal patella, according the terminology proposed by Prendini *et al.* (in prep.), under UV light. A, dorsal aspect. B, external aspect. C, ventral aspect. D, internal aspect.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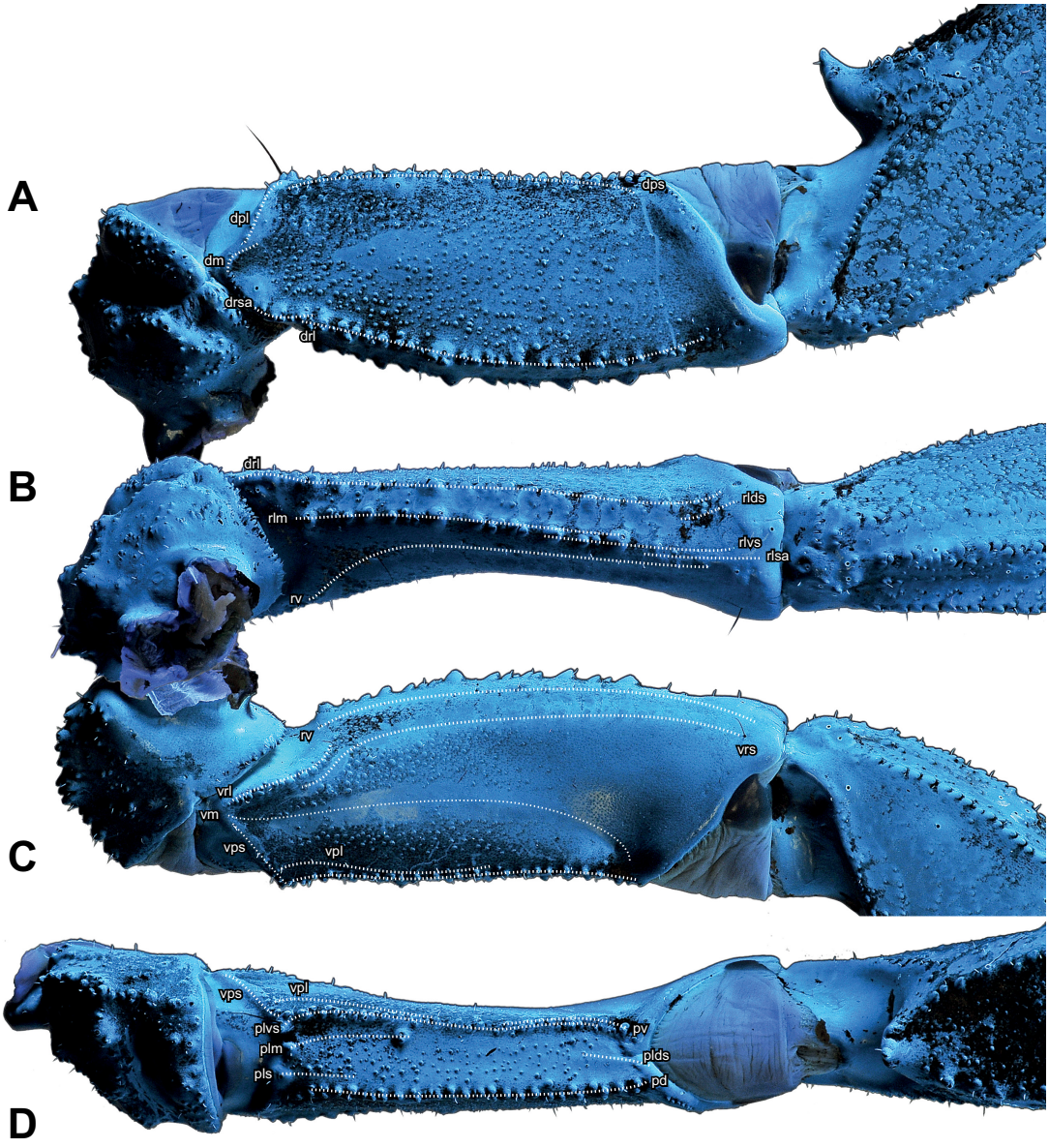
rls
vrl
C
vrl
vrs
vm
vps
vpl
pv
plvs
vpl
pv
vps
plvs
plm
pls
pd
plds
D

Fig. 28. *Hormurus ankistros* n. sp. from Sindik (Saudaun Province, Papua New Guinea), female (LP 4339). Carinal pattern of the pedipalpal femur, according to the terminology proposed by Prendini *et al.* (in prep.), under UV light. A, dorsal aspect. B, external aspect. C, ventral aspect. D, internal aspect.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pls
pd

recent scorpion, although some variability may exists in their vertical development. Invoking the existence of “fused double” carinae and their simultaneous or independent expression to account for dissimilarities in carinal longitudinal development between different taxa is much more parsimonious than invoking a modification of the muscular organisation. Under this conjecture, a complete carina results from the expression of the two distinct units whereas a partial carina results from the expression of only one.

The following characters of the pedipalp carination provide some important phylogenetic signals at the suprageneric level:

(1) When present, the dorsal retrol*at*eral (*drl*) carina of the chela (Prendini, 2000) is visible as a smooth ridge in *C. ochropus*, *O*. (*N*.) *laevipes*, *Palaeocheloctonus*, *Opisthacanthus* (*Monodopisthacanthus*), *I. politus*, *O*. (*O*.) *lecomtei*. Conversely, it is costate to granular in *Chiromachetes*, *Hormiops*, most *Hormurus*, *Liocheles*, the Indian *Iomachus* and *O.* (*O.*) *elatus*. A smooth carina is considered here as plesiomorphic. The derived granular carina may have evolved three time independently, in the groups (*Chiromachetes* + Indian *Iomachus*), (*Hormiops* + *Hormurus* + *Liocheles*), and in *O. (O*.) *elatus* respectively. It is considered synapomorphic for the first two groups and autapomorphic for *O*. (*O*.) *elatus*. Few Australian *Hormurus* reverted to the plesiomorphic state, i.e. *H. agastachys* n. sp., *H. dodecatrichos* n. sp., *H. glaphyroscytos* n. sp., *H. khangalu* n. sp., *H. laevitropis* n. sp., *H. ochyroscapter* n. sp., *H. scopaeus* n. sp., and *H. xerogaios* n. sp.. [Character 65]

(2) In the patella, the presence of the ventral retrolateral (*vrl*) carina is considered plesiomorphic, whereas its absence or obsolescence provides a potential synapomorphy for (Indian *Iomachus* + *Chiromachetes*) and (*I. politus* + *Opisthacanthus* (*Opisthacanthus*)), and an autapomorphy for *C. ochropus*. The occurrence of a distinct *vrl* carina in *O*. (*O*.) *lecomtei* is attributed to a reversal. [Character 82]

(3) The prolateral subdorsal (*pls*) and prolateral median (*plm*) carinae are vestigial to absent in the femur of most taxa included here. When visible, they are distinguishable only by one to four large spiniform granules. The presence and number of these granules is a good indicator of phylogenetic relationships among the different genera. The *pls* carina bears few larger granules in all liochelids in the study except in the clade (*Hormiops* + *Hormurus* + *Lio-*

cheles) for which the absence of granules is considered synapomorphic. Similarly, all liochelids in the study possess a *plm* carina with large granules except for most species of *Hormurus* and the character is probably synapomorphic for at least some phylogenetic groupings within the genus if not for the whole genus. Few *Hormurus* species possess a *plm* carinae with larger granules; it is considered as a reversal and autapomorphic for these taxa. [Characters 87–89]

Pedipalp ornamentation, macrosculpture [Characters 93–114]

#93. Chela, fingers, macrosculpture, granulation: 1, smooth or nearly so; 2, granular (at least sparsely on proximal half) [PCW03/26].

#94. Chela, fixed finger, dorsal surface, surface around *db*/*dsb*/*dst* trichobothria, macrosculpture, granulation: 1, trichobothria not in distinct depressions, surrounding areas smooth; 2, *db*-*dsb*-*dst* trichobothria in distinct smooth depressions, surrounding areas granular (at least in the most proximal part).

#95. Chela, fixed finger, dorsal surface, depression around *dst*/*dsb*/*db* trichobothrium: 1, a single large smooth depression grouping the 3 trichobothria; 2, 3 distinct depressions (one around each trichobothrium).

#96. Chela, dorsal intercarinal surface, macrosculpture, distribution [additive]: 1, absent; 2, limited to prolateral and retrolateral edges, absent from the median part; 3, present, across entire surface.

#97. Chela, dorsal intercarinal surface, macrosculpture, shape [additive]: 1, granulation vestigial, at most low granules or shallow reticulation; 2, distinct spiniform granules; 3, network of ridges and dimples (reticulation) [BHL 17, 18, HWC 61, LP01/51, 52, PCW03/29, 30] [modified].

#98. Chela, dorsal intercarinal surface, macrosculpture, if granular, size of granules: 1, medium-sized spiniform granules; 2, very minute spiniform granules [BHL 17, 18, HWC 60, 61, LP01/50, PCW03/28] [modified].

#99. † Chela, dorsal intercarinal surface, macrosculpture, if granular, density of granules: 1, densely granular; 2, sparsely granular.

#100. Chela, retrolateral intercarinal surface, macrosculpture, granulation: 1, gran-

ular; 2, smooth or nearly so (only few scattered granules) [LP01/55, 56, PCW03/33, 34].

#101. Chela, ventral intercarinal surface, macrosculpture, granulation, distribution [additive]: 1, absent; 2, present along prolateral and retrolateral edges only, smooth medially; 3, distributed across entire surface.

#102. Chela, prolateral ventral intercarinal surface, macrosculpture, granulation: 1, smooth or nearly so; 2, granular at least along prolateral edge.

#103. Patella, dorsal intercarinal surface, macrosculpture, granulation: 1, smooth or nearly so, prolateral edge and proximal end may be weakly granular; 2, entirely granular, at least a reticulated network of granules [LP01/66, HWC03/40].

#104. Patella, ventral intercarinal surface, macrosculpture, granulation: 1, smooth or nearly so; 2, entirely granular, at least a reticulated network of granules.

#105. Patella, retrolateral dorsal intercarinal surface (between *drl* and *rlm* carinae), macrosculpture, granulation: 1, smooth or nearly so; 2, at least sparsely granular [BHL79/32, HWC81/37, LP01/67, PCW03/40] [split into two characters].

#106. Patella, retrolateral ventral intercarinal surface (between *rlm* and *vrl* carinae), microsulpture, granulation: 1, smooth or nearly so; 2, at least sparsely granular [BHL79/33, HWC81/37, LP01/67, PCW03/40] [split into two characters].

#107. Patella, prolateral intercarinal surface, macrosculpture, granulation, distribution: 1, surface smooth or nearly so, sometimes with few scattered bigger spiniform granules proximally; 2, proximal half at least sparsely granular, distal half usually less granular.

#108. Femur, dorsal intercarinal surface, macrosculpture, granulation, distribution: 1, granulation absent or limited to the proximal and retrolateral edges; 2, granular except distal end.

#109. † Femur, dorsal and prolateral intercarinal surfaces, macrosculpture, if granular, size of granules: 1, small to medium-sized spiniform granules; 2, larger spiniform granules.

#110. Femur, dorsal intercarinal surface, macrosculpture, if granular, density of

granules: 1, densely granular; 2, sparsely granular.

#111. Femur, dorsal retrolateral intercarinal surface, macrosculpture, granulation: 1, smooth or nearly so; 2, at least sparsely granular.

#112. Femur, retrolateral ventral intercarinal surface, macrosculpture, granulation: 1, smooth or nearly so; 2, at least sparsely granular.

#113. Femur, ventral intercarinal surface, macrosculpture, granulation, distribution: 1, granulation absent or vestigial and limited to the retrolateral edge; 2, granular proximally, distal part without granulation (sometimes reduced to the extremity).

#114. Femur, prolateral intercarinal surface, macrosculpture, granulation: 1, granulation absent or nearly so; 2, at least sparsely granular.

Intercarinal surfaces. Besides their own morphological characteristics, carinae are landmarks to delineate the different intercarinal cuticular surfaces of the chela, patella and femur that are recognized according to the structural plane of the segments and used in taxonomic descriptions since Koch (1837a), i.e. dorsal, external (= retrolateral), internal (= prolateral) and ventral surfaces. Based on observations of the granulation's patterns, Lamoral (1979) considered the retrolateral surface of the patella as two independent units, i.e. the "dorsoexternal" and "ventroexternal" surfaces. In a similar way, the prolateral surface of the chela and the retrolateral surface of the patella are split in the present work into two distinct units in order to better diagnose the different granulation patterns observed. Eight surfaces can then be recognized on each segment of the liochelid pedipalps: (1) the dorsal surface is located between the *dpl* and *drl* carinae; (2) the retrolateral surface lies between the *drl* and *vrl* carinae and can be further split into a retrolateral dorsal surface (between *drl* and *rlm* carinae) and a retrolateral ventral surface (between *rlm* and *vrl* carinae); (3) the ventral surface lies between *vrl* and *vpl* carinae; (4) the prolateral surface lies between *vpl* and *dpl* carinae and can be further split into a prolateral ventral surface (between *vpl* and *plvs* carinae) and a prolateral dorsal surface (between *plvs* and *dpl* carinae).

Apart from carinae, two type of cuticular ornamentation are presently recognized:

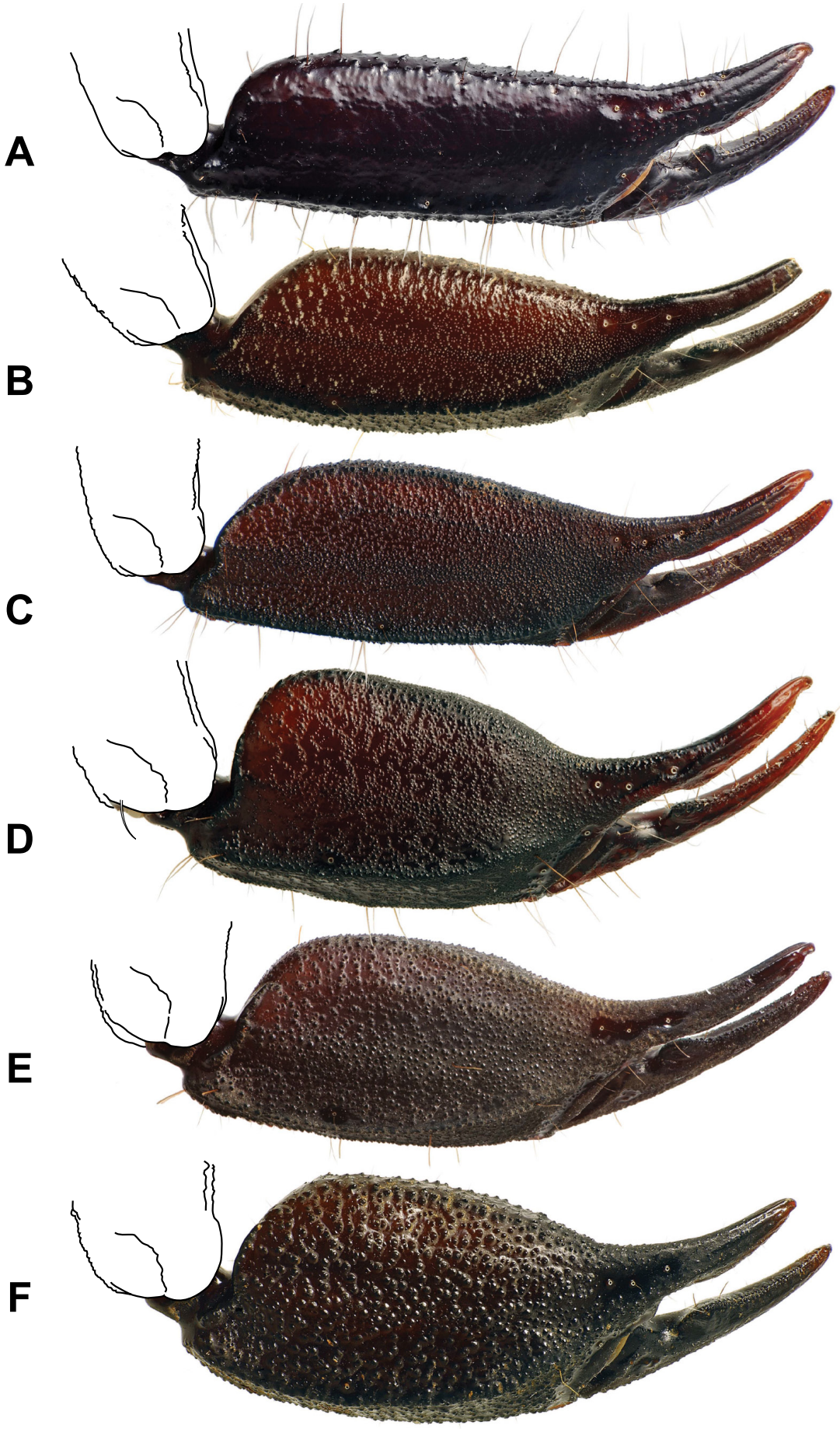
(1) punctation: the tegument can be covered with numerous minute perforations (the term “minutely pitted” is often used); and (2) “macrosculpture” which refers here to any patterned carving that gives his surface texture to the tegument (as opposed to “structural” outgrowths/ depressions such as carinae, sulci and apophysis which are the outer expression of the internal morphology): it can either be totally smooth, devoid of any morphosculpture or finely engraved. Whereas the cuticle of a scorpion is either punctated or not, there is a lot more variability observed in macrosculpture, therefore lending to the development of multiple characters to appropriately describe and diagnose the different aspects of these structures. In the present work, the presence or absence of macrosculpture on each surface of each segment was first examined. Four additional characters pertaining to macrosculpture (fig. 29) were also inspected on each surface and scored accordingly when applicable: (1) the distribution; (2) the “type” (the most common type is granulation but in some taxa the granules can be “fused” into a reticulated network of ridges and dimples); (3) the size of granules and (4) the density of granules.

The variation of the ornamentation and sculpturing of the intercarinal surfaces of the pedipalp provides important phylogenetic signals. Generally speaking, a smooth intercarinal surface is plesiomorphic, whereas macrosculpture is a derived state. Reversals from a granular to smooth tegument are however not uncommon:

(1) In most taxa of this study, granulation on the dorsal intercarinal surface of the chela is absent or vestigial and limited to the prolateral and retrolateral edges. Conversely, this surface is granular in *O*. (*O*.) *elatus* and in most *Hormurus* species. Thus, it may be autapomorphic for the former and synapomorphic for the later. However, several species within *Hormurus* including *H. penta* display the plesiomorphic state, possessing pedipalp chelae that are dorsally non-granular. The position of these species in the cladogram will determine if this character is synapomorphic for the genus with subsequent reversals. [Character 96]

(2) The ventral side of the chela is provided with at least vestigial granulation in all species belonging to the genus *Hormurus* except *H. penta*, whereas it is smooth in all other taxa except *Liocheles suspectus* (Thorell, 1888). If *H. penta* is excluded, ventrally granular chelae represent another potential synapomorphy for *Hormurus*. Depending on its position on the phylogenetic reconstructions, absence of granulaltion in these two taxa can either represent

Fig. 29. Dorsal aspect of pedipalp chelae in the family Liochelidae Fet & Bechly, 2001, males. Macrosculptures. A, *Iomachus politus* Pocock, 1896 fom Hadeni (Tanzania), male (AMNH): granulation absent [Character 96/1]. B, *Liocheles longimanus* (Werner, 1939) from Mangani (Sumatra, Indonesia), male (CAS): granulation vestigial limited to prolateral and retrolateral edges [Characters 96/2, 97/1]. C, *Hormurus chydaeostigmata* n. sp. from Maret Island (Western Australia, Australia) (WAM-T62943): entirely granular, dense and minute spiniform granules [Characters 96/3, 97/2, 98/2, 99/1]. D, *Hormurus aethes* n. sp. from Mount Obree (Central Province, Papua New Guinea), male (LP3001): entirely granular, dense and minute spiniform granules [Characters 96/3, 97/2, 98/2, 99/1]. E, *Hormurus solomonensis* n. sp. from Haruligo (Guadalcanal, Solomon Islands), male (LM): entirely granular, dense and medium spiniform granules [Characters 96/3, 97/2, 98/1, 99/1]. F, *Hormurus penta* from Mount Austen (Guadalcanal, Solmon Islands), male (NHML): granulation vestigial limited to prolateral and retrolateral edges [Characters 96/2, 97/1].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a plesiomorphy (if the species is basal to all other *Hormurus*) or a reversal (if it appears to be more derived). [Character 101]

(3) The ventral side of the patella is smooth in the basal liochelids of the study and granular in most *Hormurus*. *H. agastachys* n. sp., *H. chydaeostigmata* n. sp., *H. dodecatrichos* n. sp., *H. ischnoryctes* n. sp., *H. khangalu* n. sp., *H. penta* n. sp., and *H. scopaeus* n. sp. possess the primitive state. The position of these taxa on the phylogenetic reconstructions will clarify if the granulation is a valid synapomorphy for *Hormurus* with several reversals within the genus. [Character 104]

Prosomal carapace and mesosomal tergites [Characters 115–128]

#115. Carapace anterior margin, median notch development]: 1, strongly excavated, with protruding frontal lobes; 2, weakly excavated (shallow), with weak frontal lobes; 3, frontal notch almost absent [WRL4, LP00/3, PCW03/5, LP03/3, VP08/4] [modified.

#116. Carapace, anterior furcated suture/sulci: 1, present, distinct; 2, obsolete or absent [LP01/9].

#117. Prosomal carapace, median ocular tubercle, position: 1, anteromedial; 2, medial/posteromedian [BHL79/3; LP01/15].

#118. † Prosomal carapace, median ocelli: 1, presence; 2, absence.

#119. Prosomal carapace, median ocelli, interocular distance: 1, separated by at least half a diameter of a median ocular; 2, close together (less than a diameter); -, inapplicable [LP unpublished].

#120. Prosomal carapace, median ocelli, size relative to lateral ocelli [additive]: 1, slightly smaller than (= larger lateral ocelli); 2, equal (= similar median and lateral ocelli); 3, larger (= large median ocelli, at least twice the size of lateral ocelli); -, inapplicable [LP01/19].

#121. Prosomal carapace, median ocular tubercule, size compared to carapace width: 1, small (usually 1/9 of the width); 2, medium (usually around 1/7 of the width); 3, large (median ocular tubercle occupied 1/5 of the width); -, inapplicable.

#122. Prosomal carapace, lateral ocelli, number of pairs: 1, two; 2, three [S89/21, S89/25, J94/14, LP00/1 (part), G02/5, S&F03.5/102, LP03/1, VP08/5].

#123. † Prosomal carapace, lateral ocelli: 1, present and distinct; 2, extremely reduced, vestigial.

#124. † Prosomal carapace, lateral ocelli, first ocellus, size relative to second ocellus or second and third ocelli: 1, smaller than; 2, equal to [LP01/20].

#125. Prosomal carapace, lateral ocelli, third ocellus, size relative to first and second ocelli: 1, smaller than (2 anterior eyes in a cluster); 2, equal to or larger than; -, inapplicable [LP01/20].

#126. Prosomal carapace, lateral ocelli, interocular distance: 1, third ocellus apart from first and second ocelli; 2, first ocellus apart from second and third ocelli; 3, ocellus equidistant, apart from each other; 4, ocellus equidistant, close together, almost touching each other.

#127. Prosomal carapace, median occular tubercle, elevation: 1, raised at least slightly; 2, not elevated [LP00/2, LP03/2, VP08/7].

#128. Prosomal carapace, superciliary carinae: 1, absent; 2, present [LP unpublished].

Prosomal carapace and tergites ornamentation [Characters 129–154]

#129 Prosomal carapace, superciliary carinae, granulation: 1, without granules; 2, with at least few granules; -, inapplicable.

#130. Prosomal carapace, rostrolateral margin of carapace, portion next to posterior lateral ocelli, granulation: 1, markedly more granular than the rest of the carapace border; 2, granulation absent or vestigial, similar to the rest of the carapace margins.

#131. Tergites I–VII, posterior margins: 1, straight or nearly so, without distinct prominence; 2, with two distinct submedial projections.

#132. Prosomal carapace, anteromedian area, macrosculpture, granulation, ♂ [additive]: 1, entirely smooth or nearly so; 2, frontal lobes (area I) smooth, granular

along median longitudinal sulci and anterior furcated sulci (areas II–IV); 3, entirely granular, at least sparsely [BHL79/4, LP01/31, PCW03/17].

#133. Prosomal carapace, central area, macrosculpture, granulation, ♂: 1, smooth or nearly so; 2, at least sparsely granular.

#134. Prosomal carapace, posteromedian area, macrosculpture, granulation, ♂: 1, entirely smooth or nearly so; 2, at least sparsely granular [BHL79/7, LP01/37].

#135. Prosomal carapace, anterolateral areas, macrosculpture, granulation, ♂: 1, smooth or nearly so; 2, at least sparsely granular [BHL79/6, LP01/33, PCW03/19] [modified].

#136. Prosomal carapace, mediolateral and posterolateral areas, macrosculptures, granulation, ♂: 1, smooth or nearly so; 2, at least sparsely granular [BHL79/6, LP01/36] [modified].

#137. Tergites I–VII, pretergites, posterior margin, macrosculpture, ♂: 1, smooth: 2, crenulate (small spiniform granules).

#138. Tergites I–VI, posttergites, macrosculpture, granulation, distribution, ♂ [additive]: 1, entirely smooth or nearly so; 2, median area smooth, lateral areas at least sparsely granular posteriorly; 3, entirely granular, at least sparsely on posterior half; granulation may be absent or vestigial on ridges [BHL79/23, HWC81/91, PCW03/74] [modified].

#139. Tergite VII, posttergite, macrosculpture, granulation, distribution, ♂ [additive]: 1, completely smooth or nearly so; 2, anteromedian and posteromedian areas smooth; lateral area granular; 3, anteromedian area smooth; lateral and posteromedian areas granular; 4, entirely granular, at least sparsely.

#140. Tergites III–VII, posttergites, macrosculpture, reticulated network of ridges and dimples, ♂: 1, absent (even surface); 2, distinct (uneven surface).

#141. Prosomal carapace, anteromedian area, macrosculpture, granulation, ♀ [additive]: 1, entirely smooth or nearly so; 2, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); 3, entirely granular, at least sparsely [BHL79/5, LP01/32, PCW03/18].

#142. Prosomal carapace, posteromedian area, macrosculpture, granulation, ♀: 1, smooth or nearly so; 2, at least sparsely granular [BHL79/8, LP01/38].

#143. Prosomal carapace, anterolateral areas, macrosculpture, granulation, ♀: 1, smooth or nearly so; 2, at least sparsely granular [BHL79/6, LP01/33, PCW03/19] [modified] [split into three characters].

#144. Prosomal carapace, mediolateral area, macrosculpture, granulation, ♀: 1, smooth or nearly so; 2, at least sparsely granular [BHL79/6] [modified] [split into three characters].

#145. Prosomal carapace, posterolateral areas, macrosculpture, granulation, ♀: 1, smooth or nearly so; 2, at least sparsely granular [BHL79/6, LP01/36] [modified] [split into three characters].

#146. Tergites I–III, posttergites, macrosculpture, ♀ [additive]: 1, mesial and lateral areas smooth; 2, mesially smooth, laterally granular; 3, entirely granular [BHL79/23, HWC81/91, PCW03/74] [modified].

#147. Tergites IV–VI, posttergites, macrosculpture, distribution, ♀ [additive]: 1, mesial and lateral surfaces smooth (or nearly so); 2, mesially smooth, laterally granular; 3, mesial and lateral surfaces granular [BHL79/23, HWC81/91, PCW03/74] [modified].

#148. Tergite VII, posttergite, macrosculpture, granulation, distribution, ♀: 1, entirely smooth or nearly so; 2, granular at least posteriorly.

#149. Tergites III–VII, macrosculpture, reticulated network of ridges and dimples, ♀: 1, absent or vestigial, even surface; 2, distinct, uneven surface [LP unpublished] [modified].

#150. Prosoma, macrosculpture, granules, size: 1, minute spiniform granules; 2, larger spiniform granules at least on anteromedian surface (areas I-V), rest of prosoma usually with sparse smaller spiniform granules.

#151. Prosoma, macrosculpture, granules, density: 1, evenly and sparsely distributed; 2, granules extremely dense giving the tegument a sand-like appearance; 3, inapplicable.

#152. Tergites I–VII, posttergites, macrosculpture, granules, size: 1, minute spiniform granules; 2, larger spiniform granules.

#153. Tergites I–VII, posttergites, macrosculpture, granules, density: 1, uniformly and sparsely distributed; 2, extremely densely distributed.

#154. Tergites I–VI, lateral transversal sulcus: 1, absent or vestigial (extremely shallow); 2, present.

The morphosculpture of the prosomal carapace and tergites is an important source of diagnostic and phylogenetic data. However, the difficulty in examining and accurately assessing inter and intra-specific variation and the ensuing difficulty in appropriately scoring the characters in a morphological matrix has hindered the use of these characters in phylogenetic reconstructions. The development of a new examination and imaging technique using the cuticle photoluminescence of scorpions (see paragraph 1.1; Volschenk, 2002, 2005; Prendini, 2003A) now allows an improved evaluation and comparison of tegument morphosculptures and therefore facilitates the incorporation of these characters into phylogenetic matrices.

As for the pedipalp carinal pattern, skeletomuscular anatomy is a determining factor for the external morphology of the prosomal carapace and mesosomal tergites. Sites of muscles attachment are visible on the cuticle as sulci (sutural grooves) and apodemes (smooth patches) and their locations appear to be very conserved across the order even between distantly related taxa (see fig. 30; Shultz, 2007a). Based on observations of the morphosculpture and infuscation patterns, Lamoral (1979) divided the tegument surfaces of the carapace and tergites into smaller areas delineated by the sulcus and apodemes and treated each of these “sub-surfaces” as a distinct character. In his phylogenetic analysis of the scorpionid genus *Opisthophthalmus* C. L. Koch, 1937, Prendini (2001E) recognized seven “sub-surfaces” for the carapace (fig. 31), i.e. frontal lobes (*fl*), interocular (*ios*), circumocular (*cos*), anterolateral (*als*), mediolateral (*mls*), posterolateral (*pls*), and posteromedian (*pms*), and three for the tergites, i.e. pretergite, lateral and median of posttergite. The liochelid carapace is divided in the present study into 13 distinct areas (fig. 32; tab. 6). Areas I, III, V, IX, [X + XI], XII and XII correspond to Prendini’s *fl*, *ios*, *cos*, *als*, *mls*, and *pls* respectively. However, Prendini’s posteromedian surface (*pms*) is divided here

into three areas (VII, VIII and IX). This incongruence is due to the pronounced morphological differences between *Opisthophthalmus* and liochelid genera. In *Opisthophthalmus*, because of the posterior position of the median ocelli, the posteromedian area is extremely reduced which hampers the distinction of potential “sub-surfaces”. On the contrary, the posteromedian area is larger in liochelids, allowing the recognition of several distinct areas. Finally, areas II, IV and IV were added to Prendini’s in order to diagnose the presence/absence of granulation along the anterior furcated, anteromedian and posteromedian longitudinal sulci respectively. Precise granulation maps of the carapace (figs 33–34) were then produced for each species allowing the identification of general patterns and the reduction of the number of areas to six consistent, independent and phylogenetically meaningful units that were scored accordingly: (1) the anteromedian surface (areas I–IV), (2) the median surface (area V), (3) the posteromedian surface (areas VI–IX), (4) the anterolateral surface (area X), (5) the mediolateral surface (areas XI–XII) and the poserolateral surface (area XIII). Moreover, tergites I–VI were divided into three distinct areas (fig. 32) following Prendini (2001E), i.e. (1) pretergite, (2) posttergite median area, (3) posttergite lateral area. An additional area was recognised for tergite VII (fig. 32), i.e. (1) pretergite, (2) posttergite anteromedian area, (3) posttergite lateral area, and (4) posttergite posteromedian area.

The same criteria as for pedipalp intercarinal surfaces are used to describe the texture of prosomal and tergal surfaces, i.e. (1) the presence of punctation and (2) the presence of macrosculpture. Reticulated networks of ridges and dimples giving an uneven appearance to the cuticle (fig. 37) were observed on the posterior tergites of some species. These reticulations were either smooth or covered by minute granules depending on the taxon and the sex. Each subsurface of the carapace and the tergites was scored independently depending on the presence/absence of macrosculpture. The size and density of granules (fig. 35) provided additional diagnostic characters and were also coded in the phylogenetic matrix. Furthermore, two types of “structural” cuticular markings were identified on the tergites and included in the matrix: the presence of (1) two submedial projections on the posterior margins (fig. 36), and of (2) lateral transversal sulcus (fig. 32, 37). Furthermore, the sexual dimorphism of tegument sculpturing can be pronounced (fig. 32), males being usually much more granular than females. Therefore,

Fig. 30. Prosomal carapace, dorsal aspect. A, *Heterometrus spinifer* (Ehrenberg, 1828), approximate sites of prosomal muscles attachment on pleural membrane (after Shultz, 2007a), colors indicate the appendage associated with each muscle. B, *Hormurus macrochela* n. sp. from Palm Island (Queensland, Australia), female (QM-S59206), sites of muscle attachment are visible as sulcus (suture grooves) and apodemes (smooth patches) on the carapace.

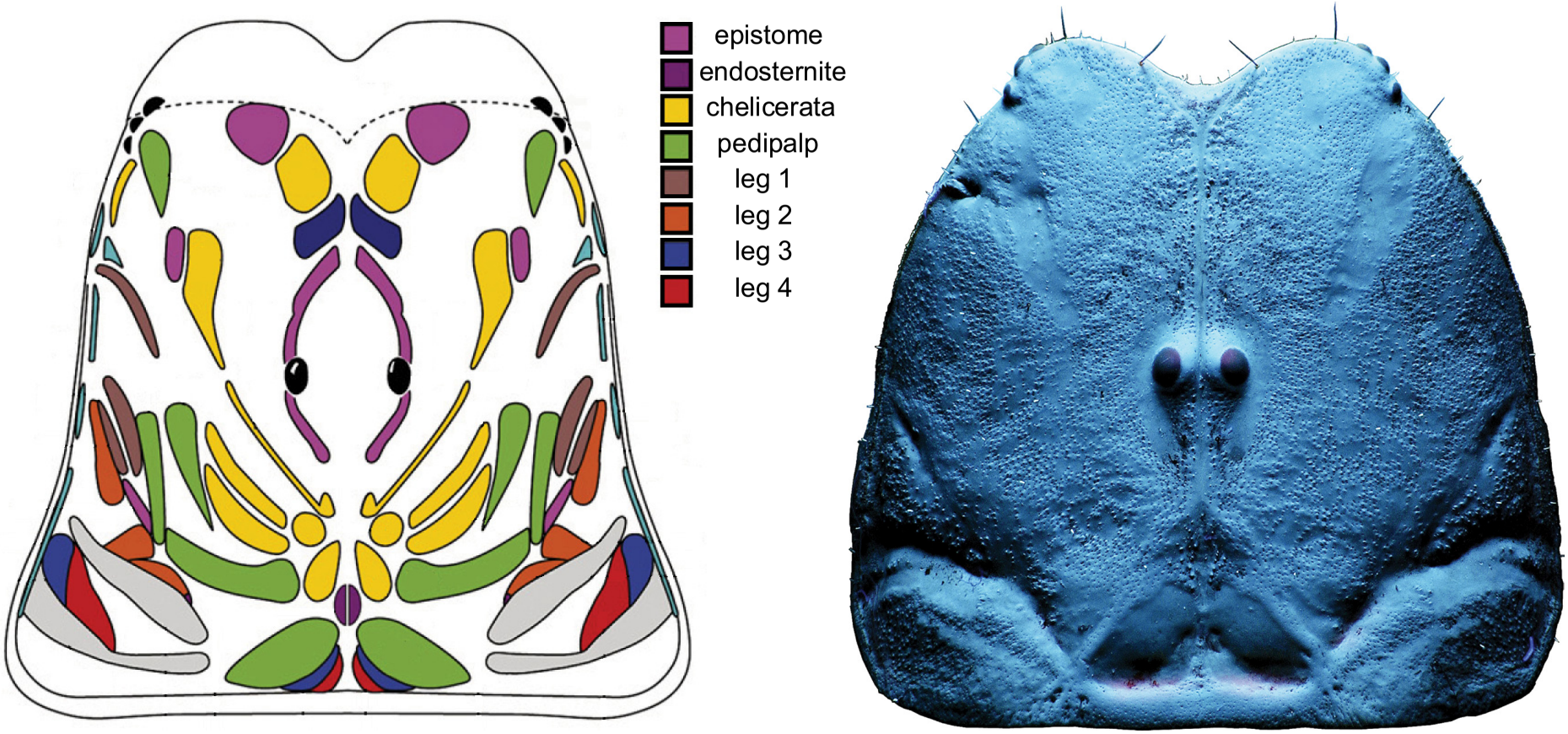
epistome
endosternite
chelicerata
pedipalp
leg 1
leg 2
leg 3
leg 4

Fig. 31. *Opisthophthamus* C.L. Koch, 1937. Prosomal carapace, sub-surfaces recognized by Prendini (2001E). Legend: *als* = anterolateral surface; *cos* = circumocular surface; *fl* = frontal lobes; *ios* = interocular surface; *mls* = mediolateral surface; *pls* = posterolateral surface; *pms* = posteromedian surface. From Prendini (2001E).

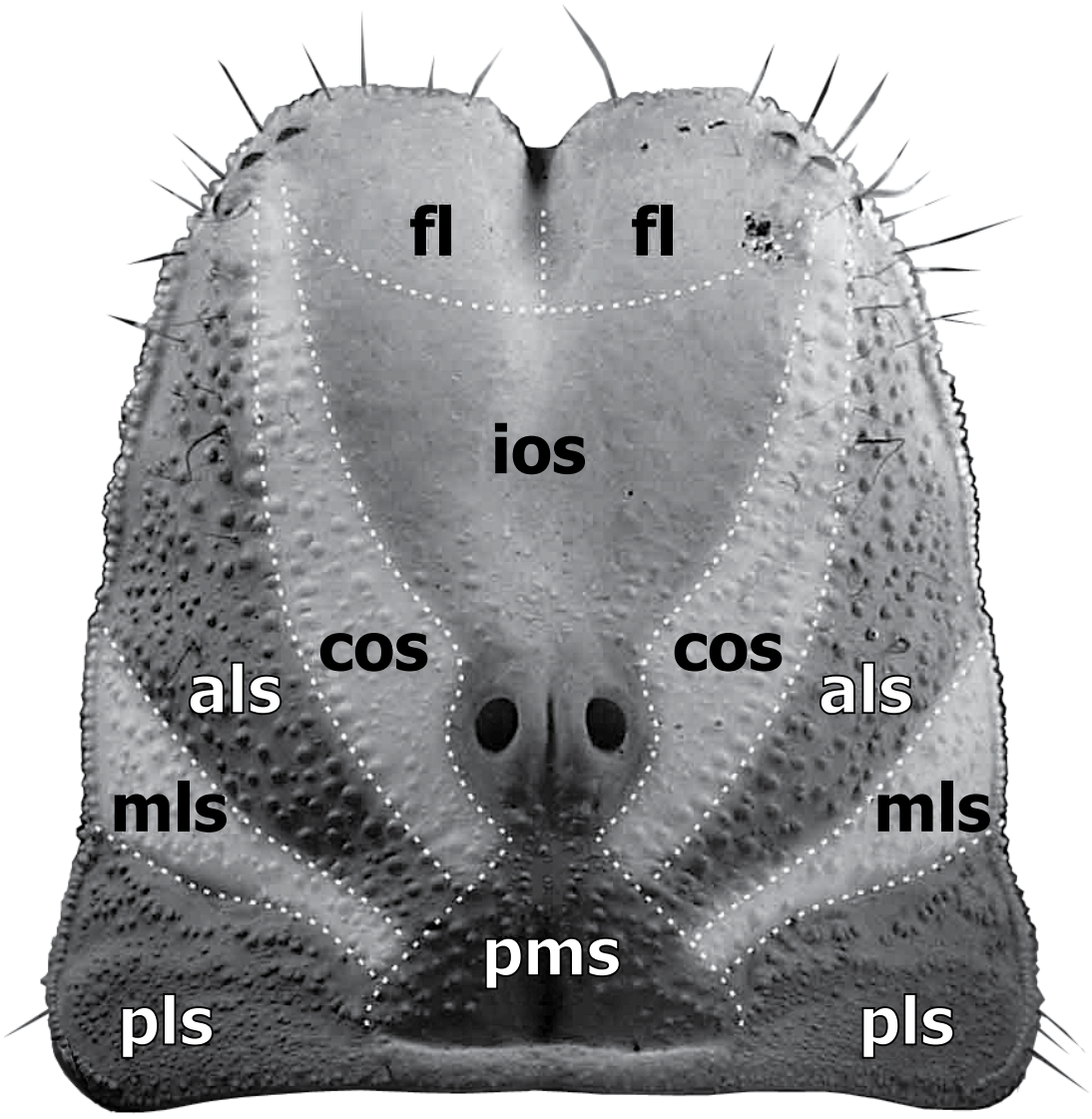
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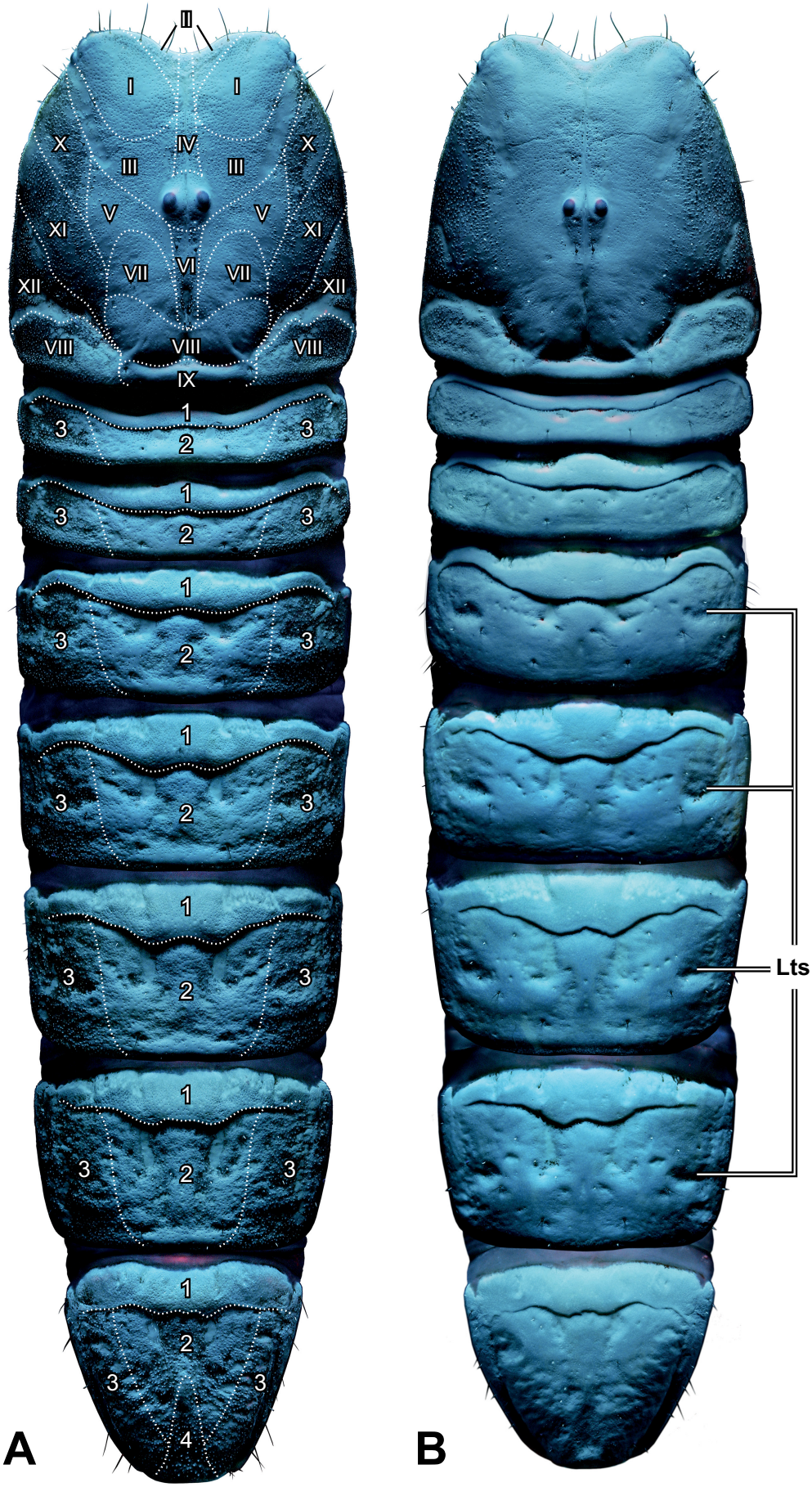
Fig. 32. Sexual dimorphism in the ornamentation and sculpturing of prosomal carapace and mesosomal tergites in the genus *Hormurus*. *Hormurus ischnoryctes* n. sp. from Mount Mulligan Cattle Station, Queensland, Australia (to be deposited in the collection of the QM). A, male. B, female. The tegument is clearly more granular in the male than in the female. The prosomal carapace is divided into 13 areas numbered from I to XIII (refer to text for detailed explanation). Legend: 1 = pretergite; 2 = median surface of posttergite; 3 = lateral surface of posttergite; 4 = posteromedian surface of postergite; Lts = lateral transversal sulcus.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VIII
IX
1
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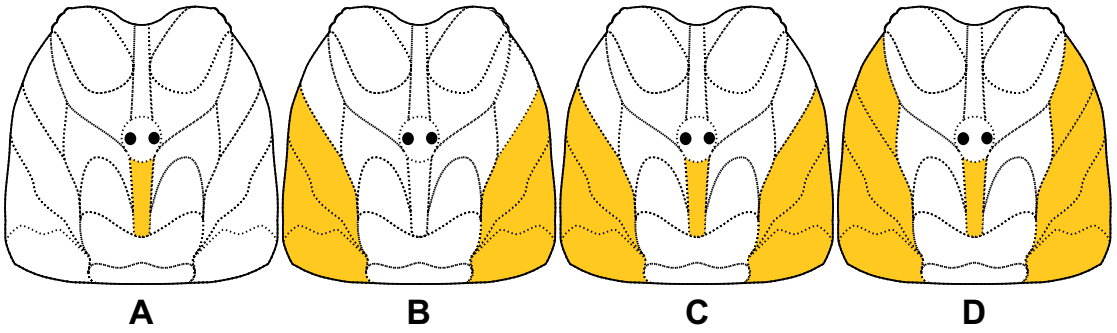
Fig. 33. Granulation maps of the prosomal carapace of Indo-Pacific Liochelidae, males. White indicates smooth areas while orange indicates granular areas.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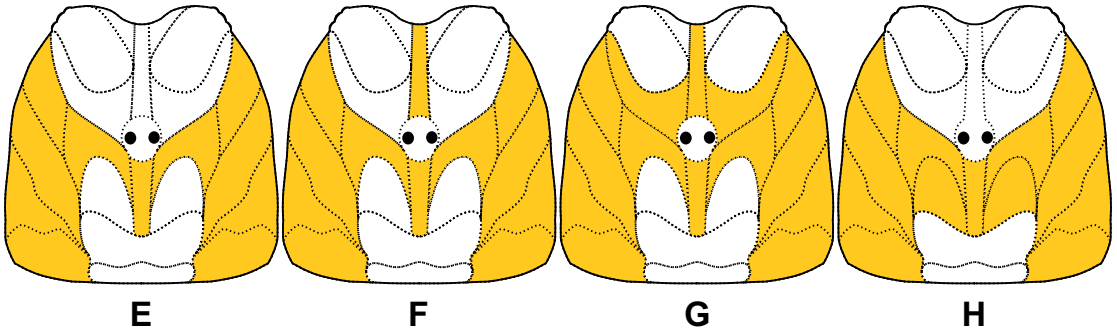
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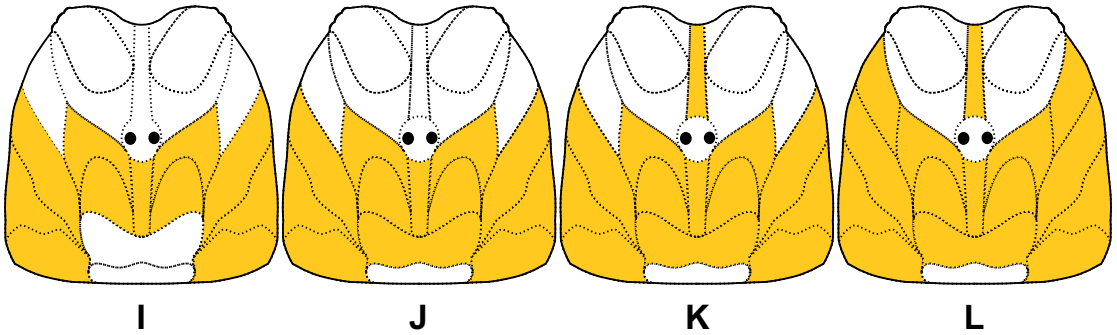
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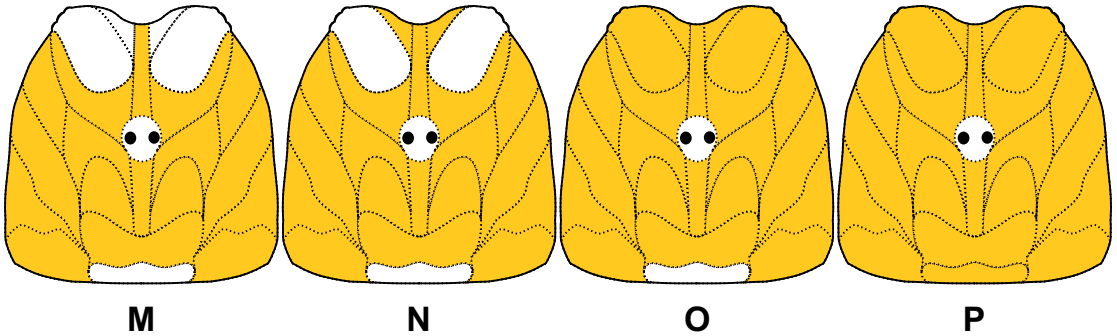
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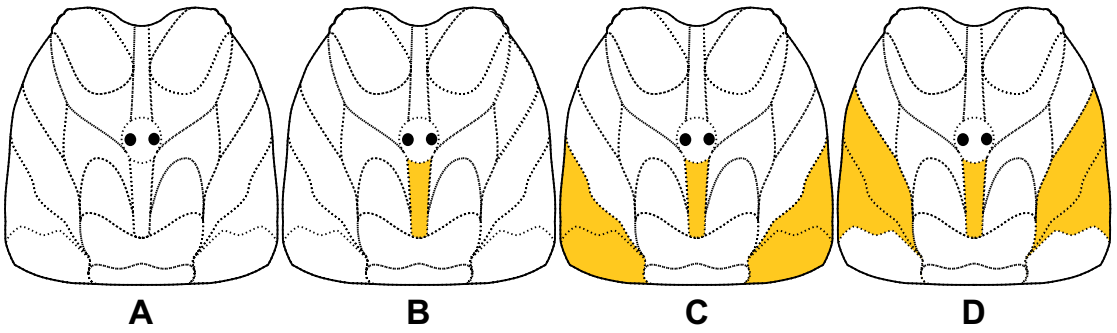
Fig. 34. Granulation maps of the prosomal carapace of Indo-Pacific Liochelidae, females. White indicates smooth areas while orange indicates granular areas.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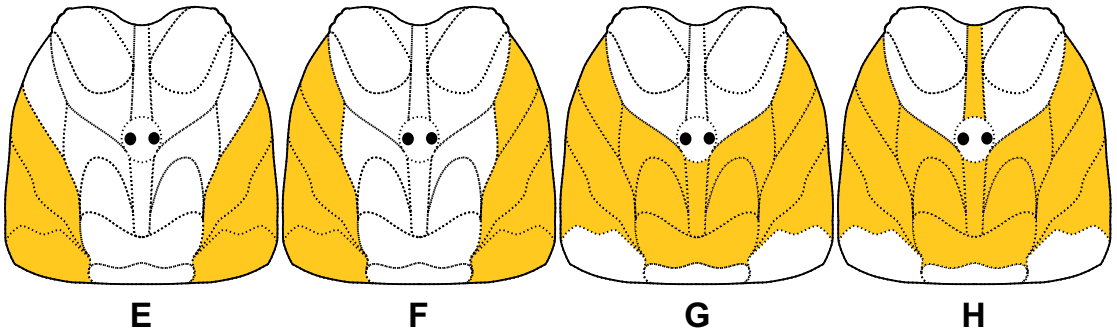
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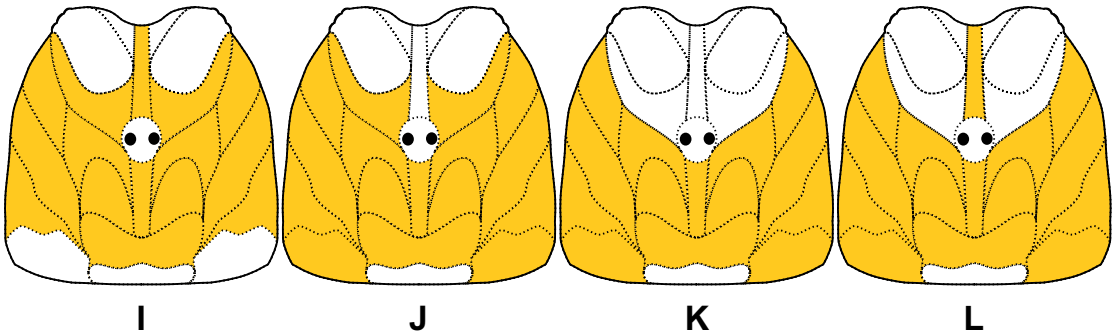
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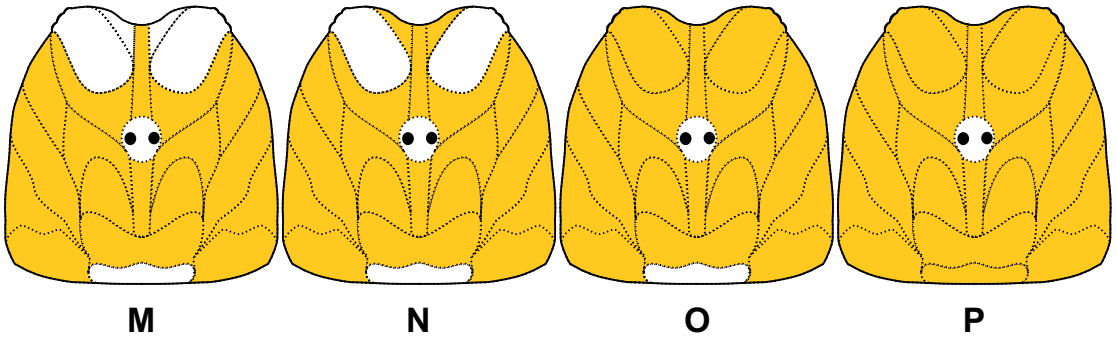
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Table 6. Sub-surfaces of the prosomal carapace. Terminology according to Prendini (2001E) and correspondence with the nomenclature used in the present study. The sign "—" indicates surfaces included in each of the six areas recognized as important for the present phylogenetic analysis.

PRENDINI, 2001[E]	SURFACES RECOGNISED BASED ON GRANULATION DISTRIBUTION	SURFACES RETAINED FOR PHYLOGENETIC ANALYSIS (PATTERNS)
frontal lobe (fl)	I	anteromedian surface
	II	—
interocular surface (ios)	III	—
	IV	—
circumocular surface (cos)	V	median surface
	VI	posteromedian surface
posteromedian surface (pms) [part]	VII	—
posteromedian surface (pms) [part]	VIII	—
posteromedian surface (pms) [part]	IX	—
anterolateral surface (als) [part]	X	anterolateral surface
anterolateral surface (als) [part]	XI	mediolateral surface
mediolateral surface (mls)	XII	—
posterolateral surface (pls)	XIII	posterolateral surface

genders are scored independently for each species in the present work, an approach previously adopted by Prendini (2001E) and Prendini *et al.* (2003).

As for the ornamentation of pedipalp intercarinal surfaces, the smoothness of the tegument is generally indicative of ancestral condition whereas granulation is a derived state. Reversals from a granular to a smooth cuticle apparently occurred several times in the Liochelidae. The following characters changes were recognized as phylogenetically informative in the present context:

(1) Few of the taxa examined in the present study exhibit a very peculiar type of granulation on the carapace and tergites: the tegument is densely covered with numerous minute granules giving it a sand-like appearance (=shagreened). This type of engraving is only observed in *Hormiops*, *Hormurus extensus* Locket, 1997, *Hormurus polisorum* Volschenk, Locket & Harvey, 2001, *Opisthacanthus* (*Monodopisthacanthus*), *O.* (*O.*) *elatus*, *Palaeocheloctonus*. It is probably synapomorphic for *Hormiops* and (O. (*Monodopisthacanthus*) + *Palaeocheloctonus*) and independently derived in the others three species. [Characters 150-151]

(2) In *C. ochropus*, *O.* (*O.*) *cayaporum*, *O.* (*O.*) *elatus*, *H. agastachys*, and most Melanesian *Hormurus* species, granulation of the prosoma is coarser with larger spiniform granules than in any other species of the study. Whereas this is probably an autapomorphy for *C. ochropus* and *H. agastachys*, it is potentially synapomorphic for (*O.* (*O.*) *cayaporum* + *O.* (*O.*) *elatus*) and the Melanesian *Hormurus*. [Character 150]

(3) The presence of lateral transverse sulci on tergites I–VI is reported in *C. ochropus*, *Opisthacanthus* (*Opisthacanthus*), *Liocheles* and *Hormurus* species. It is a putative synapomorphy for (*Liocheles* + *Hormurus*) and autapomorphic for both *C. ochropus* and *Opisthacanthus* (*Opisthacanthus*). [Character 154]

(4) The presence of a distinct network of small ridges and shallow dimples on tergites III–VII is only reported in *Hormurus* (the reticulation is absent in females of few species) making it a potential synapomorphy for the genus with few reversals in females. [Characters 140, 149]

Coxae [Character 155]

#155. Coxae III, antero-distal tip, shape: 1, without swelling or bulge; 2, with a dis-

Fig. 35. Prosomal carapace, males. Macrosculpture. A, *Hormurus chydaeostigmata* n. sp. from Maret Island (Western Australia, Australia) (WAM-T62943): carapace granular excepted frontal lobes, minute spiniform granules [Characters 132/2, 133/2, 134/2, 135/2, 136/2, 150/1]. B, *Hormurus ischnoryctes* n. sp. from Mount Mulligan Cattle Station, Queensland, Australia (to be deposited in the collection of the QM): carapace granular except frontal lobes and posteromedian surface, minute spiniform granules [Characters 132/2, 133/2, 134/1, 135/2, 136/2, 150/1]. C, *Hormurus aethes* n. sp. from Mount Obree (Central Province, Papua New Guinea), male (LP3001): carapace completely granular, minute spiniform granules [Characters 132/3, 133/2, 134/2, 135/2, 136/2, 150/1]. D, *Hormurus agastachys* n. sp. from Mazeppa National Park (Queensland, Australia) (QM-S39695): carapace completely granular, larger spiniform granules [Characters 132/3, 133/2, 134/2, 135/2, 136/2, 150/2].

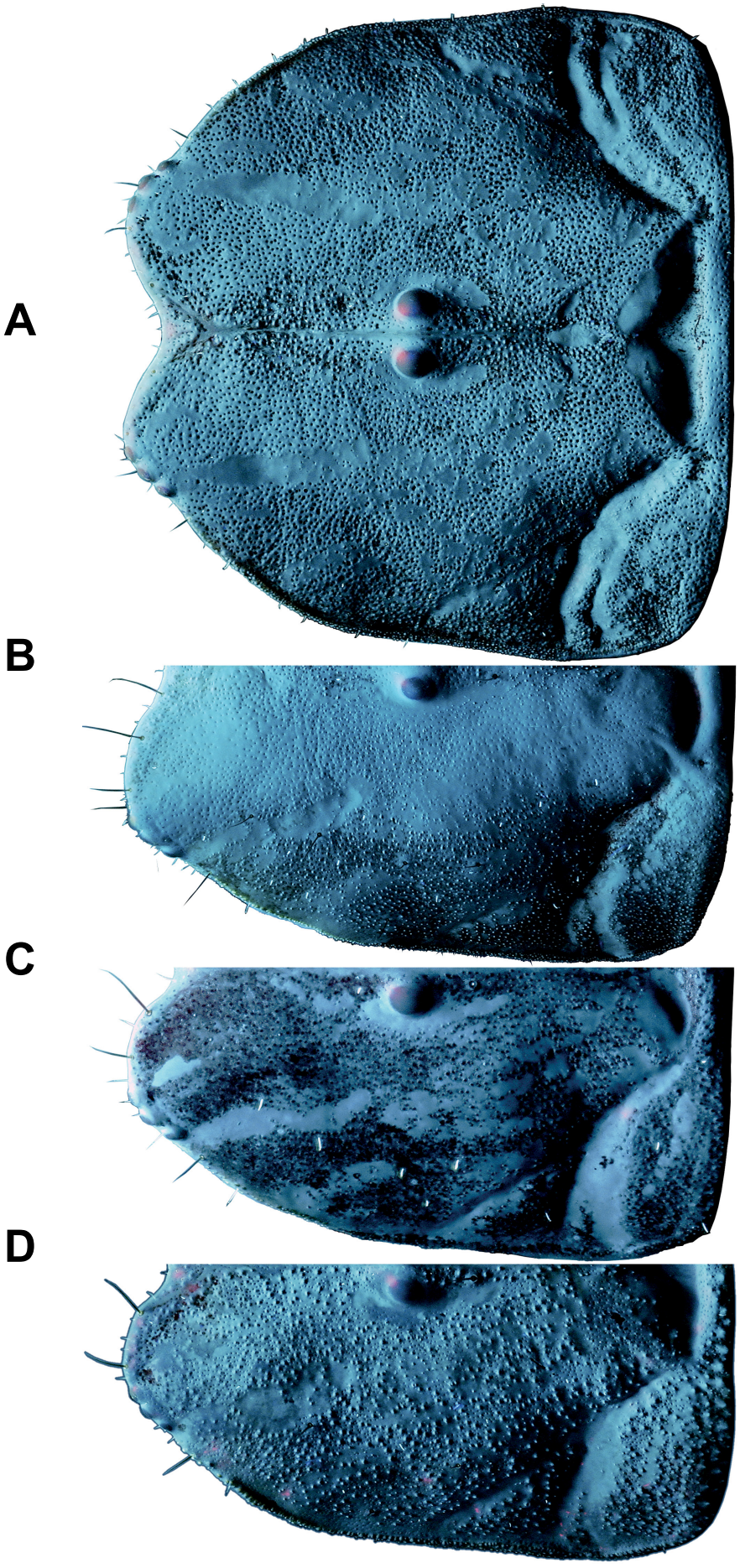
A
B
C
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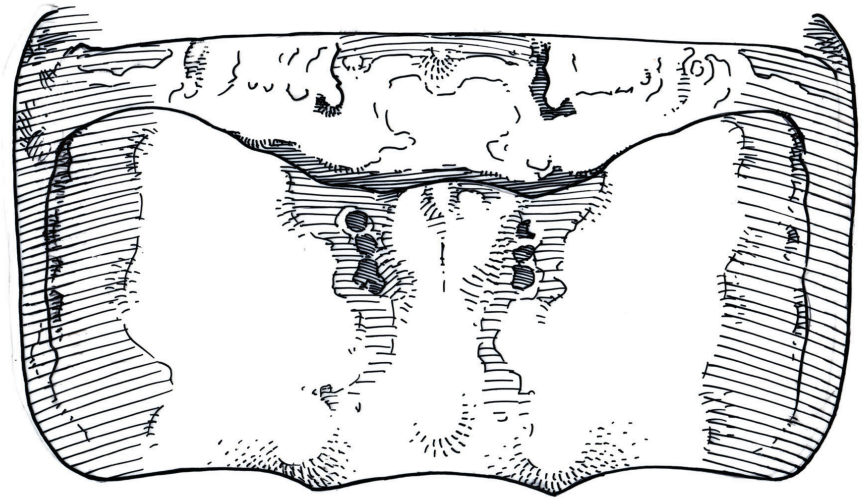
Fig. 36. Mesosoma, tergite V. A, *Opisthacanthus* (*Monodopisthacanthus*) *piceus* Lourenço & Goodman, 2006 from Tolongoina Mountain (Madagdascar), male (LP 6260A): two submedial projections are present on the posterior margin. B, *Hormurus asychnachaena* n. sp. from Bukaua (Morobe Province, Papua New Guinea), female (MHNG).

A



B

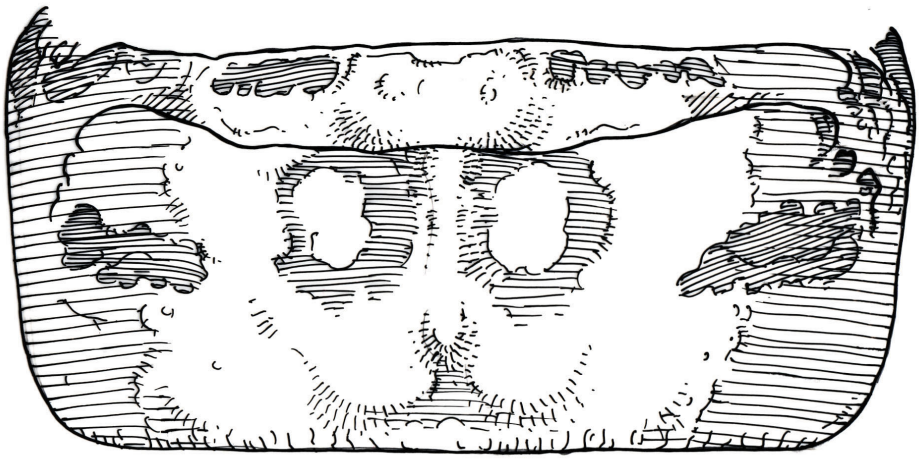


Fig. 37. Interspecific differences of the ornamentation and morphosculptures of prosomal carapace and mesosomal tergites in the genus *Hormurus* Thorell, 1876. A, *Hormurus agastachys* n. sp. from Mazeppa National Park (Queensland, Australia), male (QM-S39695). B, *Hormurus macrochela* n. sp. from Palm Island (Queensland, Australia), male (QM-S59212). C, *Hormurus chydaeostigmata* n. sp. from Maret Island (Western Australia, Australia), male (WAM-T62943). Longitudinal transversal furrows and reticulated network of small ridges and dimples are visible on the tergites of the three species.Carapace and tergites of *H. agastachys* are covered with strong spiniform granules (autapomorphy) whereas those of *H. chydaeostigmata* lack any granulation but are densely punctulated, a character the species shares with *H. dodecatrichos* n. sp. from the northern Kimberley (Western Australia, Australia). The granules on the carapace and tergites of *H. macrochela* are much smaller than in *H. agastachys*.

A
B
C

tinct swelling/bulge oriented posteriorly, at least weak, usually more pronounced in males; 3, hook-like.

Sternum [Characters 156–157]

#156. Sternum shape: 1, anterior width approximately equal to slightly less than posterior width (1<pw/aw<1.5) [=subpentagonal]; 2, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal] [L80/3,12,18, S89/28-30, LP00/9, LP03/8, S&F03.5/68].

#157. Sternum shape, length/posterior width: 1, length less than or equal to posterior width; 2, length greater than width [S&S01/70 (part), S&F03.5/67].

Reproductive anatomy, ♀ [Character 158–163]

#158. Genital operculum, width compared to sternum: 1, approximately same width as sternum, maybe slightly narrower; 2, distinctly wider than sternum.

#159. Genital operculum sclerites, median suture: 1, completely fused, with no clear median suture; 2, partly fused, clear median suture [L80/12 (part), S89/105, S89/107, LP00/80] [modified] [split into two characters].

#160. Genital operculum, posterior notch: 1, absent; 2, present, at least weakly developed.

#161. Genital operculum, shape: 1, sub-pentagonal to pentagonal; 2, oval to semi-oval [WRL11].

#162. Genital operculum, shape (if subpentagonal/pentagonal): 1, not pointed posteriorly; 2, heart-shaped/subtriangular (posterior part elongated and pointed); -, inapplicable.

#163. Genital operculum, proportions: 1, as wide as long (or wider than long); 2, longer than wide.

Pectines [Characters 164–168]

#164. Pecten length, expressed relative to length of coxa of leg IV, ♂: 1, long, distal

edge reaching beyond distal edge of coxa; 2, moderate, distal edge reaching to, but not beyond distal edge of coxa; 3, short, distal edge not reaching to distal edge of coxa [PCW03/60].

#165. Pecten length, expressed relative to length of coxa of leg IV, ♀: 1, long, distal edge reaching beyond distal edge of coxa; 2, moderate, distal edge reaching to, but not beyond distal edge of coxa; 3, short, distal edge not reaching to distal edge of coxa [LP unpublished].

#166. † Pectines, fulcrae: 1, present; 2, absent.

#167. Pectines, marginal lamellae, number: 1, three; 2, two.

#168. Pectinal teeth, shape: 1, short, curved, sensory papillae covering distal portion only; 2, short, not curved, sensory papillae covering distal portion only; 3, long, straight, sensory papillae entirely covering [WRL8, PCW03/63] [modified].

Pectines are ventral comb-like sensory structures, unique to scorpions. They primarily act as chemoreceptors, mechanoreceptors, and proprioceptors much like antennae of other arthropod groups (Cloudsley-Thompson, 1955; Carthy, 1966, 1968; Swoveland, 1978; Ivanov & Balashov, 1979; Foelix & Müller-Vorholt, 1983; Krapf, 1986; Gaffin & Brownell, 1992; Gaffin *et al.*, 1992; Brownell, 1988, 1989, 1998; Wolf, 2008). They allow the scorpion to detect moisture, pheromones and motionless prey that were stung but managed to escape, to perceive ground-vibrations, and to select an appropriate substrate for habitat construction and spermatophore deposition. Pectines consist of an assemblage of four different types of segments/plates, i.e. the marginal lamellae, the median lamellae, the fulcrae and the pectinal teeth or “pegs” (Hjelle, 1990). Whereas most scorpions usually possess three marginal lamellae, the number of median lamellae, fulcrae and pectinal teeth varies widely between taxa and to some extent between the sexes of the same species, males usually having longer pectines with more teeth than females. Several taxa examined during the course of this study possess only two marginal lamellae (fig. 38B-D) instead of the usual three (fig. 38A). This reduction apparently happened independently several times in the Liochelidae and is considered uninformative from a phylogenetic perspective, although it can be useful for specific differentiation. As for the number of

pegs, it is correlated with the length of the pectines and therefore dependent on environmental factors. Scorpions from arid habitats have long pectines with numerous teeth whereas scorpions inhabiting mesic habitats tend to have shorter pectines with fewer teeth and in some case fewer marginal lamellae.

Stigma [Characters 169–170]

#169. Stigma (spiracle), shape: 1, slit-like (straight); 2, half-moon shaped (with a distinct curve); 3, round/oval [L80/20 (part), S&F03.5/101] [modified].

#170. Stigma (spiracle), length: 1, short (less than 1/3 of sternite width); 2, long (at least 1/3 of sternite width).

Sternites [Character 171]

#171. † Sternite VII, longitudinal carinae: 1, four carinae (paired ventrosubmedian and ventrolateral); 2, carinae absent or obsolete [PCW03/100].

Metasoma [Characters 172–216]

#172. Metasoma, lateral compression: 1, markedly flattened laterally (thicker than large); 2, not modified (as thick as large or slightly thicker, more rounded).

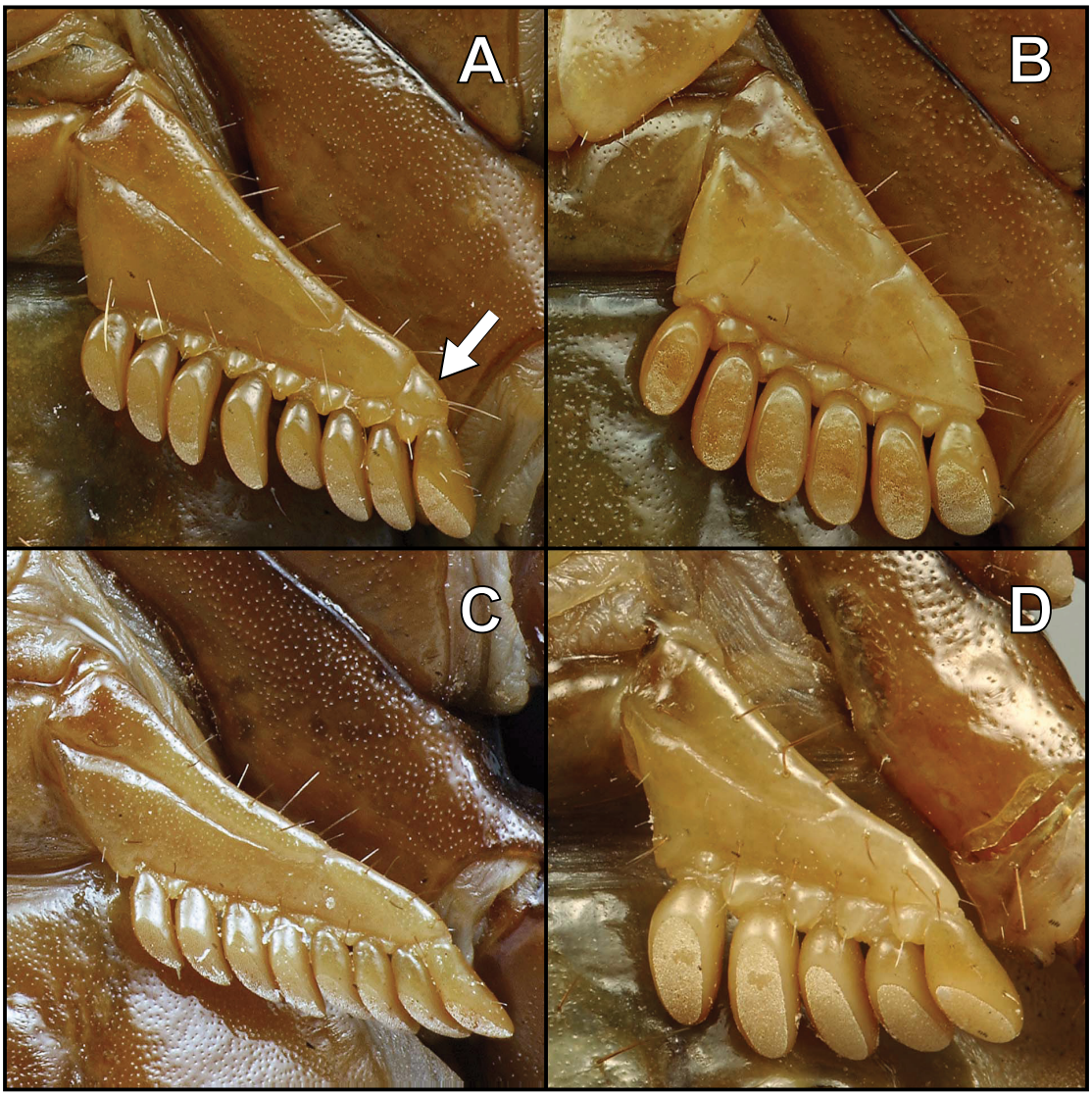
#173. † Metasoma, segments length, ♂: 1, similar to or slightly longer than female; 2, much longer than female [VP08/38].

#174. Metasoma, anal arch, macrosculpture: 1, crenulate, at least with few reduced tooth; 2, with few large conical tooth; 3, with elongated spines; 4, serrate [PCW03/87] [modified].

#175. Metasomal segments I–IV, median furrow: 1, shallow, weak to absent or only visible on segments I–III; 2, distinct on at least segments I–IV, sometimes also in segment V; usually deep.

#176. Metasoma, segments I–IV, dorsosubmedian carinae: 1, present or distinct on at least some segments; 2, absent or obsolete on all segments [BHL79/39, 44, 49, 57, LP01/120].

Fig. 38. Pectines, males. A, *Hormurus macrochela* n. sp. from Palm Island (Queensland, Australia) (QM-S59212). B, *Hormurus tytthognaphos* n. sp. from Mount Lewis (Queensland, Australia) (to be deposited in the QM). C, *Hormurus chydaeostigmata* n. sp. from Maret Island (Western Australia, Australia) (WAM-T62943). D, *Hormurus aethes* n. sp. from Mount Obree (Central Province, Papua New Guinea) (LP3001). The distal marginal lamella is indicated in A by an arrow, it is absent in the three other species.


A
B
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#177. Metasoma, segments I–IV, dorsolateral carinae: 1, present and distinct on at least some segments; 2, absent or obsolete on all segments [VP08/39].

#178. Metasoma, segments I–IV, ventrolateral carinae: 1, present and distinct on at least some segments; 2, absent or obsolete on all segments [BHL79/41, 46, 47, 52, 53, LP01/125].

#179. Metasoma, segments I–IV, ventral carinae: 1, present and distinct on a least some segments; 2, obsolete or absent on all segments [BHL79/40, 45, 50, 51, 59, LP00/95, LP01/126, PCW03/81 (part)].

#180. † Metasoma, segments I–IV, ventral carinae, shape: 1, paired ventrosubmedian carinae; 2, single ventromedian carinae; -, inapplicable [S89/132, LP00/95, LP03/77, VP08/46].

#181. † Metasoma, segment I, width: 1, less than or equal to height; 2, greater than height [LP unpublished].

#182. Metasomal segment I, median lateral carina, ♂: 1, present and distinct; 2, absent or obsolete [VP08/41].

#183. Metasomal segment I, median lateral carina, ♀: 1, present and distinct; 2, absent or obsolete [LP unpublished].

#184. † Metasoma, segment I, dorsosubmedian carinae: 1, separated distally; 2. merging distally; -, inapplicable [LP unpublished].

#185. † Metasoma, segment I, dorsosubmedian carinae, posterior spiniform granules: 1, weak to absent (not noticeably larger than preceding granules); 2, moderate to strong (distinctly larger than preceding granules) [PCW03/78] [split into four characters, 185/187/189/190].

#186. Metasomal segment I, dorsomedian posterior spiniform granules: 1, weak to absent; 2, present, more strongly developed.

#187. Metasoma, segment II, dorsosubmedian carinae, posterior spiniform granules: 1, weak to absent (not noticeably larger than preceding granules); 2, moderate to strong (distinctly larger than preceding granules) [PCW03/78] [split into four characters, 185/187/189/190].

#188. † Metasomal, segment II, dorsomedian posterior spiniform granules: 1, weak to absent; 2, present, more distinct and strongly developed.

#189. Metasoma, segment III, dorsosubmedian carinae, posterior spiniform granules: 1, weak to absent (not noticeably larger than preceding granules); 2, moderate to strong (distinctly larger than preceding granules) [PCW03/78] [split into four characters, 185/187/189/190].

#190. Metasoma, segment IV, dorsosubmedian carinae, posterior spiniform granules: 1, weak to absent (not noticeably larger than preceding granules); 2, moderate to strong (distinclty larger than preceding granules) [PCW03/78] [split into four characters, 185/187/189/190].

#191. Metasoma, segment I, ventral surface, posterior spiniform granules: 1, absent; 2, 1 or 2 pairs, well developed [LP unpublished] [split into three characters, 191/192/193].

#192. Metasoma, segment I, ventrosubmedian carinae, sub-posterior spiniform granules: 1, weak to absent; 2, 1 or 2 pairs, moderate to strong [LP unpublished] [split into three characters, 191/192/193].

#193. Metasoma, segment I, ventrosubmedian carinae, medial granules: 1, weak to absent; 2, 1–3 pairs, well developed [LP unpublished] [split into three characters, 191/192/193].

#194. Metasoma, segment II, ventrolateral carinae, posterior spiniform granules [LP00/102] [split into four characters, 194–197]: 1, absent; 2, vestigial; 3, well developed.

#195. Metasoma, segment II, ventrosubmedian carinae, posterior spiniform granules: 1, absent; 2, 2 or 3 pairs, well developed [LP00/102] [split into four characters, 194–197].

#196. Metasoma, segment II, ventrosubmedian carinae, sub-posterior granules [additive]: 1, absent; 2, 1–3 pairs, small/vestigial; 3, 1 pair, well developed [LP00/102] [split into four characters, 194–197].

#197. Metasoma, segment II, ventrosubmedian carinae, medial granules [additive]:

1, absent; 2, 1 or 2 pairs, small/vestigial; 3, 1–3 pairs, well developed [LP00/102] [split into four characters, 194–197].

#198. Metasoma, segment III, ventrosubmedian carinae, subposterior spiniform granules: 1, absent; 2, 1 pair, well developed.

#199. Metasoma, segment III, ventrosubmedian carinae: 1, no visible ridge, when visible smooth ridges or nearly so (sometimes with a few reduced spiniform granules); 2, ridges with at least a few small/medium spiniform granules; -, inapplicable.

#200. Metasoma, segment III, ventrolateral carinae; 1, no visible ridges, when visible smooth ridges or nearly so; 2, with at least few minute/small spiniform granules; 3, with numerous spiniform granules; -, inapplicable.

#201. † Metasomal segment IV, ventrosubmedian carinae, larger subposterior spiniform granules: 1, absent; 2, 1 pair.

#202. Metasoma, segment IV, ventrosubmedian carinae: 1, ridges with distinct spiniform granules; 2, ridges with at least few reduced spiniform granules distally; 3, no ridges visible, when visible smooth ridges or nearly so (sometimes with few reduced spiniform granules on posterior half); -, inapplicable.

#203. Metasoma, segment IV, ventrolateral carinae [additive]: 1, with well developed spiniform granules; 2, with minute/small spiniform granules; 3, no ridges visible, when visible smooth ridges or nearly so; -, inapplicable.

#204. † Metasoma, segment V, dorsal surface, macrosculptures: 1, smooth; 2, granular [BHL 48, PCW03/79, 80].

#205. Metasoma, segment V, dorsolateral carinae: 1, present and distinct; 2, absent or obsolete [PCW03/77, VP08/40].

#206. Metasoma segment V, ventromedian carina: 1, present and distinct; 2, absent or obsolete [LP unpublished].

#207. Metasoma, segment V, ventromedian carina: 1, complete; 2, partial, expressed only in posterior half; -, inapplicable.

#208. Metasoma, segment V, ventral surface, smooth and shiny depression on

posterior half between ventrolateral carinae: 1, absent; 2, present.

#209. Metasoma, segment V, ventromedian carinae, shape: 1, as a single ridge; 2, as a double ridge; -, inapplicable [BHL79/68; LP01/132].

#210. Metasoma, segment V, ventromedian carina, distal portion: 1, straight; 2, bifurcating; -, inapplicable [LP00/99, LP03/81, PCW03/86, SFK05/81].

#211. Metasoma, segment V, ventromedian carina, macrosculptures: 1, with distinct spiniform granules, at least distally; 2, ridges absent/smooth or nearly so.

#212. † Metasoma, segment V, ventrolateral carinae, distal part: 1, divergent; 2, subparallel to convergent; -, inapplicable [BHL 53, PCW03/83].

#213. † Metasoma, segment V, ventrolateral carinae: 1, present and distinct; 2, absent or obsolete [LP unpublished].

#214. Metasoma, segment V, ventrolateral carinae, anterior half: 1, with at least few small spiniform granules; 2, smooth or nearly so; -, inapplicable [BHL 52, PCW03/84] [split into two characters, 214–215] [modified].

#215. Metasoma, segment V, ventrolateral carinae, posterior half: 1, with at least small spiniform granules; 2, smooth or nearly so (rarely one pair of vestigial granules posteriorly); -, inapplicable [BHL 52, PCW03/84][split into two characters, 214–215].

#216. Metasomal segment V, ventrolateral carinae, posterior half, spiniform-conical granules [additive]: 1, strong conical tooth; 2, medium spiniform granules more strongly developed than preceding granules (anterior half); 3, small/vestigial spiniform granules not noticeably larger than preceding granules (anterior half); -, inapplicable [HWC 113, PCW03/85] [modified].

The metasoma comprises of five segments. Ornamentations on these segments, such as carination and macrosculpture, are important diagnostic characters at familial, generic and specific levels. Variation in the metasomal carination was thus utilized in various phylogenetic analyses (Stockwell, 1989; Prendini, 2000, 2001B, 2001E, 2003; Prendini *et al.*, 2003, 2010; Soleglad & Fet, 2003; Volschenk & Prendini, 2008), with characters pertaining to (1) the pres-

ence/absence, (2) the strength of sclerotization or vertical development, (2) the longitudinal development (complete or partial carinae), and (2) the macrosculpture or ornamentation. These concepts are applied in the present study. The presence of large spiniform granules on the ventral surfaces of metasomal segments I–II is particularly informative to distinguish species in the family Liochelidae and the character was mentioned in early descriptions of *Hadogenes* and *Liocheles* species (Simon, 1877A, 1888; Kraepelin, 1894). Later, Prendini (2000) considered the occurrence of spiniform granules on the ventral metasomal segment II as a relevant character and incorporated it in his phylogenetic analysis of the superfamily Scorpionoidea. Monod (2000) noticed that in *Liocheles* species spiniform granules were actually located on the ventrosubmedian and ventrolateral carinae of metasomal segments I and II and confirmed their taxonomic importance for the genus. Based on new observations, nomenclature of the carinal granulation of the ventral surface of metasomal segments I–II is refined here. In species of the *Hadogenes tityrus* complex, spiniform granules on the ventrosubmedian and ventrolateral carinae are numerous and evenly distributed along the length of the segments. However, in the genera *Hormiops*, *Hormurus* and *Liocheles,* spiniform granules on the metasomal ventrolateral carinae are in most cases present only on the posterior end and rarely along the carinae itself. If so, they are usually smaller/vestigial and randomly placed without a distinct clustering. However, on the metasomal ventrosubmedian carinae, spiniform granules are organised in three distinct “clusters” (fig. 39), i.e. posterior, sub-posterior and medial granules. These three groups of granules appear to be independently expressed and were therefore coded as distinct characters in the present phylogenetic analysis. Four of these characters derived from the ventral carinal spination of metasomal segments I and II were especially informative in the phylogeny:

(1) The presence of strong posterior spiniform granules on the ventral surface of metasomal segment I and on the ventrolateral and ventrosubmedian carinae of metasomal segment II is synapomorphic for *Liocheles* sensu stricto, and for *Hormiops* and *Liocheles* sensu stricto, respectively. [Characters 191 and 194]

(2) The presence of medial granules on the ventrosubmedian carinae of metasomal segment I is observed in *Liocheles malaya* n. sp., *Liocheles australasiae* (Fabricus, 1775), *Liocheles complanatus* (C. L. Koch, 1837), *L. suspectus*, *Hormurus boholiensis* Kraepelin, 1914,

Hormurus dechangei (Becker, 1880), and *H. neocaledonicus*. It is considered here as apomorphic for (*Hormurus* + *Liocheles*). [Character 193]

(3) The presence of strong sub-posterior granules on the ventrosubmedian carinae of metasomal segment II is observed in all *Hormiops* and *Liocheles* species except *Liocheles nigripes* (Pocock, 1897) and in putatively basal *Hormurus* species, i.e. *H. boholiensis*, *H. dechangei*, *H. neocaledonicus*, *H. penta*, *H. samoa* n.sp, and *Hormurus weberi* Pocock, 1894. This character is considered here apomorphic for (*Hormiops* (*Hormurus* + *Liocheles*)) and plesiomorphic for (*Hormurus* + *Liocheles*). [Character 196]

Telson [Characters 217–220]

#217. † Telson, vesicle, surface macrosculpture: 1, longitudinal rows of granules on ventral and lateral surfaces; 2, two or more longitudinal rows of granules on all or part of ventral surface only; 3, smooth, without granules [LP00/111 (modified), LP03/91, PCW03/89, VP08/53].

#218. Telson, size compared to metasomal segment V: 1, shorter than; 2, same size or slightly longer.

#219. † Telson vesicle, shape, ♂: 1, unmodified; 2, elongated with pair of distal lobes; 3, elongated without pair or distal lobes [LP00/109, LP03/89, VP08/49].

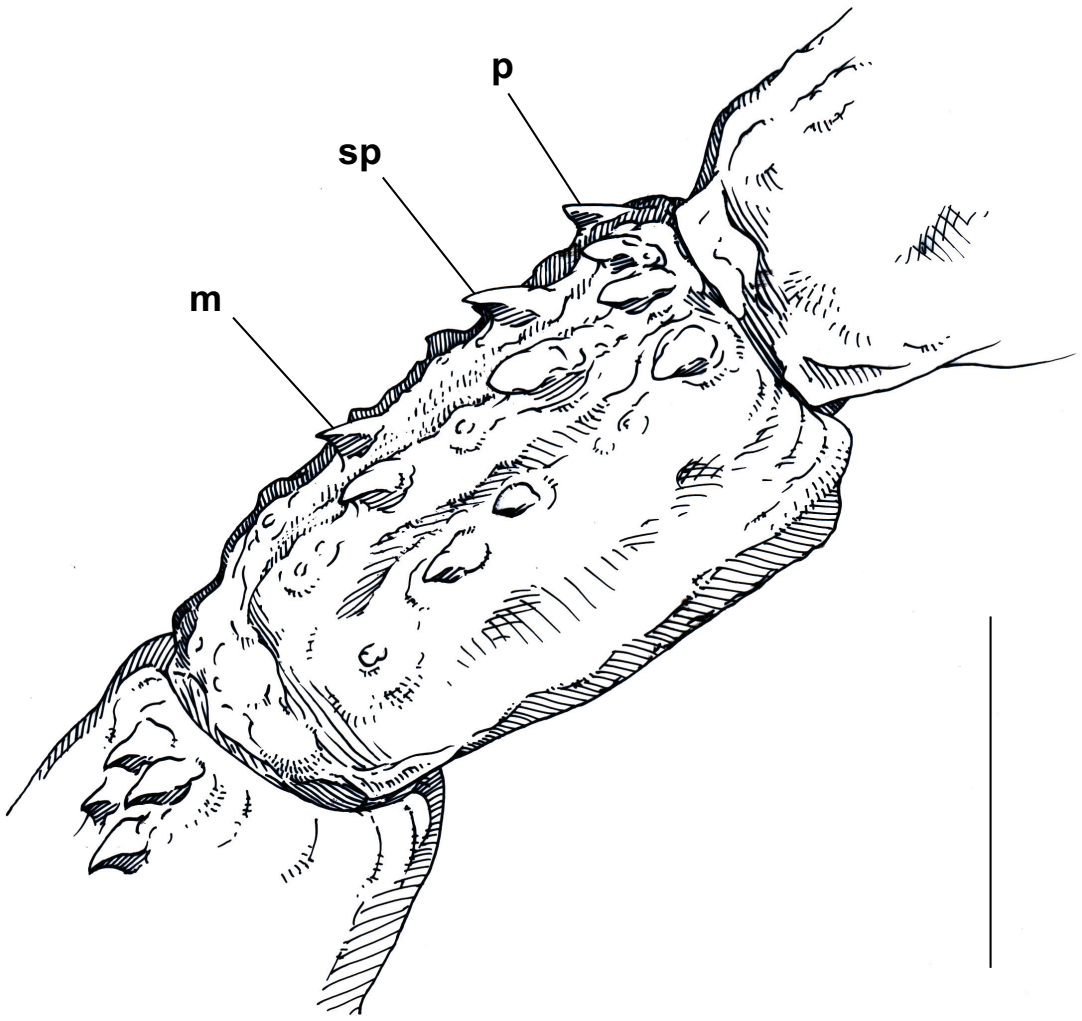
#220. † Telson, vesicle shape, ♀: 1, unmodified; 2, laterally compressed [LP00/108, LP03/88, VP08/51].

Legs [Characters 221–233]

#221. † Legs, femora, ventromedian surfaces: 1, unicarinate, no discernable carina demarcating anterior and posterior surfaces; 2, unicarinate, distinct anterior and posterior surfaces marked by macrosetae and usually granules; 3, bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed [PCW03/65].

#222. Leg IV, femora, ventromedian carinae: 1, absent or obsolete (only expressed

Fig. 39. *Liocheles australasiae* (Fabricius, 1775) from Mount Raro (Tetepare, Solomon Islands), female (LM). Metasomal segment II, ventral surface. Legend: m = medial; p = posterior; sp = sub-posterior. Scale bar = 1 mm.


p
sp
m

distally) or no distinct carinae (only scattered granules); 2, present.

#223. † Tibia I, retrolateral margin, setation: 1, no spiniform macrosetae; 2, a row of spiniform macrosetae [PCW03/66] [split into two characters, 223-224].

#224. † Tibia II, retrolateral margin, setation: 1, no spiniform macrosetae; 2, a row of spiniform macrosetae [PCW03/66] [split into two characters, 223-224].

#225. † Basitarsi I, prolateral margin, setation: 1, no spiniform macrosetae; 2, few spiniform macrosetae [1–4]; 3, many spiniform macrosetae [9-12] [LP unpublished].

#226. † Basitarsi I, retrolateral margin, setation: 1, no spiniform macrosetae; 2, few spiniform macrosetae [1–5]; 3, many spiniform macrosetae [9-12] [LP01/102].

#227. Telotarsi, ventrosubmedian rows of macrosetae (except distal pair), type [additive]: 1, stout spiniform; 2, slender spiniform; 3, few secondarily setiform; 4, numerous secondarily setiform [L80/9, S89/93, 94, 97, LP00/68, 70, S&S01/83, 84, 88, 89, S&F03.5/57 F, S&F03.5/58, LP03/58, VP08/32].

#228. Telotarsi I–IV, distal macrosetae of ventrosubmedian rows, type: 1, spiniform; 2, setiform.

#229. Telotarsi I–IV, distal setiform macrosetae of ventrosubmedian rows, number of pair: 1, one pair; 2, two pairs; -, inapplicable.

#230. Telotarsi, distinct ventromedian row of spinules: 1, present; 2, absent or vestigial [L80/9, S89/97 (part), LP00/68, LP03/56].

#231. Telotarsi, basal spinules: 1, present (at least one, usually a short row); 2, absent.

#232. Telotarsi, terminal ventromedian spinules: 1, present, several spinules arranged into a crown; 2, present, single median spinule; 3, present, a pair of submedian spinules; 4, absent.

#233. Telotarsi, ungues, size: 1, shorter than telotarsus; 2, approximately the same size as telotarsus or longer.

HEMISPERMATOPHORES [CHARACTERS 234–259]

#234. Hemispermatophore, distal lamina, shape: 1, straight or nearly so; 2, curved at least slightly [WRL3].

#235. Hemispermatophore, antero-distal lamina, distal crest: 1, present; 2, absent [WRL2, LP00/87].

#236. Hemispermatophore, distal part and basal part relative sive: 1, distal part distinctly longer than basal part; 2, distal part of approximately the same size as basal part or slightly longer.

#237. † Hemispermatophore, lamellar hook: 1, single; 2, double [LP00/90].

#238. Hemispermatophore, position of lamellar hook [additive]: 1, basal (in basal 1/3 of distal lamina or below; at least less than mid-length); 2, sub-distal, not more than mid-lamina; 3, distal, at least mid-lamina (usually in distal 1/3); 4, extremely distal, in distal 1/4 [LP00/89, LP03/73] [modified].

#239. Hemispermatophore, basal extrusion of distal lamina: 1, present; 2, absent.

#240. Hemispermatophore, transverse ridge: 1, present and distinct; 2, weak to absent.

#241. Hemispermatophore, transverse ridge, merging point with anterior edge: 1, merging below base of lamellar hook; 2, merging with base of lamellar hook; 3, merging above base of lamellar hook; -, inapplicable.

#242. Hemispermatophore, transverse ridge and lamellar hook, relative position [additive]: 1, transverse ridge at approximately same level as base of hook; 2, transverse ridge below base of hook; 3, transverse ridge well below base of hook; -, inapplicable.

#243. Hemispermatophore, capsular region, lamella, shape: 1, thin elongated and pointed lamella (with tip narrower than base), folded longitudinally on both sides, forming a narrow groove; 2, broad lamella folded only basally (wide groove) and unfolded into a wide lobe distally ('spoon' type); 3, lamella broad basally, forming a wide groove; distally only folded anteriorly; tip much narrower than base; 4, broad lamella (tip not markedly thinner), folded longitudinally on both sides (forming a

groove); 5, thin lamella, folded only proximally and unfolded to a flattened distal extremity (tip and base approximately the same width).

#244. Hemispermatophore, capsular region, lamella, longitudinal 'spine' (*ls*) on external surface: 1, present; 2, absent to weak.

#245. Hemispermatophore, capsular region, lamella, accessory hook (*lah*) on distal part of external surface, oriented toward basal part: 1, presence; 2, absence (simple lamella).

#246. Hemispermatophore, capsular region, accessory lobe (*Lac*) on basal part of posterior surface of lamella: 1, presence; 2, absence (simple lamella).

#247. Hemispermatophore, capsular region, lamella and lamellar hook, relative position [additive]: 1, lamellar tip below base of lamellar hook; 2, lamellar tip at approximately same level with apex of lamellar hook or slightly above; 3, lamellar tip at approximately same level with base of lamellar hook, sometimes slightly below.

#248. Hemispermatophore, capsular region, lamella and distal lobe, relative position: 1, lamellar tip below or at approximately same level as tip of distal lobe; 2, lamellar tip above tip of distal lobe.

#249. Hemispermatophore, capsular region, distal lobe: 1, well developed, as an elongated protuberance; 2, well developed, forming a distinct hump; 3, weak (low hump) or absent.

#250. Hemispermatophore, capsular region, distal lobe, shape: 1, hook-like shape; 2, without a distinctive hook-like shape; -, inapplicable.

#251. Hemispermatophore, capsular region, distal lobe, accessory hook on anterior surface: 1, absence; 2, presence.

#252. Hemispermatophore, capsular region, distal lobe, accessory hook, shape: 1, large hook; 2, small to medium hook, pointing downward; 3, small hook, pointing upward; 4, triangular structure; -, inapplicable.

#253. † Hemispermatophore, capsular region, distal lobe, accessory carinae pointing upward on posterior half: 1, absence; 2, presence.

#254. † Hemispermatophore, capsular region, distal lobe, accessory crest on ante-

ro-distal part: 1, absence; 2, presence.

#255. Hemispermatophore, capsular region, basal lobe: 1, well developed ('spoon' shaped), merging with accessory anterior basal lobe; 2, weak to absent.

#256. Hemispermatophore, capsular region, posterior edge of basal lobe and lamella relative orientation: 1, forming a 90° angle; 2, forming a 135-150° angle; -, inapplicable.

#257. Hemispermatophore, capsular region, anterior edge of basal lobe, orientation: 1, forming a 90° angle with lamella; 2, in same plan as lamella (180 °); -, inapplicable.

#258. Hemispermatophore, capsular region, anterior edge of basal lobe, shape: 1, forming a fold towards the posterior part; 2, no accessory fold toward posterior part.

#259. † Hemispermatophore, capsular region, posterior edge of basal lobe, shape: 1, with an accessory distal fold, forming a median groove; 2, no accessory fold (no groove).

Internal morphology in phylogenetics. Diagnostic characters used in scorpion systematics are currently mostly derived from the external morphology, despite numerous publications documenting phylogenetically informative character systems from the internal anatomy (Laurie, 1890, 1891, 1896a, 1896b; Pavlovsky, 1924a, 1924b, 1924c, 1924d, 1925, 1926; Vachon, 1950; Rosin & Shulov, 1963). The external macrostructures of scorpions have been extensively studied for more than 200 years and the most valuable in a systematic framework are currently well known. Progress in our understanding of these character systems are still made but they are usually limited to the addition of newly gathered data and/or to reinterpretations of homology hypotheses and nomenclatural systems (for instance, the "placeholder" paradigm proposed by Prendini & Volschenk (2007) to assess trichobothrial homology and the new pedipalp carinae terminology based on a complete revision of homologous relationships across the order Scorpiones proposed by Prendini *et al.* (in prep.); see paragraphs 1.4-1.5). Since external macromorphological aspects of scorpion taxonomy are largely exhausted, scorpion taxono-

mists were prompted to redirect their investigation efforts towards other domains of research, i.e. external microstructures, internal morphology, ecology and behaviour. Recent development of new imaging technologies (Klaus *et al.*, 2003; Betz *et al.*, 2007; Heethoff & Norton, 2009) now allows the study of internal biological anatomy without the need of dissection or histological serial sectioning. These new techniques open a wide range of possibilities and for instance, the exploration of the internal morphology of fossils is now made possible. Exploration of external microstructures has also benefited from the progresses of scanning electron microscopy (SEM) technology over the last 20 years and several interesting features have recently been discovered on the metasoma (Fet *et al.*, 2003, Fet *et al.*, 2006a, 2006b, 2009) and the pectines (Lourenço, 2002; Lourenço & Goodman, 2002; Prendini *et al.*, 2006). The ultrastructures of the spermatozoa of various scorpion taxa has been recently studied in detail (Peretti & Battán-Horenstein, 2003; Vignoli *et al.*, 2008; Michalik & Mercati, 2009) and their utility for phylogenetic studies clearly demonstrated (Michalik & Mercati, 2009). Furthermore, several extensive comparative studies on the respiratory system (Kamenz *et al.*, 2005; Kamenz & Prendini, 2009), circulatory system (Wirkner & Prendini, 2007), and female reproductive system (Volschenk *et al.*, 2008) were conducted across the order with a critical assessment of the phylogenetic value of each trait. Internal morphology appears to be particularly informative at the deeper nodes of evolution of scorpion lineages because it is arguably less prone to be affected by environmental pressures and habitat adaptation and more stable thereof than external morphology. It is potentially a better indicator of evolutive relationships at the familial and genus level than external features.

Although it is becoming more frequent in scorpion taxonomic publications, investigation of the diagnostic value of the internal anatomy remains minimal probably because it is not as easily implemented as examination of the external macromorphology. Study of the internal anatomy may indeed be hampered by one or a combination of the following factors: (1) the need of freshly caught specimens: internal organs are made of soft tissues and they degrade quickly if the specimens are not properly fixed, internal organs of old collection specimens tend to decompose or become extremely brittle and are therefore unsuitable for dissection and analysis; (2) the implementation of a complex and time-consuming procedure before the sample is

ready for analysis: whereas examination of external macrostructures can be readily carried out when specimens are available, examination of microstructures and internal anatomy required some sort of preparation of the biological material before it can be conducted, either dissection, coating (SEM) or embedding/sectioning/staining (histology); (3) the need for sophisticated and expensive tools and equipment (scanning electron microscope, microtome). The male reproductive system has received more attention than other internal organs probably because it is the easiest to dissect. It is less fragile than other organs and usually relatively well preserved even in old specimens probably because of its partial sclerotization. Dissection from the male specimen and subsequent removal of paraxial organ tissues either manually or chemically (with Proteinase K or Trypsine) is a rapid procedure easily implemented with microsurgery scissors and forceps.

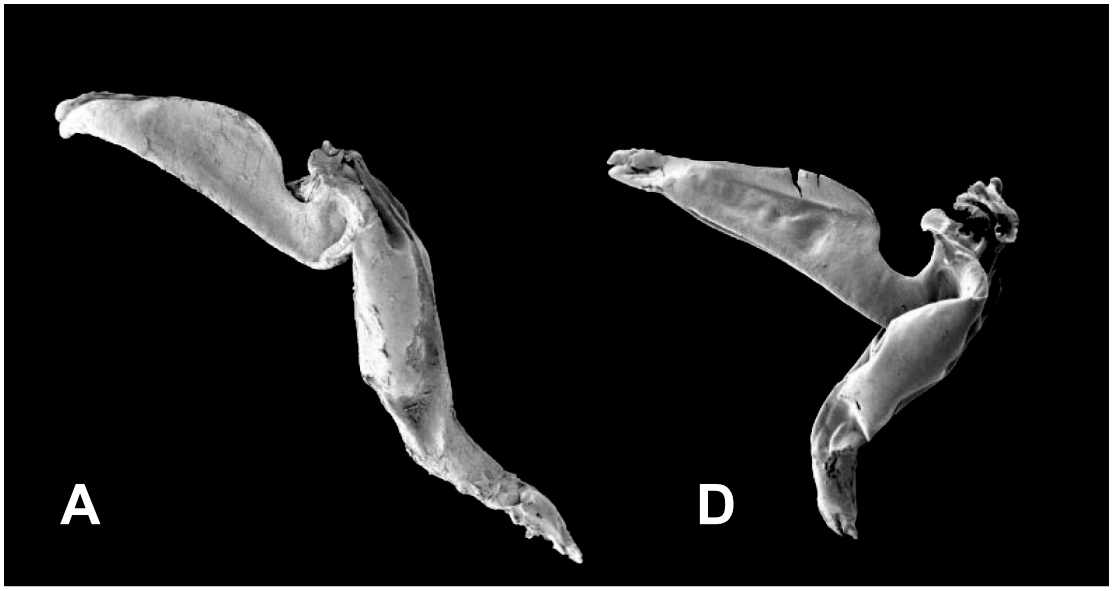
Hemispermatophores in phylogenetics. Scorpions use sclerotized spermatophores for sperm transfer (fig. 40), a common reproductive mechanism in arachnids. These structures are produced in the paraxial organs of the male and provide reliable characters for the identification of specimens to family, genus, and even species level. Pavlovsky (1924) was the first to conduct an extensive investigation of the male genitalia (hemispermatophores and paraxial organs) across the order Scorpiones. Several taxonomists (Vachon, 1952; San Martín, 1969; Maury, 1975b, 1980; Francke, 1979) subsequently used hemispermatophores as descriptive and diagnostic characters in their respective revisionary works. Lamoral (1979) pointed out that earlier terminologies were based on positional criteria rather than homologous structures and proposed his own revised nomenclature. However, Stockwell (1989) subsequently falsified homologies postulated by Lamoral and emphasized that the erroneous conclusions were presumably due to the fact that he attempted to homologize the buthid hemispermatophores with the most complex scorpionoid hemispermatophores (Bothriuridae, Liochelidae and Scorpionidae) without examining those of other scorpion lineages that are phylogenetic intermediate between Buthoidea and Scorpionoidea. Stockwell was the first to study the male reproductive system of all scorpion families and to provide a complete comparative overview of these structures. He clearly demonstrated the phylogenetic value of both hemispermatophores and paraxial organs

and proposed a consensus regarding their terminology and hypotheses of homology. Prendini (2000), Soleglad & Sissom (2001), Prendini *et al.* (2003), Soleglad & Fet (2003) subsequently incorparated in their respective phylogenetic studies characters pertaining to hemispermatophores, that were for the most part adapted from Stockwell's (1989) characters. More recently, several publications presented comprehensive interpretations of the functional morphology of these reproductive structures (Peretti, 2003; Jacob *et al.*, 2004a) as well as detailed comparisons of their fine structures with more emphasis on phylogeny and taxonomy (Mattoni & Peretti, 2004).

Hemispermatophore categories. Scorpion spermatophores were first categorized into three different morphological types by Pavlovsky (1924), i.e. the "complex" type only present in the Buthidae, the "intermediate" type only observed in *Chaerilus* Simon, 1877 (family Chaerilidae) and *Calchas* Birula, 1899 (family Iuridae), and the "simple type" occuring in all other scorpions. Francke (1979) recognized only two types of hemispermatophores, i.e. the "flagelliform" type of the buthids and the "lamelliform" type characteristic of all non-buthid scorpions. He was undecided concerning the "intermediate" type of Pavlovsky and suggested that it might either be lamelliform or of an undescribed type. Lamoral (1979, 1980) followed Francke's categorization although he used the terms "rod-like" and "fusiform", instead of "flagelliform" and "lamelliform" respectively. The hemispermatophore of *Chaerilus* was deemed by Stockwell (1989) as the simplest known. As Pavlovsky before, Stockwell established that the male reproductive system of *Chaerilus* combined features of both the lamelliform and the flagelliform hemispermatophore and concluded that its unique morphology warranted its assignment to a separate category which he designated as "fusiform". The hemispermatophores of the recently described genus *Pseudochactas* Gromov, 1998 (Pseudochactidae Gromov, 1998) also present a very unusual shape associated with primitive state (Prendini *et al.*, 2006) and cannot be assigned to one of the three categories currently recognized. Therefore scorpion hemispermatophores are currently separated into four different morphological types:

(1) The "flagelliform" type (Buthidae; figs 41A-B) is characterized as having a long, slender trunk, very simple sperm duct, and a long filamentous projection at the distal end re-

Fig. 40. Spermatophore of *Euscorpius italicus* (Herbst, 1800). A–C. Before sperm transfer. A. Lateral view of spermatophore in toto, SEM. B. Lateral view of hemispermatophore in toto, drawing; arrow shows the down and backward motion of the distal lamella against that triggers sperm expulsion during mating. C. Lateral view of the capsular region. D–F. After sperm transfer. D. Lateral view of spermatophore in toto, SEM. E. Lateral view of hemispermatophore in toto, drawing; arrow shows the direction of sperm expulsion and capsular eversion. F. Lateral view of the capsular region. dl, distal lamina; sd, sperm duct; tr, trunk. (modified after Jacob *et al.*, 2004).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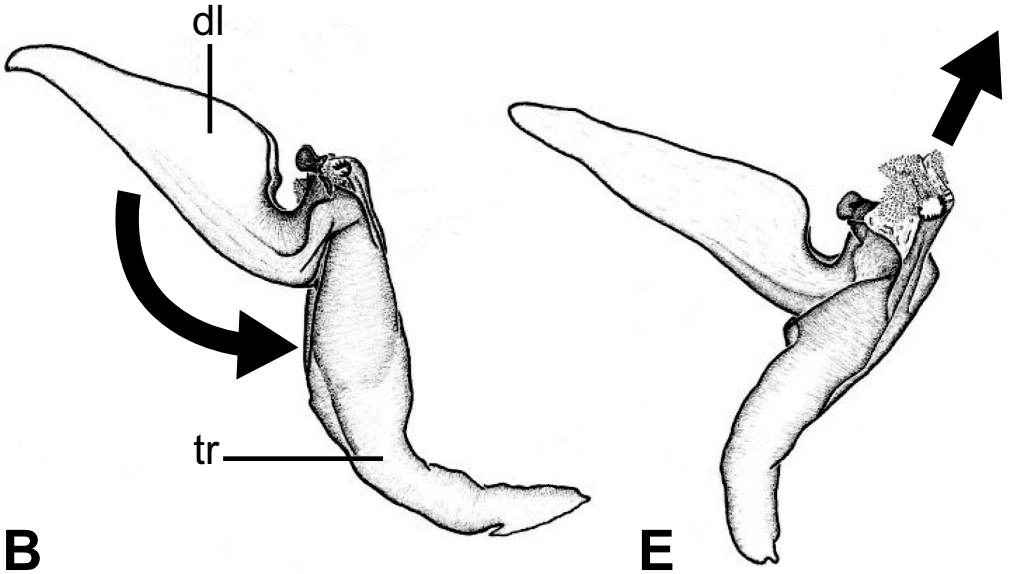
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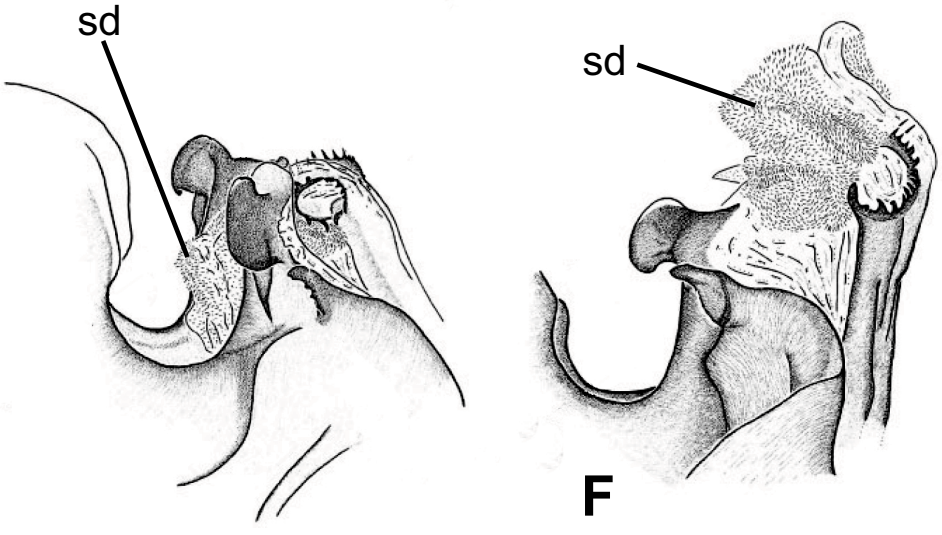
sd
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ferred to as the flagellum. Sperm transfer is triggered by the flexing and compressing of the entire trunk against the foot and substrate (Alexander 1959).

(2) The “lamelliform” type (most non-buthid scorpions; figs 40, 41F–N, 42–48) is characterized by a long, distal lamellate projection, called distal lamella or lamina. The flexing of this structure posteriorly and downward against the trunk (Alexander 1957; Francke 1979; Peretti, 2003; Jacob *et al.*, 2004a; fig. 40) is allowed by the presence of a truncal flexure between the two parts and triggers the sperm expulsion. The shape of lamelliform hemispermatophores varies greatly. The sperm duct may be very simple or highly elaborate with sclerotized projections and detachable mating plugs. All scorpionoid genera produce lamelliform hemispermatophores with a complex capsular structure. In these taxa, the sperm duct is composed of a lamella that projects into a distinct through (figs 41L-N, 42-48). This character is considered apomorphic. On the other hand, the capsule of other lamelliform hemispermatophores is much simpler : the membranous evertile invaginations forming the sperm duct are poorly developed without a distinct lamella (figs 40, 41F–K).

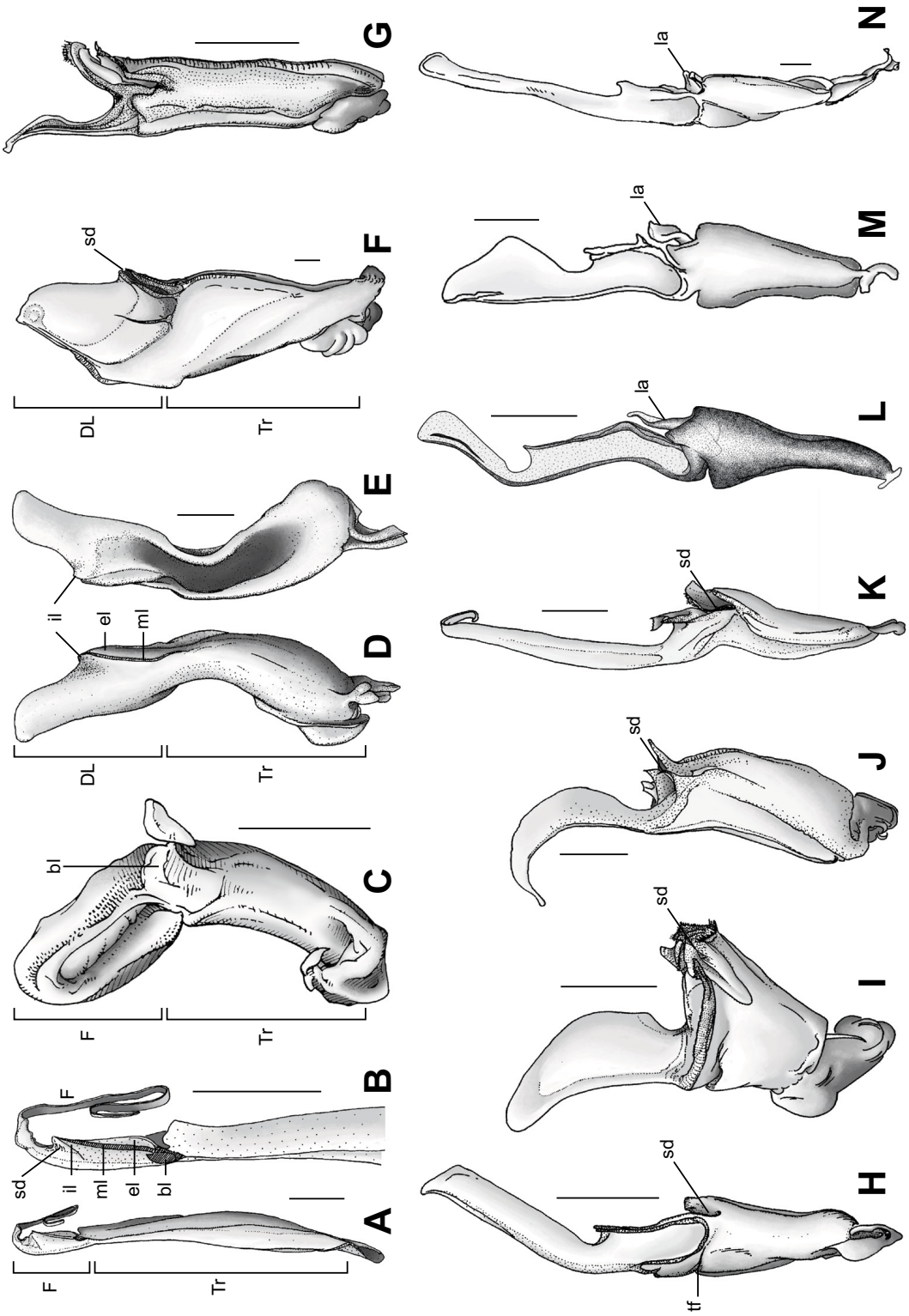
(3) The “fusiform” type (Chaerilidae; figs 41D-E) is characterized by a poorly developed and short lamella that resemble those of non-buthid scorpions. Networks of external carinae and a truncal flexure like those observed in most lamelliform hemispermatophores are absent. Chaerilid hemispermatophore possess a long, narrow trunk, a keel-like median lobe, and a simple sperm duct, all of which bear remarkable resemblances to the elongated trunk, median lobe, and simple sperm duct of buthid hemispermatophores. It is considered by Stockwell (1989) to be plesiomorphic.

(4) The hemispermatophore of Pseudochactidae (fig. 41C), is composed of a shaft, connecting distally to a thick, folded tubular process. Prendini *et al.* (2006) considered this structure as homologous to the flagellum of buthids. They also regarded the large cuticular process on the capsule as a potential homologue to the structure referred to as the basal lobe in buthid hemispermatophores. They concluded that the male reproductive system of Pseudochactidae is more similar to that of the Buthidae.

Hemispermatophores as diagnostic characters. The male reproductive system remains

hitherto poorly studied or even completely unexplored in several scorpion families, i.e. the Chactidae and the Scorpiopidae. On the other hand, the structure is relatively well known in Buthidae (Alexander, 1959; Francke, 1979; Locket, 1990; Gantenbein *et al.*, 2000), Bothriuridae (see references below), Diplocentridae (Rosin & Shulov, 1963; Sissom, 1994), Hemiscorpiidae (Monod & Lourenço, 2005; Lowe, 2010), Heteroscorpionidae (Lourenço, 1985, 1989, 1996b; Lourenço *et al.*, 2003), Liochelidae (see references below), Scorpionidae (Vachon, 1952; Lamoral, 1979; Couzijn, 1981), Typhlochactidae (Francke, 1982), Urodacidae (Koch, 1977; Volschenk *et al.*, 2000) and Vaejovidae (Francke, 1979; Sissom, 1991). Hemispermatophore morphology was most extensively studied in the Bothriuridae. Four generations of taxonomists from Latin America successfully used the structure for specific and generic identifications within the family (Abalos, 1955; San Martin, 1965, 1969; San Martin & Gambardella, 1967, 1974; Maury, 1968, 1973a, 1973b, 1975b, 1975c, 1980; Maury & San Martin, 1973; Acosta, 1985, 1997; Acosta & Ochoa, 2000; Mattoni, 2002a, 2002b, 2002c, 2007; Ochoa & Acosta, 2002a, 2002b, 2003a, 2003b; Ochoa, 2002a, 2002b, 2004a, 2004b; Mattoni & Acosta, 2005, 2006; Ochoa & Ojanguren-Affilastro, 2007; Ojanguren *et al.*, 2007a, 2007b). Several authors have also used these internal structures for generic and specific diagnoses within Liochelidae, e.g. Koch (1977), Lamoral (1979), Lourenço (1985, 1988, 1989, 1997), Lourenço & Monod (1999), Locket (1995), Newlands & Prendini (1997), Prendini (2001a, 2005b, 2006), Volschenk & al. (2001) and Scorpionidae (Lamoral, 1979; Prendini *et al.*, 2003). Following Lamoral's (1979) terminology of scorpionid hemispermatophores, Monod & Volschenk (2004) provided a detailed description of the median microstructure in *Liocheles*, e.g. number, length and shape of the different inner lobes and the presence or absence of small hooks. These characteristics proved to be very informative for determining relationships among liochelid genera and species groups, and related scorpionoid taxa (Monod & Lourenço, 2005). Although it is a sclerotized structure, hemispermatophores can easily be distorted, especially the softer basal part, if the specimens are thrown alive into alcohol, or if they subsequently dry out. Hence description of new species should not be based on minute differences in the shape of a single hemispermatophore without a precise knowledge of the intraspecific variability. It is recommended that several males are dissected, preferably from the same population before any taxonomic decisions are made. For

Fig. 41. Right hemispermatophores. Flagelliform type. *Centruroides vittatus* (Say, 1821) (Buthidae). A, *in toto*, external aspect. B, detail of capsular region, external aspect. C, *Pseudochactas ovchinnikovi* Gromov, 1998 (Pseudochactidae Gromov, 1998), external aspect. Fusiform type, *Chaerilus granosus* Pocock, 1900 (Chaerilidae Pocock, 1893). D, external aspect. E, internal aspect. Lamelliform type. F, *Anuroctonus phaiodactylus* (Wood, 1863) (Iuridae Thorell, 1876), external aspect. G, *Nullibrotheas allenii* (Wood, 1863) (Chactidae Pocock, 1893), external aspect. H, *Serradigitus* sp. (Vaejovidae Thorell, 1876), external aspect. I, *Megacormus gertschi* Díaz Najera, 1966 (Euscorpiidae Laurie, 1896), external aspect. J, *Troglocormus willis* Francke, 1981 (Euscorpiidae Laurie, 1896), external aspect. K, *Scorpiops montanus Karsch*, 1879 (Scorpiopidae Kraepelin, 1905), external aspect. L, *Orobothriurus grismadoi* Ojanguren-Affilastro, Fernández Campón, Silnik & Mattoni, 2009 (Bothriuridae Simon, 1880), external aspect. M, *Orobothriurus wawita* Acosta & Ochoa, 2000 (Bothriuridae Simon, 1880), external aspect. N, *Heterometrus spinifer* (Ehrenberg, 1828) (Scorpionidae Latreille, 1802), external aspect. Abbreviations: bl = basal lobe; DL = distal lamina; el = external lobe; il = internal lobe; F = flagellum; la = lamella; ml = median lobe; sd = sperm duct; tf = truncal flexure; Tr = trunk. Scale bars = 1 mm (all except C and M), 50 µm (C), 0.5 mm (M). All drawings are modified from Stockwell, 1989 except C modified from Prendini *et al.*, 2006, L modified from Ojanguren-Affilastro *et al.*, 2009 and M modified from Acosta & Ochoa, 2000.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instance, Ojanguren-Affilastro *et al.* (2009) justified the description of a new species of *Orobothirurus* Maury, 1975 (family Bothriuridae) by providing illustrations of several hemispermatophores from the new taxon and its close relative along with a statistical assessment of the inter and intraspecific variations. On the other hand, hemispermatophores may be uninformative for specific diagnosis in some taxonomic groups (Jacob *et al.*, 2004B).

Hemispermatophore nomenclature. The terminology proposed by Stockwell (1989) is not detailed enough to accurately describe the complexity of the median capsular structure of the scorpionoid hemispermatophore. In that regard, the terminology created by Lamoral (1979) is more appropriate. It was slightly modified by Monod & Volschenk (2004) and Monod & Lourenço (2005) to accommodate a few characters specific to Liochelidae and that were previously unknown. Several other important features were discovered in the course of the present study which prompted further revision of Lamoral's terminology and the introduction of new terms (tabs. 7–8): (1) the lamellar 'spine' refers to the longitudinal ridge or carinae that is present in some taxa on the external side of the capsular lamella, apparently strengthening it; (2) a distinction is made between the anterior and posterior edges of the basal lobe because the morphology and orientation of these membranous folds appears to be quite variable and phylogenetically informative within Liochelidae (characters 256–259; figs 42–48); (3) an accessory structure that can take various shapes (usually a hook, rarely a carina or crest) is reported on the distal lobe of the capsular region of several *Hormurus* species (characters 252–254; fig. 43). Besides, Monod & Volschenk (2004) and Monod & Lourenço (2005) used the term "flagellum" to describe the distal part of the distal lamina. The same name is also used to describe the distal part of buthid hemispermatophores. However, the flagellum does not refer to homologous structures in the two systems. The buthid flagellum is homologous to the distal lamina of other scorpions, whereas the flagellum of Monod & Volschenk (2005) refers to the portion of the lamina that is above the lamellar hook. The "flagellum" of Monod & Volschenk is renamed here "distal part of distal lamina" in order to remove homonymy with the flagellum of buthids hemispermatophores.

Numerous characters were found to be extremely informative for phylogenetic recon-

struction purposes in the hemispermatophores of Liochelidae:

(1) The absence of an anterior distal crest on the distal lamina (Lourenço, 1985; Prendini, 2000) is reported only for the derived taxa *Hormiops*, *Hormurus*, *I. politus*, *Liocheles* and *Opisthacanthus* (*Opisthacanthus*) and is therefore potentially synapomorphic for this group and symplesiomorphic for the remaining taxa (figs 44–45). [Character 235]

(2) Among the taxa studied, the basal extrusion of the distal lamina is only present in *C. ochropus* (fig. 46), *I. politus*, *O*. (*N*.) *laevipes*, and *Opisthacanthus* (*Opisthacanthus*) (fig. 42). This is a plesiomorphic character since it is observed in *O*. (*N*.) *laevipes*. The occurrence of a similar swelling on the hemispermatophore of *I. politus*, *C. ochropus* and the subgenus *Opisthacanthus* may represent reversal to the primitive state depending on where these taxa nest in the cladogram. [Character 239]

(3) There is no transverse ridge in the hemispermatophores of *C. ochropus* (fig. 46), the Indian *Iomachus* (fig. 47), and the Malagasy *Monodopisthacanthus* and *Palaeochelonus*. Besides, in the same taxonomic groups, the anterior edge of the basal lobe is in line with the lamella whereas it is oriented at 90° angle compared to the lamella in all other taxa (figs 42–45, 48). These two characters might potentially be synapomorphies for a monophyletic assemblage of *C. ochropus*, the Indian *Iomachus* and (*Monodopisthacanthus* + *Palaeochelonus*) but it is so far impossible to assert because it is unclear whether these taxonomic groups are closely related or not. [Character 240]

(4) The capsular lamella of the Indian *Iomachus* hemispermatophore (fig. 47) has a very peculiar shape, unique among the taxa studied in the present study. It can be described as a spoon-like process: it is broad and short, the tip never reaching the apex of the distal lobe contrary to all other liochelids of the study. Furthermore, the anterior edge of the basal lobe forms a fold towards the posterior part, another feature that is only observed in the Indian *Iomachus*. [Character 243]

(5) A longitudinal ‘spine’ on the capsular lamella is present in *I. politus*, *O*. (*N*.) *laevipes*, *Monodopisthacanthus*, *Opisthacanthus* (*Opisthacanthus*) and *Palaecheloctonus* whereas it is absent in all other species. Like the previous character, its occurrence in *O*. (*N*.) *laevipes* suggests that it is an ancestral state. The loss of this longitudinal carinae then corresponds to a

Table 7. Terminology of hemispermatophore gross morphology. Synonymies with recent nomenclatural systems are summarized.

	LAMORAL, 1979	STOCKWELL, 1989	MONOD & VOLSCHENK, 2004
Distal lamina (Dl)	distal lamina (DL)	distal lamella (DL)	distal lamellum
Spatula (sp)			flagellum
Basal part of distal lamina (bpDL)			basal part of lamella
Sperm duct (Sd)		sperm duct (sd)	
Capsule median structure			capsule region
Truncal flexure (tf)	median transverse cleavage (mtc)	truncal flexure (tf)	
Basal trunk (Bt)	basal portion (BP)	trunk (Tr)	basal part
	basal cleavage (bc)		
Pedicel (P)	stalk		
	foot	pedicel	

Fig. 42. *Opisthacanthus* (*Opisthacanthus*) *cayaporum* Vellard, 1932. A, Right hemispermatophore *in toto*, external aspect. B, left hemispermatophore, detail of the capsular median structure, internal aspect. Abbreviations: aebl = anterior edge of basal lobe; bl = basal lobe; beDL = basal extrusion of distal lamina; bpDL = basal part of distal lamina; DL = distal lamina; dl = distal lobe; dpDL = distal part of distal lamina; etDL = external through of distal lamina; h = lamellar hook; La = lamella; lah = lamellar accessory hook; lac = lamellar accessory lobe; lc = longitudianl carina; ls = lamellar spine; mtt = median transverse through; pebl = posterior edge of basal lobe; pl = posterior lobe; Sd = sperm duct; tf = truncal flexure; tr = transverse ridge. Scale bars = 1mm.

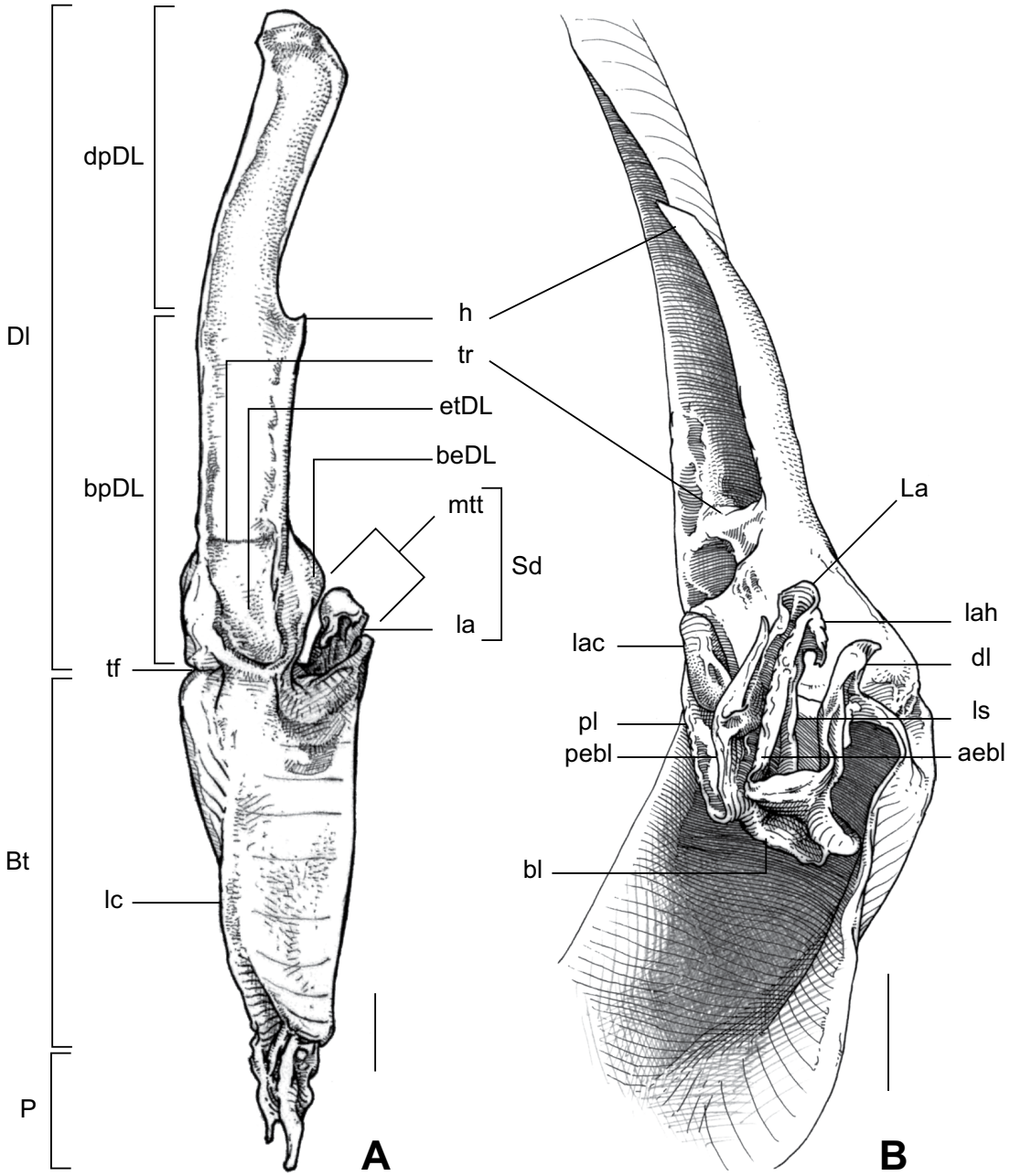
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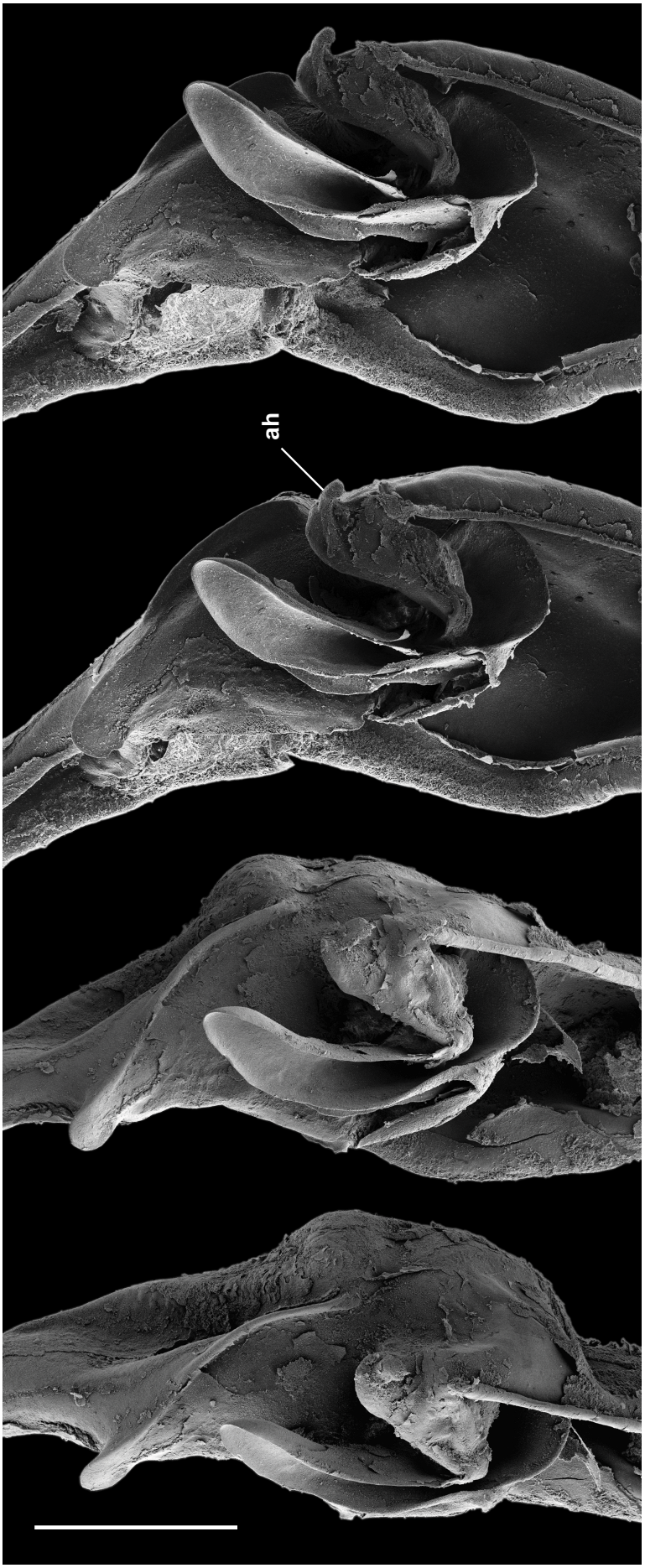
Table 8. Terminology of hemispermatophore detailed morphology. Synonymies with previous nomenclatural systems are summarized.

		LAMORAL, 1979	STOCKWELL, 1989	MONOD & VOLSCHENK, 2004	MONOD & LOURENCO, 2005
Distal part of distal lamina		pars bireflecta (pbrf) (Buthidae)		flagellum	flagellum
		pars recta (pr) (Buthidae)			
		pars refelcta (prf) (Buthidae)			
	distal crest of distal lamina (dcr)	distal crest of distal lamina (dcr)	distal crest		
		lateral crest (lcr)			
	hook (h)	hook (h)		hook (h)	hook (h)
		hook apex (ha)			
		hook notch (hn)			
		dorsal through of hook (dth)			
Basal part of distal lamina	**external through of distal lamina (etDL)**	dorsal through of distal lamina (dtDL)			
		sub-apical lateral margin of hook (salmh)			
	basal extrusion of distal lamina (beDL)	median lobe (ml)			
		basal scallop of hook (bsh)			
	transverse ridge (tr)	distal crest of median lobe (dcrml)		transverse ridge (Tr)	transverse ridge (Tr)
		ectal crest of median lobe (eccr)			

Table 8. Terminology of hemispermatophore detailed morphology. Synonymies with previous nomenclatural systems are summarized. (Continued)

		LAMORAL, 1979	STOCKWELL, 1989	MONOD & VOLSCHENK, 2004	MONOD & LOURENCO, 2005
Capsular region	**median transverse through (mtt)**	median transverse through (mtt)			
	distal lobe (dl)	basal lobe (bl)		distal lobe (Ld)	distal lobe (Ld)
	accessory hook of distal lobe (ah)				
	lamella (La)	inner lobe (il)	internobasal reflexion of sperm duct (ibr)	lamella (La)	capsule lamella (La)
	lamellar spine (ls)				
	lamellar accessory hook (lah)				accessory hook
	lamellar accessory lobe (lac)				accessory lobe (Lac)
	posterior lobe (pl)			posterior lobe (Pl)	posterior lobe (Pl)
	basal lobe (bl)			basal lobe (Lb)	basal lobe (Lb)
	posterior edge of basal lobe (pebl)				
	anterior edge of basal lobe (aebl)				
Basal part		lateral lobe (ll)			
		outer lobe (ol)			
		axial rib (ar)			
	longitudinal carina (lc)	diagonal rib (dr)			

Fig. 43. *Hormurus macrochela* n. sp. from Magnetic Island (Queensland, Australia). Left hemispermatophore, detail of the capsular median structure, internal aspect under several orientations. Legend: ah = accessory hook of distal lobe. Scale bar = 1 mm.


ah

derived state. The fact that it is also observed in (*I. politus* + *Opisthacanthus* (*Opisthacanthus*)) and (*Monodopisthacanthus* + *Palaeocheloctonus*) might indicate several reversals since at least the first group is among the more terminal clades within the family Liochelidae. [Character 244]

(6) The morphology of the capsular lamella provides two synapomorphies for the monophyletic grouping of *I. politus* and *Opisthacanthus* (*Opisthacanthus*) (fig. 42). In these taxa, the lamina bears an additional lobe and a additional hook whereas it is devoid of any complex accessory structures in all other taxa. On the other hand, the absence of a distal lobe is synapomorphic for (*Palaeocheloctonus* + *Monodopisthacanthus*) and the presence of a well developed basal lobe is synapomorphic for (*Liocheles* + *Hormiops* + *Hormurus*) (figs 43-45). [Characters 245–246, 249, 255]

(7) The posterior edge of the basal lobe forms a 90° angle with the capsular lamella in *Hormiops* and *Liocheles* (fig. 45) whereas this angle is less acute in *Hormurus* (approximately 135-150°) (figs 43-44) making the basal lobe much wider in this genus than in the two other genera. This provide a synapomorphy for *Hormurus*. [Character 256]

Book lungs [Characters 260–262]

#260. Book lungs, lamellar surface, fine structure: 1, simple trabeculae; 2, branched trabeculae [S89/131, KP08].

#261. Book lungs, Lamellar edge, fine structure: 1, bristles or spines; 2, arcuate bow-like structures [KP08].

#262. Book lungs, Posterior spiracle edge, fine structure: 1, chisel-like structures; 2, hillocklike structures; 3, hexagonal 'tiles' [KP08].

The respiratory organs of scorpions are composed of numerous thin, leaflike lamellae organized in layers much like the pages of a book, hence their name. Morphology of the book lungs was first investigated and illustrated by Lankester (1883). Laurie (1896A, 1896B) and subsequently Pavlovsky (1926) published the first comparative surveys of the structure across a range of families. Based on the literature, Stockwell (1989) recognized two characters

Fig. 44. *Hormurus* sp. from Halmahera, North Maluku, Indonesia (NNHM). A, Right hemispermatophore *in toto*, external aspect. B, left hemispermatophore, detail of the capsular median structure, internal aspect. Scale bars = 1 mm.

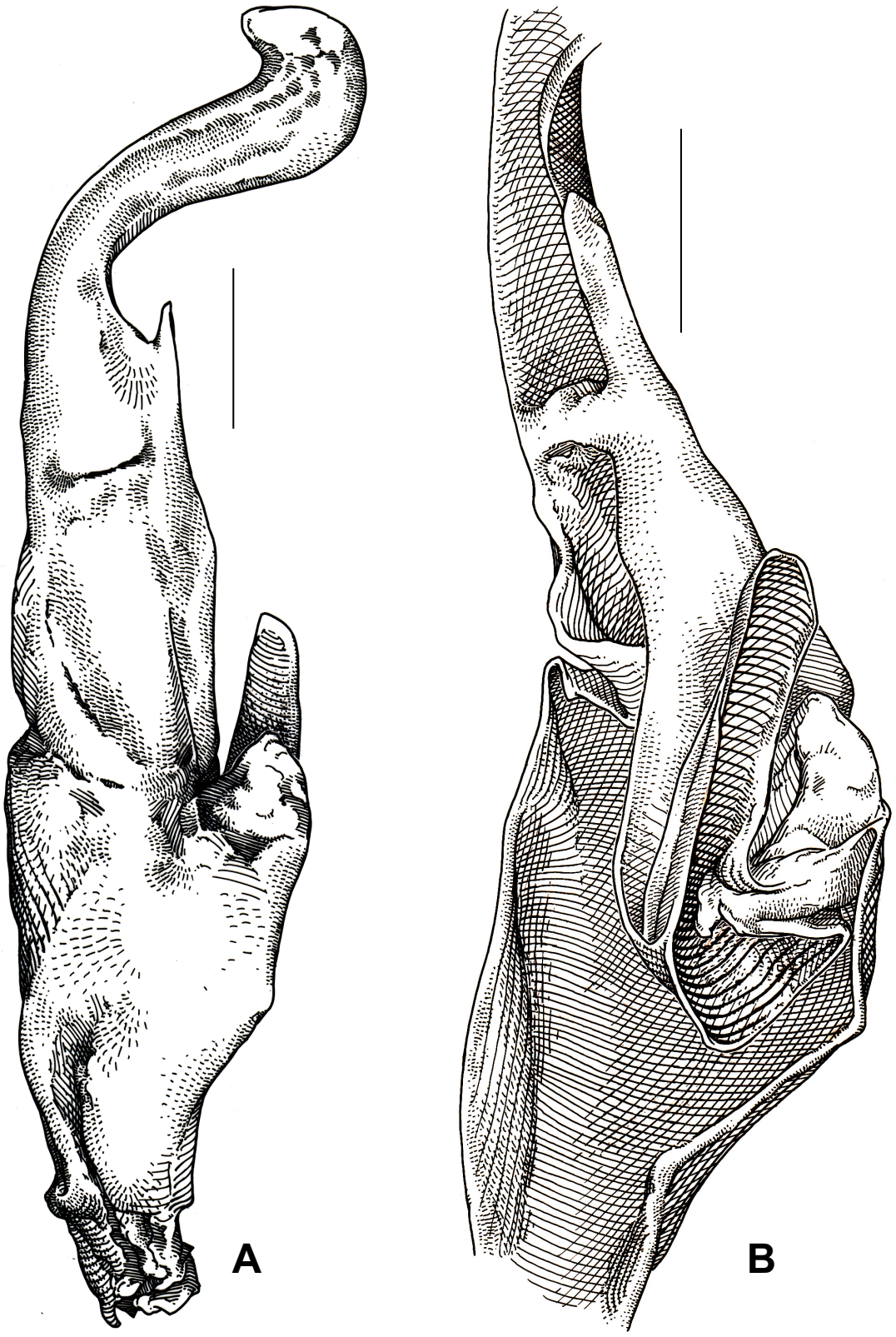

A
B

Fig. 45. *Liocheles australasiae* (Fabricius, 1775) from Tanna Island, Vanuatu (BPBM). A, Right hemispermatophore *in toto*, external aspect. B, left hemispermatophore, detail of the capsular median structure, internal aspect. Scale bars = 0.5 mm.

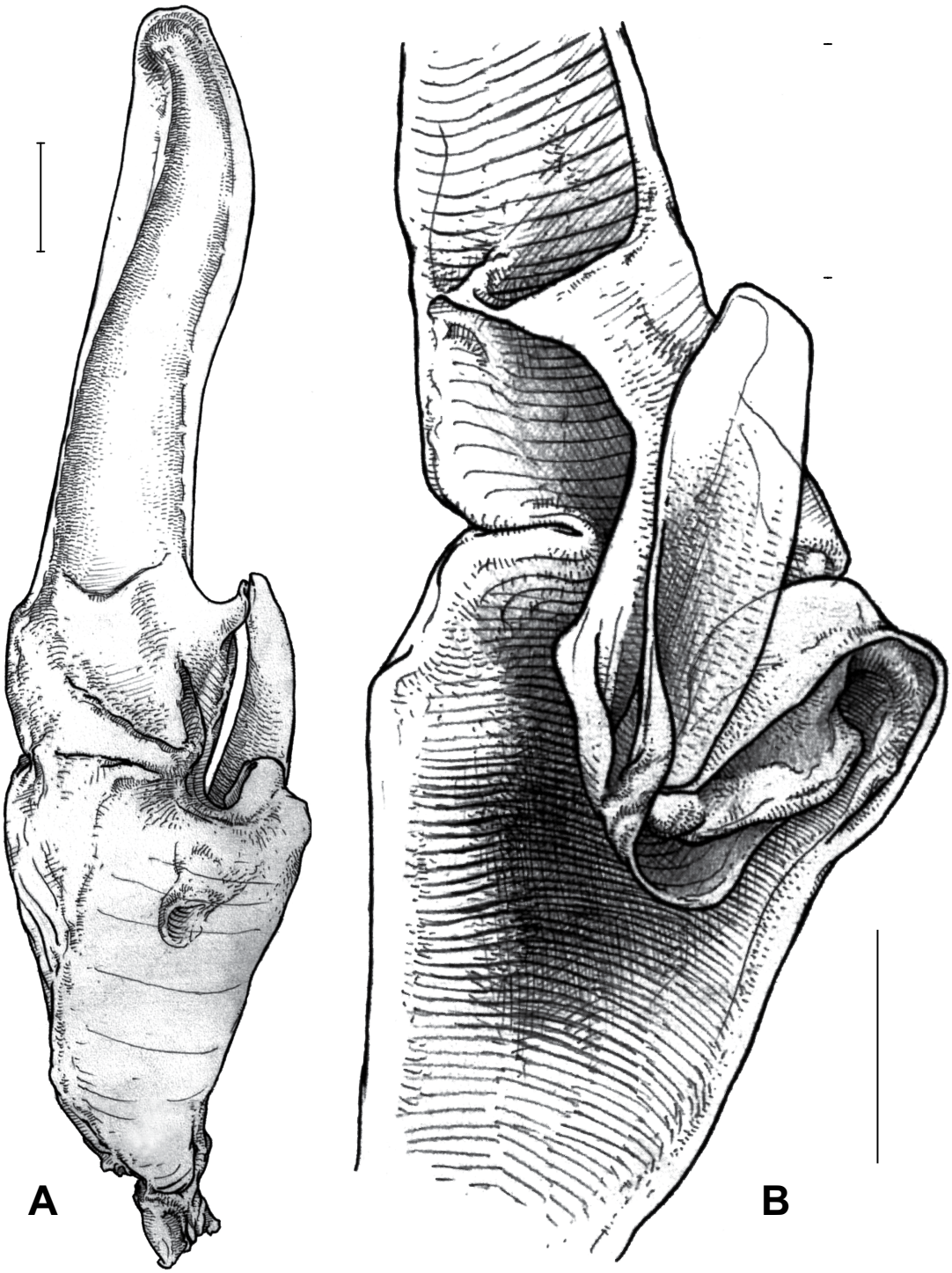

A
B

Fig. 46. *Chiromachus ochropus* (C. L. Koch, 1837) from Fregate Island, Seychelles (USNM). A, Right hemispermatophore *in toto*, external aspect. B, left hemispermatophore, detail of the capsular median structure, internal aspect. Legend: dcr = distal crest. Scale bars = 1 mm.

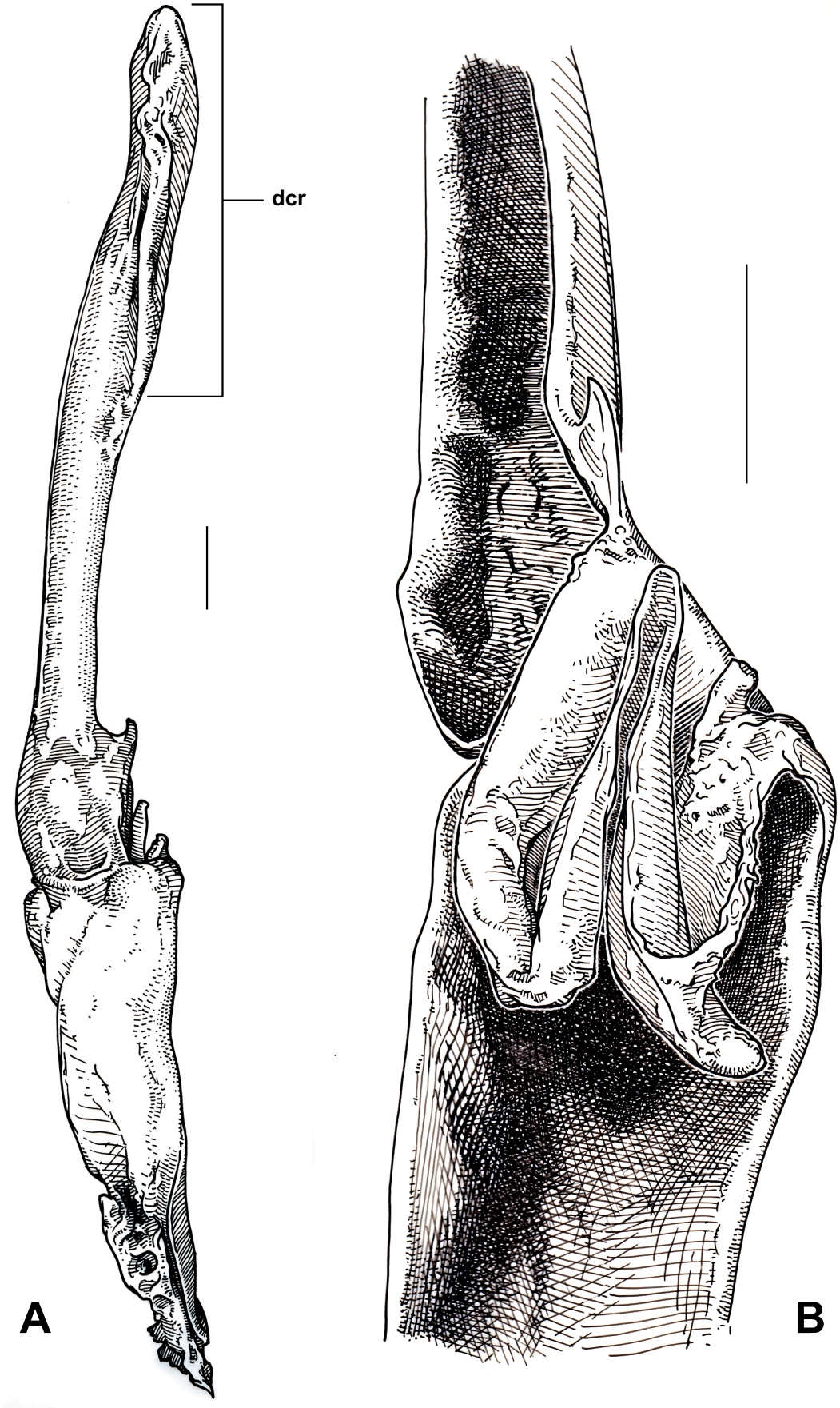

dcr
A
B

Fig. 47. *Iomachus malabarensis* Pocock, 1900 from Mangalore, Karnataka, India (NHML 1896.7.30.75.80, paratype). A, right hemispermatophore *in toto*, external aspect. B, left hemispermatophore, detail of the capsular median structure, internal aspect. Legend: dcr = distal crest. Scale bars = 1 mm.

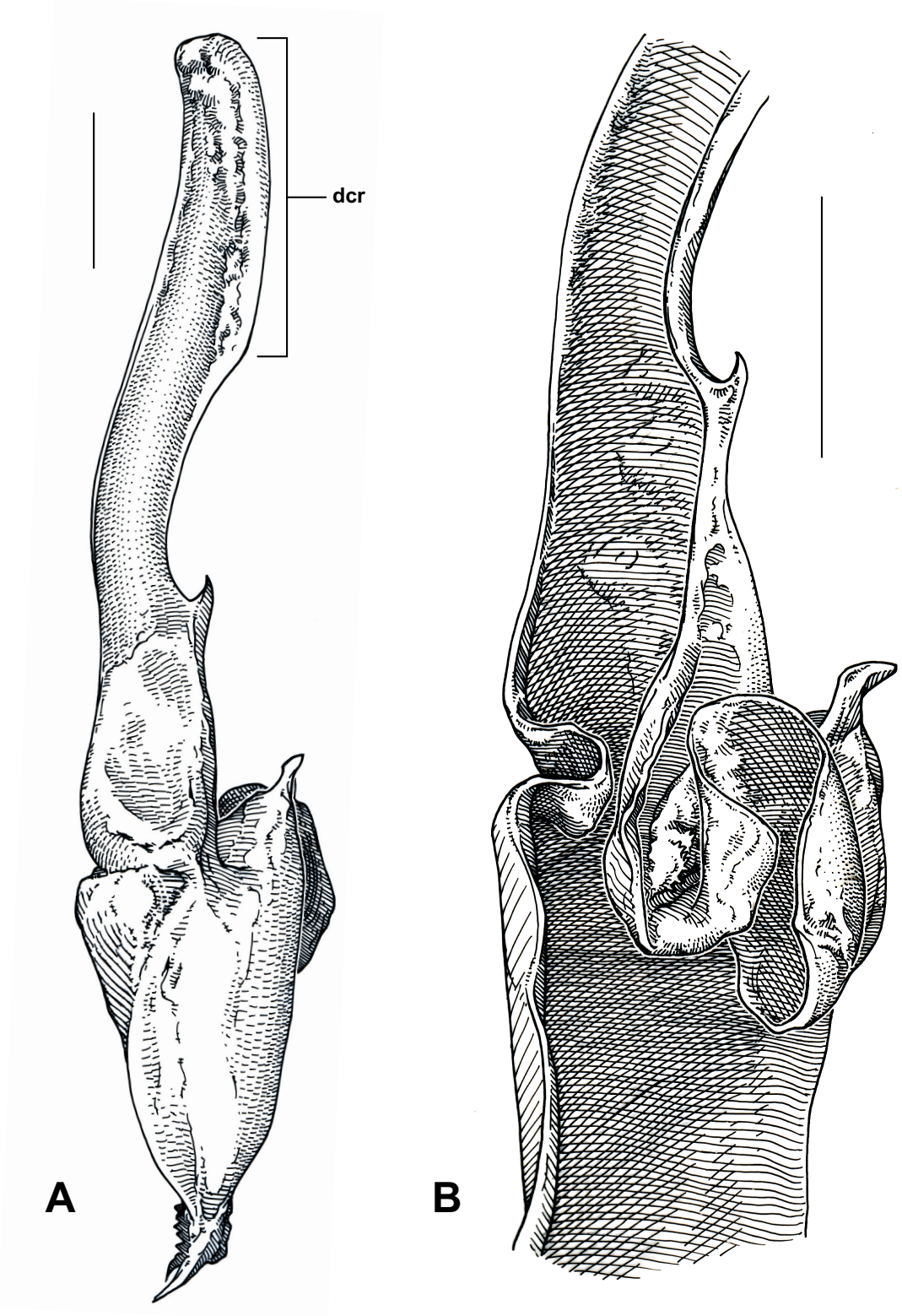
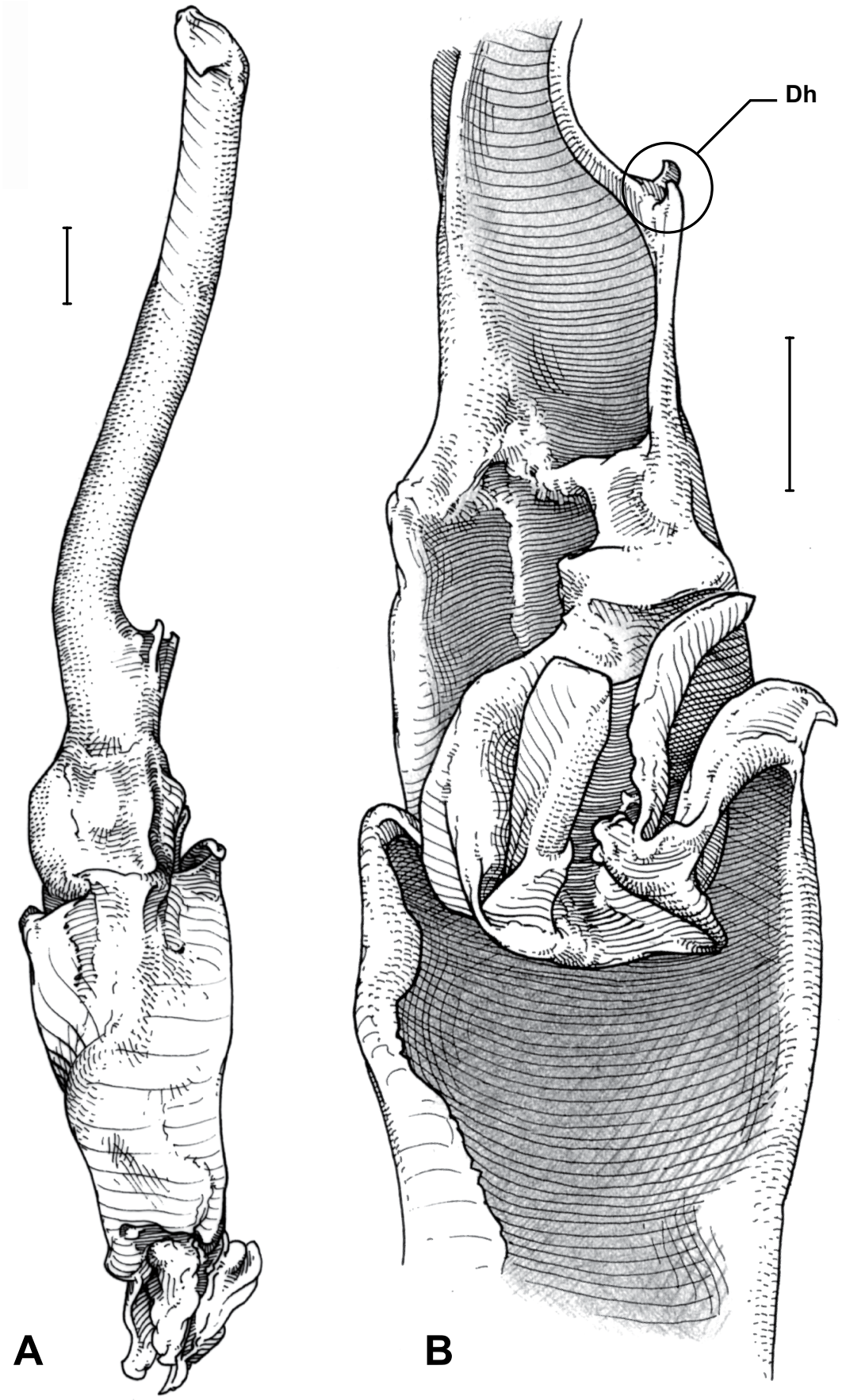

dcr
A
B

Fig. 48. *Hadogenes troglodytes* (Peters, 1861) from Zimbabwe (NHMW 1703). A, Right hemispermatophore *in toto*, external aspect. B, left hemispermatophore, detail of the capsular median structure, internal aspect. Scale bars = 1 mm.


Dh
A
B

pertaining to the book lungs morphology that may be potentially informative for phylogenetic reconstruction, but he included only one in his analysis, i.e. the reticulation of lamellae [Character 261], arguing that the observations made by earlier authors, although not inexact, did not encompass the entire morphological variation of the structure and that a thorough reinvestigation was necessary before more precise phylogenetic hypotheses can be formulated. Fine structures of the books lungs of scorpions were finally reexamined and documented using modern SEM techniques (Kamenz *et al.*, 2005; Scholtz & Kamenz, 2006; Kamenz & Prendini, 2008), revealing a substantial diversity of forms clearly informative at various taxonomic levels, although it was not tested in a phylogenetic framework. Only ten species included in the present analysis were studied in these recent publications, and data for the major part of the taxon sampling are thus unavailable. Although they will probably provide little phylogenetic signal due to the incomplete dataset, the three characters defined by Kamenz & Prendini (2008) are nonetheless incorporated in the present matrix mainly for descriptive purpose.

CHAPTER II
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PHYLOGENETIC ANALYSIS

2.1 PHILOSOPHICAL CONSIDERATIONS

Currently, parsimony (Kluge & Farris, 1969; Farris, 1970, 1983; Kluge, 1984), maximum likelihood (Farris, 1973; Felsenstein, 1973, 1981; Swofford *et al.*, 1996; Huelsenbeck & Crandall, 1997) and Bayesian Inference (Mau & Newton, 1997; Rannala & Yang, 1996; Yang & Rannala, 1997) are the three most commonly used methods of phylogenetic inference, each with its own inherent flaws and advantages (see Brooks *et al.*, 2007, Huelsenbeck *et al.*, 2001, 2002; Swofford *et al.*, 2001 for reviews and criticisms of the different methods). Prendini *et al.* (2003) argued that analytical methods should be chosen *a priori* by the authors according to philosophical preferences. They considered that the use of various methods cannot be justified on the grounds that hypotheses are more robust if supported simultaneously by different analytical procedures: “methodological concordance” that is congruence between trees generated with different methods cannot be considered as an evidence of the robustness of phylogenetic reconstructions (Grant & Kluge, 2003; Bergsten, 2005). Besides, methods with widely differing assumptions are not expected to necessary yield congruent results. A survey of 20 studies including both cladistic and model-based analysis (Brooks *et al.*, 2007) suggests that there is considerably more agreement than disagreement among the results using different methods and that more data leads to congruent results from all methods. Phylogenetic tree topologies based on the same datasets but inferred from model-based and parsimony methods were generally quite similar, with an average of 88% identical nodes. Moreover similarity between trees derived with different methods increased as the number of gene sequences used increased. Studies using only one gene sequence have the biggest variation in tree topologies, while studies using 6 gene sequences showed identical trees regardless of the method used for analysis. Therefore the resolution of the phylogeny depends more on the adequacy of empirical data and their inherent phylogenetic information content than on the methods used. Analysis of an appropriate and complete dataset should therefore yield reliable results independently of the method chosen.

Parsimony is chosen as the optimality criterion in the present investigation. Parsimony analysis is an accurate and robust method and algorithms recently implemented are extremely efficient and allow computation of very large phylogenies in reasonable times (Goloboff *et al.*,

2009). Long-branch attraction (LBA) is one of the major criticisms of parsimony (P) methods (Felsenstein, 1978). It is a phenomenon that can occur when distantly related taxa exhibit high amounts of divergence. Such taxa are likely to group together on the basis of convergent evolution rather than shared ancestry, parsimony erroneously interpreting homoplasy as synapomorphy (Huelsenbeck, 1995; Huelsenbeck & Hillis, 1993; Pol & Siddall, 2001; Swofford *et al.*, 2001). It is proven that LBA is a real bias of P (Bergsten, 2005), but inference methods such as maximum likelihood can likewise be subject to LBA artifacts (Huelsenbeck, 1995; Lockhart *et al.*, 1996; Yang, 1997) although they remain overall less sensitive to the problem (Pol & Siddall, 2001; Swofford *et al.*, 2001). The risk of having an outcome affected by LBA can be avoided or at least diminished by "breaking up" the long branches, that is adding taxa closely related to those with the long branches (Graybeal, 1998; Bergsten, 2005). Therefore a robust dataset without major "holes" in the taxon sampling greatly reduces the chance of long-branch attraction occurrence. As the present dataset covers most of the species and geographical diversity of the taxonomic group of interest, the risk of LBA is considered minimal.

Molecular data prove to be extremely useful in many cases to decipher "true" phylogenies and help to dissociate homoplasious characters associated with ecological adaptations from phylogenetically informative characters (Parra-Olea & Wake, 2001; Lockridge Mueller *et al.*, 2004; Wiens *et al.*, 2005; Svenson & Whiting, 2009). Because molecular analysis provide quick results with less effort, it is nowadays preferred over time-consuming morphological approaches the utility of which is increasingly questioned and criticised (Hillis & Wiens, 2000; Baker & Gatesy, 2002; Pennisi, 2003; Tautz *et al.*, 2003; Scotland *et al.*, 2003). However, the two approaches are complementary and molecules should not be regarded as an alternative to morphology but rather as a way to provide additional characters. Cladistic phylogenies are constructed based on character homology (synapomorphy) and tests of the congruence of characters. As emphasized by Mooi & Gill (2010): "The only evidence for phylogenetic relationship is homology represented as synapomorphy - presenting phylogenies without synapomorphies is not cladistics". Understanding character homology and sequence of characters changes along the branches of a tree is essential to decipher biological processes that may have induced these changes. On the other hand, genes will remain mere sequences of nucleotides with little

biological meaning when considered alone (no hypothesis can be made about the causes of a change from an A to a G). A phylogenetic study should not be limited to a dataset, a topology and some statistics, it should also provide biological insights into the organisms studied.

The 'simultaneous analysis' or 'total-evidence' approach to analyzing molecular and morphological data sets (Whiting *et al.*, 1997; Schuh, 2000; Prendini *et al.*, 2003) is here preferred over partitioned analysis (Miyamoto & Fitch, 1995) because it has the greatest explanatory power, maximizing information content and providing the most severe test of homology (Kitching *et al.*, 1998; Kluge, 1998; Grant & Kluge, 2003). Besides, as noted by Prendini *et al.* (2003), common signal between independent datasets can be amplified in a combined analysis, reducing noise. Combined partition analysis is also regarded as a means to reduce potential occurrence of LBA artefacts. Molecular data are known to be more prone to the problem than morphological data (Grant & Kluge, 2003). Inclusion of morphological data in phylogenetic inference is warranted and recommended (Jenner, 2004) contrary to the current trend towards quickly implemented DNA taxonomy. In many studies, morphology contributes to increase branch support and complementary resolution with emergence of secondary signals absent when molecules are tested alone (Jenner, 2004). Although total evidence is preferable as a final analysis, separated partitioned analyses of the morphological and molecular data were conducted here in an effort to identify the source of potential conflicts between the datasets and possible LBA artifacts (Bergsten, 2005).

2.2. MATERIAL & METHODS

2.2.1 CLADISTIC ANALYSIS OF MORPHOLOGICAL DATA

TAXON SAMPLING

The use of supraspecific taxa in the context of a phylogenetic analysis has been previously criticized (Prendini, 2000, 2001d; Giribet 2002; Prendini *et al.*, 2003), mainly on the grounds that the monophyly of supraspecific terminals is assumed *a priori* and not empirically tested therefore reducing the explanatory power of an analysis. The exemplar approach was thus implemented in the present study, all known species of the ingroup were included and each outgroup was represented by more than one species. The ingroup is composed of two

species (one of which is undescribed) of *Hormiops*, 62 species (48 of which are undescribed and eight were in synonymy; see chapter IV for details) belonging to the genus *Hormurus* (the *waigiensis* species group of *Liocheles s.l.*) and six species (one of which is new to science and three of which were in synonymy) belonging to the genus *Liocheles s. s*. (the *australasiae* species group of *Liocheles s.l.*). In order to polarize characters within the ingroup and to thoroughly test biogeographical hypotheses, liochelid taxa from all southern continents were included in the present phylogenetic reconstructions as outgroups: two *Chiromachetes* and four *Iomachus* from India, the Afrotropical *Iomachus politus*, two Malagasy and one Australian (new to science) *Opisthacanthus* (*Monodopisthacanthus*), one *Opisthacanthus* (*Nepabellus*) from Southern Africa, two Neotropical and one Afrotropical *Opisthacanthus* (*Opisthacanthus*), and one *Palaeocheloctonus* from Madagascar. Trees were rooted on *O*. (*N*.) *laevipes* based on the phylogeny of Liochelidae by Prendini (2000) that retrieved the South African sub-genus *Nepabellus* and its close relatives *Cheloctonus* and *Hadogenes* as basal to all other liochelids. *Tibietiomachus himalayensis* was not included in the analysis because it was not possible to examine the types. However, testing the position of this taxon in a phylogenetic analysis is not necessary to demonstrate that the genus and the species are not valid. The illustrations provided by the authors, Lourenco & Qi (2006), contradict their own diagnosis and allow *T. himalayensis* to be unambiguously synonymised with *L.nigripes* (see chapter IV for details).

CHARACTERS (SEE CHAPTER 1)

External and internal morphology of specimens belonging to the 86 species (see appendix 1) were critically examined in order to produce the morphological matrix (see appendix 2). Ten continuous characters and 253 discrete characters were scored for each species (see chapter I for the list of characters); 145 of these characters were compiled from 129 characters cited in previous publications (see chapter I for details and references); 30 were corrected and adapted, based on new information, recognition of new states or reinterpretation: four were split into two characters, three were split into three characters, two were split into four characters, and one was split into eight characters; 92 remain unaltered. Among the remaining 118 characters, 98 are new and 20 are from an unpublished matrix by L. Prendini; of the latter,

two were modified and one was split into three characters in the context of the present study. Missing entries are due to damaged or poorly preserved specimens (*H. tetrakaideca* n. sp., *H. waigiensis*) or to the absence of adult males in the material examined (*C. fergusoni*, *H. boholiensis*, *H. dechangei*, *H. nesiotes* n. sp., *L. complanatus*, *Opisthacanthus* (*M.*) *apios* n. sp.) or adult females (*C. tirupati*, *H. agastachys* n. sp., *H. oreopsyridus*, *H. penta*, *H. samoa* n. sp., *H. scopaeus* n. sp., *H. waigiensis*). 188 of the 253 discrete characters were coded into binary states and 66 were coded into multistates. A few characters were scored as polymorphic in some taxa based on observation of the material. Characters were edited with the data manager DELTA version 1.04 (Dallwitz *et al.*, 2000) which enable automated descriptions to be generated for each species and interactive species keys to be produced. A matrix of all morphological characters was generated in Nexus format from DELTA and further edited in Nexus Data Editor version 0.5.0 (Page, 2001).

CHARACTERS EXCLUSION

57 uninformative characters [Characters 10, 18, 19, 29, 31, 33, 39, 41, 44, 51, 52, 54, 55, 56, 58, 60, 63, 64, 66, 67, 69, 70, 72, 78, 80, 84, 86, 92, 99, 109, 118, 123, 124, 166, 171, 173, 180, 181, 184, 185, 188, 201, 204, 212, 213, 217, 219, 220, 221, 223, 224, 225, 226, 237, 253, 254, 259] were detected with the “mop uninformative chars” function in Winclada version 1.00.08 (Nixon, 1999a) and were excluded from the analysis which is thus based on 206 phylogenetically informative characters (including 10 continuous characters). Hence, tree statistics were calculated for these 206 informative characters only. Invariant and autapomorphic characters are considered uninformative in the context of a phylogenetic analysis. Autapomorphies cannot contribute to homoplasy because they are unique to a single taxon and therefore imply only a single transformation. Consequently, they artificially inflate the consistency index by adding evidence for the distinctiveness of terminal taxa not by increasing the congruence among informative characters (Bryant, 1995). Nonetheless, uninformative characters are included in the character list and data matrix because they constitute potential synapomorphies at a higher taxonomic level. These characters may be uninformative in the present study due to its limited scope but they can prove useful in future studies that will encompass the whole liochelid fam-

ily and/or closely related families (i.e., Hemiscorpiidae, Heteroscorpionidae and Urodacidae). Among these characters, several are already known to diagnose synapomorphies for the family Liochelidae or for intrafamilial clades [Characters 18, 51, 52, 54, 55, 56, 58, 63, 67, 69, 70, 72, 78, 84, 86, 92, 124, 171, 173, 180, 184, 204, 212, 219, 220, 221, 237]. For instance, the basal liochelid genus *Hadogenes* possesses hemispermatophores bearing a double hook (fig. 48; Lamoral, 1979; Prendini, 2001a, 2005b, 2006) whereas all other liochelid genera have hemispermatophores with a single lamellar hook. Hence, the “double hook” [Character 237, state 2] represents a good synapomorphy for *Hadogenes* and the “single hook” [Character 237, state 1] a good symplesiomorphy for the remaining liochelids. Besides, the matrix also has a descriptive purpose and was used to generate descriptions and diagnosis. It is therefore essential to also include any characters that can provide descriptive details at the specific level even though they are not useful for phylogenetic reconstruction (autapomorphies).

Evolutionary sequences could not be inferred for 38 multistate characters [Characters 18, 24, 37, 39, 41, 44, 50, 55, 56, 57, 66, 74, 81, 85, 91, 115, 121, 126, 151, 155, 165, 168, 169, 174, 194, 200, 202, 217, 219, 221, 225, 226, 232, 241, 243, 249, 252, 262] that were then treated as nonadditive (unordered) (Fitch, 1971). This approach is justified here on the grounds that all character transformations should be considered equiprobable if there is no apparent reason for regarding one event to be more likely than its alternatives (Wilkinson, 1992). On the other hand, linear transformation series were applied to the remaining 28 multistate characters [Characters 16, 20, 21, 26, 27, 28, 42, 68, 88, 89, 96, 97, 101, 120, 132, 138, 139, 141, 146, 147, 196, 197, 203, 216, 227, 238, 242, 247]. It was argued that ordering multistate characters is equivalent to assuming *a priori* an hypothesis of character transformation which should rather be tested by cladistic analysis (Wilkinson, 1992; Griswold *et al.*, 1998). However, disregarding nested similarity is equivalent to omitting evidence which is epistemologically unacceptable (Pimentel & Riggins, 1987; Lipscomb, 1992; Prendini, 2000), especially when considering multistate characters which should logically reflect a gradual evolutionary transition, for instance discretized continuous characters such as those pertaining to the length of appendages (short; medium; long) or to the extent of textured tegumental surface (smooth; partially textured; completely textured). Characters were not weighted *a priori*.

TREE SEARCH

Parsimony analysis was implemented in TNT version 1.1 (Goloboff *et al.*, 2003, 2008). TNT allows quantitative and continuous characters to be included in cladistic analysis and treated as such without discretization (Goloboff *et al.*, 2006). Heuristic search strategies using the new technology search, i.e. sectorial searches, tree-drifting and tree-fusing (Goloboff, 1999) were adopted because they eventually allow a fast recovery of optimal trees even for very large datasets. Sectorial search splits the trees in different sectors or sub-trees that are then reanalyzed separately by traditional strategies, i.e. multiple random addition sequences (RAS) and tree bisection reconnection branch-swapping (TBR). When better configurations of sectors are found, they are incorporated in the complete topology replacing the previous sub-trees. Tree-drifting allows suboptimal solutions to be accepted during branch swapping with a certain probability. Accepting suboptimal solutions ensure that the "tree landscape" is adequately explored without the analysis being trapped in a local optimum (Kirkpatrick *et al.*, 1983). The probability of accepting a suboptimal solution depends on both the relative fit difference and the length difference between the tree being currently swapped and the original tree used to start the drifting procedure. Tree-fusing exchanges sub-groups of 5 or more taxa between different suboptimal trees. Each sub-group is likely to be in an optimal configuration in at least one tree. All possible exchanges between suboptimal trees are calculated but only the exchanges that improves (reduce the length of) the tree are conserved. It is actually a way to compare all available configurations for each sub-group and select the better one to be incorporated in the target tree.

An equal weights (EW) analysis was initially performed with 100 random taxon addition replicates as starting points. Using several independent starting points for an analysis minimizes the risks of the different searches becoming trapped in a local optimum and maximizes their chances of ending in a global optimum. Constraint and random sectorial search with 200 parsimony ratchet (Nixon, 1999b) iterations, 50 iterations of tree drifting and 5 rounds of tree fusing were performed on each replication that was initially auto-constrained with Wagner and previously inferred trees. The maximum number of trees held in memory was initially set to

10’000. Cladograms presented here were generated as metafiles from TNT and Winclada version 1.00.08 (Nixon, 1999a) and subsequently edited in Illustrator CS3 (Adobe Systems, San Jose, CA, USA).

BRANCH SUPPORT

The relative degree of support for each node in the optimal trees selected was assessed with absolute (Bremer, 1988, 1994) and relative (Goloboff & Farris, 2001) Bremer support, as well as symmetric resampling percentages (Goloboff *et al.*, 2003).

Bremer support. The Bremer support (Källersjö *et al*., 1992) also called decay index (Donoghue *et al*., 1992) for a given node in the shortest unconstrained tree is the number of extra steps required to “collapse” that node. The absolute Bremer value evaluates only the favourable evidence when calculating support for a given node, whereas the relative support (RFD) considers both favourable and contradictory evidence. For instance, the relative Bremer support will be much higher for a node supported by 2 characters and contradicted by none than for a node supported by 100 characters and contradicted by 98, although both nodes will have an absolute Bremer support of 2. Absolute Bremer and relative Bremer indices (setting the maximum number of trees held in memory to 10’000) were calculated for the preferred trees by retaining suboptimal trees up to 100 steps longer and with a relative fit difference up to 0.9 respectively.

Jackkniffing. Group supports in a phylogenetic reconstruction can also be assessed by means of resampling methods. These methods are based on perturbation of the dataset by a series of random resamplings. The frequency with which a given group is retrieved in the trees obtained from the resampled matrices is used as a measure of its support. The amount of support for a group is then the result of iteration between the characters that favours the group and those that contradict the group. Traditional resampling measures (i.e., bootstrapping and jackknifing) may be influenced by heterogeneous prior weights and state transformation costs and then under- or overestimate actual group supports. However, jackknifing with symmetric resampling (Goloboff *et al.*, 2003) is not impaired by the distortion of frequencies observed under bootstrap or jackknifing. The method allows each character to be changed with a prob-

ability chosen by the user, and if changed, the character can be duplicated or deleted with equal probability. Symmetric resampling can be applied to any weighting scheme: successive weighting (Farris, 1969), implied weighting (Goloboff, 1993), or weighting of state transformations, including asymmetries in transformation costs. Symmetric resampling is the method of choice in the present study because it shows lower error rates than other methods and is therefore considered to produce better indicators of support (Kopuchian & Ramírez, 2010). The probability to increase and decrease character weight was set to the default value (P = 0.33). 5000 pseudoreplicates were used to calculate the frequencies; suboptimal trees were generated by traditional search with TBR. Frequencies were reported on the trees as GC scores (for 'Group present/Contradicted') which represent the difference in frequency between a group and its most frequent contradictory group (Goloboff *et al.*, 2003). Only percentages above 50% are considered meaningful.

WEIGHTING

Implied weighting. The postulate that characters with a greater tendency to homoplasy are less reliable to reconstruct phylogenetic history is the basis of weighting schemes currently used in cladistic practice. The purpose of weighting against homoplasy is to find topologies supported by the most consistent characters. Farris's (1969) successive approximations weighting (SW) was the first iterative procedure implemented, in which characters are assigned weights *a posteriori* depending on their consistencies with the most parsimonious tree(s): highly homoplasious characters are downweighted more heavily than characters with less or no homoplasy. Data are reanalysed with the newly assigned weights. The procedure is repeated until a stable solution is achieved. Successive weighting as been criticised because of the lack of an objective criterion to evaluate and compare the optimal trees found (Goloboff, 1993; Swofford *et al.*, 1996). Unlike successive weighting, non-iterative weighting methods, i.e. implied weighting (IW) and self-weighted optimization (Goloboff, 1993, 1997) provide an optimality criterion (maximum fit) for tree selection and allow characters weights to be adjusted according to their fit to the tree simultaneously with topology searches. The procedure resolves conflicts in favor of less homoplastic characters. Three forms of fitting functions, i.e. linear, concave, and convex,

can be used to adjust the cladistic consistency of a character onto a cladogram (Farris, 1969). Linear function ignores homoplasy and is therefore equivalent to equal weighting and convex function favours characters with greater homoplasy. Therefore, concave function is the best estimator of character fit to a given tree (Farris, 1969). Implied weighting as implemented in PIWE and TNT searches for trees which maximise the total fit of a tree $F = \Sigma fi$, where *fi*, the fit of an individual character *i*, is considered as a concave function of homoplasy and calculated with the formula $fi = K/(K+ESi)$ (*ESi* being the number of extra steps for character i) (Goloboff, 1993). The program allows the influence of homoplasious character to be varied according to a constant of concavity *K* chosen by the user. Low values of *K* (indicative of strongly concave functions) weight more heavily against homoplastic characters whereas high *K* values (functions approaching linearity) allow more influence to homoplastic characters. Consequently, results obtained with the latter do not differ significantly from results obtained with equal weights analyses. The method was criticized on the ground that *K* value must be arbitrarily assigned (Turner & Zandee, 1995). Goloboff, (1993, 1995) and Goloboff *et al.* (2008) advised against the use of very mild functions and of very strong functions but did not provide theoretical justification for the choice of a particular value over another. The default $K = 3$ was used in several published studies (Griswold *et al.*, 1998; Geisler & Theodor, 2009). More recently, Goloboff *et al.* (2008) demonstrated that IW improves group supports. The authors reported a clear increase of jackknife frequencies and other resampling measures under IW compared to EW. Trees obtained with IW also appeared much more stable than trees derived from EW. Finally, when new characters or taxa were added to the original dataset, reanalyses produce topologies with fewer discrepancies with the original topologies when inferred under IW.

Sensitivity analysis can be defined as an evaluation of the topological stability of a phylogenetic analysis to variation of analytical parameters such as differential weighting schemes (Wheeler, 1995; Giribet, 2003). The choice of any particular parameter set is arbitrary; therefore multiple parameter sets should be used to discern between supported and spurious phylogenetic groupings. Under this methodological framework, the monophyly of a taxonomic group only supported under a very specific combination of parameters cannot be considered as firmly established contrary to the monophyly of a clade which is supported under a wider range and

combination of parameters (Whiting *et al.*, 1997). Nodal support is not a synonym of nodal stability. As Giribet (2003) pointed out: “many examples exist in the literature (....) decoupling support from stability in both directions: high stability with low support and low stability with high support. While the first example can be explained under the circumstance of few but uncontradicted evidence, the second may be a way to detect pernicious long-branch-attraction phenomenon (....). The use of multiple models for a given method of tree analysis may well constitute the best and most secure way to detect artificially well-supported nodes.” Therefore, topological stability is probably more important than branch support when evaluating the phylogenetic status of taxa and more confidence can be given to clades that are retrieved under a wide range of parameter sets even though their supports are low. Prendini (2000) and Prendini *et al*. (2003) evaluated the effects of weighting against homoplasy on tree topologies and characters length and fit. He performed a series of analyses under successive weighting and implied weighting with different concavity values and used the results obtained to compare the different trees and select those with maximum fit and minimum length. Following a similar procedure, a sensitivity analysis consisting in 10 IW analyses under *K* values ranging from 1 to 10 was undertaken here in order to assess the robustness of clade supports and the stability of tree topologies under different weighting regimes. Goloboff *et al.* (2008) doubted the relevance of using sensitivity analysis as a metacriterion to maximize resolution, i.e. selecting optimal trees based on their robustness to resampling (Ramírez, 2003), and argued that optimal trees should rather be selected according to the tree topologies and taxonomic groupings that were retrieved under the widest range of parameters sets. In previous publications (Prendini, 2000; Prendini *et al.*, 2003), topological results of sensitivity analysis were presented by means of a strict consensus (SCT) and a 50% majority-rule consensus (MCT) (Margush & McMorris, 1981) of the MPTs generated from the separares analyses. The use of majority rule consensus trees is justified here because it provide a graphical representation of the nodes that are most frequently retrieved under the different weighting regimes. These nodes can thus be considered as more robustly supported by the data than other alternative nodes which were retrieved only under specific weighting regimes. In the present study, because of the important difference between the number of trees obtained under EW (91 trees) and the number of trees obtained with

each IW analysis (between 1 and 14 trees depending on the *K* value) and in order to avoid bias toward topologies obtained under EW and to reflect the most frequently retrieved topologies, strict consensus trees were generated for each of the 11 separate analyses and subsequently used to produce a global SCT and a global MCT. For each analysis (morphological partition, molecular partition and combined partitions), trees that were congruent with topological results of the sensitivity analysis, and that maximize fit and minimize length were finally selected as optimal tree.

CONSTRAINED SEARCHES

Alternative hypotheses of phylogenetic relationships in Indo-Pacific liochelids were investigated by forcing the monophyly of some clades, previously recognized in the literature as valid but not retrieved as monophyletic in unconstrained analyses. These constrained searches were performed under the weighting regime that is considered to generate optimal phylogenetic hypotheses. The difference in length and fit between unconstrained and constrained trees was then evaluated as in Prendini (2000).

2.2.2 CLADISTIC ANALYSIS OF MOLECULAR DATA AND COMBINED ANALYSIS

TAXON SAMPLING

The number of species represented in the molecular dataset is smaller than for the morphological dataset because fresh material suitable for DNA sequences or samples were not available for all species at the time of writing. However, several samples from geographically distant localities were sometimes available from the same species and were included in the analysis in order to identify potential cryptic species. The morphological matrix was thus reduced by deleting taxa not available for DNA and entries for species represented by multiple localities were duplicated to accommodate the number of samples. 101 samples representing 42 taxa were included in the molecular matrix (see appendix 1). The ingroup is composed of one *Hormiops* (one of two species in the genus), 29 *Hormurus* (45% of the species in the genus), and four *Liocheles* (67% of the species in the genus) which represent approximately

half of the known diversity for these three genera. The outgroups are represented as follow: *C. ochropus*, one Indian *Iomachus*, *I. politus*, two Malagasy *Opisthacanthus* (*Monodopisthacanthus*), one African *Opisthacanthus* (*Nepabellus*), two *Opisthacanthus* (one Neotropical and one Afrotropical species).

GENETIC MARKERS

It is now widely accepted that combining multiple sources of data leads to a better resolution of phylogenetic relationships and that the use of several gene loci is mandatory in the context of molecular phylogenetic reconstructions (Doyle, 1992). Five gene loci, commonly used in arthropod phylogenetic studies (Giribet *et al.*, 2001; Prendini *et al.*, 2003, 2005; Boyer *et al.*, 2005, 2007; Giribet & Edgecombe, 2006; Murienne *et al.*, 2008) were selected for the present investigation because (1) primers that consistently amplify large fragments are available for each of them (see table 9) and (2) they are known to evolve at different rates and thus are phylogenetically informative at different, overlapping taxonomic levels. Three labile fragments of the mitochondrial genome, i.e. the Cytochrome C oxidase subunit I gene (COI), the large-subunit ribosomal RNA gene (16S rDNA), and the small-subunit ribosomal RNA gene (12S rDNA) possess sufficient conserved regions to be informative at the interspecific and intraspecific level. In addition, the D3 region of the nuclear genome, i.e. the large-subunit ribosomal RNA gene (28S rDNA) and the small-subunit ribosomal RNA gene (18S rDNA) are less variable and give phylogenetic information on relationships at the family-genus levels.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

DNA samples were isolated from pedipalp or leg muscle tissues dissected from specimens fixed in 95-100% ethanol and stored at –20°C (Fet & Vezzeti, 1994; Prendini *et al.*, 2002). DNA extraction and purification were performed with the Dneasy Tissue Kit: Dneasy Protocol for Animal Tissues (Qiagen, Venlo, The Netherlands). The gene fragments were subsequently amplified using the Polymerase Chain Reaction (PCR) on an Eppendorf Mastercycler Epgradient S thermocycler (Eppendorf, Hamburg, Germany). Each PCR was run with PureTaq-Ready-To-Go PCR Beads (GE Healthcare, Little Chalfont, United Kingdom). PCR products

Table 9. Primers used in amplification and sequencing of Liochelidae Fet & Bechly, 2001.

GENE REGION	PRIMER NAME	SEQUENCES	REFERENCE
16S	16Sar	5’-CGCCTGTTTATCAAAAACAT-3’	Simon *et al.*, 1991
	16Sbr	5’-CTCCGGTTTGAACTCAGATCA-3’	Simon *et al.*, 1991
12S	12Sai	5’-AAACTAGGATTAGATACCCTATTAT-3’	Kocher *et al.*, 1989
	12Sbi	5’-AAGAGCGACGGGCGATGTGT-3’	Kocher *et al.*, 1989
28S	28Sa	5’-GACCCGTCTTGAAGCACG-3’	Nunn *et al.*, 1996
	28Sbout	5’-CCCACAGCGCCAGTTCTGCTTACC-3’	Prendini *et al.*, 2005
18S	18S1F	5’-TACCTGGTTGATCCTGCCAGTAG-3’	Prendini *et al.*, 2005
	18S5R	5’-CTTGGCAAATGCTTTCGC-3’	Prendini *et al.*, 2005
	18S3F	5’-GTTCGATTCCGGAGAGGGA-3’	Prendini *et al.*, 2005
	18Sbi	5’-GAGTCTCGTTCGTTATCGGA-3’	Prendini *et al.*, 2005
	18SA2.0	5’-ATGGTTGCAAAGCTGAAAC-3’	Prendini *et al.*, 2005
	18S9R	5’-GATCCTTCCGCAGGTTCACCTAC-3’	Prendini *et al.*, 2005
COI	LCO	5’-GGTCAACAAATCATAAAGATATTGG-3’	Folmer *et al.*, 1994
	LE1r	5’-GTAGCAGCAGTAAARTARGCYCGAGTATC-3’	Esposito, unpublished
	HCOoutout	5’-GTAAATATATGRTGDGCTC-3’	Prendini *et al.*, 2005
	CruzR	5’-CATACCCAAAGARCCAAAAGG-3’	Valdez-Cruz *et al.*, 2004

were verified on a 1% agarose/TBE electrophoresis gel stained with SYBR Safe (Invitrogen, Carlsbad, CA, USA). Amplification products were then cleaned using Ampure Magnetic Beads (Beckman-Coulter, Brea, CA, USA) on a Beckman Coulter Biomek NX robot and subsequently re-suspended in DNA grade water. The clean PCR products were labeled using dye-labelled terminators (ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction Kit; Applied Biosystems, Inc., Foster City, CA, USA) and cycle-sequenced with AmpliTaq DNA Polymerase FS (Perkin Elmer, Inc., Waltham, MA, USA) in an Eppendorf Mastercycler Epgradient S thermocycler. Dye-labeled cycle-sequence products were cleaned using CleanSeq magnetic beads (Beckman-Coulter) on a Biomex NX robot (Beckman-Coulter). Cleaned cycle-sequence products were re-suspended in EDTA, heat-sealed in a Plateloc heat-sealer (Agilent Technologies, Santa Clara, CA, USA), and briefly spun on an Eppendorf Mastercycler Epgradient S Centrifuge to remove bubbles. Finally the dye-labeled DNA was sequenced using the dideoxy termination method (Sanger *et al.*, 1977) on an ABI Prism 3730xl automated DNA sequencer.

SEQUENCE EDITING AND ALIGNMENT

Sequence editing. Complementary strands of all fragments were independently amplified and sequenced in order to control the accuracy of sequences. When complementary strands strongly disagreed, probably as a result of contamination, the sample was reamplified and resequenced to resolve discrepancies. DNA sequence chromatograms were edited using Sequencher version 4.5 (Gene Codes Corporation, Ann Arbor, MI, USA): minor mismatches were corrected, primer sequences were removed, and consensus sequences resulting from the complementary strands were exported into FASTA format for subsequent analyses. In total, 485 sequences representing 4163–4186 sampled base-pairs per species were generated in the course of this investigation. The 18S rDNA and COI fragments were exactly 1,761 bp, and 1,078 bp respectively, in all species, whereas the 12S rDNA, 16S rDNA, and 28S rDNA fragments varied from 330 to 335 bp, from 480 to 486 bp and from 514 to 526 bp respectively.

Sequence alignment. Alignment is fundamental in molecular systematics and evolution because it is the basis for primary homology statements, on which all subsequent analyses depend (Doyle & Davis, 1998; Giribet & Wheeler, 1999; Prendini *et al*., 2003). The quality of

the initial alignment is crucial for the accuracy of subsequent analyses. Up to the mid 1980s, sequences were manually aligned. But this procedure lacks objectivity and optimality criteria (Whiting *et al.*, 1997; Doyle & Davis, 1998), and it prompted the development of more objective and automated methods. However aligning numerous sequences with sometimes greatly different lengths entail severe computational challenges (Doyle & Davis, 1998; Giribet & Wheeler, 1999; Phillips *et al.*, 2000). The first MSA (multiple sequence alignment) methods implemented (Needleman & Wunsch, 1970; Lipman *et al.*, 1989) were prohibitively slow and impractical for alignment of more than a few sequences. Eventually several programs based on a heuristic search strategy referred to as 'progressive alignment' (Feng & Doolittle, 1987) and allowing quick and simple alignments of numerous distantly related sequences were developed (Hogeweg & Hesper, 1984; Barton & Sternberg, 1987; Higgins & Sharp, 1988). 'Progressive alignment' is performed in two distinct steps: (1) combination by pairwise comparison of the most similar sequences and (2) progressive addition of less related sequences or groups until the entire query set has been incorporated into the solution. This method is strongly impaired by the propagation of early errors through to the final result - that is once an error has been incorporated into the solution it is not removed in later steps. The problem is corrected in 'iterative refinement' methods (Barton & Sternberg, 1987; Berger & Munson, 1991; Gotoh, 1993, 1996) by a secondary objective weighting function that assigns scores to alignments. The algorithms add sequences to the growing MSA while repeatedly reassessing previous alignment subsets so that their scores are maximized. Alignments are thus gradually improved until an optimum is reached.

MAFFT version 6 (Katoh *et al.*, 2002; Katoh *et al.*, 2005; Katoh & Toh, 2008), currently recognized as one of the most efficient MSA programs for nucleotide sequences (Golubchik *et al.*, 2007; Wilm *et al.*, 2006), was used to align sequences in the present study. In general there is a trade-off between speed and accuracy, the most accurate algorithms being the most computationally intensive. The present dataset was relatively small (less than 200 samples), and the length variation among fragments was minimal: there was no length variation among the 18S rDNA and COI fragments, and very little among the 12S rDNA and 16S rDNA fragments, which respectively exhibited length variation of five and six bp between the shortest and the

longest sequences. On the other hand, the 28S rDNA fragment shows a length variation of 12 bp due to the presence of a large insertion in five taxa. Apart from this insertion, this fragment is extremely conserved with 87.8% invariable sites across the dataset. Thus, alignment of this dataset involves no major difficulties. G-INS-i (Katoh & Toh, 2008), one of the most accurate and computationally intensive algorithms implemented in MAFFT, is recommended by the developers for alignment of sequences with global homology and was used to align the present molecular dataset. The G-INS-i algorithm first generates a guide tree for progressive alignment. A tree-based iteration strategy is then used to refine the alignment by optimizing an objective function combining the weighted sum-of-pairs (WSP) score (Gotoh, 1995) and a consistency-based score (Notredame *et al.*, 1998). Each pairwise alignment is given a score according to its accuracy; the higher the occurrence of mismatches or gaps the lower the score. The scores of each pair are then weighted according to the guide tree, scores of closely related pairs are downweighted while scores of more divergent pairs are upweighted. The WSP score of an MSA is then calculated by summing weighted scores of all the pairs present, the higher the better. On the other hand, the consistency score is attributed according to the congruence between a MSA and all pairwise alignments, in other words the MSA with the highest level of similarity with a collection of pairwise alignments obtains the highest score. The accuracy of the alignments obtained with MAFFT was verified in BioEdit Sequence alignment Editor version 7.0.5.2 (Hall, 1999). The final alignment of the present molecular dataset is presented in appendix 3. Basic statistics from the aligned molecular sequences (nucleotides frequencies, number of constant, variable and informative positions) were then computed with MEGA version 4.1 (Tamura *et al.*, 2007; Kumar *et al.*, 2008).

SENSITIVITY ANALYSIS AND CONSTRAINED SEARCHES

Inclusion of indels (treated as fifth state) is justified on the grounds that it maximizes explanatory power (Giribet & Wheeler, 1999; Phillips *et al.*, 2000). Therefore, a first series of analysis was conducted on the molecular dataset alone with gaps treated as a fifth state. The same heuristic strategies as for the morphological dataset were used in TNT to produced the trees. An initial analysis under equal weighting was performed, followed by 10 analyses under

implied weighting with concavity constants ranging from 1 to 10. Then, a second series of tests also consisting of an EW and 10 IW analyses was conducted but indels were treated here as missing data (Whiting *et al.*, 1997; Giribet *et al.*, 1999a; Prendini *et al.*, 2003). A total of 22 parameter combinations (use of equal and implied weighting, with indels treated as missing or as a fifth state) were thus applied to the aligned DNA sequences. Results of this sensitivity analysis are summarised by means of a strict consensus tree and a 50% majority-rule consensus of all the MPTs obtained from the 22 separates analyses. The same sequence of analyses was repeated on morphological and molecular data simultaneously and results are presented in a similar way. Additional heuristic searches in which the monophyly of some clades was constrained were finally performed under the optimal weighting regime assessed and topologies and statistics retrieved were compared with unconstrained trees.

2.3 RESULTS

2.3.1 SEQUENCE DATA ANALYSIS

Results of the analysis of the sequences performed with MEGA are presented in table 10 and appendix 3. The 12S rDNA sequences are composed of 114 constant sites and 225 variable sites (including gaps), 193 of which are informative and 30 are singletons (autapomorphies). On the other hand, the 16S rDNA sequences comprises 228 constant sites and 263 variable sites (including gaps), 257 of which are informative and 36 are singletons. The frequencies of variable, informative and singletons sites (including gaps) in the 12S DNA alignment (64.8, 55.6 and 8.6% respectively) are slightly greater than those in the 16S rDNA alignment (52.7, 45.3 and 7.2% respectively). As typically observed in arthropod genomes (Prendini *et al.*, 2003), both loci have a high percentage of AT nucleotides.

The mitochondrial 1078-bp COI sequences (359 codons) contains 561 constant sites and 517 variable sites, 430 of which are informative and 87 are singletons. The frequencies of variable and informative sites in this locus (47.9 and 39.9% respectively) are lower than those in the 12S rDNA and 16S rDNA alignments. Like in other protein-coding genes, most of the variation is in the third codon position: 319 of 339 variable third positions are informative, compared with 82 of 110 variable first positions and 29 of 68 variable second positions. The frequencies of

Table 10. Distribution of constant,variable, phylogenetically informative and singleton positions and frequencies of nucleotides, transitions and transversions in aligned sequences of five gene loci (12S rDNA, 16S rDNA, 18S rDNA, 28S rDNA and COI) among Indo-Pacific Liochelidae Fet & Bechly, 2001. '+ gaps' denotes counts in which gaps (in the 12S rDNA, 16S rDNA and 28S rDNA) were included.

GENOME	Nuclear		Mitochondrial						Total
FUNCTION	Ribosomal		Ribosomal		Protein-coding				
GENE LOCUS	18S rDNA	28S rDNA	12S rDNA	16S rDNA	COI	1rst	2nd	3rd	
Length	1761	527	347	499	1078				4212
Constant	1714 (97.3%)	463 (87.8%)	114 (32.8%)	228 (45.7%)	561 (52%)	249 (44.4%)	291 (51.9%)	21 (3.7%)	3080 (73.1%)
Variable + gaps	47 (2.7%)	63 (11.9%)	225 (64.8%)	263 (52.7%)	517 (47.9%)	110 (21.3%)	68 (13.2%)	339 (65.6%)	1115 (26.5%)
Variable	-	61 (11.6%)	215 (62%)	257 (51.5%)	-	-	-	-	1097 (26%)
Informative + gaps	29 (1.6%)	41 (7.8%)	193 (55.6%)	226 (45.3%)	430 (39.9%)	82 (19.1%)	29 (6.7%)	319 (74.2%)	919 (21.8%)
Informative	-	39 (7.4%)	188 (54.2%)	223 (44.7%)	-	-	-	-	909 (21.6%)
Singleton + gaps	18 (1%)	22 (4.2%)	30 (8.6%)	36 (7.2%)	87 (8.1%)	28 (32.2%)	39 (44.8%)	20 (23.0%)	193 (4.6%)
Singleton	-	19 (3.6%)	28 (8.1%)	34 (6.8%)	-	-	-	-	186 (4.4%)
NUCLEOTIDES									
A	25.4	22.0	40.6	34.2	20.0	25.6	15.0	19.3	142.2
C	23.5	26.9	8.4	11.7	12.2	11.3	23.5	2.0	82.7
G	27.7	32.0	16.1	16.7	24.5	33.1	17.8	22.8	117.0
T	23.5	19.2	35.0	37.4	43.3	30	44	56	158.3
Transition (ts)	4.0	5.0	26.0	34.0	67.0	9.0	4.0	55.0	136.0
AG	1.0	2.0	17.0	19.0	53.0	6.0	2.0	46.0	92.0
CT	3.0	3.0	9.0	15.0	14.0	3.0	2.0	9.0	44.0
Transversions (tv)	1.0	4.0	22.0	30.0	50.0	6.0	2.0	44.0	107.0
AC	1.0	1.0	2.0	2.0	2.0	0.0	0.0	1.0	8.0
AT	0.0	1.0	18.0	22.0	24.0	3.0	1.0	21.0	65.0
CG	0.0	1.0	0.0	1.0	2.0	0.0	1.0	1.0	4.0
GT	0.0	1.0	3.0	5.0	24.0	3.0	0.0	21.0	33
tv/ts	0.25	0.80	0.85	0.88	0.75	0.67	0.50	0.80	0.79

informative sites in the first, second and third positions (19.1, 6.7 and 74.2% respectively) are relatively similar to the percentages previously observed in the family Scorpionidae by Prendini *et al.* (2003) (16, 2 and 81% respectively) although the COI fragment sequenced for that study was shorter (658 bp) than the fragment included in the present analysis (1078 bp). Like the two mitochondrial fragments previously discussed, the COI sequences are rich in AT nucleotides especially at the third codon position.

The nuclear 28S rDNA and 18S rDNA are considerably more conserved than the first three loci discussed. The 28S rDNA fragment is 527 bp long with 463 constant sites and 63 variable sites (with gaps), 41 of which are informative and 22 are singleton. The frequencies of variable, informative and singleton sites are only 11.9, 7.8 and 4.2% respectively. These values differ from the findings of Prendini *et al.* (2003) on the genome of the family Scorpionidae, the 28S rDNA fragment proving to be much more informative for the family Liochelidae. Like in liochelids, the 28S rDNA is extremely conserved in the scorpionids, with 9% of variable sites. However, there was only 4% of informative sites which is approximately half of what is observed in the Liochelidae. The 18S rDNA alignment is 1761 bp long with 1714 constant sites and only 47 variable sites, 29 of which are informative and 18 are singleton. This is the most conserved of the molecular markers sampled for the present analysis. Percentages of variable, informative and singleton sites for this loci are 2.7, 1.6 and 1% respectively. Besides, the proportion of GC nucleotides is higher in the 18s rDNA and 28S rDNA fragments than in the other genes.

The combined alignment of the five fragments comprised 4212 sites, of which 3080 are constant, 1097 variable and 193 singletons. Including gaps, 919 sites are informative, which represent approximately 21.8% of the total sequence. The estimated transversion/transition ratio for combined data is 0.79. Most of the changes are AG transitions, CT transitions and AT transversions. GT transversions are numerous in the protein-coding gene but much less common in the ribosomal loci. These observations are congruent with those of Prendini *et al.* (2003).

2.3.2 SEPARATE ANALYSIS OF THE MORPHOLOGICAL DATA

Parsimony analysis of the 263 informative characters with equal weights located 90

most parsimonious trees (MPTs) that were 1219 steps long. Implied weights analyses with *K = 7* and *K = 9–10* located a single most parsimonious tree each, and IW analyses with *K = 4–5* and *K = 8* located three MPTs each. IW analyses with *K = 1*, *K = 2* , *K = 3* and *K = 6* located ten, fourteen, five and six MPTs respectively. As expected, the trees produced by implied weighting analyses were longer than the trees from the analyses with equal weights. As the concavity constant increased, tree lengths decreased, progressively approaching the length of MPTs under EW. As reported by Turner & Zande (1995), Prendini (2000) and Prendini *et al.* (2003), trees obtained by IW analyses with K < 3 were less fit than those obtained with EW whereas IW with moderate to mild concavity (K ≥ 3) located trees fitter than those obtained with EW. Topological results of the sensitivity analysis are synthesized in a strict consensus and a 50% majority-rule consensus tree (figs 49–50) and a statistical comparison of the trees obtained under the different weighting regimes is presented in table 11. As expected for a matrix of this size, the CI is uninformative (Farris, 1989). As the number of taxa increases, values of CI are known to decrease irrespective of the phylogenetic information conveyed. That is because the CI measures homoplasy but not character fit. On the other hand, the RI values measured for the trees produced by the different analyses indicate that grouping information (synapomorphies) and homoplasy were reasonable (Sanderson & Donoghue, 1989; Hauser & Boyajan, 1997).

Based on previous knowledge and on the results obtained in the present analysis, the phylogenetic status of major taxonomic groups (that is whether a group is retrieved as monophyletic or not in a particular analysis) was assessed in the different topologies. Results are compiled in table 12. Each clade is color-coded the same way in the different cladograms to facilitate visual comparison. Many nodes are collapsed in the strict consensus of the MPTS obtained from the 11 separate analyses which indicate a rather high sensitivity to parameter variation. However, all nodes are retrieved in the majority rule consensus tree with at least 63%, except within the genus *Hormurus*, where resolution remained quite low with many collapsed nodes. The single MPT obtained with IW under *K = 7* is selected as the optimal tree and presented in fig. 51. Absolute and relative Bremer supports as well as symmetric resampling frequencies (GC values) were computed for this tree and are indicated. Although the MPTs derived from IW analyses with *K = 8–10* were shorter and fitter, they were not retained as optimal

Table 11. Summary of statistical and topological differences among the most parsimonious trees (MPTs) obtained by separate analysis of the morphological dataset under equal weights (EW) and implied weights (IW) with ten values for the concavity constant (*K*).

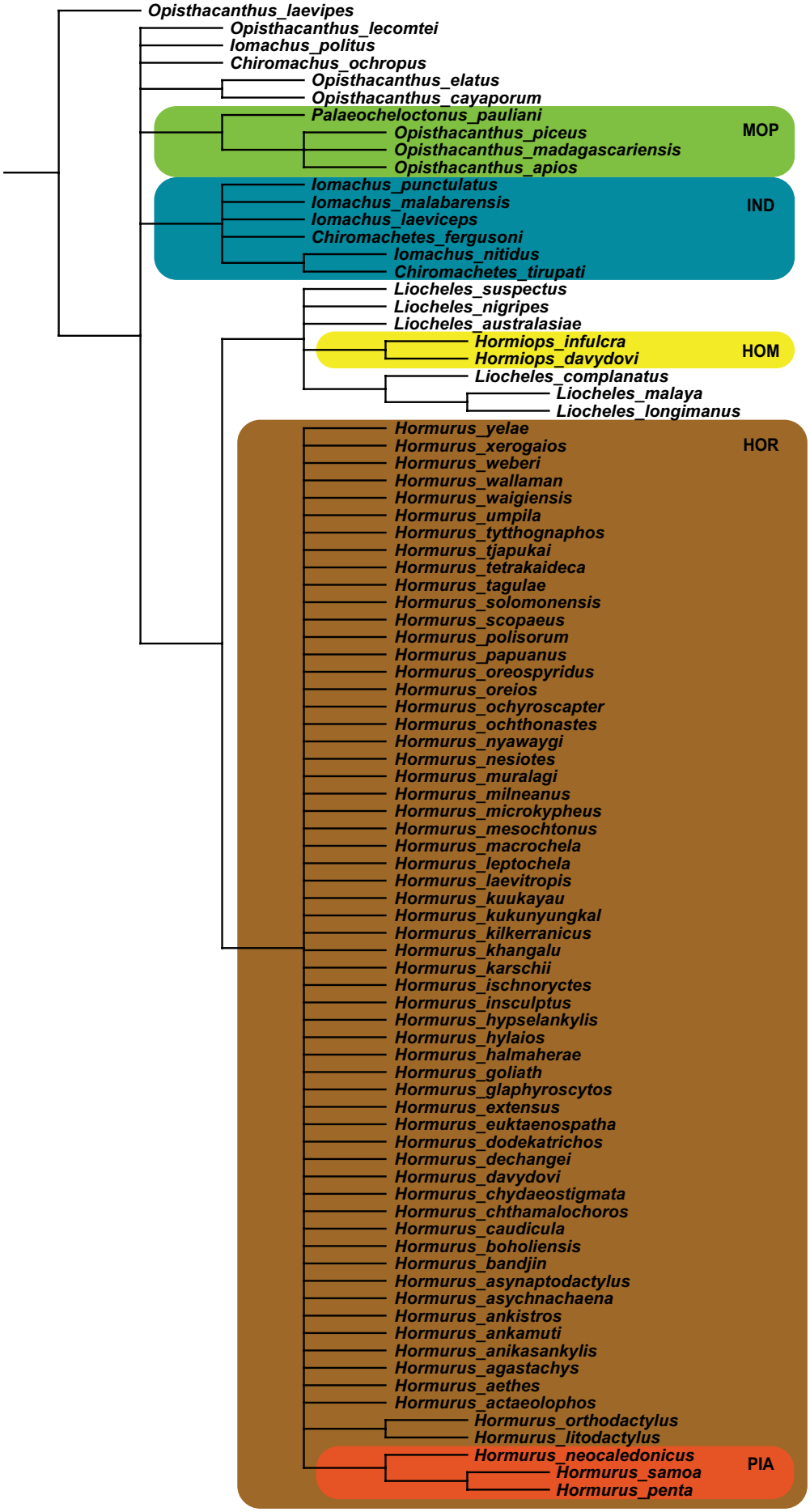
	MPTs	Length	Total fit (*Fi*)	Adjusted homoplasy	CI	RI
EW	90	1219	134.38-135.78 (56.7-57.3%)	101.31-102.62 (42.8-43.3%)	0.272	0.707
IW, *K=1*	10	1311	99.14 (41.8%)	137.86 (58.2%)	0.253	0.677
IW, *K=2*	14	1272	122.48 (51.7%)	114.52 (48.3%)	0.261	0.69
IW, *K=3*	5	1269	138.14 (58.3%)	98.86 (41.7%)	0.262	0.691
IW, *K=4*	3	1261	149.49 (63.1%)	87.51 (36.9%)	0.263	0.693
IW, *K=5*	3	1261	158.23 (66.8%)	78.77 (33.2%)	0.263	0.693
IW, *K=6*	6	1261	165.22 (69.7%)	71.78 (30.3%)	0.263	0.693
IW, *K=7*	1	1255	170.98 (72.1%)	66.02 (27.9%)	0.265	0.695
IW, *K=8*	3	1245	175.86 (74.2%)	61.14 (25.8%)	0.267	0.698
IW, *K=9*	1	1234	180.06 (76%)	56.94 (24%)	0.269	0.702
IW, *K=10*	1	1234	183.71 (77.5%)	53.29 (22.5%)	0.269	0.702

Table 12. Sensitivity data for the major taxonomic groups derived from trees (MPTs or SCTs) obtained by separate analysis of the morphological dataset under equal weights (EW) and implied weights (IW) with ten values for the concavity constant (*K*). Taxonomic groups: AU = Australian *Hormurus* (including *Hormurus polisorum*); CAF = *Iomachus politus* + *Opisthacanthus lecomtei*; CHI = *Chiromachetes sensu lato*; CTI= *Chiromachetes tirupati* + *Iomachus nitidus*; HHL = *Hormiops* + *Hormurus* + *Liocheles* (*Liocheles* sensu lato); HML = *Hormiops* + *Liocheles*; HOL = *Hormurus* + *Liocheles*; HOR = *Hormurus*; INC = IND + *Chiromachus* ochropus; IND = *Chiromachetes* + Indian *Iomachus*; IOM = *Iomachus sensu lato*; LIO = *Liocheles sensu stricto*; MIC = MOP + IND + *Chiromachus ochropus*; MOP = *Monodopisthacanthus* + *Palaeochelocto-nus*; OP = *Opisthacanthus* (*Opisthacanthus*); OPH = OPI + HHL; OPI = *I. politus* + *Opisthacanthus* (*Opisthacanthus*); PIA = Pacific island arc *Hormurus* (see text for detailed list of species). Legend: M = resolved monophyly under those conditions; Para = resolved paraphyly under those conditions; Poly= resolved polyphyly under those conditions.

	IOM	CHI	CTI	IND	MOP	INC	MIC	OP	OPI
Ew	Poly	Poly	M	M	M	Poly	Poly	Para	Para
IW, *K=1*	Poly	Para	M	M	M	M	M	Para	M
IW, *K=2*	Poly	Para	M	M	M	M	M	Para	M
IW, *K=3*	Poly	Para	M	M	M	M	M	Para	M
IW, *K=4*	Poly	Para	M	M	M	M	M	Para	M
IW, *K=5*	Poly	Para	M	M	M	M	M	Para	M
IW, *K=6*	Poly	Para	M	M	M	M	M	Para	M
IW, *K=7*	Poly	Para	M	M	M	M	M	Para	M
IW, *K=8*	Poly	Poly	M	M	M	Para	Para	Para	M
IW, *K=9*	Poly	Poly	M	M	M	Poly	Poly	Para	Para
IW, *K=10*	Poly	Poly	M	M	M	Poly	Poly	Para	Para

	CAF	OPH	HHL	HOL	HML	LIO	HOR	PIA	AU
Ew	Para	Para	M	Para	M	Para	M	M	Para
IW, *K=1*	M	M	M	Para	M	M	M	M	Para
IW, *K=2*	M	M	M	Para	M	M	M	M	Para
IW, *K=3*	M	M	M	Para	M	M	M	M	M
IW, *K=4*	M	M	M	Para	M	M	M	M	M
IW, *K=5*	M	M	M	Para	M	M	M	M	M
IW, *K=6*	M	M	M	Para	M	M	M	M	M
IW, *K=7*	M	M	M	Para	M	M	M	M	M
IW, *K=8*	M	M	M	Para	M	M	M	M	M
IW, *K=9*	Para	Para	M	Para	M	M	M	M	Para
IW, *K=10*	Para	Para	M	Para	M	M	M	M	Para

Fig. 49. Strict consensus of the MPTs generated from the eleven separate analyses of the morphological data in which weighting regime was varied.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Chiromachus_ochropus
Opisthacanthus_elatus
Opisthacanthus_cayaporum
Palaeocheloctonus_pauliani
Opisthacanthus_piceus
Opisthacanthus_madagascariensis
Opisthacanthus_apios
MOP
Iomachus_punctulatus
Iomachus_malabarensis
Iomachus_laeviceps
Chiromachetes_fergusoni
Iomachus_nitidus
Chiromachetes_tirupati
IND
Liocheles_suspectus
Liocheles_nigripes
Liocheles_australasiae
Hormiops_infulcra
Hormiops_davydovi
HOM
Liocheles_complanatus
Liocheles_malaya
Liocheles_longimanus
Hormurus_yelae
Hormurus_xerogaios
Hormurus_weberi
Hormurus_wallaman
Hormurus_waigiensis
Hormurus_umpila
Hormurus_tytthognaphos
Hormurus_tjapukai
Hormurus_tetrakaideca
Hormurus_tagulae
Hormurus_solomonensis
Hormurus_scopaeus
Hormurus_polisorum
Hormurus_papuanus
Hormurus_oreospyridus
Hormurus_oreios
Hormurus_ochyroscapter
Hormurus_ochthonastes
Hormurus_nyawaygi
Hormurus_nesiotes
Hormurus_muralagi
Hormurus_milneanus
Hormurus_microkypheus
Hormurus_mesochtonus
Hormurus_macrochela
Hormurus_leptochela
Hormurus_laevitropis
Hormurus_kuukayau
Hormurus_kukunyungkal
Hormurus_kilkerranicus
Hormurus_khangalu
Hormurus_karschii
Hormurus_ischnoryctes
Hormurus_insculptus
Hormurus_hypselankylis
Hormurus_hylaios
Hormurus_halmaherae
Hormurus_goliath
Hormurus_glaphyroscytos
Hormurus_extensus
Hormurus_euktaenospatha
Hormurus_dodekatrichos
Hormurus_dechangei
Hormurus_davydovi
Hormurus_chydaeostigmata
Hormurus_chthamalochoros
Hormurus_caudicula
Hormurus_boholiensis
Hormurus_bandjin
Hormurus_asynaptodactylus
Hormurus_asychnachaena
Hormurus_ankistros
Hormurus_ankamuti
Hormurus_anikasankylis
Hormurus_agastachys
Hormurus_aethes
Hormurus_actaeolophos
Hormurus_orthodactylus
Hormurus_litodactylus
HOR
Hormurus_neocaledonicus
Hormurus_samoa
Hormurus_penta
PIA

Fig. 50. Majority rule (>50%) consensus of the MPTs generated from the eleven separate analyses of the morphological data in which weighting regime was varied. Frequencies with which nodes were retrieved are indicated.Nodes retrieved in less than 50% of the analyses are collapsed.

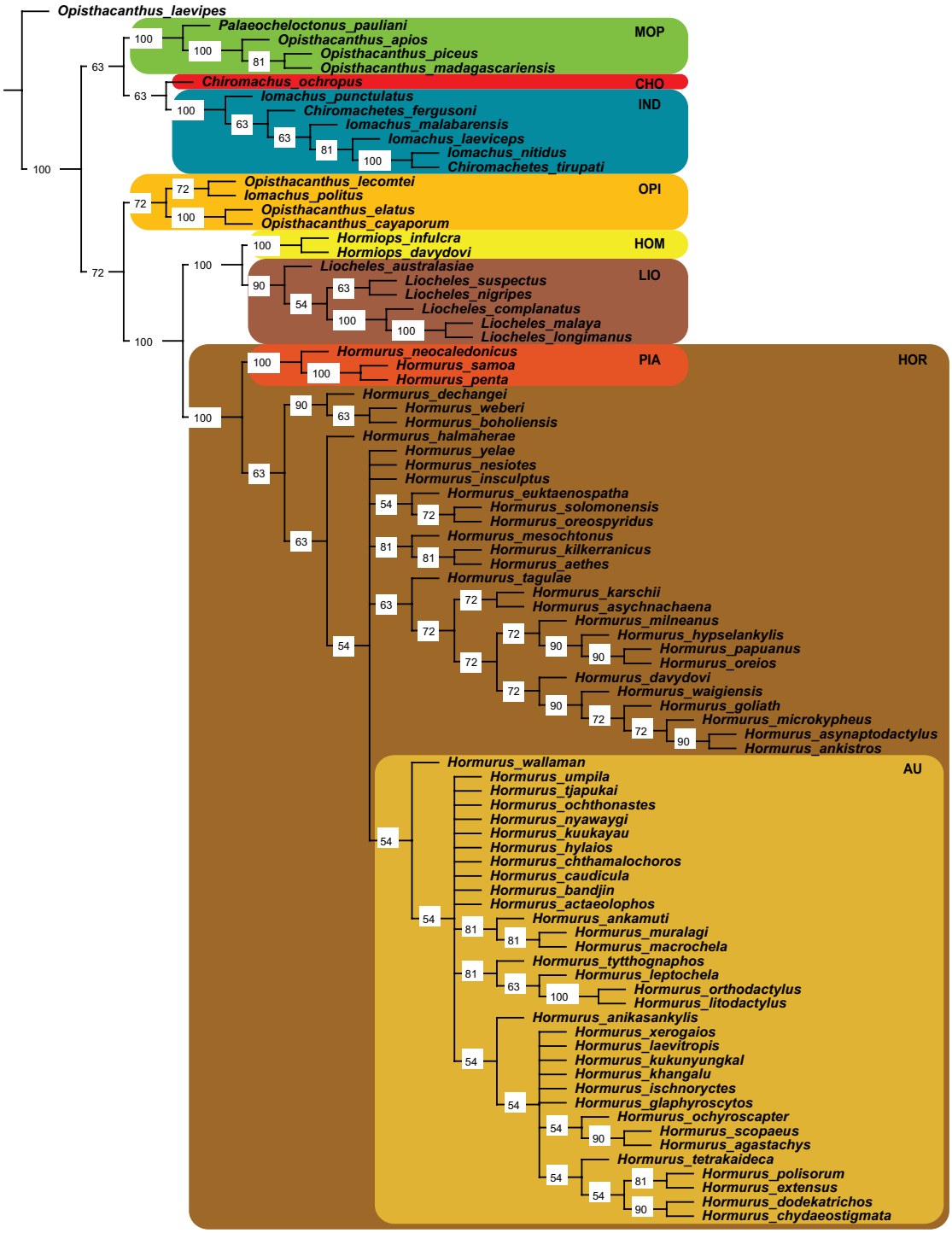
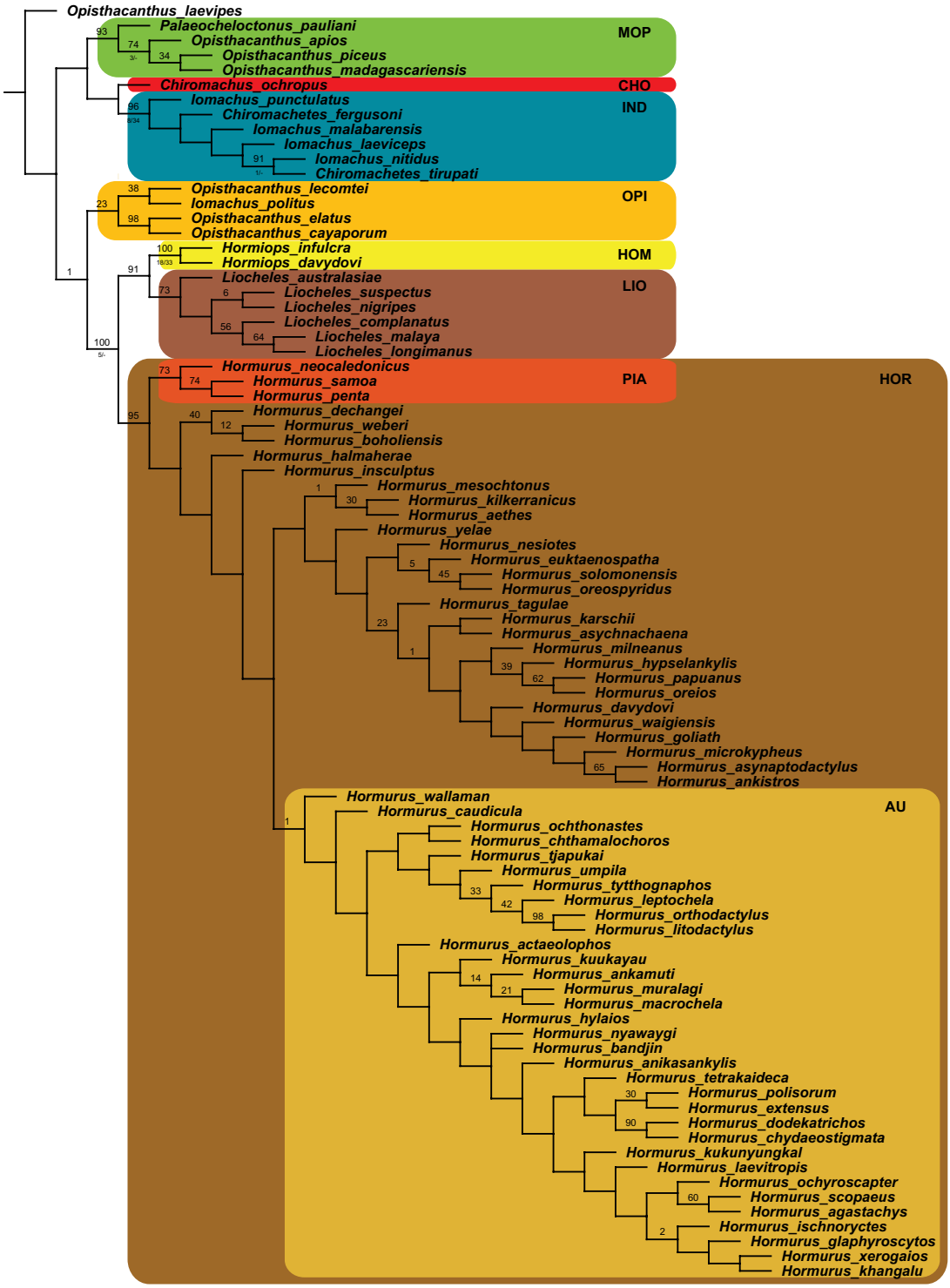

Opisthacanthus_laevipes
Palaeocheloctonus_pauliani
Opisthacanthus_apios
Opisthacanthus_piceus
Opisthacanthus_madagascariensis
MOP
Chiromachus_ochropus
CHO
Iomachus_punctulatus
Chiromachetes_fergusoni
Iomachus_malabarensis
Iomachus_laeviceps
Iomachus_nitidus
Chiromachetes_tirupati
IND
Opisthacanthus_lecomtei
Iomachus_politus
Opisthacanthus_elatus
Opisthacanthus_cayaporum
OPI
Hormiops_infulcra
Hormiops_davydovi
HOM
Liocheles_australasiae
Liocheles_suspectus
Liocheles_nigripes
Liocheles_complanatus
Liocheles_malaya
Liocheles_longimanus
LIO
Hormurus_neocaledonicus
Hormurus_samoa
Hormurus_penta
PIA
HOR
Hormurus_dechangei
Hormurus_weberi
Hormurus_boholiensis
Hormurus_halmaherae
Hormurus_yelae
Hormurus_nesiotes
Hormurus_insculptus
Hormurus_euktaenospatha
Hormurus_solomonensis
Hormurus_oreospyridus
Hormurus_mesochtonus
Hormurus_kilkerranicus
Hormurus_aethes
Hormurus_tagulae
Hormurus_karschii
Hormurus_asychnachaena
Hormurus_milneanus
Hormurus_hypselankylis
Hormurus_papuanus
Hormurus_oreios
Hormurus_davydovi
Hormurus_waigiensis
Hormurus_goliath
Hormurus_microkypheus
Hormurus_asynaptodactylus
Hormurus_ankistros
Hormurus_wallaman
Hormurus_umpila
Hormurus_tjapukai
Hormurus_ochthonastes
Hormurus_nyawaygi
Hormurus_kuukayau
Hormurus_hylaios
Hormurus_chthamalochoros
Hormurus_caudicula
Hormurus_bandjin
Hormurus_actaeolophos
Hormurus_ankamuti
Hormurus_muralagi
Hormurus_macrochela
Hormurus_tytthognaphos
Hormurus_leptochela
Hormurus_orthodactylus
Hormurus_litodactylus
Hormurus_anikasankylis
Hormurus_xerogaios
Hormurus_laevitropis
Hormurus_kukunyungkal
Hormurus_khangalu
Hormurus_ischnoryctes
Hormurus_glaphyroscytos
Hormurus_ochyroscapter
Hormurus_scopaeus
Hormurus_agastachys
Hormurus_tetrakaideca
Hormurus_polisorum
Hormurus_extensus
Hormurus_dodekatrichos
Hormurus_chydaeostigmata
AU

Fig. 51. Optimal tree of the separate analysis of the morphological data under weighting regime that minimised length et maximised fit, and remains congruent with the majority rule consensus tree of the sensitivity analysis (single most parsimonious tree obtained by IW analysis under $K = 7$). Symmetric resampling frequencies (GC scores) are indicated above each branch and Bremer supports (absolute and relative) below.


Opisthacanthus_laevipes
Palaeocheloctonus_pauliani
Opisthacanthus_apios
Opisthacanthus_piceus
Opisthacanthus_madagascariensis
MOP
Chiromachus_ochropus
CHO
Iomachus_punctulatus
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Iomachus_malabarensis
Iomachus_laeviceps
Iomachus_nitidus
Chiromachetes_tirupati
IND
Opisthacanthus_lecomtei
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Opisthacanthus_cayaporum
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Hormiops_davydovi
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Liocheles_suspectus
Liocheles_nigripes
Liocheles_complanatus
Liocheles_malaya
Liocheles_longimanus
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Hormurus_neocaledonicus
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Hormurus_penta
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HOR
Hormurus_dechangei
Hormurus_weberi
Hormurus_boholiensis
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Hormurus_insculptus
Hormurus_mesochtonus
Hormurus_kilkerranicus
Hormurus_aethes
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Hormurus_solomonensis
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Hormurus_oreios
Hormurus_davydovi
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Hormurus_goliath
Hormurus_microkypheus
Hormurus_asynaptodactylus
Hormurus_ankistros
Hormurus_wallaman
Hormurus_caudicula
AU
Hormurus_ochthonastes
Hormurus_chthamalochoros
Hormurus_tjapukai
Hormurus_umpila
Hormurus_tytthognaphos
Hormurus_leptochela
Hormurus_orthodactylus
Hormurus_litodactylus
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Hormurus_muralagi
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Hormurus_laevitropis
Hormurus_ochyroscapter
Hormurus_scopaeus
Hormurus_agastachys
Hormurus_ischnoryctes
Hormurus_glaphyroscytos
Hormurus_xerogaios
Hormurus_khangalu

because their topologies were noticeably different from the MCT of the sensitivity analysis and therefore do not reflect the phylogenetic groupings that were most frequently retrieved. Despite being shorter than any trees obtained with IW, the MPTs obtained with EW were not considered in the choice of the optimal topology because their overall fit was considerably lower than that of the trees obtained with the milder concavity constants.

Taxonomic implications. *Opisthacanthus* (*M*.) *apios* n. sp. from Cape York (Australia) and three taxa from Madagascar, i.e. *O*. (*M*.) *madagascariensis*, *O*. (*M*.) *piceus*, *Palaeocheloctonus pauliani* form a monophyletic clade (**MOP**), regardless of the weighting scheme. On the other hand, none of the analyses diagnosed the monophyly for the genus *Iomachus* (**IOM**) as presently recognized, i. e. including African and Indian species. The Western African *I. politus* was consistently placed outside of the IND clade (see below). The two described species of *Chiromachetes* (**CHI**), i.e. *C. fergusoni* and *C. tirupati*, were not monophyletic in any analyses. However, *C. tirupati* and *I. nitidus* form a clade (**CTI**) in all analyses. A grouping of all Indian *Iomachus* and *Chiromachetes* species (Indian clade, **IND**) is also reported in all analyses. *Chiromachus ochropus* is placed as sister to the Neotropical *Opisthacanthus* (*Opisthacanthus*) under EW and under IW with *K* = *9–10*, and as sister to (OPI + HHL) under IW with *K* = *8*. Under IW with *K* = *1–7*, *C. ochropus* is part of the **INC** clade as sister to IND. INC and MOP nest together in the **MIC** clade that is therefore most exclusively composed of taxa from India, Madagascar and the Seychelles (if *O*. (*M*.) *apios* is excluded). In the optimal tree, IND and MOP receive high branch support (symmetric resampling frequencies (SR) = 93% and 96% respectively), whereas INC and MIC are not supported at all.

The monophyly of subgenus *Opisthacanthus* (**OP**) is never reported in any of the trees. *O.* (*O*.) *lecomtei* never grouped monophyletic with the two Neotropical species. However, it formed a monophyletic clade with *I*. *politus* (Central African clade, **CAF**) in reconstructions obtained under IW with *K* = *1–8*. The monophyly of (*I. politus* + *Opisthacanthus* (*Opisthacanthus*)) (**OPI**) is reported in trees obtained under IW with *K* = *1–8*, and *C. ochropus* nests within the OPI clade under EW and IW with *K* = *10*. Regardless of the inclusion of *C. ochropus* under these two weighting regimes, OPI is always diagnosed as sister to (*Hormiops* + *Hormurus* +

Liocheles) in the **OPH** clade. OPI and CAF are not strongly supported in the preferred topology, with symmetric resampling values of 24% and 38% respectively, and branch support for OPH is also extremely low (SR = 1%).

Hormiops, *Hormurus* and *Liocheles* always form a monophyletic assemblage (**HHL** clade) which receive high branch support (SR = 100%) in the optimal tree. However, the phylogenetic relationships between the three genera is not unambiguously resolved in the analysis. Monophyly of *Liocheles s. l.* (*Hormurus* + *Liocheles*) (**HOL**) is never reported, *Hormiops* nesting with *Liocheles s. s*. in all trees (**HML**). However, the monophyly of *Liocheles s. s.* (**LIO**) and its placement as sister to *Hormiops* are supported in all trees except those produced by EW analysis. In the SCT of the EW analysis, relationships within HML are not resolved, and *Hormiops* is placed in a pectinate arrangement with other *Liocheles s. s.* species. Symmetric resampling values for HML and LIO in the preferred tree are 91% and 73% respectively.

The monophyly of *Hormurus* (**HOR**) is unambiguously supported in all analyses and branch support for the genus is high in the prefered phylogenetic scenario (SR = 95%). The Pacifc island arc clade (**PIA**) that includes *H. neocaledonicus*, *H. penta*, and *H. samoa* n. sp. is consistently retrieved across the analyses. Its position varies depending on the weighting regime: it is placed basally as sister to all remaining *Hormurus* species under IW with *K* = *1* and *K* = *3–8*, whereas under EW and IW with *K* = *2* and *K* = *9–10*, it nests within a more derived group comprising all Melanesian species. Branch support in Another clade grouping all Australian species (**AU**) is observed in trees generated under IW with *K* = *3–8* (weighting regimes that also place PIA as basal to all other *Hormurus*). Under IW with *K* = *2* and *K* = *9–10*, Australian *Hormurus* do not form a monophyletic cluster but are nonetheless placed basally together, species from Queensland inland savannahs (*H. agastachys* n. sp., *H. glaphyroscytos* n. sp., *H. ischnoryctes* n. sp., *H. khangalu* n. sp., *H. ochyroscapter* n. sp., *H. scopaeus* n. sp., and *H. xerogaios* n. sp.) and north Western Australia (*H. chydaeostigmata* n. sp. and *H. dodecatrichos* n. sp.) being the more basal. In the strict consensus tree of the EW analysis, these latter species are also basal to all other *Hormurus* that form an unresolved polytomy. Melanesian *Hormurus* species form a monophyletic unit with PIA in trees from IW analyses with *K* = *2* and *K* = *9–10*. Under IW with *K* = *3*, they are intermediate between PIA and AU, whereas under IW with *K* =

Table 13. Comparison of alternative hypotheses of phylogenetic relationships in Indo-Pacific Liochelidae Fet & Bechly, 2001 based on morphological evidence.

Constrained topology	Step difference	Total fit difference
Monophyletic *Chiromachetes*	6	0.38 (0.16%)
Monophyletic *Iomachus*	17	2.29 (0.97%)
Stockwell (1989): (*Iomachus* sensu lato + *Liocheles* sensu lato (including *Hormiops*))	22	1.81 (0.76%)
Monophyletic *Liocheles* sensu lato, excluding *Hormiops*	7	0.42 (0.18%)

3–8, only some (*H. boholiensis*, *H. dechangei*, *Hormurus halmaherae* n. sp., *Hormurus weberi* Pocock, 1894) are consistently retrieved as transitional taxa between PIA and AU (*Hormurus insculptus* Thorell, 1888 and *Hormurus nesiotes* n. sp. fall into this group in IW with *K* = *3* and IW with *K* = *4–8*, respectively) with the remaining species forming a clade sister to AU. Within *Hormurus*, PIA is the only clade to receive significant branch support (SR = 74 %) in the chosen phylogeny, most of the other nodes are unsupported or only weakly supported (AU, SR = 1%).

Constrained searches. Results of the constrained searches under IW with *K* = *7* are presented in table 13. The greatest number of extra steps and loss of fitness occurred when phylogenetic relationships between *Iomachus s. l.* and *Liocheles s. l.* as proposed by Stockwell (1989) and Prendini (2000) were constrained (22 extra steps and 0.76 % loss in fitness), and when *Iomachus s. l.* was constrained for monophyly (17 extra steps and 0.97 % fitness loss). In contrast, constraining the monophyly of *Chiromachetes* cost only six extra steps on the optimal tree with 0.16% loss in fitness. Seven extra steps and a 0.18% fitness loss are required to constrain HOL (*Hormurus* + *Liocheles*) for monophyly [= constrain *Hormiops* to be sister to HOL].

2.3.3 SEPARATE ANALYSIS OF THE MOLECULAR DATA

Parsimony analysis of the aligned DNA sequences with equal weights located 6 MPTs whether gaps were included or not. The MPTs were 6588 (with gaps) and 6274 steps (without gaps) respectively. Each IW analysis located three MPTs. As for the morphological data, IW yielded trees that were longer than trees from the EW analyses (tab. 14). Trees obtained with strong concavity (*K* < *3)* were also less fit than those obtained with EW whereas IW with moderate to mild concavity (K ≥ 3) located trees fitter than those obtained with EW. Topological results of the sensitivity analysis are presented in the same way as results of the analysis of the morphological data, i.e. a strict consensus tree, a 50% majority-rule consensus tree (figs 52–53) and two tables comparing the topologies and statistics of the different trees obtained (tabs. 14–15). The fitness, CI and RI values are slightly greater than those obtained for the morphological data alone. Besides, the MPTs obtained by analyses in which gaps were included have a slightly greater fitness and CI than the MPTs obtained when gaps were excluded. Using

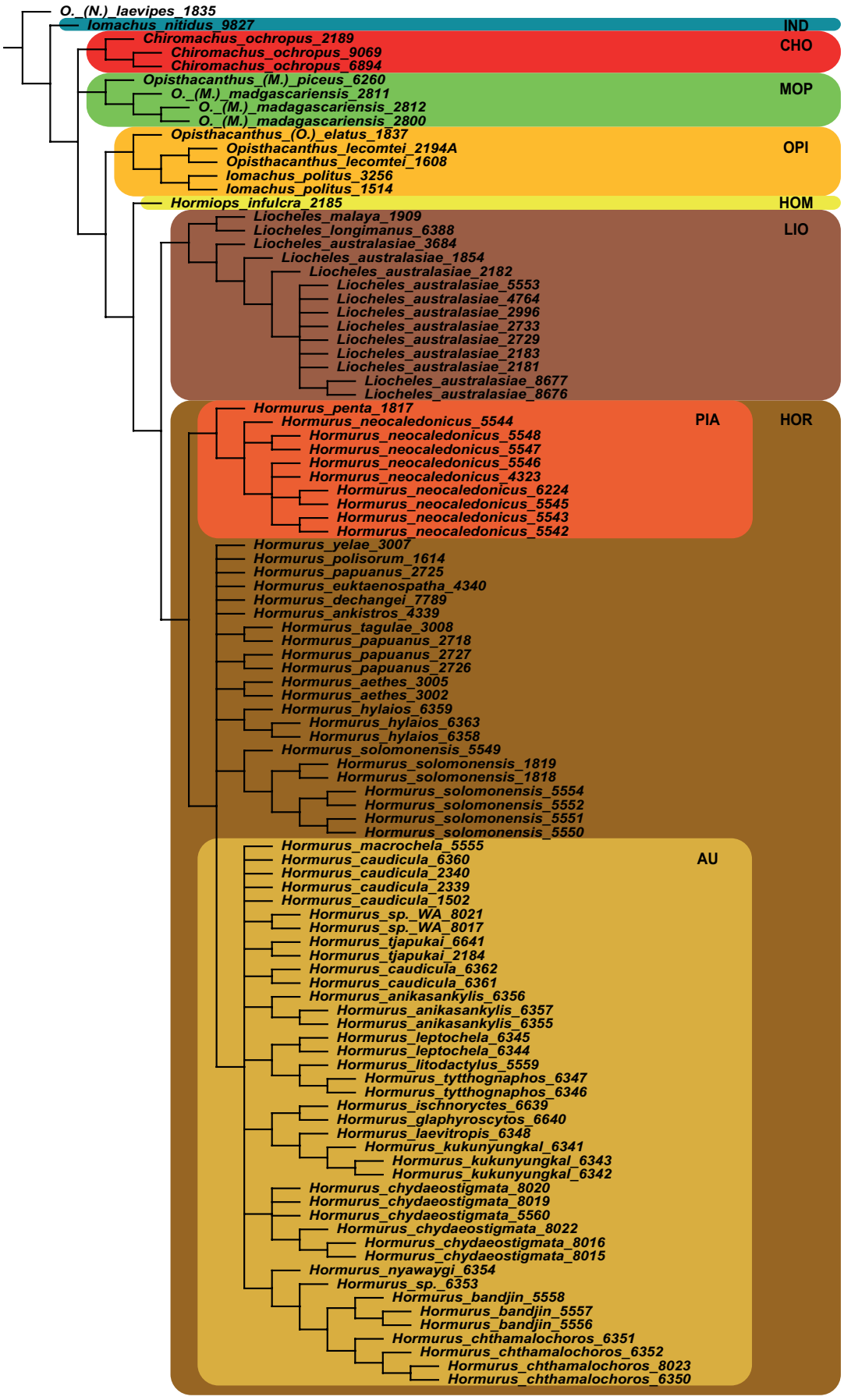
Table 14. Summary of statistical and topological differences among the most parsimonious trees (MPTs) obtained by separate analysis of the aligned molecular data (gaps included or excluded) under equal weights (EW) and implied weights (IW) with 10 values for the concavity constant (*K*).

		MPTs	Length	Total fit	Adjusted homoplasy	CI	RI
Gaps included	EW	6	6588	481.17-481.39 (53%)	426.61-426.83 (47%)	0.313	0.69
	IW, *K=1*	3	6736	331.11 (36.5%)	576.89 (63.5%)	0.306	0.68
	IW, *K=2*	3	6672	423.47 (46.6%)	484.53 (53.4%)	0.309	0.684
	IW, *K=3*	3	6672	484.20 (53.3%)	423.80 (46.7%)	0.309	0.684
	IW, *K=4*	3	6669	528.64 (58.2%)	379.36 (41.8%)	0.309	0.684
	IW, *K=5*	3	6670	563.20 (62%)	344.80 (38%)	0.309	0.684
	IW, *K=6*	3	6668	591.14 (65.1%)	316.86 (34.9%)	0.309	0.684
	IW, *K=7*	3	6666	614.36 (67.7%)	293.64 (32.3%)	0.309	0.684
	IW, *K=8*	3	6608	634.21 (69.8%)	273.79 (30.2%)	0.312	0.688
	IW, *K=9*	3	6608	651.34 (71.7%)	256.66 (28.3%)	0.312	0.688
	IW, *K=10*	3	6608	666.28 (73.4%)	241.72 (26.6%)	0.312	0.688
Gaps excluded	EW	6	6274	459.84-460.06 (52.3%)	418.94-419.16 (47.7%)	0.285	0.689
	IW, *K=1*	3	6390	312.37 (35.5%)	566.63 (64.5%)	0.279	0.681
	IW, *K=2*	3	6336	401.76 (45.7%)	477.24 (54.3%)	0.282	0.684
	IW, *K=3*	3	6312	461.04 (52.5%)	417.96 (47.5%)	0.283	0.686
	IW, *K=4*	3	6290	504.7 (57.4%)	374.3 (42.6%)	0.284	0.688
	IW, *K=5*	3	6291	538.77 (61.3%)	340.23 (38.7%)	0.284	0.687
	IW, *K=6*	3	6291	566.36 (64.4%)	312.64 (35.6%)	0.284	0.687
	IW, *K=7*	3	6291	589.32 (67%)	289.68 (33%)	0.284	0.687
	IW, *K=8*	3	6291	608.81 (69.3%)	270.19 (30.7%)	0.284	0.687
	IW, *K=9*	3	6291	625.61 (71.2%)	253.39 (28.8%)	0.284	0.687
	IW, *K=10*	3	6291	640.28 (72.8%)	238.72 (27.2%)	0.284	0.687

Table 15. Results of the sensitivity analysis derived from the SCTs obtained by separate analysis of the molecular dataset (gaps included or excluded), under equal weights (EW) and implied weights (IW) with ten values for the concavity constant (*K*). Taxonomic groups: AU = Australian *Hormurus* (including *Hormurus polisorum*); CAF = *Iomachus politus* + *Opisthacanthus lecomtei*; HHL = *Hormiops* + *Hormurus* + *Liocheles* (*Liocheles* sensu lato); HML = *Hormiops* + *Liocheles*; HOL = *Hormurus* + *Liocheles*; HOR = *Hormurus*; INC = *Iomachus nitidus* + *Chiromachus* ochropus; IOM = *Iomachus sensu lato*; LIO = *Liocheles sensu stricto*; MIC = *Opisthacanthus* (*Monodopisthacanthus*) + *I. nitidus* + *C. ochropus*; MOC = *Opisthacanthus* (*Monodopisthacanthus*) + *C. ochropus*; OP = *Opisthacanthus* (*Opisthacanthus*); OPH = OPI + HHL; OPI = *I. politus* + *Opisthacanthus (Opisthacanthus)*; PIA = Pacific island arc *Hormurus* (see text for detailed list of species). Legend: M = resolved monophyly under those conditions; Para = resolved paraphyly under those conditions; Poly= resolved polyphyly under those conditions.

		IOM	INC	MOC	MIC	OP	OPI	CAF	OPH	HHL	HOL	HML	LIO	HOR	PIA	AU
Gaps included	Ew	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	Para
	IW, *K=1*	Poly	Para	Para	Para	Para	M	M	M	M	M	Para	M	M	M	Para
	IW, *K=2*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=3*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=4*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=5*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=6*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=7*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=8*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=9*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=10*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
Gaps excluded	Ew	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	Para
	IW, *K=1*	Poly	Para	Para	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=2*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=3*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=4*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=5*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=6*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=7*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=8*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=9*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K=10*	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M

Fig. 52. Strict consensus of the MPTs obtained by 22 separate analyses of the aligned molecular data in which weighting regime was varied and gaps were included or excluded.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IND
Chiromachus_ochropus_2189
Chiromachus_ochropus_9069
Chiromachus_ochropus_6894
CHO
Opisthacanthus_(M.)_piceus_6260
O._(M.)_madagascariensis_2811
O._(M.)_madagascariensis_2812
O._(M.)_madagascariensis_2800
MOP
Opisthacanthus_(O.)_elatus_1837
Opisthacanthus_lecomtei_2194A
Opisthacanthus_lecomtei_1608
Iomachus_politus_3256
Iomachus_politus_1514
OPI
Hormiops_infulcra_2185
HOM
Liocheles_malaya_1909
Liocheles_longimanus_6388
Liocheles_australasiae_3684
Liocheles_australasiae_1854
Liocheles_australasiae_2182
Liocheles_australasiae_5553
Liocheles_australasiae_4764
Liocheles_australasiae_2996
Liocheles_australasiae_2733
Liocheles_australasiae_2729
Liocheles_australasiae_2183
Liocheles_australasiae_2181
Liocheles_australasiae_8677
Liocheles_australasiae_8676
LIO
Hormurus_penta_1817
Hormurus_neocaledonicus_5544
Hormurus_neocaledonicus_5548
Hormurus_neocaledonicus_5547
Hormurus_neocaledonicus_5546
Hormurus_neocaledonicus_4323
Hormurus_neocaledonicus_6224
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Hormurus_neocaledonicus_5542
PIA
Hormurus_yelae_3007
Hormurus_polisorum_1614
Hormurus_papuanus_2725
Hormurus_euktaenospatha_4340
Hormurus_dechangei_7789
Hormurus_ankistros_4339
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Hormurus_hylaios_6358
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Hormurus_solomonensis_1818
Hormurus_solomonensis_5554
Hormurus_solomonensis_5552
Hormurus_solomonensis_5551
Hormurus_solomonensis_5550
Hormurus_macrochela_5555
Hormurus_caudicula_6360
Hormurus_caudicula_2340
Hormurus_caudicula_2339
Hormurus_caudicula_1502
Hormurus_sp._WA_8021
Hormurus_sp._WA_8017
Hormurus_tjapukai_6641
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Hormurus_anikasankylis_6355
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Hormurus_litodactylus_5559
Hormurus_tytthognaphos_6347
Hormurus_tytthognaphos_6346
Hormurus_ischnoryctes_6639
Hormurus_glaphyroscytos_6640
Hormurus_laevitropis_6348
Hormurus_kukunyungkal_6341
Hormurus_kukunyungkal_6343
Hormurus_kukunyungkal_6342
Hormurus_chydaeostigmata_8020
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Hormurus_chydaeostigmata_5560
Hormurus_chydaeostigmata_8022
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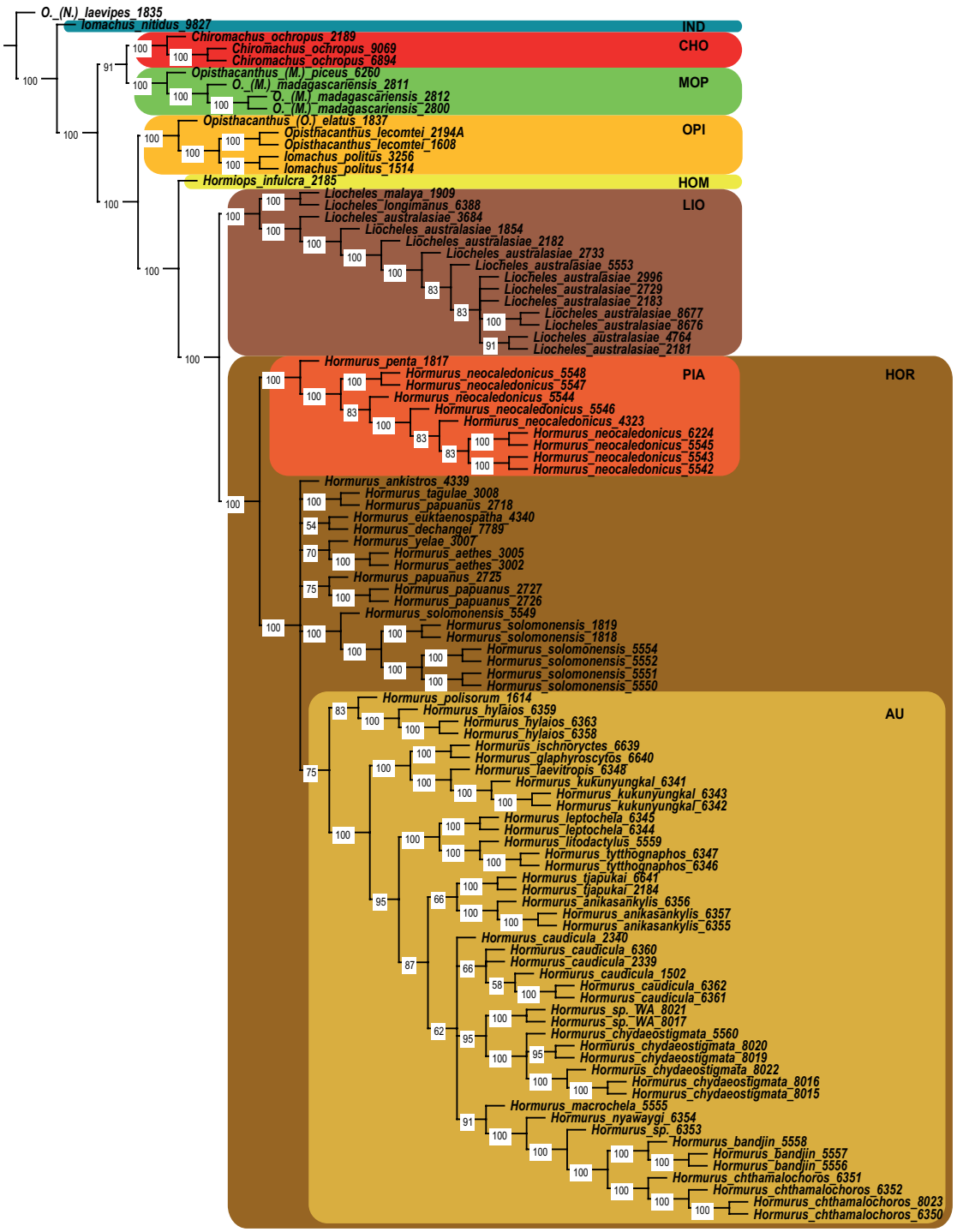
Hormurus_chydaeostigmata_8015
Hormurus_nyawaygi_6354
Hormurus_sp._6353
Hormurus_bandjin_5558
Hormurus_bandjin_5557
Hormurus_bandjin_5556
Hormurus_chthamalochoros_6351
Hormurus_chthamalochoros_6352
Hormurus_chthamalochoros_8023
Hormurus_chthamalochoros_6350
AU
HOR

Fig. 53. Majority rule (>50%) consensus of the MPTs obtained by 22 separate analyses of the aligned molecular data in which weighting regime was varied and gaps were included or excluded. Frequencies with which nodes were retrieved are indicated. Nodes retrieved in less than 50% of the analyses are collapsed.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Iomachus_nitidus_9827
IND
Chiromachus_ochropus_2189
Chiromachus_ochropus_9069
Chiromachus_ochropus_6894
CHO
Opisthacanthus_(M.)_piceus_6260
O._(M.)_madagascariensis_2811
O._(M.)_madagascariensis_2812
O._(M.)_madagascariensis_2800
MOP
Opisthacanthus_(O.)_elatus_1837
Opisthacanthus_lecomtei_2194A
Opisthacanthus_lecomtei_1608
Iomachus_politus_3256
Iomachus_politus_1514
OPI
Hormiops_infulcra_2185
HOM
Liocheles_malaya_1909
Liocheles_longimanus_6388
Liocheles_australasiae_3684
Liocheles_australasiae_1854
Liocheles_australasiae_2182
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Liocheles_australasiae_2996
Liocheles_australasiae_2729
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Liocheles_australasiae_4764
Liocheles_australasiae_2181
LIO
HOR
Hormurus_penta_1817
Hormurus_neocaledonicus_5548
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Hormurus_neocaledonicus_5545
Hormurus_neocaledonicus_5543
Hormurus_neocaledonicus_5542
PIA
Hormurus_ankistros_4339
Hormurus_tagulae_3008
Hormurus_papuanus_2718
Hormurus_euktaenospatha_4340
Hormurus_dechangei_7789
Hormurus_yelae_3007
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Hormurus_papuanus_2725
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Hormurus_glaphyroscytos_6640
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Hormurus_tjapukai_2184
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Hormurus_anikasankylis_6355
Hormurus_caudicula_2340
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Hormurus_caudicula_2339
Hormurus_caudicula_1502
Hormurus_caudicula_6362
Hormurus_caudicula_6361
Hormurus_sp._WA_8021
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Hormurus_nyawaygi_6354
Hormurus_sp._6353
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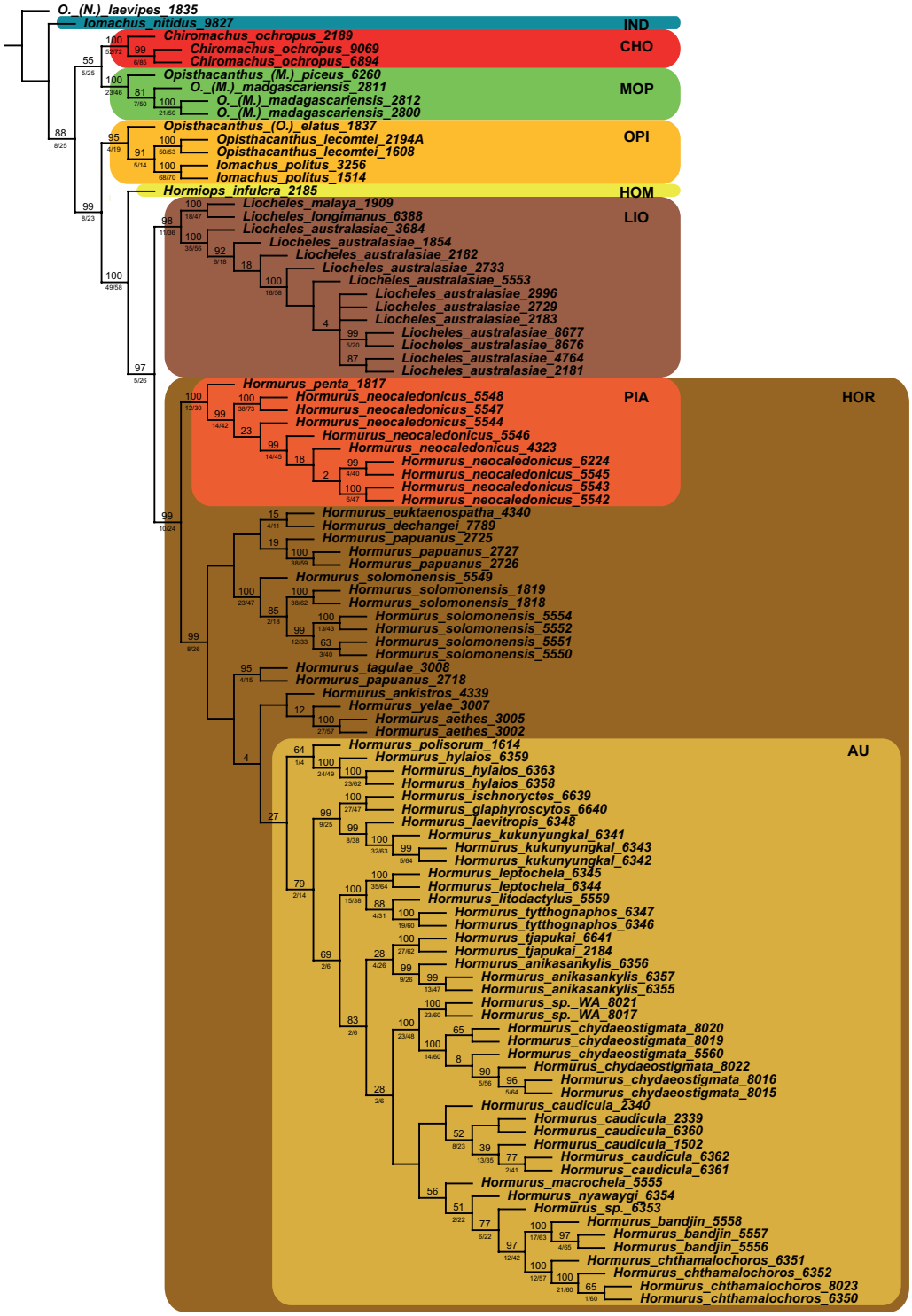
Hormurus_chthamalochoros_6351
Hormurus_chthamalochoros_6352
Hormurus_chthamalochoros_8023
Hormurus_chthamalochoros_6350
AU

the same optimality criteria as for the separate analysis of morphological data (fitness, length, and congruence with MRT of the sensitivity analysis), the three MPTs retrieved under IW with *K = 10* and when gaps were excluded are chosen as optimal phylogenetic hypotheses and a SCT is presented (fig. 54). The same groups as in the analysis of the morphological dataset are considered and discussed. Although the taxon sampling was smaller, most of the groups are represented by at least one species. The topologies obtained here are congruent for the most part with the prefered phylogeny generated from analysis of morphological data; only a few nodes at the base of the trees differ.

Taxonomic implications. The **MOP** clade is represented here by two species of *Opisthacanthus* (*Monodopisthacanthus*) (4 samples) that are always grouped together. The genus *Iomachus* (**IOM**) appeared to be polyphyletic in all analyses. *Iomachus nitidus* (the sole representative of the **IND** clade) is consistently retrieved as sister to the rest of the taxa and thus placed more basally than in the morphological analysis. However, this position may be a sampling artefact, other Indian *Iomachus* and the closely related genus *Chiromachetes* being absent from the dataset. On the other hand, *I. politus* is always placed within the subgenus *Opisthacanthus* (**OPI**) where it forms a monophyletic cluster with *O.* (*O.*) *lecomtei* (**CAF**). This makes the subgenus *Opisthacanthus* as currently defined (**OP**) paraphyletic. Besides, the OPI group is diagnosed as sister to the HHL clade in all analyses (**OPH**). *Chiromachus ochropus* and *Opisthacanthus* (*Monodopisthacanthus*) form a monopheletic group (**MOC**) except in IW analyses with *K = 1* (both with and without gaps) where *C. ochropus* is sister to (MOP (OPI (*Hormiops* (*Hormurus* + *Liocheles*)))). In the optimal tree, CAF, OPH and OPI are all strongly supported with symmetric resampling frequencies of 91%, 99% and 95% respectively, whereas MOC receive only 55% of support.

Hormiops, *Hormurus* and *Liocheles* are grouped in a monophyletic unit (**HHL**) in all trees and strongly supported in the prefered topology (SR = 99%). The following arrangement (*Hormiops* (*Hormurus* + *Liocheles*)) was consistently and unambiguously retrieved regardless of weighting regimes and the monophyly of all three genera is significantly supported in the optimal tree (*Liocheles s. s.* (**LIO**), SR = 98%; *Hormurus* (**HOR**), SR = 99%). Besides, (*Hormurus*

Fig. 54. Optimal tree of the separate analysis of the molecular data under weighting regime that minimised length and maximised fit, and remains congruent with the MRT of the sensitivity analysis (strict consensus of the three MPTs obtained by IW analysis under *K = 10* and gaps excluded). Symmetric resampling frequencies (GC scores) are indicated above each branch and Bremer supports (absolute and relative) below.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O._(M.)_madgascariensis_2811
O._(M.)_madagascariensis_2812
O._(M.)_madagascariensis_2800
MOP
Opisthacanthus_(O.)_elatus_1837
Opisthacanthus_lecomtei_2194A
Opisthacanthus_lecomtei_1608
Iomachus_politus_3256
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OPI
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HOM
Liocheles_malaya_1909
Liocheles_longimanus_6388
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LIO
Hormurus_penta_1817
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PIA
HOR
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Hormurus_chthamalochoros_6352
Hormurus_chthamalochoros_8023
Hormurus_chthamalochoros_6350
AU

Table 16. Comparison of alternative hypotheses of phylogenetic relationships in Indo-Pacific Liochelidae Fet & Bechly, 2001 based on molecular data.

Constrained topology	Step difference	Total fit difference
Monophyletic *Iomachus*	60	4.2 (0.48%)
MIC (*C. ochropus* + *I. nitidus* + *Opisthacanthus* (*Monodopisthacanthus*) + *Palaeocheloctonus*)	8	0.59 (0.07%)
(*C. ochropus* + *I. nitidus*)(*Opisthacanthus* (*Monodopisthacanthus*) + *Palaeocheloctonus*)	19	1.08 (0.12%)

+ *Liocheles*) (**HOL**) also receive a high branch support (SR = 97%). The **PIA** clade (represented here by two species) is retrieved in all analyses and diagnosed as a basal clade, sister to all other *Hormurus*. For the remaining portion of the genus, there is less topological concordance between the different trees obtained and most nodes are collapsed in the strict consensus. However, Australian species are grouped in a monophyletic clade (**AU**) under IW with *K = 2–10* when gaps are excluded and under IW with *K = 2–10* when gaps are included. In EW analyses (with and without gaps) and in IW analysis with *K = 1* when gaps are included, *Hormurus polisorum* Volschenk, Locket & Harvey, 2001 and *Hormurus hylaios* n. sp. cluster outside of AU with *Hormurus ankistros* n. sp. and/or *Hormurus yelae* n. sp. both from Papua New Guinea. Symmetric resampling frequencies for PIA and AU in the optimal topology are 100% and 27% respectively.

Constrained searches. Results of the constrained searches under IW with *K = 10* when gaps are excluded are presented in table 16. Forcing the monophyly of *Iomachus* s.l. on the optimal topology cost 60 extra steps and a fitness loss of 0.48%. On the other hand, only eight extra steps and a 0.07% loss in fitness are required to constrain the monophyletic grouping (*C. ochropus* + *I. nitidus* + *Opisthacanthus* (*Monodopisthacanthus*)+ *Palaeocheloctonus*), and 19 extra steps and a 0.12% of fitness loss to obtain the phylogenetic relationships reported between these taxa in the morphological analysis, i.e. (*C. ochropus* + *I. nitidus*)(*Opisthacanthus* (*Monodopisthacanthus*) + *Palaeocheloctonus*).

2.3.4 SIMULTANEOUS ANALYSIS OF THE MORPHOLOGICAL AND MOLECULAR DATA

Simultaneous parsimony analysis of the morphology and aligned DNA sequences with equal weights located 9 MPTs when gaps were included and 17 when gaps were excluded. The MPTs were 7525 (with gaps) and 7212 (without gaps) steps long respectively. Each IW analysis located three MPTs. The remarks made about the topological and statistical results (Fitness, CI and RI depending on the different *K* values) of the separate analyses of the morphological and the molecular data also apply to the simultaneous analysis of both partitions (tab. 17). The CI, RI and fitness values were slighlty greater than those obtained for the corresponding

Table 17. Summary of statistical and topological differences among the most parsimonious trees (MPTs) obtained by simultaneous analysis of the morphological and aligned molecular data (gaps included or excluded) under equal weights (EW) and implied weights (IW) with 10 values for the concavity constant (*K*).

		MPTs	Length	Total fit (Fi)	Adjusted homoplasy	CI	RI
Gaps included	EW	9	7525	630.48-630.74 (55.3%)	510.26-510.52 (44.7%)	0.316	0.717
	IW, *K=1*	3	7645	440.45 (38.6%)	700.55 (61.4%)	0.311	0.711
	IW, *K=2*	3	7621	557.38 (48.9%)	583.62 (51.1%)	0.312	0.712
	IW, *K=3*	3	7606	633.73 (55.5%)	507.27 (44.5%)	0.313	0.713
	IW, *K=4*	3	7600	689.39 (60.4%)	451.71 (39.6%)	0.313	0.713
	IW, *K=5*	3	7601	732.2 (64.2%)	408.8 (35.8%)	0.313	0.713
	IW, *K=6*	3	7601	766.66 (67.2%)	374.34 (32.8%)	0.313	0.713
	IW, *K=7*	3	7601	795.13 (69.7%)	345.87 (30.3%)	0.313	0.713
	IW, *K=8*	3	7540	819.19 (71.8%)	321.81 (28.2%)	0.321	0.717
	IW, *K=9*	3	7540	839.96 (73.6%)	301.04 (26.4%)	0.316	0.717
	IW, *K=10*	3	7535	858.03 (75.2%)	282.97 (24.8%)	0.316	0.717
Gaps excluded	EW	17	7212	608.77-609.22 (54.8%)	502.78-503.23 (45.2%)	0.292	0.717
	IW, *K=1*	3	7329	421.92 (37.9%)	690.08 (62.1%)	0.287	0.71
	IW, *K=2*	3	7298	535.71 (48.2%)	576.29 (51.8%)	0.288	0.712
	IW, *K=3*	3	7252	610.54 (54.9%)	501.46 (45.1%)	0.29	0.715
	IW, *K=4*	3	7233	665.25 (59.8%)	446.75 (40.2%)	0.291	0.716
	IW, *K=5*	3	7233	707.59 (63.6%)	404.41 (36.4%)	0.291	0.716
	IW, *K=6*	3	7227	741.68 (66.7%)	370.32 (33.3%)	0.291	0.716
	IW, *K=7*	3	7224	769.89 (69.2%)	342.11 (30.8%)	0.291	0.716
	IW, *K=8*	3	7224	793.71 (71.4%)	318.29 (28.6%)	0.291	0.716
	IW, *K=9*	3	7224	814.16 (73.2%)	297.84 (26.8%)	0.291	0.716
	IW, *K=10*	3	7224	831.94 (74.8%)	280.06 (25.2%)	0.291	0.716

analyses of the molecular data partition only. Results of the sensitivity analysis are presented by means of a strict consensus, a 50% majority-rule consensus tree (figs 55–56), and two tables presenting the statistical and topological differences between the different trees obtained (tabs. 17–18). Consensus trees obtained by separate analysis of the molecular data and by simultaneous analysis of morphological and molecular datasets are identical for the most part, slight topological differences are only observed within the genus *Hormurus*. In the simultaneous analysis, *H. dechangei* is placed in an intermediate position between PIA and the remaining species whereas it nests within the Indonesian species in the analysis of the molecular partition. Finally, based on fitness, length and congruence with MRT of the sensitivity analysis, The MPTs recovered by the analysis with implied weighting under *K = 9* and in which gaps were included may be regarded as the optimal trees according to the three optimality creteria used for the previous analyses, i.e. length, fitness and congruence with the results of the sensitivity analysis. A SCT of these three trees is presented in figure 57.

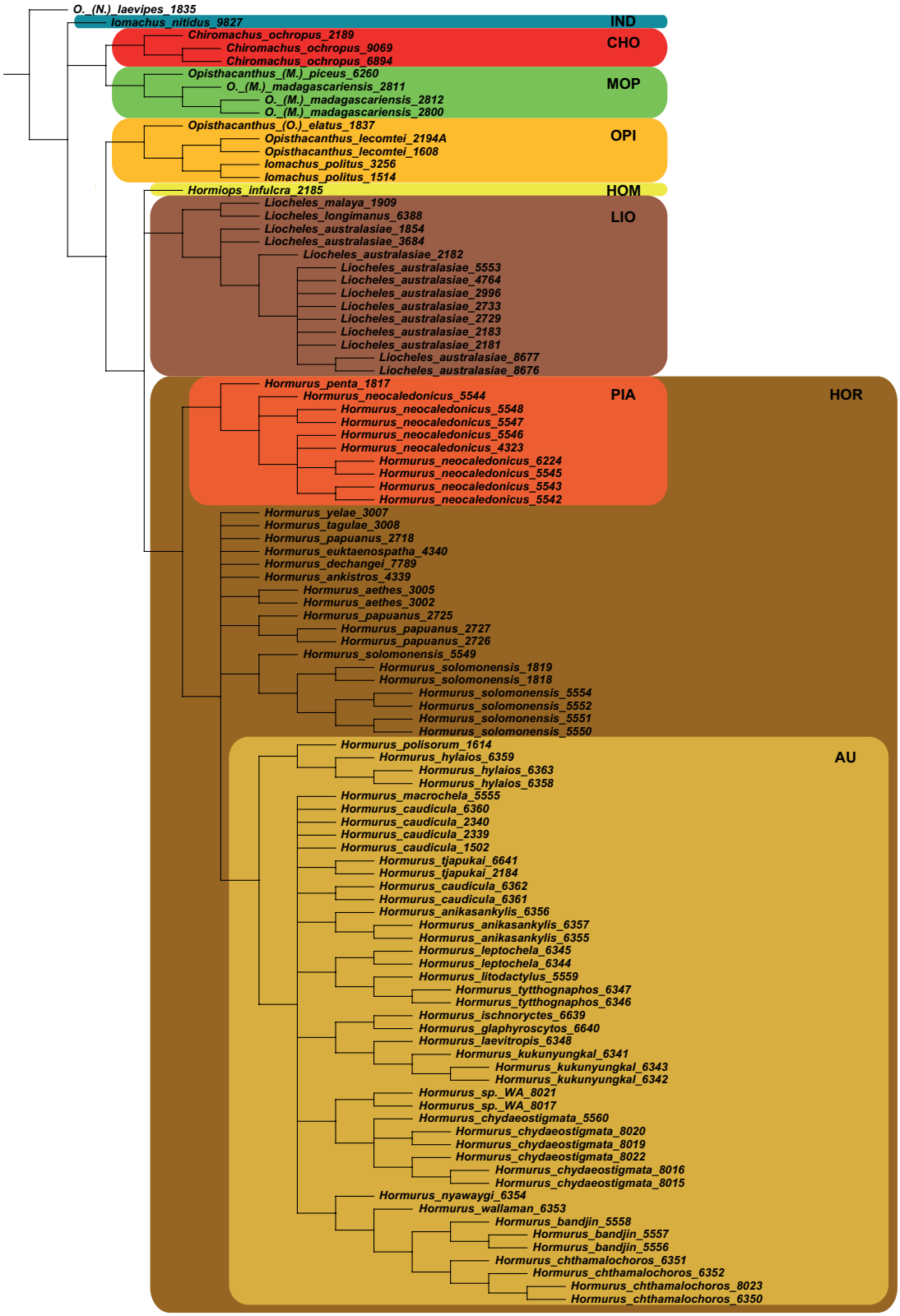
Taxonomic implications. The genus *Iomachus* (**IOM**) is polyphyletic in all simultaneous analyses of the morphological and molecular data, with *I. nitidus* retrieved as sister to the rest of the taxa and *I. politus* nesting within the subgenus *Opisthacanthus* (**OPI**) as sister to *O.* (*O.*) *lecomtei* (**CAF**). OPI appear to be sister to HHL in all analyses (**OPH**). *Chiromachus ochropus* is clustered with *Monodopisthacanthus* to form the **MOC** clade in all analyses. A monophyletic grouping of *C. ochropus*, *I. nitidus* and *Opisthacanthus* (*Monodopisthacanthus*) (**MIC**) is observed under IW with *K = 1–2* with or without gaps, with *I. nitidus* as sister to (*C. ochropus* + *Opisthacanthus* (*Monodopisthacanthus*)). As in the separate analysis of molecular data, branch supports for CAF, OPH and OPI in the optimal tree are robust with symmetric resampling frequencies of 88%, 99% and 99% respectively. Besides, MOC received a higher support (SR = 73%) than in the analysis with DNA alone.

Monophyletic groupings of *Hormiops*, *Hormurus* and *Liocheles* (**HHL**), all *Hormurus* species (**HOR**), and all *Liocheles* s.s. species (**LIO**), were retrieved in all trees with strong support in the prefered topology (SR = 100%, 100% and 97% respectively). (*Hormurus* + *Liocheles*) (**HOL**) is observed in all analyses except those under IW with *K = 1–2* (*Hormiops* is

Table 18. Sensitivity data for the major taxonomic groups derived from the SCTs obtained by simultaneous analysis of the morphological and molecular dataset (gaps included or excluded), under equal weights (EW) and implied weights (IW) with ten values for the concavity constant (*K*). Taxonomic groups: AU = Australian *Hormurus* (including *Hormurus polisorum*); CAF = *Iomachus politus* + *Opisthacanthus lecomtei*; HHL = *Hormiops* + *Hormurus* + *Liocheles* (*Liocheles* sensu lato); HML = *Hormiops* + *Liocheles*; HOL = *Hormurus* + *Liocheles*; HOR = *Hormurus*; INC = *Iomachus nitidus* + *Chiromachus* ochropus; IOM = *Iomachus sensu lato*; LIO = *Liocheles sensu stricto*; MIC = *Opisthacanthus* (*Monodopisthacanthus*) + *I. nitidus* + *C. ochropus*; MOC = *Opisthacanthus* (*Monodopisthacanthus*) + *C. ochropus*; OP = *Opisthacanthus* (*Opisthacanthus*); OPH = OPI + HHL; OPI = *I. politus* + *Opisthacanthus (Opisthacanthus)*; PIA = Pacific island arc *Hormurus* (see text for detailed list of species). Legend: M = resolved monophyly under those conditions; Para = resolved paraphyly under those conditions; Poly= resolved polyphyly under those conditions; U = lack of resolution potentially consistent with monophyly.

		IOM	INC	MOC	MIC	OP	OPI	CAF	OPH	HHL	HOL	HML	LIO	HOR	PIA	AU
Gaps included	Ew	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=1	Poly	Para	M	M	Para	M	M	M	M	Para	M	M	M	M	M
	IW, *K*=2	Poly	Para	M	M	Para	M	M	M	M	Para	M	M	M	M	M
	IW, *K*=3	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=4	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=5	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=6	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=7	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=8	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=9	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=10	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
Gaps excluded	Ew	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=1	Poly	Para	M	M	Para	M	M	M	M	Para	M	M	M	M	M
	IW, *K*=2	Poly	Para	M	M	Para	M	M	M	M	Para	M	M	M	M	M
	IW, *K*=3	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=4	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=5	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=6	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=7	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=8	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=9	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M
	IW, *K*=10	Poly	Para	M	Para	Para	M	M	M	M	M	Para	M	M	M	M

Fig. 55. Strict consensus of the MPTs obtained by 22 simultaneous analyses of the morphological and aligned molecular data in which weighting regime was varied and gaps were included or excluded.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Chiromachus_ochropus_6894
CHO
Opisthacanthus_(M.)_piceus_6260
O._(M.)_madagascariensis_2811
O._(M.)_madagascariensis_2812
O._(M.)_madagascariensis_2800
MOP
Opisthacanthus_(O.)_elatus_1837
Opisthacanthus_lecomtei_2194A
Opisthacanthus_lecomtei_1608
Iomachus_politus_3256
Iomachus_politus_1514
OPI
Hormiops_infulcra_2185
HOM
Liocheles_malaya_1909
Liocheles_longimanus_6388
Liocheles_australasiae_1854
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Liocheles_australasiae_2183
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LIO
Hormurus_penta_1817
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Hormurus_neocaledonicus_5542
PIA
HOR
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Hormurus_papuanus_2718
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Hormurus_chydaeostigmata_8016
Hormurus_chydaeostigmata_8015
Hormurus_nyawaygi_6354
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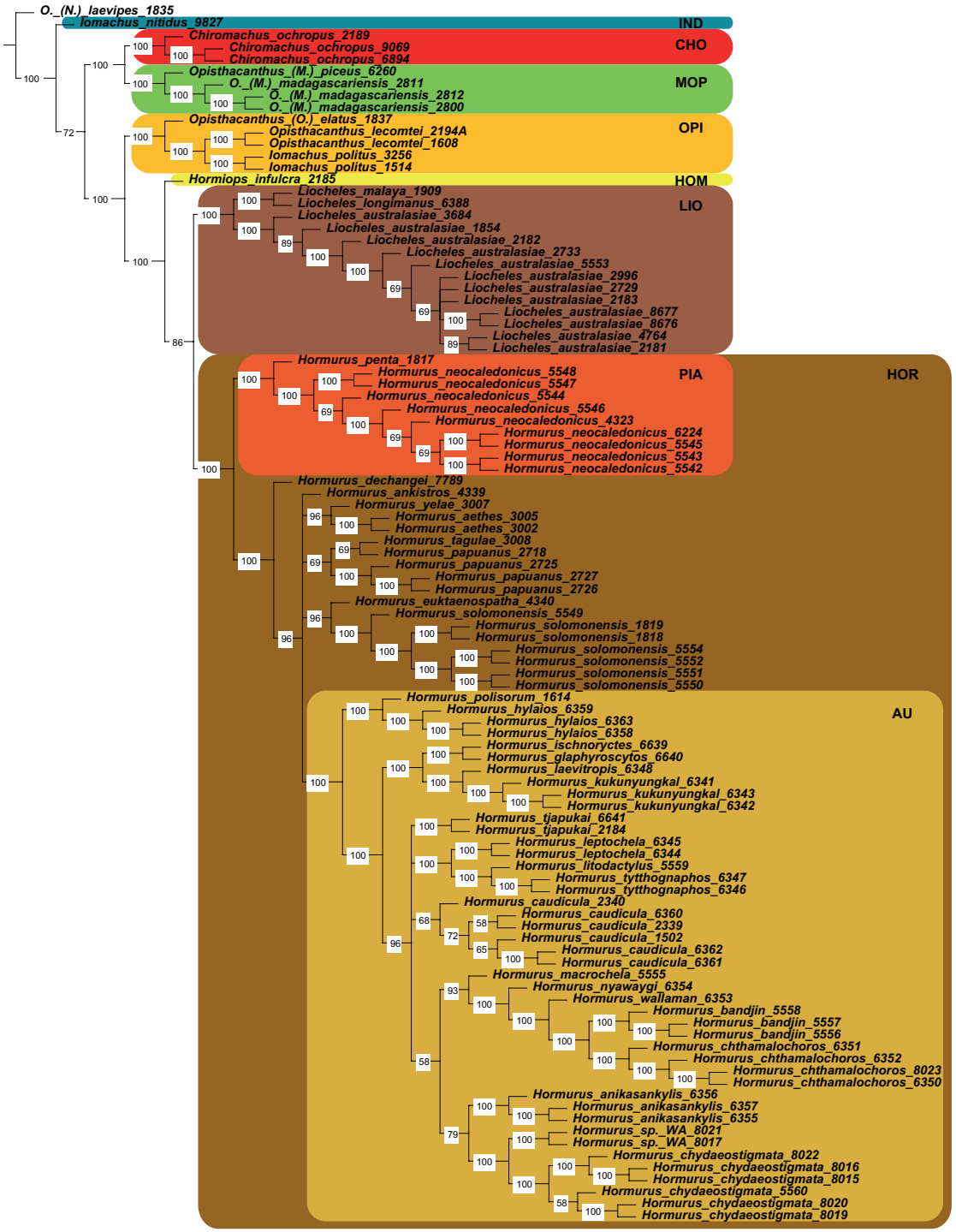
Hormurus_bandjin_5558
Hormurus_bandjin_5557
Hormurus_bandjin_5556
Hormurus_chthamalochoros_6351
Hormurus_chthamalochoros_6352
Hormurus_chthamalochoros_8023
Hormurus_chthamalochoros_6350
AU

Fig. 56. Majority rule (>50%) consensus of the MPTs obtained by 22 simultaenous analyses of the morphological and aligned molecular data in which weighting regime was varied and gaps were included or excluded. Frequencies with which nodes were retrieved are indicated. Nodes retrieved in less than 50% of the analyses are collapsed.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Chiromachus_ochropus_9069
Chiromachus_ochropus_6894
CHO
Opisthacanthus_(M.)_piceus_6260
O._(M.)_madagascariensis_2811
O._(M.)_madagascariensis_2812
O._(M.)_madagascariensis_2800
MOP
Opisthacanthus_(O.)_elatus_1837
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Iomachus_politus_3256
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OPI
Hormiops_infulcra_2185
HOM
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Liocheles_longimanus_6388
Liocheles_australasiae_3684
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LIO
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Hormurus_neocaledonicus_4323
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Hormurus_neocaledonicus_5545
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Hormurus_neocaledonicus_5542
PIA
HOR
Hormurus_dechangei_7789
Hormurus_ankistros_4339
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Hormurus_aethes_3005
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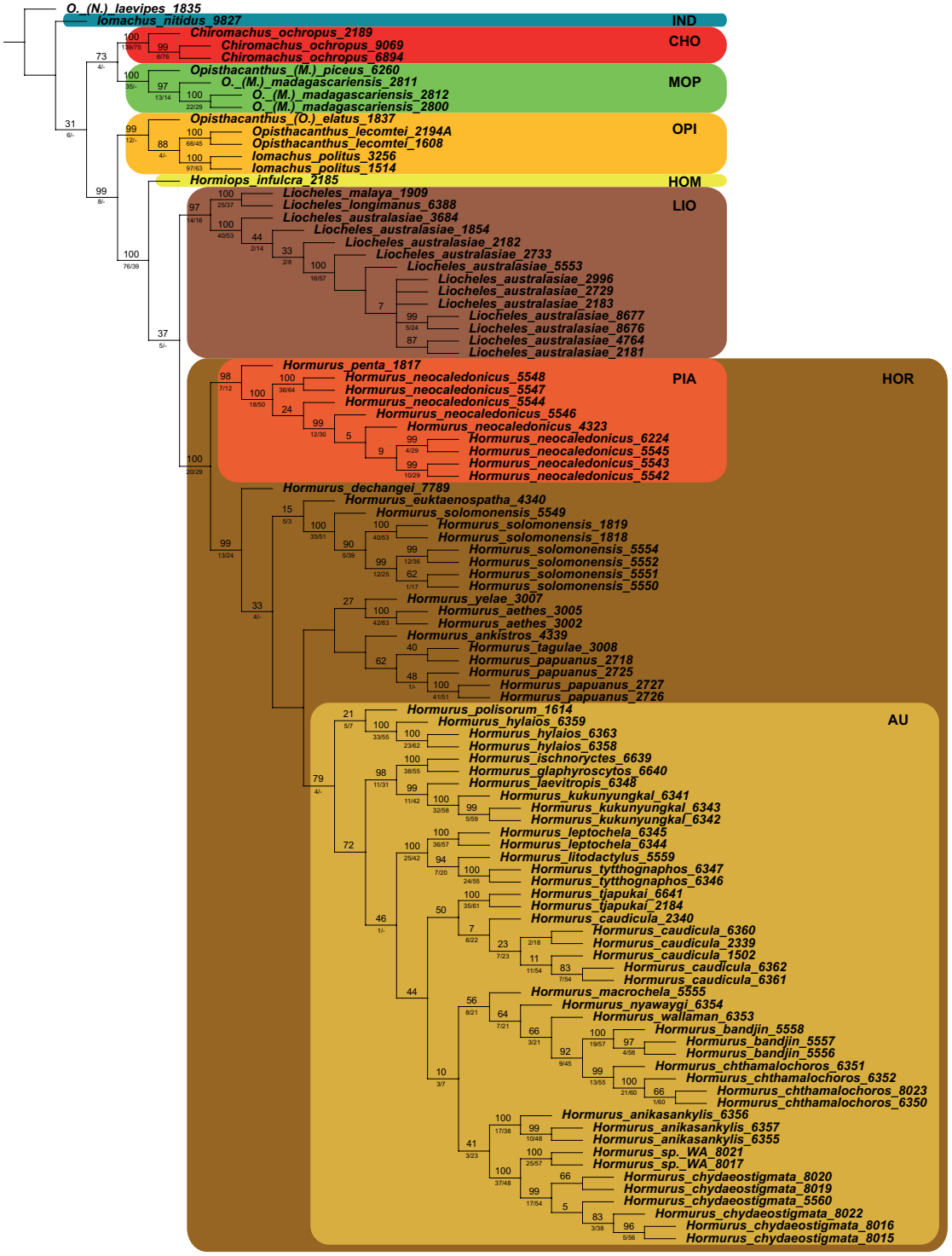
AU

Fig. 57. Optimal tree of the simultaneous analysis of the morphological and aligned molecular data under weighting regime that minimised length et maximised fit, and remains congruent with the MRT of the sensitivity analysis (strict consensus of the three MPTs obtained by IW analysis under *K = 9* and gaps included). Symmetric resampling frequencies (GC scores) are indicated above each branch and Bremer supports (absolute and relative) below.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Iomachus_politus_3256
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Hormurus_chydaeostigmata_8015
AU

Table 19. Comparison of alternative hypotheses of phylogenetic relationships in Indo-Pacific Liochelidae Fet & Bechly, 2001 based on molecular data.

Constrained topology	Step difference	Total fit difference
Monophyletic *Iomachus*	64	4.67 (0.41%)
MIC (*C. ochropus* + *I. nitidus* + *Opisthacanthus* (*Monodopisthacanthus*) + *Palaeocheloctonus*)	16	0.52 (0.05%)
(*C. ochropus* + *I. nitidus*)(*Opisthacanthus* (*Monodopisthacanthus*) + *Palaeocheloctonus*)	32	1.31 (0.12%)

then placed as the sister taxon of *Liocheles* s.s., clade **HML**) and received in the optimal tree a much lower symmetric resampling frequency (37%) than in the analysis of the molecular partition. The **PIA** clade is basal to all other *Hormurus* in all analyses and robustly supported in the optimal tree (SR = 98%). Australian species are always clustered in a monophyletic clade (**AU**) that receives a much higher branch support than in the molecular analysis (SR = 79%). The positioning of *H. dechangei* between PIA and the other *Hormurus* species is reported in all analyses except that under IW with *K = 10* when gaps are included. Besides it also receive a high branch support in the optimal tree (SR = 99%).

Constrained searches. Differences in length and fitness between topologies obtained by constrained searches under the "optimal" weighting regime (IW with *K = 9* and gaps included) and unconstrained topologies are presented in table 19. Making *Iomachus* s.l. monophyletic on the optimal topology cost 64 extra steps and a fitness loss of 0.41%. On the other hand, only 16 additional steps and a 0.05% loss in fitness, and 32 additional steps and a 0.12% loss in fitness are necessary to retrieve the monophyletic groupings (*C. ochropus* + *I. nitidus* + *Opisthacanthus* (*Monodopisthacanthus*)+ *Palaeocheloctonus*) and (*C. ochropus* + *I. nitidus*) (*Opisthacanthus* (*Monodopisthacanthus*) + *Palaeocheloctonus*) respectively.

Synthesis. A summary of phylogenetic relationships among the Indo-Pacific liochelid genera and within the genus *Hormurus* as retrieved in the simultaneous analysis of the morphological and molecular datasets is presented in figures 58 and 59 respectively. Unambiguously optimized morphological synapomorphies and the number of molecular synapomorphies are indicated for each node and terminal taxa. Besides, a list of unambiguous morphological characters changes (synapomorphies and parallel derivations of apomorphic states) supporting each node and terminal taxa is provided in appendix 4. The length (steps), fitness, consistency index (CI), and retention index (RI) of informative morphological characters on the optimal tree obtained with simultaneous analyses of morphological and molecular data (SCT of the MPTs obtained under IW with *K = 9* and when gaps were included) are presented in table 20.

Fig. 58. Summary cladogram indicating the most parsimonious reconstruction of relationships among the Indo-Pacific Liochelidae Fet & Bechly, 2001 according to the optimal tree selected for the simultaneous analyses. Legend: ■, uniquely derived apomorphic states; □, parallel derivations of apomorphic states (unambiguously optimized changes only). The number above each square corresponds to the character number, and the number below to the character state. Numbers below branches provide the count of molecular synapomorphies (gaps included) for each nodes (one to eight) and terminal taxa. Refer to chapter 1 for character list and descriptions.

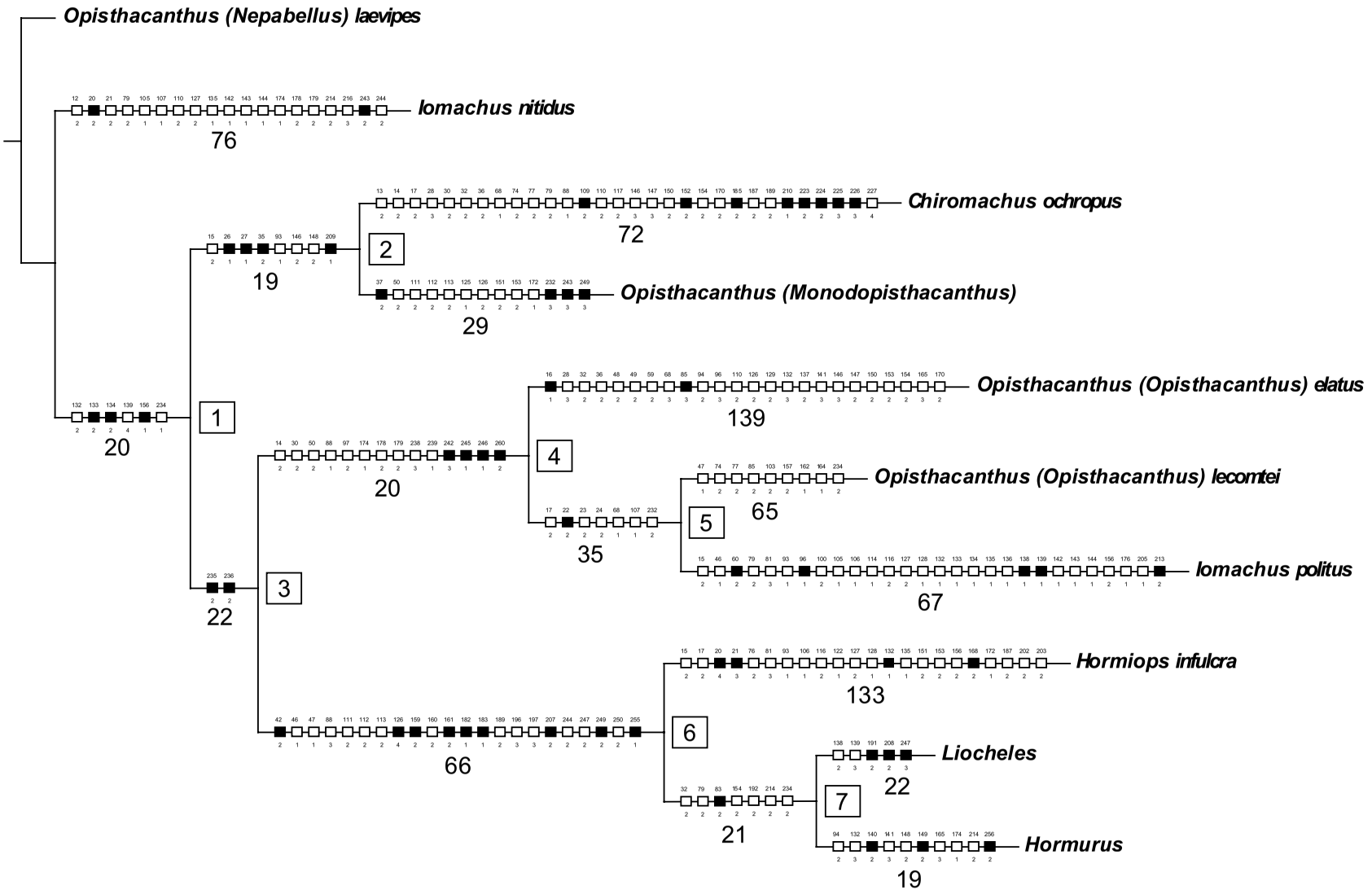
Opisthacanthus (Nepabellus) laevipes
Iomachus nitidus
76
Chiromachus ochropus
72
2
19
Opisthacanthus (Monodopisthacanthus)
29
Opisthacanthus (Opisthacanthus) elatus
139
1
20
4
20
Opisthacanthus (Opisthacanthus) lecomtei
65
5
35
Iomachus politus
67
3
22
Hormiops infulcra
133
6
66
Liocheles
22
7
21
Hormurus
19

Fig. 59. Summary cladogram indicating the most parsimonious reconstruction of relationships within the genus *Hormurus* Thorell, 187 according to the optimal tree selected for the simultaneous analyses. Legend: ■, uniquely derived apomorphic states; □, parallel derivations of apomorphic states (unambiguously optimized changes only). The number above each square corresponds to the character number, and the number below to the character state. Numbers below branches provide the count of molecular synapomorphies (gaps included) for each nodes (eight to ten) and terminal taxa.

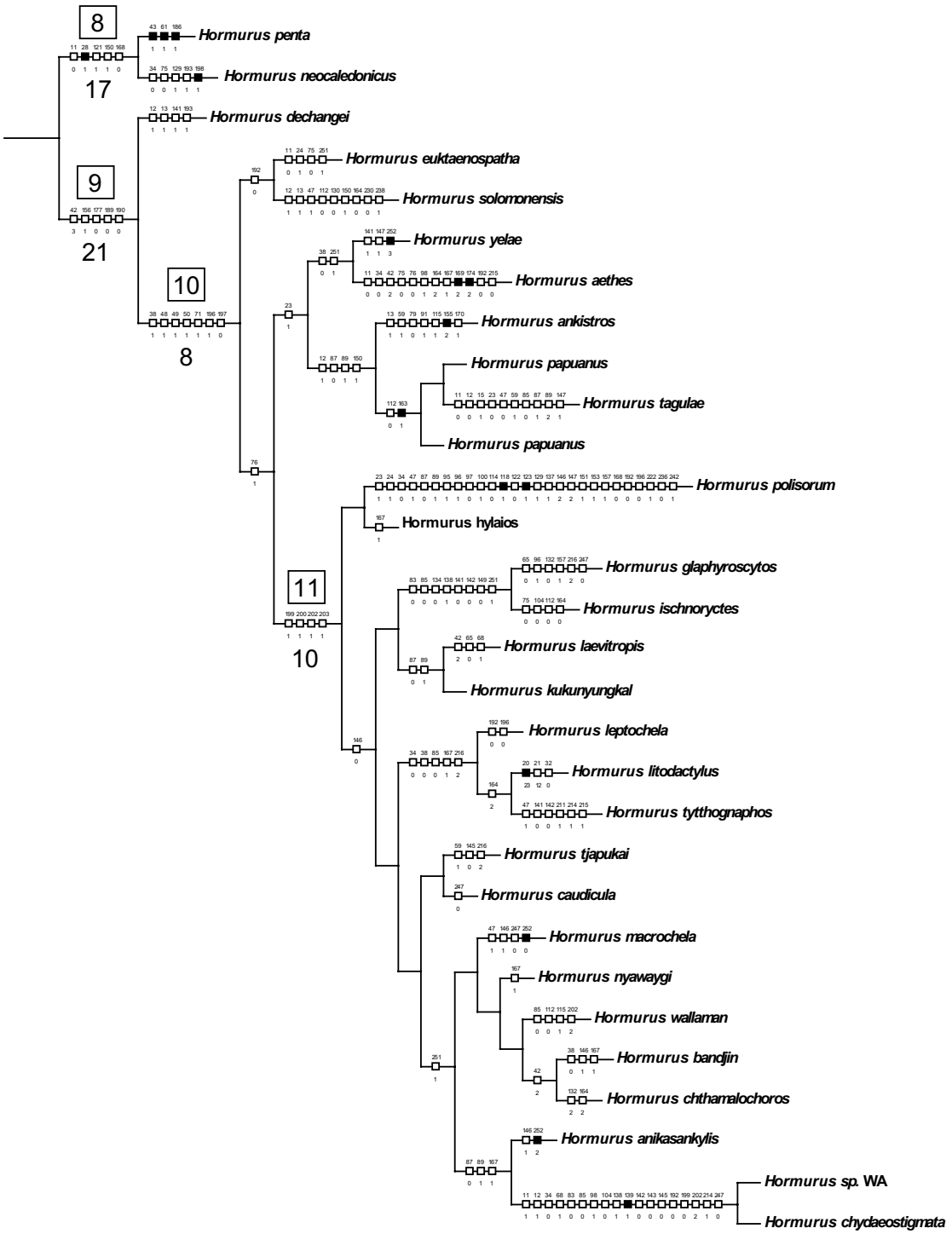
8
17
Hormurus penta
Hormurus neocaledonicus
Hormurus dechangei
9
21
10
8
Hormurus euktaenospatha
Hormurus solomonensis
Hormurus yelae
Hormurus aethes
Hormurus ankistros
Hormurus papuanus
Hormurus tagulae
Hormurus papuanus
Hormurus polisorum
Hormurus hylaios
11
10
Hormurus glaphyroscytos
Hormurus ischnoryctes
Hormurus laevitropis
Hormurus kukunyungkal
Hormurus leptochela
Hormurus litodactylus
Hormurus tytthognaphos
Hormurus tjapukai
Hormurus caudicula
Hormurus macrochela
Hormurus nyawaygi
Hormurus wallaman
Hormurus bandjin
Hormurus chthamalochoros
Hormurus anikasankylis
Hormurus sp. WA
Hormurus chydaeostigmata

Table 20. Length (steps), fit (Fi), consistency index (CI) and retention index (RI) of informative morphological characters on the optimal tree obtained by simultaneous analysis of the morphological and aligned molecular data.

Char	Steps	Fit	CI	RI
0	23	0.35	26	76
1	21	0.37	29	78
2	13	0.6	54	76
3	14	0.64	64	81
4	11	0.69	64	81
5	14	0.64	64	79
6	14	0.56	50	88
7	17	0.53	53	82
8	13	0.6	54	88
9	17	0.53	53	82
11	12	0.45	8	74
12	9	0.53	11	68
13	6	0.64	17	64
14	2	0.9	50	86
15	9	0.53	11	77
16	4	0.82	50	67
17	3	0.82	33	71
20	6	0.72	50	1
21	4	0.82	50	1
22	1	1	100	100
23	6	0.64	17	83
24	8	0.56	13	46
26	3	0.9	67	92
27	3	0.9	67	92
28	5	0.72	40	81
30	2	0.9	50	86
31	1	1	100	100
32	4	0.75	25	73
33	1	1	100	100
34	6	0.64	17	79
35	1	1	100	100
36	2	0.9	50	67
37	1	1	100	100
38	8	0.56	13	81
40	4	0.75	25	73
42	9	0.6	33	92
45	3	0.82	33	78
46	2	0.9	50	91
47	10	0.5	10	70
48	2	0.9	50	97
49	2	0.9	50	97
50	3	0.82	33	83
53	2	0.9	50	80
59	6	0.64	17	62

Char	Steps	Fit	CI	RI
60	1	1	100	100
65	5	0.69	20	69
68	8	0.54	25	86
71	7	0.6	14	83
74	3	0.9	67	75
75	6	0.64	17	67
76	5	0.69	20	90
77	3	0.82	33	60
79	5	0.69	20	56
80	1	1	100	100
81	2	0.9	50	50
82	4	0.75	25	50
83	3	0.82	33	90
85	11	0.5	18	78
87	7	0.6	14	88
88	3	0.9	67	95
89	10	0.42	20	87
90	3	0.82	33	33
91	2	0.9	50	1
93	3	0.82	33	78
94	2	0.9	50	96
95	8	0.56	13	74
96	7	0.64	29	83
97	7	0.64	29	79
98	2	0.9	50	89
100	2	0.9	50	50
101	9	0.46	22	89
102	2	0.9	50	80
103	5	0.69	20	50
104	4	0.75	25	92
105	4	0.75	25	82
106	3	0.82	33	50
107	5	0.69	20	75
108	6	0.64	17	29
109	1	1	100	100
110	3	0.82	33	50
111	3	0.82	33	82
112	7	0.6	14	76
113	3	0.82	33	82
114	2	0.9	50	50
115	6	0.69	33	60
116	3	0.82	33	33
117	2	0.9	50	67
119	4	0.75	25	50

Table 20. Length (steps), fit (Fi), consistency index (CI) and retention index (RI) of informative morphological characters on the optimal tree obtained by simultaneous analysis of the morphological and aligned molecular data. (Continued)

Char	Steps	Fit	CI	RI
120	4	0.75	25	40
121	3	0.82	33	83
122	2	0.9	50	1
125	3	0.82	33	67
126	5	0.82	60	83
127	4	0.75	25	50
128	2	0.9	50	50
129	5	0.69	20	71
130	3	0.82	33	86
132	11	0.34	18	77
133	3	0.82	33	60
134	4	0.75	25	57
135	5	0.69	20	33
136	2	0.9	50	67
137	2	0.9	50	1
138	7	0.64	29	84
139	8	0.59	38	85
140	1	1	100	100
141	12	0.29	17	79
142	7	0.6	14	79
143	5	0.69	20	84
144	4	0.75	25	82
145	8	0.56	13	78
146	11	0.35	18	84
147	10	0.42	20	77
148	6	0.64	17	89
149	2	0.9	50	97
150	5	0.69	20	85
151	3	0.82	33	60
152	1	1	100	100
153	4	0.75	25	50
154	3	0.82	33	80
156	6	0.64	17	84
157	4	0.75	25	50
158	2	0.9	50	1
159	1	1	100	100
160	2	0.9	50	92
161	1	1	100	100
162	3	0.82	33	33
163	1	1	100	100
164	8	0.6	25	68
165	2	0.9	50	96
167	9	0.53	11	71
168	5	0.75	40	83
169	4	0.82	50	78
170	4	0.75	25	40
172	2	0.9	50	75
174	5	0.75	40	86
175	4	0.75	25	91
176	2	0.9	50	50
177	3	0.82	33	93
178	2	0.9	50	80
179	2	0.9	50	80
182	1	1	100	100
183	1	1	100	100
185	1	1	100	100
187	4	0.75	25	79
189	3	0.82	33	93
190	4	0.75	25	89
191	1	1	100	100
192	6	0.64	17	86
193	3	0.82	33	90
194	2	0.9	50	93
195	2	0.9	50	93
196	6	0.65	33	92
197	8	0.54	25	92
198	1	1	100	100
199	3	0.82	33	94
200	2	0.9	50	98
202	7	0.6	14	85
203	4	0.75	25	93
205	2	0.9	50	50
206	2	0.9	50	86
207	1	1	100	100
208	1	1	100	100
209	1	1	100	100
210	1	1	100	100
211	7	0.6	14	84
213	1	1	100	100
214	8	0.56	13	83
215	6	0.64	17	81
216	6	0.65	33	80
222	9	0.53	11	62
223	1	1	100	100
224	1	1	100	100
225	1	1	100	100
226	1	1	100	100
227	5	0.8	60	50

Table 20. Length (steps), fit (Fi), consistency index (CI) and retention index (RI) of informative morphological characters on the optimal tree obtained by simultaneous analysis of the morphological and aligned molecular data. (Continued)

Char	Steps	Fit	CI	RI
228	2	0.9	50	1
230	4	0.75	25	81
231	4	0.75	25	75
232	4	0.9	75	86
234	5	0.69	20	50
235	1	1	100	100
236	2	0.9	50	89
238	6	0.64	33	81
239	2	0.9	50	80
240	2	0.9	50	86
241	3	0.9	67	89
242	4	0.82	50	85
243	4	1	100	100
244	2	0.9	50	92
245	1	1	100	100
246	1	1	100	100
247	10	0.53	20	86
249	2	1	100	100
250	2	0.9	50	88
251	4	0.75	25	88
252	3	1	100	100
255	1	1	100	100
256	1	1	100	100
257	2	0.9	50	86
260	1	1	100	100
261	1	1	100	100
262	2	1	100	100

2.4 DISCUSSION

Homoplasy and phylogenetic information of the different datasets. In the present study, the morphological and molecular datasets appear to be equally informative with very similar fitness, CI and RI indices (tab. 21). Characters from the hemispermatophores (char. 234-259) showed the highest indices of the morphological dataset (tabs 20-21), demonstrating the low level homoplasy and the high phylogenetic signal conveyed by these structures. The metasoma (char. 172-216), pedipalp finger morphosculptures (char. 17-36) and trichobothriotaxy (char. 37-61) also proved to be phylogenetically important with a relatively low level of homoplasy. However, character systems such as pedipalp carination (char. 62-92), cuticular ornamentation of the pedipalp (char. 93-114), carapace and tergites (char. 129-154) appear to be more homoplastic and therefore less informative for phylogenetic studies. In the molecular dataset, the nuclear genes (a8S and 28S) are much more informative than the mitochondrial genes (tab. 21). Among the latter, COI is the more homoplastic and less informative locus. Although not as high as those of nuclear genes, fitness, CI and RI indices of 12S and 16S are still relatively high, suggesting that these mitochondrial genes provide useful phylogenetic signals.

Liochelid systematics. The genus *Iomachus* is always retrieved as polyphyletic. The Indian *Iomachus* are either placed in a clade with *C. ochropus* and the two Malagasy genera, *Opisthacanthus* (*Monodopisthacanthus*) and *Palaeocheloctonus* (morphological analysis), or basally as sister to the remaining taxa (molecular and combined analyses) while the Afrotropical *I. politus* consistently nests with *O. lecomtei* within the subgenus *Opisthacanthus* which is then rendered paraphyletic. Prendini (2000) suggested to erect two new genera, one for the Afrotropical species *Iomachus borana* (Caporiacco, 1939) and *I. politus*, and one for *O.* (*O.*) *lecomtei* in order to improve the stability of the existing liochelid classification. The legitimacy of these propositions is confirmed by the present results. *Iomachus politus* is morphologically too distinct from *O.* (*O.*) *lecomtei* to justify its incorporation in the subgenus *Opisthacanthus*. *Opisthacanthus* (*O.*) *lecomtei* should be removed from it and placed in his own genus for phylogenetic consistency.

The Malagasy subgenus *Monodopisthacanthus* and the genus *Palaeocheloctonus*

Table 21. Means of fit (Fi), of consistency index (CI) and of retention index (RI) for the morphological and molecular datasets, the major characters systems, individual locus, the nuclear and mitochondrial genome on the optimal tree obtained by simultaneous analysis of the morphological and aligned molecular data.

	Fitness	CI	RI
Morphology	0.784285714	46.89162562	77.84729064
Hemispermatophores	0.8865	65.75	90
Metasoma	0.833611111	52.44444444	88.77777778
Pedipalp finger morphosculpture	0.829375	54.9375	73.25
Trichobothriotaxy	0.791538462	43.38461538	85.69230769
Pedipalp cuticular ornamentation	0.762857143	34.71428571	73.14285714
Pedipalp carinae	0.732222222	34.77777778	69.88888889
Carapace and tergite ornamentation	0.6968	32.84	73.8
Molecules	0.746795154	43.14867841	63.64757709
12S	0.785105263	47.25263158	69.26315789
16S	0.784566	46.031963	70.461187
18S	0.943714286	75.37142857	71.02857143
28S	0.877142857	60.2244898	59.95918367
COI	0.677325301	35.01445783	57.2939759
Nuclear genome	0.904880952	66.53571429	64.57142857
Mitochondrial genome	0.730679612	40.76456311	63.55339806

form a monophyletic group in all analyses of the morphological data. *Opisthacanthus* (*M.*) *apios* n.sp from Cape York (Australia) is also unambiguously placed in this clade. This significant new discovery dramatically changes the geographic range of the subgenus previously considered endemic to Madagascar. Taxa with similar trans-Indian Ocean disjunct distributions (with species in northern Australia/Melanesia/New Caledonia and Africa/Madagascar) have also been reported in marine and freshwater crustacea, freshwater fishes and plants (Weston & Crisp, 1996; Sparks & Smith, 2004; Page *et al.*, 2007; Myers & Lowry, 2009; Renner *et al.*, 2010; see chapter III). In regard of these results, species currently placed within *Monodopisthacanthus* should be transfered to *Palaeocheloctonus* as previously suggested by Prendini (2000).

The Seychellian monotypic genus *Chiromachus ochropus* always nests with the Malagasy taxa *Opisthacanthus* (*Monodopisthacanthus*) and *Palaeocheloctonus* in the optimal trees. However, the phylogenetic position of Indian *Iomachus* remains contentious in the present study. Two alternative hypotheses are obtained from the different analyses: (1) in the phylogeny derived from the morphology alone, Indian *Iomachus* nest in a clade with *C. ochropus*, *Monodopisthacanthus* and *Palaeocheloctonus*, as sister to *C. ochropus*, whereas (2) they are placed basally to all other taxa in molecular and combined analyses. The first scenario is preferred here considering that the phylogenetic position of Indian taxa retrieved in the molecular and combined analyses may be due to a sampling artefact. No DNA sample for the genus *Chiromachetes* was available, *Iomachus nitidus* was the only Indian taxon with molecular data in the present analysis. Besides, forcing the arrangment obtained in the morphological analysis, i.e. (*C. ochropus* + *I. nitidus*)(*Opisthacanthus* (*Monodopisthacanthus*) + *Palaeocheloctonus*), induced only a slight increase of length and loss of fitness and a monophyletic assemblage of taxa from India, Madagascar and Seychelles is congruent with the accepted sequence of Gondwana fragmentation.

The Indian genus *Chiromachetes* was paraphyletic in Prendini's study (2000), grouping with *Chiromachus*. It is also diagnosed as paraphyletic in the present analysis of the morphological data but *C. fergusoni* and *C. tirupati* are clustered with the Indian *Iomachus* in a monophyletic clade, sister to *C. ochropus*. In this clade, *C. tirupati* and *I. nitidus* always form a basal monophyletic pair in most analyses. Besides, comparison of the *C. tirupati* holotype

with *I. nitidus* specimens confirms the synonymy of the former. DNA samples from a single species of *Iomachus* from India were included in the combined study and male specimens of *C. fergusoni* remain unknown so far. No conclusive decision concerning the taxonomic status of *Chiromachetes* are taken here given the poor DNA taxon sampling of Indian liochelids and the incomplete dataset. However, the results obtained suggest that *Chiromachetes* might be a synonym of *Iomachus* but molecular samples and male specimens are needed to corroborate this statement.

Previous to this study, the generic status of *Hormiops* was never tested in a phylogenetic framework. Neither Lourenço & Monod (1999) who reinstated the genus, nor Prendini (2000) who subsequently placed it in synonymy with *Liocheles* s.l., based their decisions on phylogenetic analysis. In the present work, *Hormiops* is consistently placed as sister to (*Hormurus* + *Liocheles*) in molecular and combined analysis, whereas in the morphological analyses it is retrieved as sister to *Liocheles*, which is not surprising given the morphological similarity between the two genera and the high level of homoplasy. However, 133 molecular synapomorphies (fig. 58) diagnose *Hormiops* in the optimal tree from the simultaneous analysis and constraining its generic status in the morphological analysis cost only 7 extra steps and a slight fitness loss (0.18 %). *Hormiops* is therefore considered here as a valid genus, sister to *Liocheles* s.l.. Besides, in the majority of the trees obtained by the molecular and combined analyses, the monophyly of the two *Liocheles* s.l. species group, the *australasiae* species group (*Liocheles* s.s.) and the *waigiensis* species group (*Hormurus*), are well supported. Given their significant morphological differences and their non-overlapping distribution ranges (if the cosmopolitan *L. australasiae* is omitted), *Hormiops* and *Hormurus* are hereby reinstated. Finally, (*I. politus* + *Opisthacanthus* (*Opisthacanthus*)) is retrieved as the sister taxon to the monophyletic assemblage of *Hormiops*, *Hormurus* and *Liocheles*.

Two species, i.e. *H. neocaledonicus* from New Caledonia and *H. penta* from the Solomon Islands are consistently grouped in a basal clade (PIA) as sister to the remaining *Hormurus*. *Hormurus samoa* n. sp. from Samoa, for which there are currently no DNA samples, is unambiguously placed within the PIA clade in the morphological analysis. Moreover, four other species, *H. boholiensis* and *H. dechangei* from the Philipines Islands, *H. insculptus* from West

Papua, and *H. weberi* from Sulawesi, are diagnosed as phylogenetic intermediates between the PIA clade and the remaining species in the morphological analysis. DNA data are only available for *H. dechangei* and the position of the other species could therefore not be tested in the molecular and combined analyses. In the molecular analysis, *H. dechangei* nests within the Melanesian species, but the node received low support in the optimal tree (SR = 15 %). However, *H. dechangei* is retrieved as intermediate between PIA and the other *Hormurus* in the simultaneous analysis, obtaining a high branch support in the optimal tree (SR = 99 %). The phylogenetic relationships remain equivocal for the other Melanesian species. Most of the nodes were not stable and unsupported or with low branch supports, and were collapsed in the consensus trees of sensitivity analyses. On the other hand, all Australian species and *H. polisorum* from Christmas Island constitute a terminal clade within *Hormurus* in most analyses. This monophyletic grouping is well supported in molecular and combined analyses, but very weakly supported in the morphological analysis. The lack of resolution within the Melanesian and Australian *Hormurus* groups can probably be attributed to the uninformative morphology (high level of homoplasy and lack of unambiguous synapomorphies within the genus) and to the incomplete molecular dataset which includes so far numerous Australian species but none from Maluku/West Papua (Indonesia) and Torres Strait/Cape York Peninsula. Filling these two major gaps in the molecular dataset is crucial to clarify relationships within the genus *Hormurus*. According to the morphological analysis, the two regions mentioned above harbour species that are potentially nested between the PIA clade and Papuan species and between Papuan and Australian species respectively (see below). However, morphological data do not provide sufficient phylogenetic signal and additional molecular data are necessary to decipher the structure of this part of the tree.

Directions for future research. The lack of phylogenetic resolution within *Hormurus* is probably due to the incomplete dataset. Whereas DNA samples of Australian *Hormurus* are relatively well represented (19 species: 55% of the 34 known species and 65% of the 29 species included in the molecular dataset), no tissue samples for any species from two biogeographically important regions, i.e. East Maluku/West Papua and Cape York/Torres Strait, are

currently available for DNA isolation. The islands of Wallacea and Western Papua represent the geological and biogeographical interface between the Asian and Australian continental shelves. This region is an aggregate of terranes with Asian, Australian and Melanesian affinities (Hall, 2001; see also chapter III). It is considered a major biodiversity hotspot separating the Indo-Malayan and Australasian biogeographical realms and includes representatives from each of these regions as well as many endemics. Six endemic *Hormurus* species were described from this region (1) *Hormurus davydovi* (Birula, 1933) (Aru Islands, West Papua) and *H. weberi* Pocock, 1894 (Sulawesi), morphologically close to the basal PIA clade; *H. insculptus* Thorell, 1888 (West Papua), morphologically close to the Australian species; and *Hormurus karschii* Keyserling, 1885 (West Papua) and *Hormurus waigiensis* (Gervais, 1843) (Raja Ampat, West Papua), apparently more closely related to Papuan forms. Besides, *H. halmaherae* n. sp., an undescribed species with Melanesian affinities, has been discovered in Halmahera and several juvenile specimens from Seram and Tanimbar Islands were examined but it was not possible to assess their taxonomic status. However, they probably belong to other undescribed species. On the other hand, *Hormurus* species from the Cape York Peninsula and Torres Strait Islands are morphologically intermediate between the Australian and Papuan forms. The Cape York Peninsula is recognized as a major dispersal corridor, along which repeated biotic exchanges between northern Australia and New Guinea took place during sea levels lowstands (Lomolino *et al.*, 2006). The Cape York/Torres Strait region thus represents a second biogeographic suture zone that is extremely important to understand phylogenetic relationships within *Hormurus*. Gathering DNA sequences from the taxa in the above-mentioned areas is therefore crucial for the reconstruction of a more stable and phylogeny.

The poor resolution of the phylogenetic reconstruction within *Hormurus* is also attributed to the facts that numerous characters may be homoplasious, e.g. cuticular ornamentation, pedipalp elongation, and obscure the phylogenetic signals of the less numerous informative characters. Characters that can change rapidly in response to varying environments are unlikely to be well correlated with phylogeny and are therefore more likely to be homoplasious. Convergence may severely hinder our understanding of evolutionary relationships of organisms and lead to the development of taxonomic classification incongruent with phylogeny. Incorpo-

rating more characters less subject to ecological changes, e.g. internal anatomy, is potentially an efficient way to address the problem and yield improved phylogenetic signals. Therefore, more emphasis should arguably be placed on the study of internal morphology in order to uncover additional characters and complete the dataset for systems already studied, i.e. book lungs, ovariuterus.

2.5 APPENDICES

2.5.1 Terminal taxa, specimens and tissues samples used for cladistic analysis of the Indo-Pacific Liochelidae. Depositories for material examined are abbreviateds as follows: AMNH, American Museum of Natural History (New York, USA); BPBM, Bernice P. Bishop Museum (Honolulu, Hawaii, USA); CAS, Californian Academy of Sciences (San Fransisco, USA); LM, Lionel Monod personal collection, to be deposited in the collection of the MHNG; LP, Lorenzo Prendini DNA tissue collection (AMNH, New York, USA); MHNG, Muséum d'histoire naturelle (Geneva, Switzerland); MNHN, Muséum National d'Histoires Naturelles (Paris, France); MRHN, Musée Royal d'Histoire Naturelle de Belgique (Bruxelles, Belgium); NHML, Natural History Museum (London, United Kingdom); NHMW, Naturhistorisches Museum Wien (Wien, Austria); NTM, NorthernTerritory Museum of Arts and Sciences (Darwin, Northern Territory, Australia); NNHM, National Natuurhistorisch Museum (Leiden, The Netherlands); RMBR, Raffles Museum of Biodiversity Research (Singapore); QM, Queensland Museum (Brisbane, Australia, Queensland); USNM, United State National Musem of Natural History (Smithsonian Institution), (Washington, DC, USA); WAM, Western Australian Museum (Perth, Australia). All the material incorporated in the molecular dataset is part of the LP DNA tissue collection.

OUTGROUP

GENUS *CHIROMACHETES* Pocock, 1899

Chiromachetes fergusoni Pocock, 1899. INDIA, KERALA, Ponmudi, Travancore, H.Ferguson, 1 ♀ (Holotype, NHML 1899.7.11.1.TYPE).

Chiromachetes tirupati Lourenço, 1997. INDIA, ANDRAPRADESH, Tirupati (13º39'Nx79º25'E), IV.1966, R.P.Sreenivasa-Reddy, 1 ♂ (Holotype, MNHN-RS 8528).

GENUS *CHIROMACHUS* Pocock, 1893

Chiromachus ochropus (C.L.Koch, 1837). SEYCHELLES, INDIAN OCEAN: S.M.S. Planet, 1904 (1053/08), 1 ♂ (ZMB 15167); S.M.S. Silhouette, Brauer, 1 ♂ (ZMB 15168), 1 ♀ (ZMB

15169); 1 ♀, (Koel1bel's NachlaB, Acquis. No. 1896.VIII.613) (NHMW 1731). Île de France, Dröger, 1 ♂ (ZMB 46). Frigate Island, 10.VII.1967, under stones, J. F. G. Lionette, 2 ♂♂, 2 ♀♀, (USNM, jar 101); 1.X.2002, J. Gerlach, 1 imm. (LP 2189); palm forest (seasonally dry) near Grande Anse, 04º35'34.3''Sx55º56'20.3''E, 93 m, 16.VII.2008, under logs and rocks partially buried on the ground, L. Monod, 1 ♂, 2 ♀, 1 imm. (LM; LP 9069). Mahé, 10–18.II.1885, Frundsberg Expedition, 1 ♀, imm. (NHMW 1732). Praslin, 1 imm. (ZMB 15185); 1.2006, W.R. Lourenço, 1 imm. (LP 6894).

Genus *Iomachus* Pocock, 1893

Iomachus laeviceps (Pocock, 1890). INDIA, TAMIL NADU, Nilgiris, 1000', J. R. Henderson, 1 ♂, 1 ♀, 4 imm. (NHML 1891.11.20.9.15). Madras (Chennai), E. Thurston, 4 ♂♂, 3 ♀♀, 3 imm. (NHML).

Iomachus malabarensis Pocock, 1900. INDIA, KARMATAKA, Mangalore, R. C. Wroughton (p.), Battie (c.), TYPES 3 ♂♂, 3 ♀♀ (NHML 1896.7.30.75-80). SOUTH INDIA, Carl & Escher, no 6811, 1 ♀, 2 imm. (MHNG); no 6813, 5 imm. (MHNG).

Iomachus nitidus Pocock, 1900. INDIA, ANDRHA PRADESH, Tirupati, 50 km SW, dry deciduous forest, on slope of hill, under medium-sized stones, 2009, 1 pedipalp (LP 9827). KARNATAKA, Biligiri Rangan Hills (NE Nilgiri), 10 km NE Dhimbam, 1200 m, sifting, 29.XI.1972, C. Besuchet & I. Löbl, 2 imm. (MHNG). INDIA, TAMIL NADU, Nilgiris, Hill-Grove, Carl & Escher, 1 imm. (MHNG).

Iomachus politus Pocock, 1896. BRITISH EAST AFRICA (= KENYA), Woi, Ph. Oberlaender, 1 ♀ (NHMW 1735). GERMAN EAST AFRICA, 1905, Steindachner, 6 ♂♂, 9 ♀♀, 1 aub./juv. (NHMW 1733). Mikindani, 1897.XXI, Reimer, 4 ♀♀ (NHMW 1734). MOZAMBIQUE, Pflanzung Nangoro near Poro Amelia, 1928/29, M. Zitzmann, 1 ♂ (NHMW 1736). TANGANYIKA, W. V. Harris, J.Omer Gosper, 1 imm. (NHML). 15 mi S of Handeni, 153.XI.1957, 630 m, E. S. Ross & R. E. Leech, 1 ♂ (CAS). 20 mi SW of Morogoro, 15.XI.1957, 450 m, E. S. Ross & R. E. Leech,

1 ♂, 1 imm. (CAS). TANZANIA, 4.VI.1999, T. Gearheart, 1 ♂, 1 imm. (LP 1514); VII.2004, R. MacInnes, 1 ♀ (LP 3256). BAGAMOYO DISTRICT, Forest Proper, Kiono Forest, Makange Forest Reserve, I.1990, collected by participants in frontier, 2 imm. (MHNG); Frontier Tanzania, Kiono Forest Reserve, VIII.1989, J. Bryant, 1 ♀ (MHNG-KMH 6612); Kiono Forest Reserve, Coast Region, 6°10'Sx35°35'E, 1050 ft asl, coastal forest, under bark of rotting/fallen tree, 29–30.III.1986, K. M. Howell, 1 ♀ (MHNG-KMH 3311); 1 ♂ (MHNG-KMH 3312); 18.I.1986, J. Kiellmann, 1 imm. (MHNG-KMH 3348); 19.I.1986, J. Kiellann, 1 ♂ (MHNG-KMH 3347). TANZANIA, TANGA REGION, Hadeni, IX.2006, J. Beraducci, 2 ♂♂, 4 ♀♀, 4 imm. (AMNH). TANZANIA, UTETE DISTRICT, Kiwengoma Forest Reserve, 8º19'–8º22'Sx38º54'–38º59'E, elev. 1000–1750 ft., J. Kingdon, 1 imm. (CAS).

Iomachus punctulatus Pocock, 1897. INDIA, KERALA/TAMIL NADU: Anamalai Hills, Attakatti, Carl & Escher, 1 ♀ (MNHG); Koimbatur, W. Davidson Esquire, 1 ♂, 1 ♀ (Types, NHML 1888.16. TYPE); Kadamparai (3500 ft), 5.VIII.1963, P. Susai Nathan (H. L. Stahnke leg.), 1 imm. (CAS, CASENT 9026735, ASU 63-1160), 1 imm. (CAS, CASENT 9026734, ASU 63-1161). SOUTH INDIA: Pa Bris…?, Kukkal, Carl & Escher (no 6815), 1 ♀, 2 imm. (MHNG). Palnis inf, Tan Dikuli, Carl & Escher (no 6814), 1 ♀, 1 imm. (MNHG).

Genus *Opisthacanthus* Peters, 1861

Subenus *Monodopisthacanthus* Lourenço, 2001

Opisthacanthus* (*Monodopisthacanthus*) *apios n. sp. AUSTRALIA, QUEENSLAND, Somerset, 8.VII.1976, under logs and bark of logs in mesic forest, E. Cameron, 1 ♀, 3 imm. (USNM 00949).

Opisthacanthus* (*Monodopisthacanthus*) *madagascariensis Kraepelin, 1894. MADAGASCAR, FIANARANTSOA PROVINCE, Forêt d'Analalava, 29.6 km 280° W Ranohira, 22°35'30''Sx45°07'42''E, 700 m, B.L. Fisher, 1.II.2003–5.II.2003, general collecting, tropical dry forest, C. E. Griswold *et al.*, 2 ♂♂ (LP 2800). Parc National d'Isalo, Ambovo Springs, 29.3 km 4° N Ranohira, 22°17'54''Sx45°21'06''E, 990 m, 9.II.2003–14.II.2003, pitfall trap in Uapaca

woodland, B. L. Fisher, C. E. Griswold *et al.*, 1 imm. (LP 2812). MAHAJANGA PROVINCE, general collecting, B. L. Fisher, C. E. Griswold *et al.*: Parc National de Namoroka, 9.8 km 300° WNW Vilanandro, 16°28'00''Sx45°21'00''E, 140 m, tropical dry forest, 4–8.XI.2002, 1 ♂ (LP 2803-CASENT 9018471/BLF6452); 16.9 km 317° NW Vilanandro, 16°24'24''Sx45°18'36''E, 100 m, general collecting, tropical dry forest, 12–16.XII.2002, 2 ♂♂ (LP 2801-CASENT 9018473/ BLF6585); 17.8 km 329° WNW Vilanandro, 16°22'36''Sx45°19'36''E, 100 m, tropical dry forest, 8–12.XI.2002, 1 ♂, 1 ♀ (LP 2802-CASENT 9018472/BLF6509). Parc National Tsingy de Bemaraha, 2.5 km 62° ENE Bekopaka, Ankidrodroa River, 19°07'56''Sx44°48'53''E, 100 m, tropical dry forest on Tsingy, 11–15.XI.2001, 1 ♂, 1 ♀ (LP 2805-CASENT 9018515/BLF4342); 3.4 km 93° E Bekopaka, Tombeau Vazimba, 19°08'31''Sx 44°49'41''E, 6–10.XI.2001, 50 m, tropical dry forest, 3 ♂♂, 1 ♀, 1 imm. (LP 2806-CASENT 9018524/BLF4231), 1 ♂ (LP 2808-CASENT 9018468/BLF4231); 10.6 km 123° ESE Antsalova, 19°42'34''Sx44°43'05''E, 150 m, tropical dry forest on Tsingy, 16–20.XI.2001, 1 ♀ (LP 2807-CASENT 9018516/BLF4435). TOLIARA PROVINCE, Lake Ranobe, 23°2.593'S 43°38.011'E, 30 m, 1.II.2003–8.II.2003, pitfall trap, spiny forest/tamarinds, 50 m from lake edge, Frontier Wilderness Project, C. E. Griswold, 1 ♂ (LP 2811).

Opisthacanthus* (*Monodopisthacanthus*) *piceus Lourenço & Goodman, 2006. MADAGASCAR, FIANARANTSOA PROVINCE, Tolongoina Mountain N, 23°57.968'S 45°38.897'E, 800 m, under rocks in annually burnt grassland on mountainside, 10.II.2006, C. Raxworthy, 1 ♂, 1 ♀ (LP 6260A). TOLIARA PROVINCE, Benenitra, 1 ♂, 4 ♀♀, 4 imm. (MNHN-RS 0300). La Sakoa, 16.X.10962, Domergue, 1 ♂ (MNHN-RS 4733).

Subenus *Nepabellus* Francke, 1974

Opisthacanthus* (*Nepabellus*) *laevipes (Pocock, 1893). SOUTH AFRICA, MPUMALANGA PROVINCE, Bushbuckridge Municipality, Bushbuckridge communal lands, ca. 7 km NNW Bushbuckridge town, 24.88676°Sx31.16365°E, 551 m, plains with ridges, broadleaf savanna, moderate S slope, 2.VII, 2004, I. Engelbrecht, 1 ♂, 1 ♀ (LP 3973); 2 ♀♀ (LP 3974). Lowveld Botanical Garden, Nelspruit, 14.VII.2000, mixed bushveld, crevice in quartz, L. Prendini, M. MacFarlane, & K. M. A. Prendini, 1 ♀ (LP 1835).

Subenus *Opisthacanthus* Peters, 1861

Opisthacanthus* (*Opisthacanthus*) *cayaporum Vellard, 1932. BRAZIL, PARA, Campos de Cayapos, savannahs, in termite mounts, 10.VI.1979, W. R. Lourenço, 3 ♂♂, 1 ♀, 19 imm. (MHNG); II.1979, II.1987, W. R. Lourenço, 2 ♂♂, 1 ♀ (MHNG).

Opisthacanthus* (*Opisthacanthus*) *elatus (Gervais, 1844). COLOMBIA, BOYACA, Otanche-Muzo, 100 km W Tunja, IV–VI.1986, Indian from Muzo Mine, 2 ♂♂, 1 ♀, 3 imm. (MHNG). PANAMA, Soberalie Nat. Park, 15.X.2000, M. Makovec, 1 ♀ (LP 1837).

Opisthacanthus* (*Opisthacanthus*) *lecomtei (Lucas, 1858). AFRICA, CAMEROON: 1 ♂ (MNHN-RS 0308). Foulassi, Sangmelima, J. L. Perret, 1953-1955, 1 ♀ (MHNG); forêt primaire, XII.1959, J. L. Perret, 1 imm. (MNHN-RS 3602). Foulassi, Lobe River, 1960, J. L. Perret, 1 imm. (MNHN-RS 3603). Mengalé, 3°06'Nx10°52'E, 616 m, 12.X.2002, under tree bark on fallen log, R. C. West, 1 ♀ (LP 2194A). GABON: Belinga, 12.II.1963, H. Coiffait, 1 ♂ (MNHN-RS 6264). Ogoue-Maritime Province, Aire d'Exploitation Rationnelle de Faune des Monts Doudou, 24.5 km 303° WNW Doussala, 630 m, 2°13'58''Sx10°23'53''E, 18.III.2000, rainforest, sifted litter, B. L. Fisher, AMC [BF 2276 (2)], 1 ♂ (LP 1608).

Genus *Palaeocheloctonus* Lourenço, 1996

Palaeocheloctonus pauliani Lourenço, 1996. MADAGASCAR, SW, S.-P. d'Ampanihy, Plateau Mahafaly, near Behahitso (after Ankalinaro), 90 m, sinkholes area, high shrubby thicket with Euphorbiaceae and Didiereaceae, hand collecting, under logs and rocks, I.1966, P. Griveaud, TYPES 5 ♂♂, 6 ♀♀, 2 imm. (MNHN-RS 4451). SW, Plateau Mahafaly, near Bihahitso, I.1966, P. Griveaud, PARATYPES 1 ♂, 1 imm. (MHNG).

Ingroup

Genus *Hormiops* Fage, 1933

Hormiops davydovi Fage, 1933. VIETNAM, Poulo-Condor Island (=Con Son Island), M. Ger-

main, 1 ♀, 11 imm. (MNHN-RS 0499); forest, under stones, II.1930/IV.1931, Dawidoff leg. 1932, TYPES 1 ♂, 2 ♀♀ (MNHN-RS 0562).

Hormiops infulcra n. sp. MALAYSIA, PAHANG, Pulau Tioman, foothills of Gunung Kajang, 02º47.139'Nx104º07.548'E, 59 m, 1–2.X.2001, rainforest, in rock crevices along a stream, L. Monod, 10 ♂♂, 13 ♀♀ (LM; LP 2185). Pulau Tulai, 23.VIII.2003, P. K. L. Ng *et al.*, 1 ♀, 4 imm. (RMBR ZRC.ARA.456), 1 imm. (RMBR ZRC.ARA.457).

Genus *Hormurus* Thorell, 1876

Hormurus actaeolophos n. sp. AUSTRALIA, N QUEENSLAND, Ella Bay National Park, 17º29'Sx146º04'30''E, QLD Museum pitfall NQ10, R. Raven, P. & E. Lawless, M. Shaw, 1 imm. (QM-S 35993). Fitzroy Island, 6.XII.2000, J. Weston, 1 ♀ (QM-S 60045); site 1, 16º56'Sx145º59'E, 20 m, VIII.1998-10.II.1999, G. B. Monteith, D. J. Cook & V. E. Davies, pitfall (2250), 1 ♂ (QM-S 73948). Graham Range, 17º17'Sx145º58'E, 550 m, 8–9.XII.1995, G. B. Monteith, Thompson & D. J. Cook, 1 ♂, 1 imm. (QM-S 35429). Junction Creek, Russell River, 50 ft., 1–6.IV.1948, Archbold Expedition, 1 ♀ (AMNH). North-South Bell Peak Saddle, Malbon Thompson Range, 19–21.XI.1990, 800–900 m, G. B. Monteith & Thompson, 1 ♂, 1 ♀, 1 imm. (QM-S 35973).

Hormurus aethes n. sp. PAPUA NEW GUINEA, CENTRAL PROVINCE, Mount. Obree, slope S of Camp 1, 1600 m, 31.I.2004, J. D. Slapcinsky & F. Kraus, 1 ♀ (LP 3003); 3.II.2004, J. D. Slapcinsky & F. Kraus, 2 ♂♂ (LP 3001); 6.II.2004, J. D. Slapcinsky & F. Kraus, 3 ♀♀ (LP 3002); ridge W of Camp 1, 4.II.2004, 1550–1640 m, J.D. Slapcinsky & F. Kraus, 1 ♀ (LP 3004); pond ~200 m S of Camp 2, 7.II.2004, F. Kraus & J.D. Slapcinsky, 1 ♀, 2 imm. (LP 3005).

Hormurus agastachys n. sp. AUSTRALIA, NE QUEENSLAND, Gemini NP, 22º29'15''Sx147º52'14''E, 26.IV.1995, K. R. McDonald, J. Covacevich & P. Cooper, 1 imm. (QM-S 26299). Glencoe Station, SE of Capella, A.Rozefelds, III.1987, 2 ♂♂ (QM-S 17196). Lords Table, W base, 22º39.6'Sx148º00.5'E, 500 m, 7.III.2006, G. B. Monteith, UV lamp, black

soil, eucalyptus woodland, 13351, 1 ♂ (QM-S 73745). Mazeppa NP, S end, 22º16'Sx147º16'E, 24.X-18.XII.2000, D. J. Cook & G. B.Monteith, brigalow, pitfall trap 9828, 240 m, 1 ♂ (QM-S 39695).

Hormurus ankamuti n. sp. AUSTRALIA, QUEENSLAND, Lockerbie, 10 mi S.S.W. of Somerset, IV.1948, 20-30.IV.1948, Lockerbie, 10 mi WSW of Somerset, Archbold Expedition, 3 ♂♂, 1 ♀, 11 imm. (AMNH).

Hormurus anekasankylis n. sp. AUSTRALIA, QUEENSLAND, Townsville, James Cook University, vine thicket, around a dry creek (gully), under stones and in rock crevices, 10.VIII.2006, 71 m, 19°20'43.5''Sx146°45'42.1''E, L. Monod, 1 ♂, 4 ♀♀, 6 imm. (QM; LP 6356); Cape Pallarenda, Many Peaks Range, Mount Marlow, vine thicket, under rocks, 9.VIII.2006, 97 m, 19°11'65.6''Sx146°44'13.4''E, L. Monod, 2 jimm. (LP 6355). Alligator Creek, Bowling Green NP, Mount Elliot section, rainforest around creek, under stones and in rock crevices, 10. VIII.2006, 34 m, 19°26'10.6''Sx146°56'51.3''E, L. Monod, 3 ♀♀, 6 imm. (QM; LP 6357).

Hormurus ankistros n. sp. PAPUA NEW GUINEA, SANDAUN PROVINCE, Sindik, 0.3 km NW Parkop village, 3 km NW Sibilanga Mission, 3.42499°Sx142.51859°E, 426 m, broadleaf, tropical hill forest, 12.V.2005, J. Slapcinsky & S. Nimbisan & K. Netchy (JS 793), 1 ♀, 1 imm. (LP 4339).

Hormurus asychnachaena n. sp. PAPUA NEW GUINEA, Morobe Province, Bukaua, 35 miles W of Lae, near shore (beach), 26.XII.1972, K.W.Ströder, 1 ♀ (MHNG). Lae, Botanical Garden, 18.VII.1964, R. Zweifel, G. Sluder, 1 ♂, 1 ♀, 1 imm. (AMNH).

Hormurus asynaptodactylus n. sp. NE PAPUA NEW GUINEA, MOROBE DISTRICT, Bulolo, 10.X.1962, H. Clissold, 1 ♀ (BPBM). Maus Bokis, Bulolo River, 800 m, 4.IX.1972, Thomas W. Davies, 2 ♀♀, 11 imm. (CAS). Mine Tunnel in Bulolo Gorge, 720 m, 10.XII.1968, R. C. A. Rice, taken from crevices and burrows on floor and walls of abandonned mine tunnel, 6 ♀♀, 3 imm.

(USNM). Wau Bulolo Gorge, Maus Bokis in old water race tunnel, 12.V.1973, 750 m, Thomas W. Davies collector, 6 ♂♂, 15 ♀♀, 49 imm. (CAS).

Hormurus bandjin n. sp. AUSTRALIA, QUEENSLAND: Hinchinbrook Island, Thorsborne trail, Zoe Falls to Mulligan Falls, 3.XII.2004, R. Wyss & L. Monod, (1) Zoe Falls (69): 21 m, 18°24'30.2''Sx146°19'20.9''E, vine thicket, in rock crevices (boulders), dry, near the falls. (2) Sweetwater Creek (70): 171 m, 18°25'33.3''Sx146°19'42.9''E, patch of rainforest around creeks, under rocks and in rock crevices. (3) Mulligan Falls (71): 42 m, 18°26'32.0''Sx146°19'28.3''S, around campsite, lowland rainforest, lots of small boulders, in crevices, 3 ♂♂, 7 ♀♀ (LM; LP 5558); Little Ramsay Bay, vine forest along a creek (not many boulders), 1.XII.2004, 17 m, 18°20'50.1''Sx146°17'53.5''E, under stones and in rock crevices. R. Wyss & L. Monod, 1 ♂, 8 ♀♀, 3 juv./sub. (LM; LP 5556); Banksia Creek to North Zoe Bay, rainforest with many big boulders), 2.XII.2004, under stones and in narrow rock crevices, 36 m, 18°22'09.7''Sx 146°18'53.1''E, 36 m / 18°22'37.1''Sx146°18'37.8''E, 34 m, R. Wyss & L. Monod, 3 ♂♂, 3 ♀♀ (LM; LP 5557).

Hormurus boholiensis Kraepelin, 1914. PHILIPPINES, LUZON, Manilla, Mr. Cuming, 1 ♀ (NHML). Mount Makiling, Baker, 1 ♀ (AMNH). Subig Bay, II.1907, S. C. Thompson, 1 imm. (CAS).

Hormurus caudicula (C. L. Koch, 1867). AUSTRALIA, SE QUEENSLAND, Amama Walking track, Amamoor State Forest, 26°21'25.7''Sx 152°38'01.9''E, 103 m, 24.VIII.2006, rainforest, near creek, scree of medium to large boulders, in rock crevices, L. Monod, 3 ♂♂, 1 ♀, 6 imm. (QM; LP 6361). Buhot Ck, Burbank, 27°35.5'S 153°10.3'E, V.2003-VI.2003, riparian forest, 1 ♂, 1 ♀ (LP 2339). Cameron Scrub, knoll top, 27º30'Sx152º44'E, 11.XI.1998-13.I.1999, 90 m, vine scrub, pitfall 7557, G. B. Monteith, D. J. Cook & Thompson, 8 ♂♂, 1 ♀ (QM-S 73960). Carnarvon National Park, Mount Moffatt section, 24°54'49"S 148°02'01"E, 13.XII.2002, pitfall trap,upper slope of steep-sided ridge, brown heavy clay, C. Eddie, R. Perry & D. Harboe, 1 ♀ (LP 2340). Connondale National Park, 26°41'50.0"Sx152°33'12.4"E, 17.III.1999, blacklight-

ing amongst boulders, E. S. Volschenk & P. A. Aitken, 1 ♀ (LP 1502). Mount Jim Crow NP, 23°12'56.2''Sx150°37'46.7''E, 117 m, 14.VIII.2006, vine thicket, under rocks and in rock crevices, L. Monod, 1 ♂, 3 ♂♂, 5 imm. (QM; LP 6360). Bank of Yabba Creek, Jimna State Forest, Peach Tree Recreation Area, Eugenia track, 26°38'15.0''Sx152°27'18.3''E, 462 m, 24.VIII.2006, vine scrub (very dry), in rock crevices (scree of medium size boulders), L. Monod, 2 ♂♂, 1 ♀, 2 imm. (QM; LP 6362).

Hormurus chthamalochoros n. sp. AUSTRALIA, NE QUEENSLAND, Dunk Island, 5.VIII.2006, (1) walking track to Coconut Beach, rainforest, under stone, 57 m, 17°55'52.0''Sx146°08'40.6''E, (2) N of Muggy Muggy Beach, coastal rainforest, near a creek, under stones and in rock crevices, 0 m, 17°55'43.7''Sx146°08'43.2''E, L. Monod, 2 ♂♂, 2 ♀♀, 8 imm. (QM; LP 6352). Mission Beach, Clump Montain NP, Bicton Hill Track, K. Edward and K. P., 1 male (WAM T80277; LP 8023); coastal road hear foothills of Mount Clump, rainforest, under stones and in rock crevices, 2/4.VIII.2006, 0 m, (1) 17°50'21.2''Sx 146°06'20.5''E, (2) 17°50'12.0''Sx146°06'05.8''E, (3) 17°50'13.4''Sx146°06'06.6''E, L. Monod, hand and black lighting collecting., 1 ♂, 2 juv./sub. (LP 6350). Tully Gorge Road, rainforest, near a creek, lots of medium sized boulders, in rock crevices, 3.VIII.2006, 90 m, 17°46'36.2''Sx145°39'22.3''E, L. Monod, 1 ♂, 10 ♀♀, 10 juv./sub. (QM; LP 6351).

Hormurus chydaeostigmata n. sp. AUSTRALIA, WESTERN AUSTRALIA, Bonaparte Archipelago, Berthier Island, 14°31'Sx124°59'E, 28.V.2004, R. Teale, 1 ♂, 1 ♀ (WAM T62944; LP 5560); 14º31'10''Sx124º59'12''E (WGS84), 21.IV.2007, under loam, basalt boulders, vine thicket, RPS consultants, 1 imm. (WAM T80239; LP 8019); site BERT04, 14º31'07.3''Sx124º59'10.2''E (WGS84), 25.III.2007, under rock, vine thicket, gully slope, J. M. Waldock & K. Edward, 1 imm. (WAM T80265; LP 8020). North Maret Island, 14°23'54''Sx124°58'40''E, 28.V.2004, R. How, R. Teale, 2 ♂♂, 2 ♀♀ (WAM T62943); site NMAR 14, 14º24'19.1''Sx124º58'49.3''E (WGS84), 20.III.2007, rocky gully, East Beach, under rock, J. M. Waldock & K. Edward, 1 ♀ (WAM T80256; LP 8022). South Maret Island, 14º26'11''Sx124º58'50''E (WGS84), 21.III.2007, in funnel trap, above North-east Beach, W. Bancroft *et al.*, 1 ♂ (WAM T66736; LP 8016); site

SMAR09, 14º26'11.7''Sx124º59'22.0''E (WGS84), 19.III.2007, under lateritic rock, Corymbia woodland on plateau above North-East Beach, 1 imm. (WAM T80259; LP 8015).

Hormurus davydovi (Birula, 1903). INDONESIA, ARU ISLANDS, S Manoembaai, 20.III.1929, I.G.9223, S.A.R. le Prince Léopold, 1 ♂, 1 ♀, 2 imm. (MRHN). IRIAN JAYA (= WEST PAPUA), Kab. Merauke, Kec. Kouh, near Kampung Manggel or Kampung Yaniruma, approx. 5°20'Sx139°50'E, VI.1993, P. M. Taylor, 1 ♀ (USNM 00751).

Hormurus dechangei (Becker, 1880). PHILLIPINES, LUZON, Zambales Mountains, 4 ♀♀, 1 juv. (LM, LP 7789).

Hormurus dodecatrichos n. sp. AUSTRALIA, WESTERN AUSTRALIA, KIMBERLEY, Crystal Creek, W-side Mitchell Plateau, 14°29'Sx125°48'E, 2.XI.1976, B. R. Wilson & C. Bryce, 1 imm. (WAM 98/1858). N side mouth of Hunter River Estuary, Prince Frederick Harbour, 15º02'Sx125º21'E, STN 2, 25.VII.1977, basalt scree, vine thicket forest, B. R. Wilson, 1 ♂ (WAM 98/1859). 'Jameson Arch', Mount Jameson, 59 km NW of Elizabeth Homestead, 16º03'50''Sx125º41'25''E (WGS84), 28.I.2004, under arch, sandstone boulders, P. G. Kendrick (K14#3), 2 imm. (WAM T54103); 16º03'47''Sx125º41'29''E (WGS84), 28.I.2004, vine thicket, base of slope, sandstone, P. G. Kendrick (K14#1), 1 ♀ (WAM T54104). Kimberley Coastal Camp, opposite Walsh Point, Mitchell Plateau, 14º34'Sx125º55'E, 23–25.IX.1995, on ground at night, A.F.Longbottom (S.1833a), 1 ♀ (WAM 98/1863). Mitchell Plateau, cliff at SE base of Warrender Hill [STN 2], 14º31'54''Sx125º49'29''E, under rock (basalt), vine thicket, 1.XI.1976, B. R. Wilson & C. Bryce, 1 ♀ (WAM 98/1957). Mitchell River NP, top of Enid Falls that drops from a plateau of King Leopold Sandstones into a deep gorge through which Rufous Creek flows southward to join the Roe River, campsite [STN E5 (4)], 15º07'Sx125º33'E, 15.VIII.1974, B. R. Wilson, 1 ♂, 2 ♀♀, 5 imm. (WAM 74/1545-1552); top of Enid Fall (by chopper), 15°07'21.7''Sx125°32'57.7''E, 157 m, vine thicket beside creek, under rocks and in crevices, 6.VIII.2009, L. Monod, 1 ♂, 1 ♀, 2 imm. (WAM, MHNG); trail to Surveyors Pool, 14°38'26.9''Sx125°46'21.9''E, 238 m, granitic boulders beside creek, under rocks and in crevices near the water, 7.VIII.2009, L.

Monod, 1 ♂, 3 ♀♀, 1 imm. (WAM, MHNG). Prince Regent Reserve, campsite [STN W6 (1)], 15º34'Sx125º33'E, in a NW/SE 300 m wide valley of King Leopold Sandstones through which Youwanjela Creek runs south-eastwards to meet a major tributary of the upper Prince Regent River, 20.VIII.1974, sandstone, under stone, B. R. Wilson, 1 imm. (WAM 74/1544).

Hormurus eukteanospatha n. sp. PAPUA NEW GUINEA, EAST NEW BRITAIN PROVINCE, Wowo, 11 km NW Marmar village on old logging road to Pakia, 5.44572°Sx151.46383°E, 23.II.2005, ca. 850 m, J. Slapcinsky & K. Netchy (JS 769), 1 ♂ (LP 4340).

Hormurus extensus (Locket, 1997). AUSTRALIA, NORTHERN TERRITORY, Gorge NE of Mount Gilruth, 13.02S 133.05E, 10-13.VII.1979, rainforest, G. B. Monteith & D. J. Cook, 1 ♀, 1 imm. (QM-S 23252). Kakadu National Park, 13º15.80'Sx139º39.0'E, 20.II.1994, under decaying bark in monsoon vine forest, G. Wallis, 1 PARATYPE ♂ (NTM A000197); Gubara Pools, 12°49'36.8''Sx132°52'49.8''E, 35 m, monsoon forest inside gorge (sandstone), in rock crevices, 20.VIII.2009, L. Monod, 1 ♀ (WAM); Jim Jim Falls, 13º17'Sx132º50'E, 31.V.1992, under rocks, M. S. Harvey & J. M. Waldock, 4 imm. (WAM 98/1852-5); Jim Jim Fall walking track, (1) 13°16'24.3''Sx132°49'56.3''E, 64 m, (2) 13°16'22.2''Sx132°49'55.3''E, 129 m, monsoon forest, in rock crevices, 21–22.VIII.2009, L. Monod, 2 ♂♂, 5 ♀♀, 2 imm. (WAM, MHNG); Koolpin Creek, 13°29'45.6''Sx132°34'29.2''E, 107 m, vine thicket by the side of the creek, in rock crevices, 24.VIII.2009, L. Monod, 3 ♀♀ (WAM, MHNG); Maguk walking trail, 13°19'01.2''Sx132°26'23.4''E, 98 m, monsoon forest by the side of the pools, in rock crevices, 23.VIII.2009, L. Monod, 3 ♂♂, 5 ♀♀, 2 imm. (WAM, MHNG); Radon Gorge, (1) 12°45'02.7''Sx132°54'17.8''E, 86 m, (2) 12°45'10.1''Sx132°54'18.7''E, 65 m, monsoon forest at foothills of sanstone outcrop beside creek, in rock crevices, 20/26.VIII.2009, L. Monod, 3 imm. (WAM). Oenpelli area, 12º23.5'Sx133º03.5'E, 21-22.VII.1992, A. Wells & J. Webber, 1 HOLOTYPE ♂ (NTM A000196).

Hormurus goliath n. sp. MISLABELLED: Efulen, Cameroon, 1 ♂ (NHML 1905.6.13.1). PAPUA NEW GUINEA, early 1943, Capt, Tinkham, 1 ♀ (AMNH); 1 ♂, 4 imm. (NHML). CENTRAL

PROVINCE, Madew (=Madiu), Saint Joseph River (=Angabunga River), Sir William Ingram (P), W. Stalker (c.), 1 ♀ (NHML 1908.10.14.1). GULF PROVINCE, Murua (near Kerema), 3 m, 17-18.XII.1964, J. L. Gressitt, 1 ♀ sub, 1 juv. (BPBM); XII.1965, W. Steffan, 1 ♀ (BPBM). MOROBE PROVINCE, Aseki, IX.1980, J. K., 1 ♂, 1 ♀, 1 imm. (MHNG). Watut, VIII.1980, J. K., 1 ♀, 2 imm. (MHNG); IX.1980, J.K., 3 ♂♂, 2 ♀♀, 1 ♂ sub. (MHNG); XI.1980, J. K., 1 imm. (MHNG).

Hormurus glaphyroscytos n. sp. AUSTRALIA, QUEENSLAND, foothills of Mount Mulligan, walking track to the swimming hole, 16-18.VII.2006, in rock crevices, vine forest with big boulders (very moist), 477 m, 16°52'11.8''Sx 144°51'48.4''E, G. Romand & L. Monod, 1 ♂, 8 ♀♀, 10 imm. (QM; LP 6640); LS 35, 14.VI.1998, Dr. J. Whittier (UQ St Lucia), 1 ♀ (QM-S 41947); IV.1985, J. Covacevich & G. Czechura, 1 ♀ (QM-S 23259).

Hormurus halmaherae n. sp. INDONESIA, HALMAHERA, Dodinga, Halmahera, 1 ♀ (ZMB 3144); Bernstein, 1 ♀ (NNHM 41); Ternate, Gilolo, M.Raffray, 1 ♂, 1 ♀ (MNHN-RS 0492).

Hormurus hylaios n. sp. AUSTRALIA, N QUEENSLAND, Cape Hillsborough National Park, coastal rainforest, big boulders (volcanic), under rocks and in rock crevices, Hidden Valley walking track, 12.VIII.2006, (1) 0 m, 20°55'53.2''Sx149°02'50.2''E, (2) 3 m, 20°55'52.9''Sx149°02'55.2''E, L. Monod, 2 ♂♂, 10 ♀♀, 5 imm. (QM; LP 6358); Beachcombers cove track, 11.VIII.2006, 18 m, 20°55'34.7''Sx149°03'06.8''E, L.Monod, 14, 7 ♀♀, 7 imm.(QM; LP 6363). Finch Hatton Gorge, Eungella NP, walking track, rainforest, big boulders with coarse grains, in rock crevices, 13.VIII.2006, 146 m, 21°04'05.0''Sx 148°38'07.1''E, L. Monod, 3 ♂♂, 5 ♀♀, 6 imm. (QM; LP 6359).

Hormurus hypselankylis n. sp. PAPUA NEW GUINEA, Milne Bay Province, D'Entrecasteaux Islands, Fergusson Island, Basima, 9°27.287'Sx150°48.259'E, 250 m, 31.VIII.2002, F. Kraus (JS-0640), 1 ♂, 4 ♀♀ (LP 2717).

Hormurus insculptus Thorell, 1888. INDONESIA, WEST PAPUA, Dorey (=Manokwari), 1877,

Raffray, 4 ♂♂, 2 ♀♀ (MNHN-RS 0495).

Hormurus ischnoryctes n. sp. AUSTRALIA, N QUEENSLAND, Mount Mulligan cattle station, 10.IX.1983, A. Williamson, 1 ♂ (QM-S 17140); camp site near the dam, 16-17.VII.2006, savannah, in vertical burrows (between 20-40 cm deep, with a terminal chambers), 340 m, 16°51'54.0''Sx144°52'45.0''E, G. Romand & L. Monod, 2 ♂♂, 6 ♀♀, 10 imm. (QM; LP 6639). Ravenshoe, alt. ca. 600 m, open Eucalyptus forest, marked cold season, low rainfall (VIII.1963), H. St Girons, 1 ♂, 1 ♀ (MNHN-RS 4209).

Hormurus karschii Keyserling, 1885. INDONESIA, WEST PAPUA, Segaar Bay, Gazelle, 1875, TYPES 2 ♂♂ (pinned specimens) (ZMB 3016). Sekroe, Maarx, 1897, S.Schädler, 1 imm. (NNHM 253); 1 ♂, 2 ♀♀ et 2 imm. (NNHM 254).

Hormurus khangalu n. sp. AUSTRALIA, QUEENSLAND, Blackdown Range, 3000 ft above sea level, C. Barnard, 1 ♂, 5 ♀♀, 5 imm. (NHML 1909.10.8.8-16). Blackdown Tableland SW Rockhampton, 5–-6.X.1982, A. Rozefelds, 1 imm. (QM-S 17091).

Hormurus kilkerranicus n. sp. PAPUA NEW GUINEA, MILNE BAY PROVINCE, D'Entrecasteaux Islands, Fergusson Island, NE slope of Mount Kilkerran, 9°27.627'Sx150°47.076'E, 1100m, 21.VIII.2002, F. Kraus, 8 ♂♂ (LP 2719); 8 ♀♀ (LP 2720); 19.VIII.2002, F. Kraus, 6 imm. (LP 2722), 6 ♀♀ (LP 2732); S slope of Oya Waka, 9°27.369'Sx150°33.575'E, 1100m, 12.VIII.2002, F. Kraus (JS-0641), 3 ♂♂, 1 ♀ (LP 2728).

Hormurus kukunyungkal n. sp. AUSTRALIA, N QUEENSLAND, Black Mountain National Park, in rock crevices, vine thicket at the borders of the boulders pile (dry), 22.VII.2006, (1) 63 m, 15°38'56.1''Sx145°13'20.8'E', (2) 88 m, 15°39'00.9''Sx145°13'14.9''E, L. Monod, 3 ♂♂, 6 ♀♀, 6 imm. (LP 6341). Mount Cook NP, Foothills of Mount Cook (walking track), in rock crevices, lowland vine forest, 22.VII.2006, 97 m, 15°28'53.8''Sx145°16'05.7''E, G. Romand & L. Monod, 2 ♂♂, 1 ♀, 7imm. (QM; LP 6342); walking track to Mount Cook Summit, in rock crev-

ices, highland vine forest (very windy, much smaller/lower vegetation type, cooler), 22.VII.2006, 228 m, 15°29'09.6''Sx145°16'02.3''E, G. Romand & L. Monod, 1 ♂, 5 ♀♀, 3 imm. (QM; LP 6343).

Hormurus kuukayau n. sp. AUSTRALIA, NE QUEENSLAND: Iron Range, 50–75 ft, 20–21. VI.1948, Archbold Expedition, 1 ♂, 5 imm. (AMNH).

Hormurus laevitropis n. sp. AUSTRALIA, NE QUEENSLAND, Gillies Range, Robsons Track, open woodland/open eucalyptus forest (dry savannah with grass), big boulders, in rock crevices, near and in the bed of a dry creek, 30.VII/1.VIII.2006, (1) 239 m, 17°09'24.7''Sx145°42'09.6''E, (2) 310 m, 17°09'26.6''Sx145°42'02.2''E, L. Monod, 2 ♂♂, 1 ♀, 5 imm. (LP 6348). Gordonvale, W. C. Dormer, 1 ♂ (QM-S 17087).

Hormurus leptochela n. sp. AUSTRALIA, NE QUEENSLAND, Home Rule, walking track to waterfall, lowland rainforest, in between stones/in rock crevices, 23.VII.2006, 191 m, 15°44'46.7''Sx145°17'47.7''E, G. Romand & L. Monod, 1 ♂, 5 ♀♀ (LP 6344). Walking track to Mount Amos Summit (start of the trail at Murgumby Lodge), rainforest, in rock crevices and in shallow burrows under stones, 24.VII.2006, (1) 575 m, S 15°42'41.0''xE 145°16'24.7'', 575 m, (2) S 15°42'44.3'' / E 145°16'22.3'', 578 m, G. Romand & L. Monod, 1 ♂, 3 ♀♀, 9 imm. (QM; LP 6345).

Hormurus litodactylus Monod & Volschenk, 2004. AUSTRALIA, NE QUEENSLAND, Daintree National Park, Mount Sorrow ridge walk, (1) 16°04'38.2''Sx145°26'21.8''E, 700 m, (2) S 16°04'37.2''Ex145°26'31.3'', 638 m, (3) 16°04'37.0''Sx145°26'19.5''E, 699 m, 7.XII.2004, highland rainforest (very humid, misty, cool), under stones, in between roots of trees. L. Monod, 6 ♂♂, 5 ♀♀ (LM-LP 5559).

Hormurus macrochela n. sp. AUSTRALIA, NE QUEENSLAND, Magnetic Island, walking track Nelly bay to Arcadia, vine forest with lots of big granite boulders, along a dry creek,

28–29.XI.2004, 41 m, 19°08’33.7’’Sx146°50’43.4’’E, in rock crevices (very narrow or in between stones), R. Wyss & L. Monod, 5 ♂♂, 8 ♀♀, 2 imm. (LM; LP 5555). Palm Island, site 4, 18º44’Sx146º35’E, 100 m, rainforest. 22.II.2001, G. B. Monteith (8325), 1 ♂ (QM-S 59212); site 1, 18º45’Sx146º36’E, 450 m, rainforest, 20-21.II.2001, G. B. Monteith (8323), 1 ♂, 1 ♀ (QM-S 59206).

Hormurus mesochtonus n. sp. PAPUA NEW GUINEA, Victoria Mount, Bwih? of O. E. Jansen, 1 ♂, 2 ♀♀, 2 imm. (NHML 1896.12.7.38-41).

Hormurus microkypheus n. sp. AUSTRALIA, NE QUEENSLAND, TORRES STRAIT, Murray Island, VII–VIII.1974, H. Heatwole & E. Cameron, 1 ♂, 1 ♀, 2 imm. (WAM 98/1869-72); 1 ♀ (USNM 00949); A. C. Hadden, 1 ♀ (NHML 1891.9.5.1), 1 imm. (NHML). Weier Island, Torres Strait, 3.VIII.1974, H. Heatwole, 1 ♀, 1 imm. (WAM 98/1867-8).

Hormurus milneanus n. sp. PAPUA-NEW GUINEA: Camp 7, Peria Creek, Kwagira River, 14.VIII–6.IX.1953, Geoffrey Tate, Archbold Expedition, 2 ♂♂, 4 ♀♀, 1 imm. (AMNH).

Hormurus muralagi n. sp. TORRES STRAIT, Badu Island, 18.XII.1976, H. Heatwole *et al.*, under rocks on hillside, vine thicket, 1 ♀, (NMNH 00306). Prince of Wales Island, 30.VI.1976, E. Cameron, under rock on rocky hillside, Sav. W’land, 1 ♂ (NMNH 00306).

Hormurus neocaledonicus (Simon, 1877). NEW CALEDONIA, PROVINCE SUD, Col des Rousettes, track, 21°25’08.0’’Sx165°27’58.9’’E, 427 m, 21.IX.2004, small patch of rainforest in between niaoulis savannah, in between stones in a scree covered by litter and tree roots, dryer habitat than previous specimens, D. Gaillard & L. Monod, 2 ♂♂, 3 ♀♀, 7 imm. (LM; LP 5544). Farino, Louis Barbou forest exploitation, 7.X.2004, C.Mille, S. Cazeres & T. Nuques (I.A.C. Pocqueureux), L. Monod, (1) 21°36’50.4’’Sx165°42’05.5’’E, 383 m, degraded humid forest, near dry creek, under stones, 3 ♂♂, 4 ♀♀ (LM; LP 5547); (2) 21°37’03.7’’Sx165°42’51.0’’E, 477 m, degraded humid forest, under stones, 2 ♂♂, 3 ♀♀ (LM; LP 5548). Mount Humbold, near mine,

21°54’24.4’’Sx166°21’14.5’’E, 505 m, 4.X.2004, degraded primary forest, vine thicket, in between stones in a scree covered by leaves litter and humus and under larger stones, L. Monod, 3 ♂♂, 2 ♀♀ (LM; LP 5546). Monts Koghis, start of tracks, 22°10’40.5’’Sx166°30’28.6’’E, 440 m, 26.IX.2004, rainforest, under rocks, D. Gaillard & L. Monod, 3 ♂♂, 3 ♀♀ (LM-LP 5545); Mount Koghis, ca. 20 km N Noumea, 4.XII.2004, S. Huber, 2 imm. (LP 6224). Rivière Bleue Natural Reserve, trail between Pont Pérignon and Giant Kaori, 22°06’14.2’’Sx166°41’12.8’’E/22°06’31 .8’’S 166°41’35.6’’E, 116–169 m, 18.IX.2004, rainforest, under stones and in rock crevices, D. Gaillard & L. Monod, 3 ♂♂, 3 ♀♀ (LM; LP 5543); Pic du Grand Kaori, 22°16.770’Sx166°53.691’E, 400 m, 11.V.2005, under dead wood branches, J. Murienne, 2 imm. (LP 4323). Road Nouméa - Rivière Bleue Forest Reserve, 22°12’47.2’’Sx166°39’59.3’’E, 177 m, 17.IX.2004, vine thicket, in rock crevices, D. Gaillard & L. Monod, 1 ♀ (LP 5542).

Hormurus nesiotes n. sp. OCEANIA, PALAU, Peleliu, 21.IV.1936, Y. Kondo, 1 ♀ (USNM 04167), 1 imm. (BPBM).

Hormurus nyawaygi n. sp. AUSTRALIA, NE QUEENSLAND, Kirrama, near Birthday Creek, rainforest, in a boulder pile, E.S.Volschenk, Easter 1996, 1 ♀ (ESV 3380). Little Crystal Creek, Paluma Range National Park (Mt Spec section), rainforest, near and in the bed of a dry creek, in rock crevices and under stones, 316 m, 19°00’53.4’’Sx146°16’23.5’’E, L. Monod, 2 ♂♂, 13 ♀♀, 7 imm. (QM; LP 6354). Mount Halifax Summit, 45 km WNW Townsville, NQld, 2.XII.1990, hand collecting, A. Graham, 1 ♂ sub., 2 imm. (QM-S 35942).

Hormurus ochthonastes n. sp. AUSTRALIA, NE QUEENSLAND, Bellenden Kerr Range, Cable Tower 5, 532 m, 17–24.X.1981, Earthwatch/QLD Museum, 1 ♂, 2 imm. (QM-S 17110), 1 ♀ (QM-S 17111); Cableway Base Station, 100 m, 17–24.X.1981, Earthwatch/QLD Museum, 2 imm. (QM-S 17109). Kirrama, vine forest, E.S.Volschenk, 5.VI.1996, 1 ♂ (ESV 3381). Mount Graham, 8 km N Abergowrie, NE QLD, 600–700 m, 26–30.XII.1986, S. Hamlet, 1 ♀, 1 imm. (QM-S 23179). Mount Tyson, 2 km W Tully, 7.V.1983, 650 m, D. K. Yeates, 1 ♀ (QM-S 17176). Yuccabine Creek, near Kirrama, rainforest, in a boulder pile, 18°13’Sx145°45’E, E. S. Vols-

chenk, 6.IV.1996, 1 ♂ (ESV 3368), 1 ♂ (ESV 3374), 1 ♂ (ESV 3375).

Hormurus ochyroscapter n. sp. AUSTRALIA, NE QUEENSLAND, Reedybrook, 18°45'S, 144°38'E, excavated from hole 6'' deep, 2.VIII.1967, J. D. Brown, 1 ♂, 1 ♀, 2 imm. (QM-S 17072). Almaden, Chillagoe District, W. D. Campbell, XI.-XII. 1925, 1 imm. (AM KS 94922).

Hormurus oreios n. sp. PAPUA NEW GUINEA, WESTERN HIGHLAND DISTRICT, Baiyer River, near Mt Hagen, 8.III.1969, P. Jolivet, 1 ♂, 2 ♀♀ (MNHN-RS 5317); under bark, 900m, 10.IV.1969, P. Jolivet, 1 ♂, 1 ♀, 1 imm. (MNHN-RS 5318).

Hormurus oreospyridus n. sp. NEW CALEDONIA, Mount Panié, 1990, R. Raven, 1 ♂ (QM-S 18801).

Hormurus orthodactylus n. sp. AUSTRALIA, NE QUEENSLAND, 12 m, Scrub, Gap Creek, 22–27.XI.1975, QM pty, 2 ♀♀, 1 imm. (QM-S 17134). Mount Hartley, SW slope, 15°46'Sx145°19'E, 8.XII.1995–16.I.1996, G. B. Monteith, D. J. Cook & Roberts, pitfall traps, 750 m, 1 ♂ (QM-S 41326). Shipton's Flat, 17–22.XI.1975, QM pty, 2 ♀♀, 4 imm. (QM-S 17065).

Hormurus papuanus Kraepelin, 1914. PAPUA NEW GUINEA, MOROBE PROVINCE, Finshhafen, IV.1944, E. S. Ross, 3 ♂♂, 3 ♀♀, 1 ♂ sub., 5 juv., 7 pullus (CAS). Kamiali Guest House, 7.29934°Sx147.13435°E, 3 m, 12.X.2003, coastal forest, J. D. Slapcinsky & F. Kraus, 1 ♀ (LP 2718). Mt. Shungol, W of Apele, near junction of Kasang Creek and Ouz River, 6.82632°Sx146.69943°E, 860 m, broadleaf forest, arboreal 1–3 meters on mossy tree trunks, 22.X.2003, J. D. Slapcinsky & F. Kraus, 2 ♂♂ (LP 2715), 1 ♀ (LP 2721). Mt. Shungol, W of Apele, Bwemamik, junction of Bwemamik Creek and Ouz River, 6.81543°Sx146.69282°E, 730 m, 17.X.2003, mature broadleaf forest, J. D. Slapcinsky & F. Kraus, 1 ♀ (LP 2725), 2 imm. (LP 2726), 1 imm. (LP 2727).

Hormurus penta (Lourenço & Francke, 1991). SE PAPUA NEW GUINEA, 10.X.1914, 1 ♂ (QM-

S 23254). Samarai, 10º36'Sx150º39'E, 5.VII.1937, S. Bemrose, 1 ♂ (WAM 37-2542). SOLOMON ISLANDS, GUADALCANAL, Chocho, ca. Tambea, 09°16'Sx159°40'E, 200 m, 27.I.1999, J. Lattke 2354, 1 ♂ (LP 1817-CAS). Mount Austen, 20.XII.1963, P. Greenslade (Royal Society B.S.I.P. 1965, 1446, Acc. No. 2182), 1 ♂, (NHML). San Jorge, IX.1965, Casuarina forest & fringing semb. (Royal Society Expedition 23/27), 1 imm. (NHML). SOLOMON ISLANDS, RUSSELL ISLANDS, XII.1944, Lt. R. B. Eads, Navy #60, 1 juv. (AMNH).

Hormurus polisorum (Volschenk, Locket & Harvey, 2001). CHRISTMAS ISLAND, INDIAN OCEAN, 19th Hole, cave CI-19, 30.III.1998, wall, dark zone (BES 5782), S. M. Eberhard, 1 paratype ♀ (WAM 98/1624; LP 1614); Bishops Cave, 120 m from light, 11.VIII.1987, N. Plumley, top of rockpile, first main chamber, 1 holotype ♂ (WAM 97/2938).

Hormurus samoa n. sp. SAMOA, M. Whitmore, 1 ♂, 1 imm. (NHML 1875.11).

Hormurus scopaeus n. sp. AUSTRALIA, QUEENSLAND, Mount Robert, 5 km SW, 21º24'Sx148º27'E, 18.XII.2000–25.III.2001, D. J. Cook & G. B. Monteith, 300 m, pitfall 9994, brigalow, 2 ♂♂ (QM-S 59213).

Hormurus solomonensis n. sp. SOLOMON ISLANDS, GUADALCANAL PROVINCE, Guadalcanal island, Haruligo Village, Vatugulan area (NE coast), 09°19'03.4''Sx159°45'34.6''E, 5 m, 17.X.2004, rainforest, under stones, F. Tungale, M. R. & B. Tavalus, V. & F. Saurono, R. Wyss, L. Monod, 2 ♂♂, 7 ♀♀, 1 imm. (LM/ LP 5549). MAKIRA-ULAWA PROVINCE, Makira island, Pue Pue River, 3 km S Kira Kira, 10°29'Sx161°55'E, 120 m, 20.I.1999, J. Lattke, 1 ♂ (LP 1818); Kira Kira, 10°28'Sx161°55'E, 22.I.1999, P. Gilbert & J. Lattke, 2 juv. (LP 1819). WESTERN PROVINCE, Ranonga Island, Niami Village, 08°02'44.0''Sx156°35'22.3''E, 22 m, 1.XI.2004, rainforest, under rocks and in rock crevices, near a creek, Veronika, Cherry, Ravia, R. Wyss, L. Monod, 3 ♂♂, 8 ♀♀, 28 imm. (LM; LP 5551); Rendova Island, Mbaniata Village, 08°37'46.1''Sx157°16'39.1''E, 62 m, 4.XI.2004, rainforest, under rotten logs, rocks and in rock crevices, usually near creeks, M. Vagi, J. Havea, R. Wyss & L. Monod, 1 ♀, 32 imm. (LM; LP

5552). Tetepare Island, N coast, Raro Bay, Raro River area, 08°42’22.5’’Sx 157°32’26.2’’E/ 08°42’21.4’’Sx157°32’33.0’’E/ 08°42’37.5’’Sx157°32’42.1’’E, 4-133 m, 9.XI.2004, rainforest, under stones and rotten logs, lots of mud crabs, R. Suka, A. Fuhi, R. Wyss & L. Monod, 3 ♂♂, 7 ♀♀, 1 imm. (LM; LP 5554). Vella Lavella Island, S tip, Mbuna Poro Village, 25.X.2004, secondary rainforest, under stones and in rock crevices, around creeks, C. Sirno, R. Wyss, L. Monod, 1 ♂, 6 ♀♀, 2 juveniles (LM; LP 5550).

Hormurus tagulae n. sp. PAPUA NEW GUINEA, MILNE BAY PROVINCE, Sudest Island, Araetha Village, 11.43624°Sx153.43008°E, 0 m, 11.IV.2004, J. D. Slapcinsky (JS-0705), 1 ♂, 1 ♀, 12 imm. (LP 3008).

Hormurus tetrakaideca n. sp. AUSTRALIA, NE QUEENSLAND, Portland Roads, 11.VII.1968, J. C. Le Souef, 1 ♂, 1 ♀ (with 1 ♂ H.kuukayau) (WAM 72-259–72-261).

Hormurus tjapukai n. sp. AUSTRALIA, NE QUEENSLAND, Crystal Cascades, near Cairns, under stones along a stream, 7.V.2000, L. Monod, 3 ♂♂, 5 ♀♀, 11 imm. (LP 2184); 10.VII.2006, rainforest, in rock cervices and in shallow burrows under stones, near a creek, 16°57’58.3’’Sx145°40’45.9’’E, 46 m, L. Monod, 4 ♂♂, 5 ♀♀, 3 imm. (LM; LP 6641).

Hormurus tytthognaphos n. sp. AUSTRALIA, NE QUEENSLAND, Devil’s Thumb walking trail, Daintree NP, rainforest, in rock crevices and in shallow burrows under stones (stones with a coarse grain), 27.VII.2006, (1) 641 m, 16°23’40.1’’Sx145°18’31.5’’E, (2) 674 m, 16°23’39.3’’Sx145°18’31.5’’E, found until 724 m, L. Monod, 7 ♀♀, 3 imm. (QM; LP 6347). Mount Lewis Forest Reserve, forest road, highland rainforest, in bed of a dry creek, in rock crevices and in shallow burrows under stones (stones with a coarse grain), 26.VII.2006, 648 m, 16°34’57.3’’Sx145°18’17.6’’E, L. Monod, 1 ♂, 10 ♀♀, 6 imm. (QM; LP 6346).

Hormurus umpila n. sp. AUSTRALIA, NE QUEENSLAND, Cape York, 66 miles N Coen, under logs, open forest, 22.VIII.1972, H. Heatwole, 1 imm. (NMNH 00306). Leo Creek Road, rocky

scrub, under logs and rocks, K. R. MacDonald, 17.III.1979, 1 ♂ (QM-S 17102). Nesbit River, Buthen Buthen, NW Coen, 1–17.VIII.1978, G. Czechure & S. van Dyck, 1 ♀, 1 imm. (QM-S 17100).

Hormurus waigiensis (Gervais, 1843). INDONESIA, WEST PAPUA, RAJA AMPAT ARCHIPELAGO, Wiaigiou Island (= Waigeo Island), 1 ♂ (Holotype, badly preserved) (MNHN-RS 0491); Salawaty Island, A. Raffray, 1 imm. (MNHN-RS 0503).

Hormurus wallaman n. sp. AUSTRALIA, NE QUEENSLAND, Wallaman Falls road, rainforest, big boulders in the bed of a dry creek, in rock crevices, 6.VIII.2006, 18°37'55.2Sx145°52'57.2''E, L. Monod, 1 ♀, 3 imm. (LP 6353-AMNH).

Hormurus weberi Pocock, 1894. INDONESIA, SULAWESI, Sulawesi Selatan, Luwu, Celebes, Dr Max Weber, 1 ♂ (Holotype, NHML 1896.10.6.6 TYPE). Sulawesi Tengah, N of Guef Boni, Habland near Djaladja, 1 ♂ (NHML); near Morowali, Ranu River Area, 27.I–20.IV.1980, 1 ♂ (NHML). Sulawesi Utara, Dumoga-Bone NP, 1985, 1 ♀ (NHML).

Hormurus xerogaios n. sp. AUSTRALIA, NE QUEENSLAND, Broken River (Montgomery Range, W of Cairns), vine forest, E. S. Volschenk, 9.VII.1994, 1 imm. (ESV 3378), 1 ♂ (ESV 3376); near entrance of 'Not a Fig Tree Cave', vine forest, near limestone cave entrance, E. S. Volschenk, 7.VII.1994, 1 ♀ (ESV 3369).

Hormurus yelae n. sp. PAPUA NEW GUINEA, MILNE BAY PROVINCE, Rossel Island, Pipikea, camp 2, 11.33481°Sx154.22486°E, 253 m, 11.V.2004, J. D. Slapcinsky (JS-0718), 1 ♂, 7 ♀♀, 5 imm. (LP 3007).

***Hormurus* sp. WA**

Australia, Western Australia, Lamarck Island, NW Kimberley, 14°47'Sx125°02'E, 4.IX-11.IX.2007, M. Bamford, 1 male (WAM T81537; LP 8017); 14°46'29"Sx125°0'28"E, 4.IX.2007, M.

Bamford, 1 male (WAM T81535; LP 8021).

Genus *Liocheles* Sundevall, 1833

Liocheles australasiae (Fabricius, 1775). FIJI, Vanua Levu Island, 16°32'21"Sx179°32'50"E, 2.VII.2008, 402 m, under bark fallen logs, D. Grimaldi, 2 females (LP 8676). Viti Levu Island, Nakobaleva Mtn. Rd., 10.VII.2008, 300 m, under bark, D. Grimaldi, 2 females, 13 imm. (LP 8677). INDIA, Tripuri, 2004, F. Kovařík, 1 imm. (LP 3684). INDIA, ANDAMAN ISLANDS, 2 ♂♂, 1 ♀, 3 imm. (ZMW 1749); 1 ♀, 1 imm. (ZMW 8253); G. Rogers, 1 ♂ (NHML 1907.7.18.4). Havelock Island, III.1999, 2 ♀♀ (LP 1854). Narcondam Island, G. Rogers, 1 ♀ (NHML 1907.7.18.06). Tugapure, 3 km S, 12.4889Nx92.4929E, 14-16.VIII.2001, J.-P. Rudloff, 1 ♀ (ZMB 34975). INDONESIA, WEST PAPUA, Sansapor, XII.1944, A.P.O. 159, R. B. Burrows, 1 ♂, 1 ♀, 3 imm. (AMNH). MALAYSIA, PAHANG, Pulau Tioman, foothils of Gunung Kajang, track from Kampung Paya to Gunung Kajang Summit, 02°47.139'Nx104°07.548'E, 59 m, 1.X.2001, rainforest, in crevices of boulders along the stream, L. Monod, 4 ♀♀ (LP 2183); SELANGOR, Batu Caves area, 3.244°Nx101.695°E, 200 m, 19.V.2005, W. Maddison, D. Li, I. Agnarsson & J. X. Zhang, 1 ♀ (LP 4764); TERRENGGANU, Pulau Perhencian Kecil, above Rock Garden Resthouse, 05°54.943'Nx102°43.386'E, 77 m, 18.IX.2001, seasonally dry tropical forest, rocky outcrop, in crevices, L. Monod, 5 ♀♀, 1 imm. (LP 2181). PAPUA NEW GUINEA, CENTRAL PROVINCE, Dorobisoro, 09°27'Sx147°55'E, 8.X.2003, J. D. Slapcinsky & F. Kraus, 1 ♀, 2 imm. (LP 2729). Laronu, 9.44387°Sx147.98383°E, 880 m, 25.I.2004, F. Kraus & J. D. Slapcinsky, 2 imm. (LP 2996). MOROBE PROVINCE, Mt. Shungol, Teron's House, 15.X.2003, F. Kraus, 25 specimens (LP 2733). MYANMAR, TANINTHARYI DIVISION, Tavoy (=Dawei), 1 ♀, 1 imm. (ZMW 1750). SOLOMON ISLANDS, WESTERN PROVINCE, Tetepare Island, N of WWF research station, around creeks, 08°43'15.4"Sx157°27'10.7"E, 10 m, 7.XI.2004, rainforest, in rock crevices, near a creek, R. Suka & L. Monod, 9 ♀♀, 18 imm. (LM; LP 5553). THAILAND, KRABI PROVINCE, Rayley Beach, Gorge, 15.IX.2001, rainforest, under bark and in rotten logs, L. Monod, 2 ♀♀, 4 imm. (LP 2182). VANUATU (NEW HEBRIDES), Tanna Island, 2km S Ipeukeul, 25m, 23.VIII.1979, W. C. Gagne, 1 ♂, 1 ♀ (BPBM Acc. No. 1979.380).

Liocheles complanatus (C. L. Koch, 1837). EAST PAKISTAN (= BANGLADESH), Lawa Chera For. Srimangal, IX.27.61, 110 m, E. S. Ross & D. Cavagnaro, 1 ♀ (CAS); Harbang For., 6 miles N Chiringa, IX.18.61, 50 ft., E. S. Ross & D. Cavagnaro, 2 imm. (CAS). INDIA, Himalayas, Keys, 1 ♀ (Holotype, NHML 13.9.1.71 TYPE), 1 ♀ (NHML 1890.7.1.228).

Liocheles longimanus (Werner, 1939). INDONESIA, SUMATRA, SUMATERA BARAT, Harau Canyon, N of Payakumbuh, 0°05'46''Sx100°39'58''E, 750 m, 7.VI.2006, old secondary forest, P. Schwendinger, 1 ♂ (LP 6388). Mangani, mine near Kota Tingge, 700 m, 21.VII.1983, E. S. Ross, 1 ♂, 1 ♀ (CAS).

Liocheles malaya n. sp. MALAYSIA, PERAK, Maxwell Hill (Bukit Larut), E of Taiping, 950-1250m, 21-25.XI.1999, G.Cuccodoro & Y.Löbl, 1 ♂ (MHNG); 9.VII.1983, under bark in forest, E. S. Ross, 1 ♀ (CAS). Banding Is., Tasik Temengor, 14.IV.2001, under lumber, damp, R. West, 1 ♀ (LP 1909).

Liocheles nigripes (Pocock, 1897). INDIA, WEST BENGAL: Janida, Jhargram, Midnapore, 30.VIII.1965, C. L. Kau (H. L. Stahnke collection), 1 ♂ (CAS ASU 65-0345 #1); 17.VIII.1965, C. L. Kau (H. L. Stahnke collection), 1 ♀ (CAS ASU 65-0331 #1).

Liocheles suspectus (Thorell, 1888). MYANMAR, BAGO DIVISION, Pegu Hills/Mountains (= Bago Yoma), 2 ♂♂ (NHML 1897.5.10.193). RAKHINE STATE, Gwa Township, Kan Thar Yar Resort, along creek near Kan Thar Yar, beach area, NW of Gwa, 17º43.5Nx094º32.5'E, 28.XI-6.XII.2000, K. J. Ribardo, 1 ♂, 1 ♀, 1 imm. (LP 2796-CAS).

2.5.2 Matrix of morphological characters. Characters 0–7 (continuous). Legend: ? = unknown; - = inapplicable; [xx] = polymorphic; † = uninformative.

	0	1	2	3	4	5	6	7
Opisthacanthus (N.) laevipes	8	7-8	3	4	3	4	3	4
Chiromachetes fergusoni	?	7-8	2	3	2	3	2	3
Chiromachetes tirupati	5	?	3	3	3	3	3	3
Chiromachus ochropus	9	9-10	10-12	12-14	10-12	12-14	10-12	12-14
Iomachus laeviceps	4-5	4-5	3	3	3	3	3	3
Iomachus malabarensis	6	6	3	3	3	3	3	3
Iomachus nitidus	5	4-5	3	3	3	3	3	3
Iomachus politus	8	8	6-7	6-7	4	4	4	4
Iomachus punctulatus	5	5-6	2	3	2	3	2	3
Opisthacanthus (M.) apios	?	7-8	3	3	3	3	3	3
Opisthacanthus (O.) cayaporum	8-9	5	4	6	4	6	4	6
Opisthacanthus (O.) elatus	?	8	4	6	4	6	5	7
Opisthacanthus (O.) lecomtei	11	10-11	3	4	3	4	3	4
O. (M.) madagascariensis	8	7-8	3	3	3	3	3	3
Opisthacanthus (M.) piceus	9	8	3	3	3	3	3	3
Palaeocheloctonus pauliani	6-7	6-7	3	3	3	3	3	3
Hormiops davydovi	7	6	4	4	4	5	4	5
Hormiops infulcra	6	5-6	4	4	4	5	4	5
Liocheles australasiae	6-7	5-6	4	4	4	4	4	4
Liocheles complanatus	?	6	4	4	4	4	4	4
Liocheles longimanus	7-8	7	4	4	4	4	4	4
Liocheles malaya	8	7	4	4	4	4	4	4
Liocheles nigripes	6-7	5-6	4	4	4	4	4	4
Liocheles suspectus	7	6	4	4	4	4	4	4
Hormurus actaeolophos	6-7	5	4	4	4	4	4-5	4-5
Hormurus aethes	5	4	4	4	4	4	5	5
Hormurus agastachys	8-9	?	4	5	4	5	5	5
Hormurus anekasankylis	8	7	4	4	4	4	5	5
Hormurus ankamuti	8-9	7	4	4	4	4	5	5
Hormurus ankistros	?	9-10	4	4	4	4	4	5
Hormurus asychnachaena	?	9-11	4	4	4	4	4-5	5
Hormurus asynaptodactylus	9	7-8	4	4	4	4	5	5
Hormurus bandjin	7	6	4	4	4	4	5	5
Hormurus boholiensis	?	6	3	4	3	4	6-7	4
Hormurus caudicula	7	6	4	4	4	4	5	4-5
Hormurus chthamalochoros	7-8	6	4	4	4	4	4-5	4-5
Hormurus chydaeostigmata	8	7	4	4	4	4	4-5	5
Hormurus davydovi	7	6-7	4	4	4	4	4	5
Hormurus dechangei	8	6	3	4	4	4	4	4
Hormurus dodecatrichos	8-9	7	4	4	4	4	5	5
Hormurus euktaenospatha	7-8	?	4	4	4	4	4	5
Hormurus extensus	7-8	6-7	4	4	4	4	5	5
Hormurus glaphyroscytos	8	7-8	4	4	4	4	5	5
Hormurus goliath	8-10	8	4	4	4	4	4	4-5
Hormurus halmaherae	7	7	4	4	4	4	4	4-5
Hormurus hylaios	7-8	6	4	4	4	4	5	5
Hormurus hypselankylis	9	7-8	4	4	4	4	5	5
Hormurus insculptus	7-8	7-8	4	4	4	4	4	5
Hormurus ischnoryctes	9-10	8-9	4	4	4	4	5	4-5
Hormurus karschii	?	9-10	4	4	4	4	5	5
Hormurus khangalu	5-6	6-7	4	4	4	4	4-5	4
Hormurus kilkerranicus	6	5	4	4	4	4	5	5
Hormurus kukunyungkal	8	6-7	4	4	4	4	5	5
Hormurus kuukayau	8	7-8	4	4	4	4	5	5
Hormurus laevitropis	9	7-8	4	4	4	4	5	5
Hormurus leptochela	7	6	4	4	4	4	4	5
Hormurus litodactylus	6-7	5-6	3	4	3	4	4	4
Hormurus macrochela	8	7	4	4	4	4	5	5
Hormurus mesochtonus	7-8	6-7	4	4	4	4	5	5
Hormurus microkypheus	10	9-10	4	4	4	4	4	4
Hormurus milneanus	7-8	7	4	4	4	4	5	5
Hormurus muralagi	9-10	6-8	4	4	4	4	4-5	5
Hormurus neocaledonicus	9	7-8	4	4	4	4	5	5
Hormurus nesiotes	9	7	4	4	4	4	5	5
Hormurus nyawaygi	7	6	4	4	4	4	4-5	5
Hormurus ochthonastes	7	5-6	4	4	4	4	4	5
Hormurus ochyroscapter	9	7	4	4	4	4	4-5	5
Hormurus oreios	8	6	4	4	4	4	5	5
Hormurus oreospyridus	10	?	4	4	4	4	4	5
Hormurus orthodactylus	7-8	4-5	4	4	4	4	4	4
Hormurus papuanus	8-9	7-8	4	4	4	4	5	5
Hormurus penta	9	?	4	4	4	4	4	5
Hormurus polisorum	8	6	4-5	4-5	5	5	5	5
Hormurus samoa	9-10	?	4	4	4	4	4	5
Hormurus scopaeus	8	?	4	4	4	4	5	5
Hormurus solomonensis	10	8	4	4	4	4	4	5
Hormurus tagulae	9-10	7	4	4	4	4	5	5
Hormurus tetrakaideca	?	?	?	?	4	4	5	5
Hormurus tjapukai	7	5-6	4	4	4	4	4-5	4-5
Hormurus tytthognaphos	6-7	5-6	4	4	4	4	4	4-5
Hormurus umpila	7	6	4	4	4	4	4-5	5
Hormurus waigiensis	?	?	?	?	?	?	?	?
Hormurus wallaman	?	6-7	4	4	4	4	5	5
Hormurus weberi	7-8	5-6	3	4	3	4	4	4
Hormurus xerogaios	8	7	4	4	4	4	5	5
Hormurus yelae	7	6	4	4	4	4	4-5	5

2.5.2 Matrix of morphological characters. Characters 8–9 (continuous). (Continued).

	8	9
Opisthacanthus (N.) laevipes	3	4
Chiromachetes fergusoni	2	3
Chiromachetes tirupati	3	3
Chiromachus ochropus	10-12	12-14
Iomachus laeviceps	3	3
Iomachus malabarensis	3	3
Iomachus nitidus	3	3
Iomachus politus	4	4
Iomachus punctulatus	2	3
Opisthacanthus (M.) apios	3	3
Opisthacanthus (O.) cayaporum	4	6-7
Opisthacanthus (O.) elatus	5	7
Opisthacanthus (O.) lecomtei	3	4
O. (M.) madagascariensis	3	3
Opisthacanthus (M.) piceus	3	3
Palaeocheloctonus pauliani	3	3
Hormiops davydovi	5	5
Hormiops infulcra	4	5
Liocheles australasiae	4	4
Liocheles complanatus	4	4
Liocheles longimanus	4	4
Liocheles malaya	4	4
Liocheles nigripes	4	4
Liocheles suspectus	4	4
Hormurus actaeolophos	4-5	5
Hormurus aethes	5	5
Hormurus agastachys	5	5
Hormurus anekasankylis	5	5
Hormurus ankamuti	5	5
Hormurus ankistros	5	5
Hormurus asychnachaena	5	5
Hormurus asynaptodactylus	5	5
Hormurus bandjin	5	5
Hormurus boholiensis	4	4
Hormurus caudicula	5	5
Hormurus chthamalochoros	5	5
Hormurus chydaeostigmata	5	5
Hormurus davydovi	4-5	5
Hormurus dechangei	4	4
Hormurus dodecatrichos	5	5
Hormurus euktaenospatha	5	5
Hormurus extensus	5	5
Hormurus glaphyroscytos	5	5
Hormurus goliath	4-5	4-5
Hormurus halmaherae	4-5	4-5
Hormurus hylaios	5	5
Hormurus hypselankylis	5	5
Hormurus insculptus	4-5	5
Hormurus ischnoryctes	5-6	5
Hormurus karschii	5	5
Hormurus khangalu	5	5
Hormurus kilkerranicus	5	5
Hormurus kukunyungkal	5	5
Hormurus kuukayau	5	5
Hormurus laevitropis	5	5
Hormurus leptochela	4	5
Hormurus litodactylus	4	4
Hormurus macrochela	5	5
Hormurus mesochtonus	5	5
Hormurus microkypheus	4-5	5
Hormurus milneanus	5	5
Hormurus muralagi	5	5
Hormurus neocaledonicus	5	5
Hormurus nesiotes	5	5
Hormurus nyawaygi	4-5	5
Hormurus ochthonastes	4	5
Hormurus ochyroscapter	5	5
Hormurus oreios	5	5
Hormurus oreospyridus	4	5
Hormurus orthodactylus	4	4
Hormurus papuanus	5	5
Hormurus penta	4	5
Hormurus polisorum	5	5
Hormurus samoa	4	5
Hormurus scopaeus	5	5
Hormurus solomonensis	5	5
Hormurus tagulae	5	5
Hormurus tetrakaideca	?	?
Hormurus tjapukai	4-5	5
Hormurus tytthognaphos	4	5
Hormurus umpila	5	5
Hormurus waigiensis	?	?
Hormurus wallaman	5	5
Hormurus weberi	4	4
Hormurus xerogaios	5	5
Hormurus yelae	5	5

2.5.2 Matrix of morphological characters. Characters 10–65 (Continued).

```
                                 1          2                 3            4         5         6
                                 0123456789 0   1  23 4  567890123456 7  890123456789012345678901234567
                                 †       †† †  †  †  †  † † †        † †  †      †† ††† † †  ††
Opisthacanthus (N.) laevipes     0000001010 0   0  00 1  0220-0-0--00 0  11000000110021010001000000100
Chiromachetes fergusoni          011001?111 ?   ?  ?? ?  ?00??0----10 0  00000001110021010000000000101
Chiromachetes tirupati           011000?011 1   1  -- -  ---0---0---0 0  10000001110021010000000000101
Chiromachus ochropus             0101111111 0   0  00 0  000201010111 0  10000001110021000000000000100
Iomachus laeviceps               011000?011 1   1  -- -  -110-0-0--00 0  10000001110021010000000000101
Iomachus malabarensis            011000?011 0   0  00 0  0000-0-0--00 0  10000001110021010000000000101
Iomachus nitidus                 0110001011 1   1  -- -  -110-0-0--00 0  10000001110021010000000000101
Iomachus politus                 0100112111 0   0  11 1  0220-1101-00 0  10100000010011000000000100100
Iomachus punctulatus             0110001111 1   1  -- -  -110-0-0--00 0  10000001110021010000000000101
Opisthacanthus (M.) apios        0100002011 ?   ?  ?? ?  ?00??0----00 1  -00000001100110100000000000100
Opisthacanthus (O.) cayaporum    0110100011 0   0  00 0  022211110001 0  00000000110021000002010011-
Opisthacanthus (O.) elatus       0111100011 0   0  00 0  022211110001 0  00000000111111000000001001101
Opisthacanthus (O.) lecomtei     0111102111 0   0  11 1  0220-110--00 0  00100000100011000000000000100
O. (M.) madagascariensis         0100012011 0   0  00 0  0000-0-0--10 1  -00000001100110100000000000100
Opisthacanthus (M.) piceus       0110011011 0   0  00 0  0000-0-0--10 1  -00000001100110100000000000100
Palaeocheloctonus pauliani       0000002011 0   0  00 0  0000-0-0--00 1  -00000001100210100000000000100
Hormiops davydovi                0100012111 3   2  -- -  -220-0-0--00 0  10101001000021000000000000101
Hormiops infulcra                0100012111 3   2  -- -  -220-0-0--00 0  10101001000021000000000000101
Liocheles nigripes               0110002011 0   0  00 2  0220-0-10100 0  00001001000021000000000000101
Liocheles longimanus             0000012011 0   0  00 0  0220-0-10100 0  00001001000021000000000000101
Liocheles malaya                 0000002011 0   0  00 0  0220-0-10100 0  00101001000021000000000000101
Liocheles australasiae           0100002011 0   0  00 0  0220-0-10100 0  00101001000021000000000000101
Liocheles complanatus            0000002011 ?   ?  ?? ?  ?2??0----00 0  00101001000021000000000000101
Liocheles suspectus              0000002011 0   0  00 1  0220-0-10100 0  10001001010021000000000000101
Hormurus actaeolophos            0000012011 0   0  00 0  0220-0-10100 0  00102001001111000000000000101
Hormurus aethes                  0000002011 0   0  01 1  0220-0-10000 0  00102001011111000000000000101
Hormurus agastachys              0000002011 0   0  00 0  0??0---101?0 0  10102001001111000000000000100
Hormurus anekasankylis           0000012011 0   0  01 0  0220-0-10100 0  10102001001111000000000000101
Hormurus ankamuti                0000012011 0   0  00 2  0220-0-10100 0  10102001001111000000000001101
Hormurus ankistros               0111002011 ?   ?  ?? ?  ?2??0----00 0  10103001011111000000001000101
Hormurus asychnachaena           0110012011 2   1  00 0  0220-0-10000 0  00103001011111000000001000101
Hormurus asynaptodactylus        0000012011 0   0  01 1  0220-0-10000 0  10103001011111000000001000101
Hormurus bandjin                 0000012011 0   0  01 0  0220-0-10100 0  00102001001111000000000000101
Hormurus boholiensis             0???002011 ?   ?  ?? ?  ?2??0----00 0  00103001001111000000001000101
Hormurus caudicula               0000012011 0   0  00 0  0220-0-10100 0  10102001001111000000000000101
Hormurus chthamalochoros         0000012011 0   0  01 0  0220-0-10100 0  10102001001111000000000000101
Hormurus chydaeostigmata         0110012011 0   0  01 0  0220-0-10000 0  10103001001111000000000000101
Hormurus davydovi                0000002011 0   0  00 0  0220-0-10100 0  10103001011111000000001000101
Hormurus dechangei               0111012011 ?   ?  ?? ?  ?2??0----00 0  00103001000021000000001000101
Hormurus dodecatrichos           0100012011 0   0  00 1  1220-0-10100 0  10113011001111000000000000100
Hormurus euktaenospatha          0000002011 0   0  00 1  0??0---101?0 0  10103001001111000000001000101
Hormurus extensus                0000012011 0   0  01 1  1220-0-0--00[12]00102001001111000000000000101
Hormurus glaphyroscytos          0000012011 0   0  00 0  0220-0-10100 0  10103001001111000000000000100
Hormurus goliath                 0111012011 0   0  00[12]0220-0-10100 0  10103001011111000000001000101
Hormurus halmaherae              0001002011 0   0  01 0  0220-0-10100 0  00103001000021000000001000101
Hormurus hylaios                 0100012011 0   0  00 0  0220-0-10100 0  10103001001111000000000000101
Hormurus hypselankylis           0110012011 0   0  01 0  0220-0-10100 0  00103001011111000000000000101
Hormurus insculptus              0000012011 0   0  00 0  0220-0-10100 0  10103001011111000000000000101
Hormurus ischnoryctes            0000012011 0   0  00 0  0220-0-10100 0  10103001001111000000000000101
Hormurus karschii                0111012011 0   0  01 0  0220-0-10100 0  10103001011111000000000000101
Hormurus khangalu                0000012011 0   0  00 0  0220-0-10100 0  10103001001111000000000000100
Hormurus kilkerranicus           0000012011 0   0  01 1  0220-0-10000 0  00103001011111000000000000101
Hormurus kukunyungkal            0100012011 0   0  00 0  0220-0-10100 0  10103001001111000000000000101
Hormurus kuukayau                0000012011 0   0  00 0  0220-0-10100 0  10103001011111000000001000101
Hormurus laevitropis             0000012011 0   0  00 0  0220-0-10100 0  10102001001111000000000000100
Hormurus leptochela              0100012011 0   0  00 0  0220-0-10000 0  00102001001111000000000000101
Hormurus litodactylus            0100012011[34][23]-- -  -220-0-0--00 0  00102001001111000000000000101
Hormurus macrochela              0000012011 0   0  00 0  0220-0-10100 0  10103001011111000000000000101
Hormurus mesochtonus             0000012011 0   0  01 1  0220-0-10000 0  10103001011111000000000000101
Hormurus microkypheus            0111002011 2   1  00 0  0220-0-10000 0  10103001011111000000001000101
Hormurus milneanus               0000012011 0   0  01 0  0220-0-10100 0  00103001011111000000001000101
Hormurus muralagi                0000012011 0   0  00 1  0220-0-10100 0  10103001011111000000001000101
Hormurus neocaledonicus          0000002011 0   0  00 0  0221-0-10000 0  00102001000021000000000000101
Hormurus nesiotes                0001002011 ?   ?  ?? ?  ?2??0----00 0  00103001001121000000001000101
Hormurus nyawaygi                0000012011 0   0  01 0  0220-0-10100 0  10103001001111000000000000101
Hormurus ochthonastes            0000012011 0   0  00 0  0220-0-10100 0  00103001001111000000001000101
Hormurus ochyroscapter           0???002011 0   0  00 0  0220-0-10100 0  10102001001111000000001000100
Hormurus oreios                  0000012011 0   0  01 0  0220-0-10100 0  10103001011111000000000000101
Hormurus oreospyridus            0001012011 0   0  01 0  0??1---10100 0  10103001001111000000001000101
Hormurus orthodactylus           0100012011 3   2  -- -  -220-0-0--00 0  00102001011111000000000000101
Hormurus papuanus                0110002011 0   0  01 1  0220-0-10100 0  10103001011111000000000000101
Hormurus penta                   0000002011 0   0  00 0  0??1---101?0 0  00102101000021000000000010101
Hormurus polisorum               0000012011 0   0  01 1  0220-0-10000 0  10103001011111000000000000101
Hormurus samoa                   0???002011 0   0  00 0  0??1---100?0 0  00102101000021000000000010101
Hormurus scopaeus                0000002011 0   0  00 0  0??0---101?0 0  10102001001111000000000000100
Hormurus solomonensis            0111012011 0   0  00 0  0220-0-10100 0  10103001011111000000001000101
Hormurus tagulae                 0000012011 0   0  00 0  0220-0-10100 0  10103001001111000000001000101
Hormurus tetrakaideca            0000012011 0   0  01 0  0220-0-10100 0  10103001001111000000100000101
Hormurus tjapukai                0000012011 0   0  00 0  0220-0-10100 0  10102001001111000000001000101
Hormurus tytthognaphos           0100012011 0   0  00 0  0220-0-10000 0  00102001011111000000000000101
Hormurus umpila                  0100002011 0   0  00 0  0220-0-10100 0  10103001001111000000000000101
Hormurus waigiensis              0???01?011 0   0  01 0  0??0---101?0 0  10103001011111000000001000101
Hormurus wallaman                0000012011 ?   ?  ?? ?  ?2??0----00 0  10103001001111000000000000101
Hormurus weberi                  0000002011 0   0  01 0  0220-0-10100 0  00103001000021000000001000101
Hormurus xerogaios               ????012011 0   0  00 2  0220-0-10100 0  10102001011111000000001000100
Hormurus yelae                   0100012011 0   0  01 0  0220-0-10100 0  00103001001111000000000000101
```

2.5.2 Matrix of morphological characters. Characters 66–133 (Continued).

```
                                                                  1         1         1         1
                                    7         8         9         0         1         2         3
                                    67890123456789012345678901234567890123456789012345678901234567890123
                                    †† †† †     † †   † †     †      †         †         †    ††
Opisthacanthus (N.) laevipes        001010-02--100101001001011010-10--00100111100000120100101011100100000
Chiromachetes fergusoni             002010-0010101-00-00000100010-10--00100010101000010000101011001010??
Chiromachetes tirupati              001010-0000001-00-00001100010-10--00100010101000120000201011211010000
Chiromachus ochropus                000010-01-0101-00000000000000-10--00110111111000100100101011201100011
Iomachus laeviceps                  001010-0000001-00-00001100010-10--00100010001000121000101011211010000
Iomachus malabarensis               001010-0010001-00-00001100010-10--00100010101000121000101011211010000
Iomachus nitidus                    001010-0000001-00-00001100010-10--00100010001000120000201011211010000
Iomachus politus                    000010-0001001-20-00000000000-0---100000000--00002100120101121O-1000
Iomachus punctulatus                001010-0000101-00-00000100010-10--00100010101000110000101011101010000
Opisthacanthus (M.) apios           001010-0010000101001001000000-10--00110111100111100000101010101101??
Opisthacanthus (O.) cayaporum       101010-0010001-00-01000110010-110-0000000100-00011000011101120111011
Opisthacanthus (O.) elatus          002010-0010000100-02000110011021000000011001000100001111010101111021
Opisthacanthus (O.) lecomtei        000010-01--100001001000010010-12--00010110100000100000211010201010011
O. (M.) madagascariensis            001010-0010000101000001000000-10--00110111100111110000201010111000011
Opisthacanthus (M.) piceus          001010-0010000101000001000000-10--00100111000111100000101010101110111
Palaeocheloctonus pauliani          001010-0010001-01000001000011110--00100010100101110000101010211000011
Hormiops davydovi                   001010-0011000121000002100000-10--00000001000111121000200O1-310-1011
Hormiops infulcra                   001010-0011000121000002100000-10--00000001000111121000200O1-310-1001
Liocheles nigripes                  001010-1000001-21001002100010-10--00100010100110120000201010001001001
Liocheles longimanus                001010-0011001-01100002100010-10--00100001000000120000201011301010000
Liocheles malaya                    002010-0011001-01100002100010-110-0010000000-00012000020101100101000
Liocheles australasiae              001010-0010001-01100002100010-10--00110010100111120000201011301010011
Liocheles complanatus               001010-0011001-01100002100010-2100001000100000001200002010113010102??
Liocheles suspectus                 001010-0010001-01101002100010-2100011100111001111210002010113010100l
Hormurus actaeolophos               00201100011001-011000122-00110210001111111100101120000201011301010011
Hormurus aethes                     00201100000001-011010122-00110211002111111100111120000201011301010021
Hormurus agastachys                 001010-0011001-11000002100011110--01110111100111120000201011301010021
Hormurus anekasankylis              00201100011001-01101002100011121000111111100111120000201011301010011
Hormurus ankamuti                   00201100011001-011010122-00110210001111111100111120000201011301010011
Hormurus ankistros                  00201100011000101101002101011021000211111110011111000020101130101O??
Hormurus asychnachaena              00201100011000101101022-00111210210211111110111120000211011301110021
Hormurus asynaptodactylus           00201100011000101100002101011021000211111110011111200002010113011l021
Hormurus bandjin                    00201100011001-011010122-00110210001111111100111120000201011301010011
Hormurus boholiensis                002010-0010001-011010122-00110210001111111100100120000201011301010??
Hormurus caudicula                  002010-0011001-011010122-00110210002111111100111120000201011301010011
Hormurus chthamalochoros            00201100011001-011010122-00110210002111111100111120000201011301010021
Hormurus chydaeostigmata            001010-0011001-01000002100011121100110111001111200002010113010101l
Hormurus davydovi                   00201100011001-011000122-00110210002111111100101120001221011301010021
Hormurus dechangei                  002010-0010001-011010122-00111210001111111100111200002010113010102?
Hormurus dodecatrichos              001010-0011001-01000002100011121100110111001011200002010113010100O
Hormurus euktaenospatha             00201100000001-011010122-00110210002111111100111120000201011301010021
Hormurus extensus                   002010-0011001-01100002100011121100111111100111200002010113010101l
Hormurus glaphyroscytos             002010-0011001-010000122-00111110001111111100111120000201011301010O1
Hormurus goliath                    00201100011000101101002100011021000211111110010112000020101130111021
Hormurus halmaherae                 002010-0011001-011000122-00110210002111111100111120000201011301010011
Hormurus hylaios                    00201100011001-011010122-00110210001111111100111200002010113010101l
Hormurus hypselankylis              00201100011001-011000122-00110210002111111100111120000201011301010011
Hormurus insculptus                 002010-0011001-011000122-00110210002111111100111120001201011301010011
Hormurus ischnoryctes               002010-0001001-010000122-00111210001101111001011200002010113010101l
Hormurus karschii                   00201100011000101101022-00110210002111111100111200002010113010102l
Hormurus khangalu                   001010-0011001-01000002100011110--01110111000111120000201011301010O1
Hormurus kilkerranicus              00201100010001-011010122-00110210002111111100101120000201011301110021
Hormurus kukunyungkal               002010-0011001-01101002100011021000111111100111120000201011301010011
Hormurus kuukayau                   00201100011001-011010122-00110210002111111100111200002010113010101l
Hormurus laevitropis                001010-0011001-01101002100011121000111111100111120000201011301010011
Hormurus leptochela                 002010-0011001-011000122-00110210002111111100111120000201011301010011
Hormurus litodactylus               00201100011001-011000122-00110210002111111100111120000201011301010011
Hormurus macrochela                 00201100011001-011010122-00111210001111111100111200002010113010101l
Hormurus mesochtonus                00201100011001-011010122-00110210002111111100101120000201011301110021
Hormurus microkypheus               00201100011001-01101002100011021000211111110010112000020101130111021
Hormurus milneanus                  00201100011001-011010122-00110210002111111100111120000211011301010021
Hormurus muralagi                   00101100011001-011010122-00111210001111111100111200002010113010101l
Hormurus neocaledonicus             002010-0000001-011010122-00111210001111111100111120000211011301110021
Hormurus nesiotes                   001010-0010001-011010122-00110210002111111100111120000201011301010??
Hormurus nyawaygi                   002010-0011001-011010122-00110210001111111100111120000201011301010011
Hormurus ochthonastes               00201100011001-011000122-00110210002111111100111200002010113010101l
Hormurus ochyroscapter              002010-1000001-01000002100011121000111111100101120000201011301010011
Hormurus oreios                     00201100011001-01100002100011021000211111110011112000120101130101021
Hormurus oreospyridus               00201100010001-011010122-00010210002111111100101120001201011301010021
Hormurus orthodactylus              00201100011001-011000122-00110210002111111100111120000201011301010011
Hormurus papuanus                   00201100011001-01101002100011021000211111110010112000120101130101021
Hormurus penta                      001010-0010001-01100002100011110--00110111100111120000211011301010021
Hormurus polisorum                  00201100011001-01101002100011110--11111111100111020O1---011130111021
Hormurus samoa                      001010-0010001-01102012200-00111210001111111100111200002110113011l021
Hormurus scopaeus                   001010-0000001-11000002100011110--01110111100111120000201011301010011
Hormurus solomonensis               00201100010001-011010122-00110210002111111100101120000201011301100021
Hormurus tagulae                    00201100011001-011000122-00110210002111111100101120000201011301010021
Hormurus tetrakaideca               002010-0011001-01100002100011121000111111100111120000201011301010011
Hormurus tjapukai                   00201100011001-011010122-00110210002111111100111120000201011301010011
Hormurus tytthognaphos              00201100011001-011000122-00110210002111111100111120000201011301010011
Hormurus umpila                     00201100001001-011010122-00111210002111111100111200002010113010101l
Hormurus waigiensis                 00201100011000101101002100011021000211111110011112000020101130101021
Hormurus wallaman                   002010-0011001-011000122-00111210002111111100101110000201011301010??
Hormurus weberi                     002010-0011001-011000122-00110210001111111100111120000201011301010021
Hormurus xerogaios                  001010-0011001-010000122-00111110--01111111000101120000201011301010O1
Hormurus yelae                      00201100011001-011010122-00110210002111111100111120000201011301010021
```

2.5.2 Matrix of morphological characters. Characters 134–193 (Continued).

```
                                    1         1          1          1         1         1
                                    4         5          6          7         8         9
                                456789012345678901 2  456789012345678 9  012345678901234567890 1 2
                                                                  †          † †      ††  ††  †
Opisthacanthus (N.) laevipes    01101201111100000000 0  00101010001101O 0  11101000000011-00000100 0
Chiromachetes fergusoni         ???????000000000--- -  0000001000?2002 0  111?0011110O?1-00000000 0
Chiromachetes tirupati          0010120?????????000 0  0010??????1?012 1  01100111110O????????0?? ?
Chiromachus ochropus            11102301111122101O1 0  10000000101100O 0  11101110000011-10101100 0
Iomachus laeviceps              00001100000000000000 0  00100000101101Z 1  01100011110011-00000000 0
Iomachus malabarensis           0000110000000000--O 0  00000000101101Z 0  01100011110011-00000000 0
Iomachus nitidus                00101200000000000000 0  00100000101101Z 1  01100111110011-00000000 0
Iomachus politus                0000000000000000--- -  00100000101100Z 1  01100001110-011-00000000 0
Iomachus punctulatus            0000110000000000--O 0  00100000102201Z 1  01100011000011-00000000 0
Opisthacanthus (M.) apios       ????????111111210010 1  00010000001200O 0  01100111000O?1-00000000 0
Opisthacanthus (O.) cayaporum   11102201111100001O0 0  10000000111201Z 0  1110001111-111-00000000 0
Opisthacanthus (O.) elatus      11112302111121001O0 1  10000000101201Z 0  11100011110011-00000000 0
Opisthacanthus (O.) lecomtei    11102300111000000000 0  00010000000100Z 1  01100011110011-00000000 0
O. (M.) madagascariensis        11101301111110100l0 1  00010000101100O 0  01001110000011-00000000 0
Opisthacanthus (M.) piceus      11101301111110100l0 1  00101000001100O 0  01001110000011-00000000 0
Palaeocheloctonus pauliani      01101300011100100l0 1  00010000000100O 0  01100111000011-00000000 0
Hormiops davydovi               10102300001000000l0 1  00100111-011011 1  01001011000000-00001100 0
Hormiops infulcra               10102300000000000l0 1  00100111-011111 1  01001011000000-00101100 0
Liocheles nigripes              01101200000000000000 0  10100111-011002 1  01101011000000-00001110 0
Liocheles longimanus            0000120000000000--O 0  10000111-011002 1  01100011000000-00001111 0
Liocheles malaya                0000120000000000--O 0  10000111-001002 1  01101011000000-00001111[12]
Liocheles australasiae          11101200000000000000 0  10000111-011002 1  01101011000000-00101111 1
Liocheles complanatus           ???????000000000--- -  10100111-07l002 1  011?1011000O?0-00001111 1
Liocheles suspectus             10101300000000000000 0  10100111-001002 1  01101011000000-00001111 1
Hormurus actaeolophos           11102311111110001000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus aethes                 11102312111111011000 0  10100111-022012 2  01102110000000-00000000 0
Hormurus agastachys             1111231?????????101 0  1010??????1?002 1  01100110000000?-00000001 0
Hormurus anekasankylis          11102311111111011000 0  10100111-012012 1  01100110000000-00000001 0
Hormurus ankamuti               11102311111111011000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus ankistros              ??????12111111011100 0  12100111-07?002 1  111?0110000O?0-00000001 0
Hormurus asychnachaena          11102312111111011100 0  10100111-111002 1  11100110000000-00000000 0
Hormurus asynaptodactylus       11102312111111011100 0  11100111-022002 1  11100110000000-00000001 0
Hormurus bandjin                11102311111111011000 0  10100111-012012 1  01100110000000-00000001 0
Hormurus boholiensis            ???????11111000100- -  10100111-07?002 1  011?0010000O?0-00000001 1
Hormurus caudicula              11102311111110001000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus chthamalochoros        11102311111110011000 0  10100111-022002 1  01100110000000-00000001 0
Hormurus chydaeostigmata        11101111100100001000 0  10100111-012012 1  01100110000000-00000000 0
Hormurus davydovi               11102312111111011100 0  11100111-112002 1  01100110000000-00000000 0
Hormurus dechangei              ???????111111111000 0  10100111-012002 1  01100010000O?0-00000001 1
Hormurus dodecatrichos          10101210001000010O0 0  10100111-012012 1  01100110000000-00000001 0
Hormurus euktaenospatha         1110231?????????000 0  1010??????1?002 1  011?0010000O?-00000000 0
Hormurus extensus               11102311111100110l0[12]10100111-011012 1  01100110000000-00001000 0
Hormurus glaphyroscytos         01101310011100000000 0  10110111-012002 1  01100110000000-00000001 0
Hormurus goliath                11102312111111011100 0  11100111-112002 1  11100110000000-00000001 0
Hormurus halmaherae             11102311111110011000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus hylaios                11102311111111011000 0  10100111-012012 1  01100110000000-00000001 0
Hormurus hypselankylis          11102312111111011100 0  10100111-112002 1  01100110000000-00000001 0
Hormurus insculptus             11102311111110011000 0  10100111-112002 1  01100110000000-00000001 0
Hormurus ischnoryctes           01101310011100000000 0  10100111-002002 1  01100110000000-00000001 0
Hormurus karschii               11102312111111111100 0  10100111-122002 1  11100110000000-00000001 0
Hormurus khangalu               01102310011100000000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus kilkerranicus          11102312111111001100 0  10100111-012002 2  01100110000000-00000001 0
Hormurus kukunyungkal           11102311111110011000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus kuukayau               11102311111111011000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus laevitropis            11102311111110011000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus leptochela             11102311111100001000 0  10100111-012012 1  01100110000000-00000000 0
Hormurus litodactylus           11102311111100001000 0  10100111-022012 1  01100110000000-00000001 0
Hormurus macrochela             11102311111111011000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus mesochtonus            11102311111111011000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus microkypheus           11102312111110011100 0  11100111-112002 1  11100110000000-00000001 0
Hormurus milneanus              11102312111111011100 0  10100111-012002 1  01100110000000-00000001 0
Hormurus muralagi               11102311111111011000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus neocaledonicus         11102312111112211100 0  10000111-012000 1  01100011000000-00001101 1
Hormurus nesiotes               ???????211111111100 0  10000111-012000 1  0110011100O?0-00000001 0
Hormurus nyawaygi               11102311111110011000 0  10100111-012012[23]01100110000000-00000001 0
Hormurus ochthonastes           11102311111110001000 0  10100111-022002[23]01100110000000-00000001 0
Hormurus ochyroscapter          11102311111110000000 0  10100111-011002 1  01100110000000-00000001 0
Hormurus oreios                 11102311111110011000 0  10100111-112002 1  01100110000000-00000001 0
Hormurus oreospyridus           1110231?????????100 0  1010??????0?002 1  0110011000000?-00000000 0
Hormurus orthodactylus          11102311111100001000 0  10100111-012012 1  01100110000000-00000001 0
Hormurus papuanus               11102312111111011100 0  10100111-112002 1  01100110000000-00000001 0
Hormurus penta                  1110231?????????100 0  1000??????1?000[23]01100011000O?-01001101 0
Hormurus polisorum              11112312111122110l0 1  10110111-012000 1  01100110000000-00000000 0
Hormurus samoa                  1110231?????????100 0  1000??????1?002 1  01100011000O?-01011101 0
Hormurus scopaeus               1110231?????????000 0  1010??????1?002 1  0110011000000?-00000001 0
Hormurus solomonensis           11102312111111111100 0  10100111-002002 1  01100110000000-00000000 0
Hormurus tagulae                11102312111111111100 0  10100111-112002 1  01100110000000-00000001 0
Hormurus tetrakaideca           1110231?????????000 0  1010????????0?2 1  01100110000000-00000001 0
Hormurus tjapukai               11102311111100001000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus tytthognaphos          11102310011100010O0 0  10100111-022012 1  01100110000000-00000001 0
Hormurus umpila                 11102311111110001000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus waigiensis             111?231?????????100 0  11????????????? 1  0??????1??????????????? ?
Hormurus wallaman               ???????111110011000 0  10100111-07?002 1  011?0110000O?0-00000001 0
Hormurus weberi                 11102310111100010O0 0  10100111-002002[23]01100010000000-00000001 0
Hormurus xerogaios              01101311111110000000 0  10100111-012002 1  01100110000000-00000001 0
Hormurus yelae                  11102311111111111000 0  10100111-012002 1  01100110000000-00000001 0
```

2.5.2 Matrix of morphological characters. Characters 194–252 (Continued).

```
                                                  2         2           2           2         2         2
                                                  0         1           2           3         4         5
                                        45 6  7890123456789012345 6  7890123456 7  8901234567890123456789012
                                                    †  †       ††     † ††† ††††           †
Opisthacanthus (N.) laevipes            00 0  0000011000001100000 1  1100200011 0  0-0000100000000001101010-
Chiromachetes fergusoni                 00 0  0000022011000-10010 2  21?0200011[23]101010?????????????????????
Chiromachetes tirupati                  ?? ?  ?????2201100--10010 2  210?200011 2  1000101000011--111100000-
Chiromachus ochropus                    00 0  0000022010000000000 1  2100211122 3  1010300000011--001101000-
Iomachus laeviceps                      00 0  0000022011-0--10010 1  2100200011 2  1000101000011--111100000-
Iomachus malabarensis                   00 0  0000022011000--10010 1  2100200011 2  1000101000011--111100000-
Iomachus nitidus                        00 0  0000022011000--10010 2  2100200011 2  1000101000011--111100000-
Iomachus politus                        00 0  0000022001-0--1-1-- -  2100200011 2  1000100110200002300001000-
Iomachus punctulatus                    00 0  0000022011000000000 1  2100200011[23]100010?????????????????????
Opisthacanthus (M.) apios               00 0  0000022010000100000 1  2100200011[23]100020?????????????????????
Opisthacanthus (O.) cayaporum           00 0  0000022011000--00000 1  2100210011[13]111030011020002300001000-
Opisthacanthus (O.) elatus              00 0  0000022011000--00000 1  2100210011[13]111030011020002300001000-
Opisthacanthus (O.) lecomtei            00 0  0000022011000--10010 1  2100200011[13]100010111010002300001000-
O. (M.) madagascariensis                00 0  0000012010000100000 1  2100200011[13]1000201000011--2011012-0-
Opisthacanthus (M.) piceus              00 0  0000022010000100000 1  2100210011 0  0-0020000011--2011012-0-
Palaeocheloctonus pauliani              00 0  0000022010000011-011 -  2100200011[23]1000201000011--2011012-0-
Hormiops davydovi                       21 2  2000022011100--10000 0  2000210011 2  1011300110010104111111110-
Hormiops infulcra                       21 2  2000011011100--10000 0  2000210011 2  1011300110010104111111110-
Liocheles nigripes                      21 0  2000022011111--00000 0  2100200011 2  1010310110010204111211110-
Liocheles longimanus                    21 2  2000022011111--1-010 0  2100200011 2  1011301110010204111211110-
Liocheles malaya                        21 2  2000022011111-10000 0  2100200011 2  1010301110010204111211110-
Liocheles australasiae                  21 2  2000022011111--00000 0  2100210011 2  1011301110010204111211110-
Liocheles complanatus                   21 2  2000012011111--00000 0  21?0200011 2  1010300?????????????????????
Liocheles suspectus                     21 2  2011011011111--00000 0  2100200011 2  1010310110010204111211110-
Hormurus actaeolophos                   00 1  1011011011-0--0-000 1  2100210011 2  1010301110010204111011110-
Hormurus aethes                         00 1  0000022011-0--1-010 1  2100200011 2  1010301110010204111111111
Hormurus agastachys                     00 1  0011011011-0--0-000[23]210?200011 2  1010301110010204111111111
Hormurus anekasankylis                  00 1  0011011011-0--0-000 1  2100200011 2  1010301110010204111111112
Hormurus ankamuti                       00 1  1011011011-0--0-000 2  2100200011 2  1010301110010204111011111
Hormurus ankistros                      00 1  0000022011-0--1-011 -  21?0200011 2  1010300?????????????????????
Hormurus asychnachaena                  00 0  0000022011-0--0-011 -  2100210011 2  1010301110110214111011110-
Hormurus asynaptodactylus               00 1  0000022011-0--0-011 -  2100210011 2  1010301110110214111011110-
Hormurus bandjin                        00 1  1011011011-0--0-000 1  2100200011 2  1010301110010204111111111
Hormurus boholiensis                    00 2  2000022011-0--1-011 -  2??0200011 2  1010300?????????????????????
Hormurus caudicula                      00 1  1011011011-0--0-000 1  2100200011 2  1010301110010204111011110-
Hormurus chthamalochoros                00 1  1011011011-0--0-000 1  2100200011 2  1010301110010204111111111
Hormurus chydaeostigmata                00[12]0001021011-0--0-010 1  2100200011 2  1010301110010204111011111
Hormurus davydovi                       00 0  0000022011-0--1-011 -  2100200011 2  1010301110110014111011110-
Hormurus dechangei                      00 2  2000022011-0--1-011 -  2100200011 2  1010300?????????????????????
Hormurus dodecatrichos                  00 1  1001021011-0--0-011 -  2100200011 2  1010301110010204111011110-
Hormurus euktaenospatha                 00 0  0000022011-0--1-011 -  210?200011 2  1010301110010204111011111
Hormurus extensus                       10 1  1011011011-0--1-010 1  2100200011 2  1010301110010204111011110-
Hormurus glaphyroscytos                 00 1  1011011011-0--0-000 2  2100200011 2  1010301110010204111011111
Hormurus goliath                        00 1  0000022011-0--1-011 -  2100200011 2  1010301110110014111011111
Hormurus halmaherae                     00 1  0000022011-0--1-011 -  2100200011 2  1010301110110204111011110-
Hormurus hylaios                        00 1  1011011011-0--0-000 1  2100200011 2  1010301110010204111011110-
Hormurus hypselankylis                  00 1  1000022011-0--1-011 -  2100200011 2  1010301100310024111011110-
Hormurus insculptus                     00 1  1000022011-0--1-010 1  2100200011 2  1010301110110204111011110-
Hormurus ischnoryctes                   00 1  1011011011-0--0-000 1  2100200011 2  1010301110010204111111111
Hormurus karschii                       00 1  0000022011-0--1-011 -  2100200011 2  1010301110110214111011111
Hormurus khangalu                       00 1  1011011011-0--0-010 1  2100200011 2  1010301110010204111011111
Hormurus kilkerranicus                  00 1  1000022011-0--1-011 -  2100200011 2  1010301110010204111011110-
Hormurus kukunyungkal                   00 1  1011011011-0--0-000 1  2100200011 2  1010301110010204111111110-
Hormurus kuukayau                       00 1  1011011011-0--0-000 1  2100200011 2  1010301110010204111011110-
Hormurus laevitropis                    00 1  1011011011-0--0-000 1  2100200011 2  1010301110010204111111110-
Hormurus leptochela                     00 0  0011011011-0--0-000 2  2100200011 2  1010301110010204111111110-
Hormurus litodactylus                   00 1  0011011011-0--0-000 2  2100200011 2  1010301110010204111111110-
Hormurus macrochela                     00 1  1011011011-0--0-000 1  2100200011 2  1010301110010204111011110
Hormurus mesochtonus                    00 1  1000022011-0--1-011 -  2100200011 2  1010301110010204111011110-
Hormurus microkypheus                   00 1  0000022011-0--1-011 -  2100200011 2  1010301110110014111011110-
Hormurus milneanus                      00 1  1000022011-0--1-011 -  2100200011 2  1010301110110014111011110-
Hormurus muralagi                       00 1  1011011011-0--1-010 1  2100200011 2  1010301110010204111011111
Hormurus neocaledonicus                 00 2  2100022011-0--1-011 -  2100200011 2  1010301110010204111111110-
Hormurus nesiotes                       00 1  0000022011-0--1-011 -  2100200011 2  1010300?????????????????????
Hormurus nyawaygi                       00 1  1011011011-0--0-000 1  2100200011 2  1010301110010204111111111
Hormurus ochthonastes                   00 1  1111111011-0--0-000 1  2100210011 2  1010301110010204111111110-
Hormurus ochyroscapter                  00 1  1111011011-0--0-000 2  2100200011 2  1010301110010204111111111
Hormurus oreios                         00 1  1000022011-0--0-011 -  2100210011 2  1010301110210014111011110-
Hormurus oreospyridus                   00 0  0000022011-0--1-011 -  210?200011 2  1010301110010204111011110-
Hormurus orthodactylus                  00 1  0011011011-0--0-000 2  2100200011 2  1010301110010204111111110-
Hormurus papuanus                       00 1  0000022011-0--1-011 -  2100210011 2  1010301110210014111011110-
Hormurus penta                          00 2  2000022011-0--1-010 1  210?200011 2  1010301110010204111111110-
Hormurus polisorum                      00 0  0011011011-0--1-011 -  2100210011 2  1010301100010214111111110-
Hormurus samoa                          00 2  2000022011-0--1-010 1  210?200011 2  1010300?????????????????????
Hormurus scopaeus                       00 1  0011011011-0--0-000 2  210?200011 2  1010301110010204111011110
Hormurus solomonensis                   00 0  0000022011-0--1-011 -  2100200011 2  1000301110110204111011110-
Hormurus tagulae                        00 1  0000022011-0--1-011 -  2100200011 2  1010300?????????????????????
Hormurus tetrakaideca                   00 1  1011011011-0--0-010 1  2100200011 2  1010300?????????????????????
Hormurus tjapukai                       00 1  1011011011-0--0-000 2  2100200011 2  1010301110010204111111110-
Hormurus tytthognaphos                  00 1  0011011011-0--1-011 -  2100200011 2  1010301110010204111111110-
Hormurus umpila                         00 1  1011011011-0--0-000 2  2100200011 2  1010301110010014111011110-
Hormurus waigiensis                     ?? ?  ?????????????????? ?  ????20???? ?  ??1030?????????????????????
Hormurus wallaman                       00 1  1011021011-0--0-000 1  21?0200011 2  1010300?????????????????????
Hormurus weberi                         00 2  2000022011-0--1-011 -  2100200011 2  1010301110110204111011110-
Hormurus xerogaios                      00 1  0011011011-0--0-010 1  2100200011 2  1010301110010204111011110
Hormurus yelae                          00 1  0000022011-0--1-011 -  2100200011 2  1010301110010204111011113
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2.5.2 Matrix of morphological characters. Characters 253–262 (Continued).

```
                                        2
                                        6
                                3456789 0  12
                                ††    †
Opisthacanthus (N.) laevipes    001-010 0  02
Chiromachetes fergusoni         ??????? ?  ??
Chiromachetes tirupati          001-101 ?  ??
Chiromachus ochropus            001-111 0  02
Iomachus laeviceps              001-101 ?  ??
Iomachus malabarensis           001-101 ?  ??
Iomachus nitidus                001-101 ?  ??
Iomachus politus                001-011 1  02
Iomachus punctulatus            ??????? ?  ??
Opisthacanthus (M.) apios       ??????? ?  ??
Opisthacanthus (O.) cayaporum   001-011 ?  ??
Opisthacanthus (O.) elatus      001-011 1  02
Opisthacanthus (O.) lecomtei    001-011 ?  ??
O. (M.) madagascariensis        001-111 0  02
Opisthacanthus (M.) piceus      001-111 ?  ??
Palaeocheloctonus pauliani      001-111[12]02
Hormiops davydovi               0000011 ?  ??
Hormiops infulcra               0000011 ?  ??
Liocheles nigripes              0000011 ?  ??
Liocheles longimanus            0000011 ?  ??
Liocheles malaya                0000011 0  10
Liocheles australasiae          0000011 ?  ??
Liocheles complanatus           ??????? ?  ??
Liocheles suspectus             0000011 0  11
Hormurus actaeolophos           0001011 ?  ??
Hormurus aethes                 0001011 ?  ??
Hormurus agastachys             0001011 ?  ??
Hormurus anekasankylis          0001011 ?  ??
Hormurus ankamuti               0001011 ?  ??
Hormurus ankistros              ??????? ?  ??
Hormurus asychnachaena          0101011 ?  ??
Hormurus asynaptodactylus       0001011 ?  ??
Hormurus bandjin                0001011 ?  ??
Hormurus boholiensis            ??????? ?  ??
Hormurus caudicula              0001011 0  10
Hormurus chthamalochoros        0001011 ?  ??
Hormurus chydaeostigmata        0001011 ?  ??
Hormurus davydovi               0001011 ?  ??
Hormurus dechangei              ??????? ?  ??
Hormurus dodecatrichos          0001011 ?  ??
Hormurus euktaenospatha         0001011 ?  ??
Hormurus extensus               0001011 ?  ??
Hormurus glaphyroscytos         0001011 ?  ??
Hormurus goliath                0001011 ?  ??
Hormurus halmaherae             0001011 ?  ??
Hormurus hylaios                0001011 ?  ??
Hormurus hypselankylis          1001011 ?  ??
Hormurus insculptus             0001011 ?  ??
Hormurus ischnoryctes           0001011 ?  ??
Hormurus karschii               0001011 ?  ??
Hormurus khangalu               0001011 ?  ??
Hormurus kilkerranicus          0001011 ?  ??
Hormurus kukunyungkal           0001011 ?  ??
Hormurus kuukayau               0001011 ?  ??
Hormurus laevitropis            0001011 ?  ??
Hormurus leptochela             0001011 ?  ??
Hormurus litodactylus           0001011 ?  ??
Hormurus macrochela             0001011 ?  ??
Hormurus mesochtonus            0001011 ?  ??
Hormurus microkypheus           0001011 ?  ??
Hormurus milneanus              0001011 ?  ??
Hormurus muralagi               0001011 ?  ??
Hormurus neocaledonicus         0001011 0  10
Hormurus nesiotes               ??????? ?  ??
Hormurus nyawaygi               0001011 ?  ??
Hormurus ochthonastes           0001011 ?  ??
Hormurus ochyroscapter          0001011 ?  ??
Hormurus oreios                 0001011 ?  ??
Hormurus oreospyridus           0001011 ?  ??
Hormurus orthodactylus          0001011 ?  ??
Hormurus papuanus               0001011 ?  ??
Hormurus penta                  0001011 ?  ??
Hormurus polisorum              0001011 ?  ??
Hormurus samoa                  ??????? ?  ??
Hormurus scopaeus               0001011 ?  ??
Hormurus solomonensis           0001011 ?  ??
Hormurus tagulae                ??????? ?  ??
Hormurus tetrakaideca           ??????? ?  ??
Hormurus tjapukai               0001011 ?  ??
Hormurus tytthognaphos          0001011 ?  ??
Hormurus umpila                 0001011 ?  ??
Hormurus waigiensis             ??????? ?  ??
Hormurus wallaman               ??????? ?  ??
Hormurus weberi                 0001011 ?  ??
Hormurus xerogaios              0001011 ?  ??
Hormurus yelae                  0001011 ?  ??
```

2.5.3 Aligned molecular sequences. Mitochondrial small-subunit ribosomal DNA 12S gene, base-pairs 1–87. Dots indicate a match with the first taxon.

```
C.ochropus 2189          aaaaatatg-ttaaattaggtaataaaggaaattctgaaacctaaagaatttggcggtgttttaagtaattggaggaacctgttatt
C.ochropus 6894          .........-.............g.....................................................................
C.ochropus 9069          .........-.............g.....................................................................
I.nitidus 9827           t.......t-........a...g..t..a.tt........t.....................a....ca.............a.
I.politus 1514           ........ta...........g.....a..t...g.........a.................ta.tt.................
I.politus 3256           ........ta...........g.....a..t...g.........a.................ta.tt.................
O.elatus 1837            t...gc..at.a.............acct...c.........a..c...........c..a.................g..
O.laevipes 1835          t.....g.a-...........g.....a.t....c.........ag................a.....a..............
O.lecomtei 1608          ........taaa.........g.....attt.............a.................ta.tt.................
O.lecomtei 2194A         ........tgaag...........atttc.............a.................ta.tt.................
O.madagascariensis 2811  t....c..t-..t.........g..t..a.t..............g..............g.a....ca............t..
O.madagascariensis 2812  t.t..c..t-...........g..t..a.t..............g..............g.a....ca............t..
O.piceus 6260            t.t..c..t-...........g..t..a.t..............g..............g.a....ca............t..
H.infulcra 2185          t.......ta.a.........g..tt.a.tt.........................a......a.............t....g..
L.australasiae 1854      t.......a-a..........g.....attt.........................a.c....a....c..............
L.australasiae 2181      t.......a-a..........g.....attt.....................a.........a.c....a....c.....
L.australasiae 2182      t.......a-g..........g.....att.a.....................c....a....c.............g..
L.australasiae 2183      t.......a-a..........g.....attt.........................a.c....a....c..............
L.australasiae 2729      t.......a-a..........g.....attt.........................a.c....a....c..............
L.australasiae 2733      t.......a-a..........g.....attt.........................a.c....a....c..............
L.australasiae 2996      t.......a-a..........g.....attt.........................a.c....a..................
L.australasiae 3684      c.......a-a..........g.....attt.....................c....a....c.............c.
L.australasiae 4764      t.......a-a..........g.....attt.................a.........a.c....a....c..............
L.australasiae 5553      t.....g.a-a..........g.....attt.........................a.c....a....c..............
L.australasiae 8676      t.......a-a..........g.....attt.........................a.c....a....c..............
L.australasiae 8677      t.......a-a..........g.....attt.........................a.c....a....c..............
L.longimanus 6388        t.......at.a.g.......g...g.attta..c..........g..............a....c............g..
L.malaya 1909            t.......aa.a.....g....g...g.agtta.............g..........c.....a....c..............
H.aethes 3002            ........ataa.........g.....a.tt.....................a.............t.................g..
H.aethes 3005            ........ataa.........g.....a.tt.....................a.............t.................g..
H.anekasankylis 6355     ........atga.........g.....attt.....................................a..................
H.anekasankylis 6356     ........atga.........g...t.attt.....................................a.................c.
H.anekasankylis 6357     ........atga.........g.....attt.....................................a..................
H.ankistros 4339         ........ataa.........g...c.attt.........................a.....a..................
H.bandjin 5556           ........atga.........g.....attt.....................................a.................c.
H.bandjin 5557           ........atga.........g.....attt.....................................a.................c.
H.bandjin 5558           ........atga.........g.....attt.....................................a.................c.
H.caudicula 1502         ........ataa.........g.....attt.....................................a..................
H.caudicula 2339         ........ataa.........g.....attt.....................................a..................
H.caudicula 2340         .g......ataa...............attt.....................................a..................
H.caudicula 6360         ........ataa.........g.....attt.....................................a..................
H.caudicula 6361         ........ataa.........g.....attt.....................................a..................
H.caudicula 6362         ........ataa.........g.....attt.....................................a..................
H.chthamalochoros 6350   ........atga.........g.....attt.....................................g.a.................c.
H.chthamalochoros 6351   ........atga.........g.....atttc.............g.....................g.a.................c.
H.chthamalochoros 6352   ........atga.........g.....attt.....................................g.a.................c.
H.chthamalochoros 8023   ........atga.........g.....attt.....................................g.a.................c.
H.chydaeostigmata 5560   ........atga.........g.....attt.....................................a..................
H.chydaeostigmata 8015   ........ataa.........g.....attt.....................................a..................
H.chydaeostigmata 8016   ........ataa.........g.....attt.....................................a..................
H.chydaeostigmata 8019   ........atga.........g.....attt.....................................a..................
H.chydaeostigmata 8020   ........atga.........g.....attt.....................................a..................
H.chydaeostigmata 8022   ........atga.........g.....attt.....................................a..................
H.dechangei 7789         .........taa.........g.....a.tt.....................................a.................g..
H.euktaenospatha 4340    g....c...taa.........g.....agtt.................c...................a.................g..
H.glaphyroscytos 6640    ........ataa.........g.....attt.....................................a..................
H.hylaios 6358           ........ataa.........g.....atttc........t.................a......a.................g..
H.hylaios 6359           ....g...ataa.........g.....atttc........t.....................a.....a.................g..
H.hylaios 6363           ........ataa.........g.....atttc........t.................a......a.................g..
H.ischnoryctes 6639      ........ataa..g.......g.....attt.....................................a..................
H.kukunyungkal 6341      ........ataa.........g.....attta.....................................a...........t.......
H.kukunyungkal 6342      ........ataa.........g.....attta.....................................a.............t.......
H.kukunyungkal 6343      ........ataa.........g.....attta.....................................a.............t.......
H.laevitropis 6348       ........ataa.........g......ttta.....................................a..................
H.leptochela 6344        ........ataa.........g.....attt.....................................a.................a.
H.leptochela 6345        ........ataa.........g.....attt.....................................a.................a.
H.litodactylus 5559      ....gc..atga.........g.....attt.....................................a.....a.............
H.macrochela 5555        ........ataa.........g.....attt.....................................a..................
H.neocaledonicus 4323    ........ataa...............agtt.....................................a.................g..
H.neocaledonicus 5542    ........ataa...............a.tt.....................................a.................g..
H.neocaledonicus 5543    ........ataa...............a.tt.....................................a.................g..
H.neocaledonicus 5544    ........ataa...............a.tt.....................................a..................
H.neocaledonicus 5545    ........ataa...............a.tt.....................................a.................g..
H.neocaledonicus 5546    ........ataa...............a.tt.....................................a.................g..
H.neocaledonicus 5547    ........ataa...............a.tt.....................................a.................g..
H.neocaledonicus 5548    ........ataa...............a.tt.....................................a.................g..
H.neocaledonicus 6224    ........ataa...............a.tt.....................................a.................g..
H.nyawaygi 6354          ........ataa.........g.....attt.....................................a..................
H.papuanus 2718          ........ataa.........g.....a..t.....................................a..................
H.papuanus 2725          ..t.gc..ataa.........g...g.agtt.........t.....................a.....................
H.papuanus 2726          ........ataa.........g...g.a.ttc.....................................a..................
H.papuanus 2727          .....g..ataa.........g...g.a.ttc.....................................a..................
H.polisorum 1614         .........taa......a...g.....attt.........t.................a......a.................g..
H.solomonensis 1819      ........ataa.........g.....agtt...........g...g.c.................a.....a..............
H.solomonensis 5549      ........ataa.........g..g..a.tt.............g.c.................a.....a..............
H.solomonensis 5550      ........ataa.........g.....agtt...c...........g.c.................a.....a..............
H.solomonensis 5551      ........ataa.........g.....agtt...c...........g.c.................a.....a..............
H.solomonensis 5552      ........ataa.........g.....agtt...c...........g.c.................a.....a..............
H.solomonensis 5554      ........ataa.........g.....agtt...c...........g.c.................a.....a..............
H.tagulae 3008           ........ataa.........g.....ag.t.....................................a..................
H.tjapukai 2184          ........ataa.........g.....attt.....................................a.................g..
H.tjapukai 6641          ........ataa.........g.....attt.....................................a.................g..
H.tytthognaphos 6346     ........atga.........g.....attt.....................................a..................
H.tytthognaphos 6347     ........atga.........g.....attt.....................................a..................
H.wallaman 6353          ........atga.........g.....attt.....................................g.a................
H.yelae 3007             .........taa.........g.....a.tt.....................................a.................g..
H.sp. WA 8017            ........atga.........g.....attt.....................................a..................
H.sp. WA 8021            ........atga.........g.....attt.....................................a..................
```

2.5.3 Aligned molecular sequences. Mitochondrial small-subunit ribosomal DNA 12S gene, base-pairs 88–174. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              ttatcgataatccacgtcatatcttaccccatt-tttgtttgtatatcgttg--taa-agacaatatttaaaaattatagtc-tgag
C.ochropus 6894              ..............................t...-.................--...-.........................-....
C.ochropus 9069              ..............................t...-.................--...-.........................-....
I.nitidus 9827               .a.............g.......a...tt.a.g.................--.tg-g..t......g.............-aaga
I.politus 1514               .a..t..a.t.....a...a........tt.c.-.................--.tt-..t.g....ca.g.g..-....a.-.att
I.politus 3256               .a..t..a.t.....a...a........tt.c.-.................--.tt-..t.g....ca.g.g..-....a.-.att
O.elatus 1837                ga..t..a.......aa...........ta...-.............a...ttctc-..t..............-.g....-aaga
O.laevipes 1835              .a......g........t...........t.a.-.................--...-..........gg............-ga.a
O.lecomtei 1608              .a..t..a......ag..a........tt...-.................--.tt-..tt...g.c..g.gg.-...ag.-at.a
O.lecomtei 2194A             .a..t..a......ag..a........tt...-.............a...--.tt-..tt.....c..g.gg.-...ag.-at.t
O.madagascariensis 2811      .a.....c.....................aa.a.-..a..a............--.tg-.................a......-.ata
O.madagascariensis 2812      .a.....c.....................aa.g.-.....a............--.tg-............g....a......-..ta
O.piceus 6260                .a.....cg....................aa.g.-.....a............--.tg-............g.g..a......-..ta
H.infulcra 2185              .a..t...gt.....aa........t..a....-.....c............tt.gt-...tt.....g......a..ga..-aa.a
L.australasiae 1854          .a.at...gg.....a..ca..t..t..tt...-.c..c...........c.tt.tt-...t.g.....gg......c.a.taaa..
L.australasiae 2181          .a.at...g......a..ta..t..t..ttg..-.c..............c.tt.tt-...t.g.............c.a.tgaa.a
L.australasiae 2182          .a.at...g......a..ta..t..t..tt...-................c.tt.tt-...t.g.....g.......c.a.t-aaga
L.australasiae 2183          .a.at...g......a..ta..t..t..tt...-.a..............c.tt.tt-...t.g.............c.a.tgaa.a
L.australasiae 2729          .a.at...g......a..ta..t..t..tt...-.c..............c.tt.tt-...t.g.............c.a.tgaa.a
L.australasiae 2733          .a.at...g......a..ta..t..t..tt...-.c..............c.tt.tt-...t.g.............c.a.tgaa.a
L.australasiae 2996          .a.at...g......a..ta..t..t..tt...-.c..............c.tt.tt-...t.g.............c.a.tgaa.a
L.australasiae 3684          .a.at...g......ag.ta..t..t..tt.a.-.c..............c.tt.tc-...ttg.....g.......c.a.t-.agt
L.australasiae 4764          .a.at...g......a..ta..t..t..tt...-.c..............c.tt.tt-...t.g.............c.a.tgaa.a
L.australasiae 5553          .a.at...g......a..ta..t..t..tt...-.c..............c.tt.tt-...t.g.............c.a.tgaa.a
L.australasiae 8676          .a.at...g......a..ta..t..t..tt...-.c..c...........c.tt.tt-...t.g.............c.a.tgaa.a
L.australasiae 8677          .a.at...g......a..ta..t..t..tt...-.c..c...........c.tt.tt-...t.g.............c.a.tgaa.a
L.longimanus 6388            .a..t.....c....a..t......t..ta...-.................tt.ttc...tt..gccgg..ggc..cga..-aaga
L.malaya 1909                .a..t...gg.....a..t......t..ttg..-.............c.....tt.tc-...t...g.cg...g.....g...-g..a
H.aethes 3002                .g..t.........aa........t..at...-.................tt.tt-...t.ga....t.....a.c.a..-g..a
H.aethes 3005                .g..t.........aa........t..at...-.................tt.tt-...t.ga....t.....a.c.a..-g..a
H.anekasankylis 6355         .a..t...g......aa.g.........t...-.................tt.tt-...tgg.....g.....a.c.a..-ga.a
H.anekasankylis 6356         .a..t..cg......aa.g.........tt...-.................tt.tt-...ttg..........a.c....-aa.a
H.anekasankylis 6357         .a..t...g......aa...........tt...-.................tt.tt-...tgg.....g.....a.c.a..-ga.a
H.ankistros 4339             .a..t...g......aa........t..tt...-.................tt.tt-...t.g.....g.....a.c.a..-gaga
H.bandjin 5556               .a..t..cg......aa.g.........tt...-.................tt.tt-...t.g..........a.c.a..-ga.a
H.bandjin 5557               .a..t..cg......aa.g.........tt...-.................tt.tt-...t.g..........a.c.a..-ga.a
H.bandjin 5558               .a..t..cg......aa.g.........tt...-.................tt.tt-...t.g..........a.c.a..-ga.a
H.caudicula 1502             .a..t...g......aa.g.........tt...-...a.............tt.tt-...t.g.....g.....a.c.a..-aa.a
H.caudicula 2339             .a..t...g......aa.g.........tt...-...a.............tt.tt-...t.g.....g.....a.c.a..-ga.a
H.caudicula 2340             .a..t...g......aa...........tt...-...a.............tt.tt-...t.g.g...g..g..a.c.a..-ga.a
H.caudicula 6360             .a..t...g......aa.g.........tt.c.-...a.............tt.tt-...t.g.....g.....a.c.a..-ga.a
H.caudicula 6361             .a..t...g......aa.g.........tt...-...a.............tt.tt-...t.g.g...g.....a.c.a..-aa.a
H.caudicula 6362             .a..t...g......aa.g.........tt...-...a.............tt.tt-...t.g.....g.....a.c.a..-aa.a
H.chthamalochoros 6350       .a..t..cg......aa.g.........tt...-.................tt.tt-...t.g..........a.c.a..-a..a
H.chthamalochoros 6351       .a..t..cg......aa.g.........tt...-.................tt.tt-...t.g..........a.c.a..-a..a
H.chthamalochoros 6352       .a..t..cg......aa.g.........tt...-.................tt.tt-...t.g..........a.c.a..-a..a
H.chthamalochoros 8023       .a..t..cg..t...aa.g.........tt...-.................tt.tt-...t.g..........a.c.a..-a..a
H.chydaeostigmata 5560       .a..t...g......aa.g.........tt...-...a.............tt.tt-...tgg.....g.....a.c.a..-aa.a
H.chydaeostigmata 8015       .a..t...g......aa.g.........tt...-.................tt.tt-...tgg.....g.....a.c.a..-aa.a
H.chydaeostigmata 8016       .a..t...g......aa.g.........tt...-.................tt.tt-...tgg.....g.....a.c.a..-aa.a
H.chydaeostigmata 8019       .a..t...g......aa.g.........tt...-...a.............tt.tt-...tgg.....g.....a.c.a..-aa.a
H.chydaeostigmata 8020       .a..t...g......aa.g.........tt...-...a.............tt.tt-...tgg.....g.....a.c.a..-aa.a
H.chydaeostigmata 8022       .a..t...g......aa.g.........tt...-...a.............tt.tt-...tgg.....g.....a.c.a..-aa.a
H.dechangei 7789             .a..t...g......a.........t..ttg..-.................tt.tt-...t.g.g.........g.c.a..-ga.a
H.euktaenospatha 4340        .a..t...g......aat.......t..tt.a.-.................tt.tt-g..tgg.g...g.....g.c.a..-g..a
H.glaphyroscytos 6640        .a..t...g......aat..........tt...-.................tt.tt-...tggg.....g....a.c.a..-g..a
H.hylaios 6358               .a..t...g......aat.....c...tt...-...a.............tt.tt-...tgg.g...g.....a.c.a..-g...
H.hylaios 6359               .a..t...g......aat..........tt...-...a.............tt.tt-...tgg.g...g.....a.c.a..-ga..
H.hylaios 6363               .a..t...g......aat......c...tt...-...a.............tt.tt-...tgg.g...g.....a.c.a..-g...
H.ischnoryctes 6639          .a..t...g......aat..........ttg..-.................tt.tt-...tggg.....g....a.c.a..-a..a
H.kukunyungkal 6341          .a..t...g......aa...........tt...-...ac............tt.tt-...t.ga.....g....ggc.a..-aaga
H.kukunyungkal 6342          .a..t...g......aa...........tt...-...ac............tt.tt-...t.ga.....g....ggc.a..-aaga
H.kukunyungkal 6343          .a..t...g......aa...........tt...-...ac............tt.tt-...t.ga.....g....ggc.a..-aaga
H.laevitropis 6348           .a..t...g......aa........g..tt...-...a.............tt.tt-...t.ga.....g..g.g.c.a..-aaga
H.leptochela 6344            .a..t...g....t.aat..........at...-.................tt.tt-g..t.g..........a.c.a..-aa.a
H.leptochela 6345            .a..t...g....t.aat..........at...-.................tt.tt-g..t.g..........a.c.a..-aa.a
H.litodactylus 5559          .a..t..cg......aat..........t...-.................tt.tt-g..t.g.....g.....g.c.a..-aa.a
H.macrochela 5555            .a..t...g......aa.g.........tt...-...a.............tt.tt-...t.g.....g.....a.c.a..-aa.a
H.neocaledonicus 4323        .a..t..........aa.....t.ct..tt...-.................tt.t.-...t.g.......g..a.c....-g...
H.neocaledonicus 5542        .a..t..........aa.....t.ct..tt...-.................tt.t.-...t.g.......g..a.c....-g...
H.neocaledonicus 5543        .a..t..........aa.....t.ct..tt...-.................tt.t.-...t.g.......g..a.c....-g...
H.neocaledonicus 5544        .a..t...g......aa.........t..tt...-.................tt.t.-...t.g..........a.c....-g...
H.neocaledonicus 5545        .a..t..........aa.....t.ct..tt...-.................tt.t.-...t.g.......g..a.c....-g...
H.neocaledonicus 5546        .a..t..........aa.....t..t..tt...-.................tt.t.-...t.g.......g..a.c....-g...
H.neocaledonicus 5547        .a..t...g......aat.......t..tt...-.................tt.t.-...t.g..........a.c....-a..a
H.neocaledonicus 5548        .a..t...g......aat.......t..tt...-.................tt.t.-...t.g..........a.c....-a..a
H.neocaledonicus 6224        .a..t..........aa.....t.ct..tt...-.................tt.t.-...t.g.......g..a.c....-g...
H.nyawaygi 6354              .a..t...gg.....aa.g.........tt...-.................tt.tt-...t.g.....g.....a.c.a..-aa.a
H.papuanus 2718              .a..t...g......aa........t..tt...-.................tt.tt-...t.g.g.........a.c.a..-ga.a
H.papuanus 2725              .a..t..cg......aa.g......t..ttg..-.................tt.tt-...t.g.....g..g..a.c.a..-ga.a
H.papuanus 2726              .a..t...g......aa........c..tt...-.aa..............tt.tc-g..ttga....t.....a.c.a..-ga.a
H.papuanus 2727              .a..t...g......aa........c..tt...-.aa..............tt.tc-g..ttga....t.....a.c.a..-ga.a
H.polisorum 1614             .a..t..........aaat.........tt...-.................tt.tt-..gt.g.....gg....a.c.a..-aa.a
H.solomonensis 1819          .a..t...g......aatga.....t...t...-.................tt.tt-...t.g.g.........a.c.a..-aa.a
H.solomonensis 5549          .a..t...g......aatg......t...t...-.................tt.tt-...tgg...........a.c.a..-aa.a
H.solomonensis 5550          .a..t...g......aatg......t..tt...-.................tt.tt-...tgg...........a.c.a..-aa.a
H.solomonensis 5551          .a..t...g......aatg......t...t...-.................tt.tt-...tgg.........g.a.c.a..-aa.a
H.solomonensis 5552          .a..t...g......aatg......t...t...-.................tt.tt-...tgg.........g.a.c.a..-aa.a
H.solomonensis 5554          .a..t...g......aatg......t...t...-.................tt.tt-...tgg.........g.a.c.a..-aa.a
H.tagulae 3008               .a..t..........a.........t..tt...-.................tt.tt-...t.g......g....a.c.a..-ga.a
H.tjapukai 2184              .a..t...g......a...........tt...-...a.............tt.tt-...t.g.g...g.....a.c.a..-ga.a
H.tjapukai 6641              .a..t...g......a...........tt...-...a.............tt.tt-...t.g.g...g.....a.c.a..-ga.a
H.tytthognaphos 6346         .a..t...g......aaa.........at...-.................tt.tt-g..t.g.....g.....g.c.a..-aa.a
H.tytthognaphos 6347         .a..t...g......aaa.........at...-.................tt.tt-g..t.g.....g.....g.c.a..-aa.a
H.wallaman 6353              .a..t...g......aa.g....c....tt...-.................tt.tt-...t.g.....g.....a.c.a..-aa.a
H.yelae 3007                 .a..t...gg.....aa.......cc...t...-.................tt.tt-...t.g.g...g.....g.c.a..-ga.a
H.sp. WA 8017                .a..t...g......aa.t.........tt...-.................tt.tt-...tgg.g...g.....a.c.a..-aa.a
H.sp. WA 8021                .a..t...g......aa.t.........tt...-.................tt.tt-...tgg.g...g.....a.c.a..-aa.a
```

2.5.3 Aligned molecular sequences. Mitochondrial small-subunit ribosomal DNA 12S gene, base-pairs 175–261. Dots indicate a match with the first taxon. (Continued)

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C.ochropus 2189          ttaa-aggttttccttaattcaaatcaaggtgcag-catattggggttgtaatgggttacaatatatt-tatatattacgga-gaat
C.ochropus 6894          ....-.a.....................-...........a.................-...........-....
C.ochropus 9069          ....-.a.....................-...........a.................-...........-....
I.nitidus 9827           .g..-.t.....aaa..g..............-.g.c..aa..g.a.............gaaggt..c..a.aacg-...a
I.politus 1514           ....-.at....aga..ta.............-....g.a...a.a................--.t.....agac.g-a.t.
I.politus 3256           ....-.at....aga..ta.............-....g.a...a.a................--.t.....agac.g-a.t.
O.elatus 1837            ...g-ttt.cccaaa...a.............-......ta....ac..............---.t.....actttg-....
O.laevipes 1835          ....-.taa...ttaa..a.............-......aa....a.............g.--at.....ataatg-...a
O.lecomtei 1608          ....-gaa.c..tta...a.............-....a.aa....a.............g..ta.....atat.g-a.tc
O.lecomtei 2194A         ....-gaa......a...a.............-....a.a.....a...............---.t.....a.at.g-agtc
O.madagascariensis 2811  ....-gaa......g...a.............-......tt...aaa.............---a.a....a.ac.g-a...
O.madagascariensis 2812  ....-.at......a...a.............-......tt...aaa.............---a.a....a.ac.g-ag..
O.piceus 6260            ....-.aa......a...a.............-......tt...aaa.............---a.a....a.ac.g-ag..
H.infulcra 2185          .a..-.at....aaaa..a.............-....a..a..g.ac....a.......g..a--ata....atac.g-a.ta
L.australasiae 1854      g.g.-tatag.c...a.....g...........c....g.aa....a.............a--.t.....agac..-at.a
L.australasiae 2181      g.g.-tataa.ca.c.......g...........-....a.aa....a.............a--.t.....agac.g-at.a
L.australasiae 2182      ..g.-taagg.ctaa.......g...........-....a.aa....ac.g...........--ct.....a.ac.g-atga
L.australasiae 2183      a.g.-tataa.ca.c.......g...........-....a.aa....a.............a--.t.....agac.g-at.a
L.australasiae 2729      a.g.-tataa.ca.c.......g...........-....a.aa....a.............a--.t.....agac.g-at.a
L.australasiae 2733      a.g.-tataa.ca.c.......g...........-....a.aa....a.............a--.t.....agac.g-at.a
L.australasiae 2996      a.g.-tataa.ca.c.......g...........-....a.aa....a.............a--.t.....agac.g-at.a
L.australasiae 3684      ..g.-tatag.cttaC......g...........-......aa....................--.t.....a.ac.g-at.a
L.australasiae 4764      g.g.-tataa.ca.c.......g...........-....a.aa....a.............a--.t.....agac.g-at.a
L.australasiae 5553      a.g.-tataa.ca.c.......g...........-....a.aa....a.............a--.t.....agac.g-at.a
L.australasiae 8676      a.g.-tacaa.ca.........g...........-....a.aa....a.............a--.t.....agac.g-at.a
L.australasiae 8677      a.g.-tacaa.ca.........g...........-....a.aa....a.............a--.t.....agac.g-at.a
L.longimanus 6388        ....-taaa...t-.......g...........-....a.ta...aa..............c..--gta..g.agac..-at.a
L.malaya 1909            ....-.aaaa...a.....a..g...........-....g.aa....a.g............gc..--gta..g.a.ac.g-at.a
H.aethes 3002            .c..-.a.a....aga..a.............-....a.a.....ac..............--gt.....a.ac.g-at.a
H.aethes 3005            .c..-.a.a....aga..a.............-....a.a.....ac..............--gt.....a.ac.g-at.a
H.anekasankylis 6355     c...-gaaaa..taaa..a.............-t...a.aa....................--gt...g.agat..-at.a
H.anekasankylis 6356     ....-gaaaa..taag..a.............-t...a.aa....................--.t.....a.at.g-at.a
H.anekasankylis 6357     c...-gaaaa..taaa..a.............-t...a.aa....................--gt...g.agat..-at.a
H.ankistros 4339         ....-gaaa....aaa..a.............-....a..a....a...............--gta....a.ac..-at.a
H.bandjin 5556           ....-gaag....aaa..a.............-....a.aa....................--gtc....a.at..-at.a
H.bandjin 5557           ....-gaag....aaa..a.............-....a.aa....................--gtc....a.at..-at.a
H.bandjin 5558           ....-gaag....aaa..a.............-....a.aa....................--gtc....a.at..-at.a
H.caudicula 1502         ....-gaag....aaa..a.............-t...a.aa....a...............--.t.....a.at..-at.a
H.caudicula 2339         ....-gaag....aaa..a.............-t...a.aa....a...............--at.....a.at..-at.a
H.caudicula 2340         ....-.aag....aaa..a.............-t...a.aa....a...............--at.....a.at..-atga
H.caudicula 6360         ....-gaag....aaa..a.............-t...a.aa....a...............--at.....a.at..-at.a
H.caudicula 6361         ....-gaag....aaa..a.............-t...a.aa....a...............--.t.....a.at..-at.a
H.caudicula 6362         ....-gaag....aaa..a.............-t...a.aa....a...............--.t.....a.at..-at.a
H.chthamalochoros 6350   ....-gaag....aaa..a.............-....a.aa....................--gt.....a.at..-at.a
H.chthamalochoros 6351   ....-gaag...taaa..a.............-....a.aa....................--gt.....a.at..-at.a
H.chthamalochoros 6352   ....-gaag....aaa..a.............-....a.aa....................--gt.....a.at..-at.a
H.chthamalochoros 8023   ....-gaag....aaa..a.............-....a.aa....................--gt.....a.at..-at.a
H.chydaeostigmata 5560   ....-gaagc...aaa..a.............-t...a.aa....a...............--at...g.a.at..-at.a
H.chydaeostigmata 8015   ....-gaagc...aaa..a.............-t...a.aa....a...............--gt...g.a.at..-at.a
H.chydaeostigmata 8016   ....-gaagc...aaa..a.............-t...a.aa....a...............--gt...g.a.at..-at.a
H.chydaeostigmata 8019   ....-gaagc...aaa..a.............-t...a.aa....a...............--at...g.a.at..-at.a
H.chydaeostigmata 8020   ....-gaagc...aaa..a.............-t...a.aa....a...............--at...g.a.at..-at.a
H.chydaeostigmata 8022   ....-gaagc...aaa..a.............-t...a.aa....a...............--gt...g.a.at..-at.a
H.dechangei 7789         c...-.aaa....aag..a.............-....a.aa....a.............c..--.t...g.agac.gaattg
H.euktaenospatha 4340    ....-ga.gg..taaa..a.............-......aa....a.............c..--.t...g.a.at.g-at.a
H.glaphyroscytos 6640    ....-.aag...taag.ga.............-....a.aa....a...............--gt.....a.ac..-at.a
H.hylaios 6358           ....-gctg....aaa..a.............-t...a.aa....ac..............gg--at...g.acac.g-atga
H.hylaios 6359           ....-.atg....aaa..a.............-t...a.aa....ac....a.........ga--gt.....atac.g-atga
H.hylaios 6363           ....-gctg....aaa..a.............-t...a.aa....ac..............gg--at.....acac.g-atga
H.ischnoryctes 6639      ....-.aag...taag..a.............-....a.aa....a...............--gt.....a.ac..-at.a
H.kukunyungkal 6341      ..g.-.aag...taag..a.............-t...a.aa....a.....a.........--at.....a.ac..-at.a
H.kukunyungkal 6342      ..g.-.aag...taag..a.............-t...a.aa....a.....a.........--at.....a.ac..-at.a
H.kukunyungkal 6343      ..g.-.aag...taag..a.............-t...a.aa....a.....a.........--at.....a.ac..-at.a
H.laevitropis 6348       ....-...g...tagg..a.............-t...a.aa....a...............--gt.....agat..-at.a
H.leptochela 6344        ....-ga.a....aaa..a.............-....a.aa....t.t.............--gt.....a.at.g-at.a
H.leptochela 6345        ....-ga.a....aaa..a.............-....a.aa....t.t.............--gt.....a.at.g-at.a
H.litodactylus 5559      c...-.aaa....aaa..a.............-....a.aa....t...............--gt.....a.atag-at.a
H.macrochela 5555        .c..-gaag....aag..a.............-t...a.aa....a...............--gt.....a.at..-at.a
H.neocaledonicus 4323    ....-gaaa...tga...a.............-....a.aa....a...............--.t.....a.at.g-at.a
H.neocaledonicus 5542    ....-g.aa...tga...a.............-....a.aa....a...............--.t.....a.at.g-at.a
H.neocaledonicus 5543    ....-g.aa...tga...a.............-....a.aa....a...............--.t.....a.at.g-at.a
H.neocaledonicus 5544    ..g.-gaaa...tga...a.............-....a.aa....a...............--.t.....a.at.g-at.a
H.neocaledonicus 5545    ....-gaaa...tga...a.............-....a.aa....a...............--.t.....a.at.g-at.a
H.neocaledonicus 5546    ....-g.aa...tga...a.............-....a.aa....a...............--.t.....a.at.g-at.a
H.neocaledonicus 5547    ....-gaaa...taa...a.............-....a.aa....a...............--.t.....a.at.g-at.a
H.neocaledonicus 5548    ....-gaaa...taa...a.............-....a.aa....a...............--.t.....a.at.g-at.a
H.neocaledonicus 6224    ....-gaaa...tga...a.............-....a.aa....a...............--.t.....a.at.g-at.a
H.nyawaygi 6354          ....-gaag....aaa..a.............-....a.aa....a...............--gt.....a.at..-at.a
H.papuanus 2718          ....-gaaa....aaa..a.............-....a.a...g...............--at...g.a.at.g-at.a
H.papuanus 2725          ....-taag....aaa..a.............-....acaa..g.a..............--at...g.a.gc..-at.a
H.papuanus 2726          ....-.aaa...taaa.ga.............-....a.a.....a.............c--.t...g.a.ac.g-atgg
H.papuanus 2727          ....-.aaa...taaa.ga.............-....a.a.....a.............c--.t...g.a.ac.g-atgg
H.polisorum 1614         ....-.aag....aga..a.............-....a.aa..a.t.............--at.....a.ac..-at.a
H.solomonensis 1819      .c..-gaag...tagg.ga.............-....a.....................a--gta....agacag-atga
H.solomonensis 5549      cc..-gaag...taaa..a.............-....g.a...c.a.............c--gt.....a.acag-atga
H.solomonensis 5550      .c..-.a.g...taga.ga.............-....a......a.............--gt.....a.acag-atga
H.solomonensis 5551      ....-.a.g...taga.ga.............-....a......a.............--gt.....a.acag-atga
H.solomonensis 5552      .c..-.a.g...taga.ga.............-....a.a....a.............--gt.....a.acag-atgg
H.solomonensis 5554      .c..-.a.g...taga.ga.............-....a......a.............--gt.....a.acag-atg.
H.tagulae 3008           ...g-.aaa...taga..a.............-....a.aa..a.a.............a--at.....a.acag-at.a
H.tjapukai 2184          ....-gaaa...taaa..a.............-t...a.aa....a.............g...--.t.....a.at..-at.a
H.tjapukai 6641          ....-gaaa...taaa..a.............-t...a.aa....a.............g...--.t.....a.at..-at.a
H.tytthognaphos 6346     ....-ga.a....aga..a.............-....a.aa....t...............--gt.....a.at.g-at.a
H.tytthognaphos 6347     ....-ga.a....aga..a.............-....a.aa....t...............--gt.....a.at.g-at.a
H.wallaman 6353          ....-gaag....aaa..a.............-....a.aa....................--gt.....a.at..-at.a
H.yelae 3007             ....-.aag....aga..a.............-....a.a.....ac..............---gtc..g.a.ac..-at..
H.sp. WA 8017            ....-gaagc...aaa..a.............-t...a.aa....a...............--gt...g.a.at..-at.a
H.sp. WA 8021            ....-gaagc...aaa..a.............-t...a.aa....a...............--gt...g.a.at..-at.a
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2.5.3 Aligned molecular sequences. Mitochondrial small-subunit ribosomal DNA 12S gene, base-pairs 262–347. Dots indicate a match with the first taxon. (Continued)

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C.ochropus 2189              tgaa-aag---aaaaaacaattaaaggtggattcaaaagtaaagtag-aattaaaaagtttatatgaattat-ttttaaaacatgc
C.ochropus 6894              ..g.-...---...g.............................a..t-.....................a..-.............
C.ochropus 9069              ..g.-...---...g.............................a..t-.....................a..-.............
I.nitidus 9827               .a.c-.g.---..t.tta.t..g.........tg.......tt..tgg.a........c.t.g.....a.gaa............
I.politus 1514               .a..-.t.---....ttttca.g...................taa.a-..a..........t.t....ga..a.......g.....
I.politus 3256               .a..-.t.---....ttttca.g...................taa.a-..a..........t.t....ga..a.......g.....
O.elatus 1837                .a.c-.t.---....ttt..acg..a..............gtt.tt-...........aa.a.c....c..aa...g........
O.laevipes 1835              .tg.-.t.---.....ta.t..g.........t........tt...-g.a...g.t....t.......a.aga............
O.lecomtei 1608              -...-...---....tta.ca.g..a.........g.....taaga-..g...g.t...ct......c...ta...........t
O.lecomtei 2194A             -..g-t..---.....ta..a.g..a.........g.....caaga-..a....t...ct.g......g.ta...........t
O.madagascariensis 2811      .t..-ttt---..t.t.t....g..........tg.......tag.a-g.c..........t..........aa..c........t
O.madagascariensis 2812      .t.t-cct---..t.t.a....g..........tg.......tag.a-..c..........t..........aa..c........
O.piceus 6260                .t.t-ctt---..t.t.a....g..........tg.......tag.a-..c..........t..........a...c........
H.infulcra 2185              -a.t-.g.---..g.tta.ta.g.....................t.ta-......t.....a.gt.....a..aa.......t....
L.australasiae 1854          at..-.t.---...tctt.t..g..........g........t.ta-............a..t.....a..ga....gg.t...t
L.australasiae 2181          at..-.t.---....ctt.t..g....c......g........t.ta-............a..t.....a..aa....gg.....t
L.australasiae 2182          at..-.t.---...tttt.t..g..........g........t.ta-............aggt.....a..aa...ggg.tg..t
L.australasiae 2183          at..-.t.---....ctt.t..g....c......g........t.ta-............a..t.....a..aa....gg.....t
L.australasiae 2729          at..-.t.---....ctt.t..g....c......g........t.ta-............a..t.....a..aa....gg.....t
L.australasiae 2733          at..-.t.---....ctt.t..g..........g........t.ta-............a..t.....a..aa....gg.....t
L.australasiae 2996          at..-.t.---....ctt.t..g....c......g........t.ta-............a..t.....a..aa....gg.....t
L.australasiae 3684          at..-.t.---....ttct.t..g..........g........t.ta-............a.at.....a..ga....g.......
L.australasiae 4764          at..-.t.---....ctt.t..g....c......g........t.ta-............a..t.....a..aa....gg.....t
L.australasiae 5553          at..-.t.---....ctt.t..g....c......g........t.ta-............a..t.....a..aa....gg.....t
L.australasiae 8676          at..-.t.---....ctt.t..g....c......g........t.ta-............a..t.....a..aac...gg.....t
L.australasiae 8677          at..-.t.---....ctt.t..g....c......g........t.ta-............a..t.....a..aac...gg.....t
L.longimanus 6388            a.t.-.t.---.....gttt..g..........g........t.ta-.....tg.....a.at.....a..gac...g......t
L.malaya 1909                aatg-.t.---....g.ttt..t....c......g.......gc.ta-..c..........gggt.....a..aa......g....t
H.aethes 3002                -a..-.t.---....tgg.c..g.....................t.t.-.....t......a.at.....a..aa.c..........
H.aethes 3005                -a..-.t.---....tgg.c..g..........tt.......t.t.-.....t......a.at.....a..aa.c..........
H.anekasankylis 6355         -a..-.t.---....tta.t..g....c..............t.ta-...c.t......a.at.....a..aa...........
H.anekasankylis 6356         -...-.t.---....tta.t..g..a................t.ta-.....t......a.at.....a..aa...........
H.anekasankylis 6357         -a..-.t.---....tta.t..g....c..............gt.ta-...c.t......a.at.....a..aa...........
H.ankistros 4339             -a..-.t.---....tga.t..g..........t.........t.t.-.....t......g.gt.....a..aa.......t....
H.bandjin 5556               -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.bandjin 5557               -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.bandjin 5558               -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.caudicula 1502             -a..-.t.---....tta.t..g.....................t.ta-.....tg.....a.at........aa....g.......
H.caudicula 2339             -...-.t.---....tta.t..g.....................t.ta-.....tg.....a.at........aa....g.......
H.caudicula 2340             -...-.t.---....tta.t..g..a..................t.ta-.....t......a.at.....a..aa....g.......
H.caudicula 6360             -...-.t.---....tta.t..g..........t.........t.ta-.....tg.....a.at........aa....g.......
H.caudicula 6361             -a..-.t.---....tta.t..g.....................t.ta-.....tg.....a.at........aa....g.......
H.caudicula 6362             -a..-.t.---....tta.t..g.....................t.ta-.....tg.....a.at........aa....g.......
H.chthamalochoros 6350       ga..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.chthamalochoros 6351       -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.chthamalochoros 6352       ga..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.chthamalochoros 8023       ga..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.chydaeostigmata 5560       -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.chydaeostigmata 8015       -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.chydaeostigmata 8016       -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.chydaeostigmata 8019       -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.chydaeostigmata 8020       -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.chydaeostigmata 8022       -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.dechangei 7789             -a.g-.t.---....t.a.t..g.....................t.ca-.....t......g.gt.....a..aa......t....
H.euktaenospatha 4340        -tg.-.t.---....t...t..g....c..............gt.t.-..a..t......g.at.....g..aa...........
H.glaphyroscytos 6640        -t..-.t.---....tta.t..g.....................t.ta-.....tg.....a.at.....a..aa...........
H.hylaios 6358               -t..-.t.---....ttagt..g.....................gt.ta-.....t......a.at.....a..aa......t....
H.hylaios 6359               -...-.t.---....tta.t..g.....................gt.ta-.....t......a.at.....a..aa......t...t
H.hylaios 6363               -t..-.t.---....ttagt..g.....................gt.ta-.....t......a.at.....a..aa......t....
H.ischnoryctes 6639          -t..-.t.---....tta.t..g.....................t.ta-.....tg.....agat.....a..aa......t....
H.kukunyungkal 6341          -t..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa...........
H.kukunyungkal 6342          -t..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa...........
H.kukunyungkal 6343          -t..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa...........
H.laevitropis 6348           -t..-.t.---....tta.t..g.....................gt.ta-.....t......a.at.....g..aa...........
H.leptochela 6344            -...-.t.---....tta.t..g..a..................t.ta-.....tg.....a.gt.....a..aa...........
H.leptochela 6345            -...-.t.---....tta.t..g..a..................t.ta-.....tg.....a.gt.....a..aa...........
H.litodactylus 5559          -a..-.t.---....tta.t..g..a.......t.........t.ta-.....tg.....a.at.....a..aa...........
H.macrochela 5555            -a..g.t.---....ttagt..g.....................t.ta-.....t.g....a.at.....a..aac...g.......
H.neocaledonicus 4323        -a..-.t.---....t.att..g..a..................t.ta-.....gg.....a.gt........aa...........
H.neocaledonicus 5542        -a..-.t.---....t.att..g..a..................t.ta-.....gg.....a.at........aa...........
H.neocaledonicus 5543        -a..-.t.---....t.att..g..a..................t.ta-.....gg.....a.at........aa...........
H.neocaledonicus 5544        -a..-.t.---....t.att..g..a..................t.ta-.....gg.....a.at........aa...........
H.neocaledonicus 5545        -a..-.t.---....t.att..g..a..................t.ta-.....gg.....a.gt........aa...........
H.neocaledonicus 5546        -a..-.t.---....t.att..g..a..................t.ta-.....gg.....aggt........aa...........
H.neocaledonicus 5547        -a..-.t.---....t.att..g.....................t.ta-......g.....a.at........aa...........
H.neocaledonicus 5548        -a..-.t.---....t.att..g.....................t.ta-......g.....a.at........aa...........
H.neocaledonicus 6224        -a..-.t.---....t.att..g..a..................t.ta-.....gg.....a.gt........aa...........
H.nyawaygi 6354              -a..-.t.---....tta.t..g.....................t.ta-..c..t......g.at.....a..aa....g..t....
H.papuanus 2718              -a.g-.t.---....tta.t..g.....................t.t.-..a..t......a.at.....g..aa...........
H.papuanus 2725              -.g.-.t.---....tga.t..g...a.................t.ta-.....tg.....a.at........a...........t
H.papuanus 2726              -tg.-.t.---....t.a.tc.g.....................tc.t.-.....t..g..ca.gt.....a..aa.....t....
H.papuanus 2727              -tg.-.t.---....t.a.tc.g.....................tc.t.-.....t..g..ca.gt.....a..aa.......t....
H.polisorum 1614             -...-.t.---....tta.t..g.....................gc.t.-.....t.....caggt..g..a..aa.......t....
H.solomonensis 1819          -.g.-.t.---....t.a.cc.g.c...................gt.ta-...c.t......a.at.....a..aa...........
H.solomonensis 5549          -ag.-.t.---....t.a.t..g.c...................gt.ta-...c.c......a.gt.....a..aa...........
H.solomonensis 5550          -.g.-gt.---...gt.a.tc.g.c...................gt.ta-...c.t......a.at.....a..aa...........
H.solomonensis 5551          -.g.-.t.---....t.att..g.c...................t.ta-...c.t......a.at.....a..aa...........
H.solomonensis 5552          -.g.-.t.---....t.a.tc.g.c...................t.ta-...c.t......a.at.....a..aa...........
H.solomonensis 5554          -.g.-.t.---....t.a.tc.g.c...................t.ta-...c.t......a.at.....a..aa...........
H.tagulae 3008               -..g-.t.---....tta.t..g.....................gt.t.-..g..t......a.at.....a..aa...........
H.tjapukai 2184              -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa...........
H.tjapukai 6641              -a..-.t.---....tta.t..g.....................t.ta-.....t......a.at.....a..aa.......t....
H.tytthognaphos 6346         -a.g-.t.---....tta.t..g..a..................t.ta-.....t......a.at.....a..aa...........
H.tytthognaphos 6347         -a..-.t.---....tta.t..g..a..................t.ta-.....t......a.at.....a..aa...........
H.wallaman 6353              -a..-.t.---....tta.t..g.....................t.ta-..c..t......a.at.....g..aa..c........t
H.yelae 3007                 -...-.t.---...gtga.t..g.....................t.t.-.....tg....ca.at.....g..aa...........
H.sp. WA 8017                -a..-.t.---....cta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
H.sp. WA 8021                -a..-.t.---....cta.t..g.....................t.ta-.....t......a.at.....a..aa....g.......
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2.5.3 Aligned molecular sequences. Mitochondrial large-subunit ribosomal DNA 16S gene, base-pairs 1–87. Dots indicate a match with the first taxon.

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C.ochropus 2189              ggtttttagttg-ttaataaaaatcaagcctgctcaatgct-tct-gtaaatagccgcggtattttaactgtgctaaggtagcataa
C.ochropus 6894              ...........a-.............................-...-.....................................
C.ochropus 9069              ...........a-.............................-...-.....................................
I.nitidus 9827               ..........at-............g.............aaaa-......t.....................................
I.politus 1514               .........aaa-...t........c.............a-.g.-............a....aa.g.....................
I.politus 3256               .........aaa-...t........c.............a-.g.-............a....aa.g.....................
O.elatus 1837                ......c..aaa-.a.t.g......c.........t.....-aa.-......g.....a.....a.........a...........
O.laevipes 1835              ..........ca-.a.........................c-caa-...................a.....................
O.lecomtei 1608              .........aatg.a.t........t.............-caa-............a.....a.g.......a...........
O.lecomtei 2194A             .........agta.a.t........t.a...........-.ag-..g.........a.....a.g.......a...........
O.madagascariensis 2800      ..........at-.a.g.........g.............-.a.-......g...........a.....................
O.madagascariensis 2811      ..........gt-.a...........g.............-ca.-...................a.....................
O.madagascariensis 2812      ..........at-.a.g.........g.............-.a.-......g...........a.....................
H.infulcra 2185              ...........t-...t........tga.....c......g-ata-.....ag.....a....cc.g.......a...........
L.australasiae 1854          .........agc-...t........tga.............-.ag-......g.....a....cc.g.......a...........
L.australasiae 2181          .........aat-...t........tg..............-.ag-......g.....a....cc.g.......a...........
L.australasiae 2182          .........aat-...t........tg..............-.ag-......g.....a....cc.g.......a...........
L.australasiae 2183          .........aat-...t........tg..............-.ag-......g.....a....c..g.......a...........
L.australasiae 2729          .........aat-...t........tg..............-.aa-......g.....a....cc.g.......a...........
L.australasiae 2733          .........aat-...t........tg..............-.ag-......g.....a....cc.g.......a...........
L.australasiae 2996          .........aat-...t........tg..............-.ag-......g.....a....cc.g.......a...........
L.australasiae 3684          .........aaa-...t........tga.............c-.tg-......g.....a....cc.g.......a...........
L.australasiae 4764          .........aat-...t........tg..............-.ag-......g.....a....cc.g.......a...........
L.australasiae 5553          .........aat-...t........tg..............-.ag-......g.....a....cc.g.......a...........
L.australasiae 8676          .........aat-...t........tg..............-.ag-......g.....a....cc.g.......a...........
L.australasiae 8677          .........aat-...t........tg..............-.ag-......g.....a....cc.g.......a...........
L.longimanus 6388            .........a.t-.c.t........tga........g....-aag-......g.....a....c..g.......a...........
L.malaya 1909                .........agt-...t........tga.............-.aa-......g.....a.......g.......a...........
H.aethes 3002                ...........t-...t........t.a.......t.....-atg-......g.....a.....a.g.......a...........
H.aethes 3005                ...........t-...t........t.a.......t.....-atg-......g.....a.....a.g.......a...........
H.anekasankylis 6355         ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.anekasankylis 6356         ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.anekasankylis 6357         ...........t-..gt........t.........t.....-atg-......g.....a.....a.g.......a...........
H.ankistros 4339             ...........a-.c.t........t.a.......t.....-ata-......g.....a.....a.g.......a...........
H.bandjin 5556               ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.bandjin 5557               ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.bandjin 5558               ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.caudicula 1502             ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.caudicula 2339             ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.caudicula 2340             ...........t-...t........t.a.......t.....-atg-......g.....a.....a.g.......a...........
H.caudicula 6360             ...........t-...t........t.a.......t.....-atg-......g.....a.....a.g.......a...........
H.caudicula 6361             ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.caudicula 6362             ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.chthamalochoros 6350       ...........t-...t........t.........t.....-ata-......g.....a.....a.g.......a...........
H.chthamalochoros 6351       ...........t-...t........t.........t.....-ata-......g.....a.....a.g.......a...........
H.chthamalochoros 6352       ...........t-...t........t.........t.....-ata-......g.....a.....a.g.......a...........
H.chthamalochoros 8023       ...........t-...t........t.........t.....-ata-......g.....a.....a.g.......a...........
H.chydaeostigmata 5560       ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.chydaeostigmata 8015       ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.chydaeostigmata 8016       ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.chydaeostigmata 8019       ...........t-...t........t.........t.....-atg-..t...g..g..a.....a.g.......a...........
H.chydaeostigmata 8020       ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.chydaeostigmata 8022       ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.dechangei 7789             ...........t-...t........t.........t.....-ata-......g.....a....ca.g.......a...........
H.euktaenospatha 4340        ...........t-...t........tg........t.....-ata-......g.....a.....a.g.......a...........
H.glaphyroscytos 6640        ...........a-...t........t.........t.....-atg-......g.....a....a..g.......a...........
H.hylaios 6358               ...........t-...t........tga.......t.....-aa.-......g.....a.....a.g.......a...........
H.hylaios 6359               ...........t-...t........tga.......t.....-.a.-......g.....a.....a.g.......a...........
H.hylaios 6363               ...........t-...t........tga.......t.....-aa.-......g.....a.....a.g.......a...........
H.ischnoryctes 6639          ...........a-...t........t.........t.....-atg-......g.....a....a..g.......a...........
H.kukunyungkal 6341          ...........t-...t........t.........t.....-ata-......g.....a.....g.g.......a...........
H.kukunyungkal 6342          ...........t-...t........t.........t.....-ata-......g..t..a.....g.g.......a...........
H.kukunyungkal 6343          ...........t-...t........t.........t.....-ata-......g.....a.....g.g.......a...........
H.laevitropis 6348           ...........t-...t........t.........t.....-atg-......g.....a.....g.g.......a...........
H.leptochela 6344            ...........t-...t........tga.......t.....-atg-......g.....a.....a.g.......a...........
H.leptochela 6345            ...........t-...t........tga.......t.....-atg-......g.....a.....a.g.......a...........
H.litodactylus 5559          ...........t-...t........t.........t....c-a.g-......g.....a.....a.g.......a...........
H.macrochela 5555            ...........t-.a.t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.neocaledonicus 4323        .........agt-...t........t.a.......t.....-atg-......g.....a.....g.g.......a...........
H.neocaledonicus 5542        .........agt-...t........t.a.......t.....-atg-......g.....a.....g.g.......a...........
H.neocaledonicus 5543        .........agt-...t........t.a.......t.....-atg-......g.....a.....g.g.......a...........
H.neocaledonicus 5544        .........agt-...t........t.a.......t.....-atg-......g.....a.....g.g.......a...........
H.neocaledonicus 5545        .........agt-...t........t.a.......t.....-atg-......g.....a.....g.g.......a...........
H.neocaledonicus 5546        .........agt-...t........t.a.......t.....-atg-......g.....a.....g.g.......a...........
H.neocaledonicus 5547        .........agt-...t........t.a.......t.....-aag-......g.....a.....g.g.......a...........
H.neocaledonicus 5548        .........agt-...t........t.a.......t.....-aag-......g.....a.....g.g.......a...........
H.neocaledonicus 6224        .........agt-...t........t.a.......t.....-atg-......g.....a.....g.g.......a...........
H.nyawaygi 6354              ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.papuanus 2718              ..........ct-...t........g.........t.....-atg-......g.....a.....a.g.......a...........
H.papuanus 2725              ...........t-...t........t..t......t.....-.ta-......g.....a.....g.g.......a...........
H.papuanus 2726              ...........t-...t........t.a.......t.....-.tga......g.....a.....g.g.......a.......g....
H.papuanus 2727              ...........t-...t........t.a.......t.....-.tga......g.....a.....g.g.......a...........
H.penta 1817                 .........g..-...t........tga.......t.....-aaa-......g.....a.....a.g.......a...........
H.polisorum 1614             ..........ac-...t........t.a.......t....a-at.-......g.....a.....a.g.......a...........
H.solomonensis 1818          ...........t-.c.t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.solomonensis 1819          ...........t-.c.t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.solomonensis 5549          ...........t-.c.t........t.........t.....-atg-......g.....a....ca.g.......a...........
H.solomonensis 5550          ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.solomonensis 5551          ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.solomonensis 5552          ...........t-...t........t.........t.....-atg-......g.....a.....g.g.......a...........
H.solomonensis 5554          ...........t-...t........t.........t.....-atg-......g.....a.....g.g.......a...........
H.tagulae 3008               ...........t-...t........g.........t....c-a.g-......g.....a.....a.g.......a..........g.
H.tjapukai 2184              ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.tjapukai 6641              ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.tytthognaphos 6346         ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.tytthognaphos 6347         ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.wallaman 6353              ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.yelae 3007                 ...........t-...t........t.a.......t.....-ctg-......g.....a....ca.g.......a...........
H.sp. WA 8017                ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
H.sp. WA 8021                ...........t-...t........t.........t.....-atg-......g.....a.....a.g.......a...........
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2.5.3 Aligned molecular sequences. Mitochondrial large-subunit ribosomal DNA 16S gene, base-pairs 88–174. Dots indicate a match with the first taxon. (Continued)

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C.ochropus 2189              tcaatagccttttaattgggggctggtatgaatggtttttctgaataagtttgtctcataattatattttgaatttaatttttttagt
C.ochropus 6894              ...................a..................................................................
C.ochropus 9069              ...................a..................................................................
I.nitidus 9827               ...t...ttc......t...a..............aa..a.....t......t...g.a..........a..t.........
I.politus 1514               .a.t...t..........aa.a....a.....a....aga.........a......t.....a.c.a......c..t..a.......
I.politus 3256               .a.t...t..........aa.a....a.....a....aga.........a......t.....a.c.a......c..t..a.......
O.elatus 1837                .a.t...t..c......t...a....a.....c..c.aga..a.g...a.cc......a..ag.c.c.c.......t..a.......
O.laevipes 1835              ...t...tt........taa.a.............cc.ca..a....gtcc.....tg....a..........a..t.c.....ga.
O.lecomtei 1608              ...t...t.........ta..a....a..........gga........ag.............a.............t..g.......
O.lecomtei 2194A             ...t...t.........ta..a....a..........gaa....g....a.......g...ca.............t..a.......
O.madagascariensis 2800      ...t...t.........ta..a....a.....a...c.....a.g...t.......t.....a.............t..a....g..
O.madagascariensis 2811      ...t...t.........t...a....a.....a...c.....a.g...t.......t.....g.............t..a....g..
O.madagascariensis 2812      ...t...t.........ta..a....a.....a...c.....a.g...t.......t.....a.............t..a....g..
H.infulcra 2185              ...t...t.........t.a.a....a.....a.....ga..atgc..a..........g..a......ca.....t..aa......
L.australasiae 1854          ...t...t.c.......t...a....a.........ccga..atg..gt.a.....tg..g.a..........a..t..g.......
L.australasiae 2181          ...t...t.c.......t...a....a.........ccga..atg...t.a.....t...g.a..........a..t..a.......
L.australasiae 2182          ...t...t.c.......t...a....a.........ccga..atg...t.a.....t...g.a..........a..t..a.......
L.australasiae 2183          ...t...t.c.......t...a....a.........ccga..atg...t.g.....tg..g.a..........a..t..a.......
L.australasiae 2729          ...t...t.c.......t...a....a.........ccga..atg...t.a.....tg..g.a..........a..t..a.......
L.australasiae 2733          ...t...t.c.......t...a....a.........ccga..atg...t.a.....tg..g.a..........a..t..a.......
L.australasiae 2996          ...t...t.c.......t...a....a.........ccga..atg...t.a.....tg..g.a..........a..t..a.......
L.australasiae 3684          ...t...t.........t.a.a....a..........cga...tg..tc.a.....t...g.a..........a..t.........
L.australasiae 4764          ...t...t.c.......t...a....a.........ccga..atg...t.a.....t...g.a..........a..t..a.......
L.australasiae 5553          ...t...t.c.......t...a....a.........ccga..atg...t.a.....tg..g.a..........a..t..a.......
L.australasiae 8676          ...t...t.c.......t...a....a.........ccga..atg...t.a.....tg..g.a..........a..t..a.......
L.australasiae 8677          ...t...t.c.......t...a....a.........ccga..atg...t.a.....tg..g.a..........a..t..a.......
L.longimanus 6388            ...t...t.c.......t........a.....c...c.ga.ca.gc...a......t..t..a...c......a..g.........
L.malaya 1909                ...t...t...a.....t.a......a.....c.....ga...ggcg.ag......t.....a..........a..t.........
H.aethes 3002                ...t...t.........t...a....a..........ga..at.c....c.....tt.gt.a..........a..t.........
H.aethes 3005                ...t...t.........t...a....a..........ga..at.c....c.....tt.gt.a..........a..t.........
H.anekasankylis 6355         ...t...t.........t...a....a..........ga...tgc....c.....tt..t.a..........a..t.........
H.anekasankylis 6356         ...t...t.........aa..a....a..........ga....gc....c.....tt..t.a..........a..t..a.......
H.anekasankylis 6357         ...t...t.........t...a....a..........ga...tgc....c.....tt..t.a..........a..t.........
H.ankistros 4339             ...t...t.........t.a.a....a..........ga...tgc...........t..tca..........a..t.........
H.bandjin 5556               ...t...t..c......t...a....a..........ga..atgc....c.....tt..t.g..........a..t..a.......
H.bandjin 5557               ...t...t..c......t...a....a..........ga..atgc....c.....tt..t.g..........a..t..a.......
H.bandjin 5558               ...t...t..c......t...a....a..........ga..atgc....c.....tt..t.g..........a..t..a.......
H.caudicula 1502             ...t...t.........t...a....a..........ga....gc....c.....tt..t.a..........a..t..a.......
H.caudicula 2339             ...t...t.........t...a....a..........ga..aggc....c.....tt.gt.a..........a..t..a.......
H.caudicula 2340             ...t...t.........t.a.a....a..........aa....gc..a.c.....tt..t.a..........a..t..a.......
H.caudicula 6360             ...t...t.........t...a....a..........ga..aggc....c.....tt....a..........a..t..a.......
H.caudicula 6361             ...t...t.........t...a....a..........ga....gc....c.....t..t.a..........a..t..a.......
H.caudicula 6362             ...t...t.........t...a....a..........ga....gc....c.....tt..t.a..........a..t..a.......
H.chthamalochoros 6350       ...t...t..c......t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.chthamalochoros 6351       ...t...t..cc.....t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.chthamalochoros 6352       ...t...t..c......t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.chthamalochoros 8023       ...t...t..c......t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.chydaeostigmata 5560       ...t...t.........t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.chydaeostigmata 8015       ...t...t..c......t...a....a..........ga..atg.....c.....tt..t.a..........a..t..a.......
H.chydaeostigmata 8016       ...t...t..c......t...a....a..........ga..atg.....c.....tt..t.a..........a..t..a.......
H.chydaeostigmata 8019       ...t...t.........t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.chydaeostigmata 8020       ...t...t.........t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.chydaeostigmata 8022       ...t...t..c......t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.dechangei 7789             ...t...t.........t...a....a..........ga..atg...a.c.....tt..t.a..........a..t.........
H.euktaenospatha 4340        ...t...t.........t...a....a..........aa..atg.....c.....tt..t.a..........a..t.........
H.glaphyroscytos 6640        ...t...t.........t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.hylaios 6358               ...t...t..c......t...a....a..........aa..atgc....c.....tt..t.a..........a..t..a.......
H.hylaios 6359               ...t...t..c......t...a....a..........aa..atgc....c.....tt..t.a..........a..t..a.......
H.hylaios 6363               ...t...t..c......t...a....a..........aa..atgc....c.....tt..t.a..........a..t..a.......
H.ischnoryctes 6639          ...t...t.........t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.kukunyungkal 6341          ...t...t.........t...a....a..........ga....gc....c.....tt..t.a..........a..t..a.......
H.kukunyungkal 6342          ...t...t.........t...a....a..........ga....gc....c.....tt..t.a..........a..t..a.......
H.kukunyungkal 6343          ...t...t.........t...a....a..........ga....gc....c.....tt..t.a..........a..t..a.......
H.laevitropis 6348           ...t...t.........t...a....a..........ga..a.g.....c.....tt..t.a..........a..t..a.......
H.leptochela 6344            ...t...t.........t.a.a....a..........ga..atgc...........t..t.a.......t..a..t..a.......
H.leptochela 6345            ...t...t.........t.a.a....a..........ga..atgc...........t..t.a.......t..a..t..a.......
H.litodactylus 5559          ...t...t.........t.a.a....a..........ga..atgc....c.....tt..t.a.......t..a..t..a.......
H.macrochela 5555            ...t...t..c......t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.neocaledonicus 4323        ...t...t.........ta..a....a..........ga....g.....c.....tt....a..........a..t.........
H.neocaledonicus 5542        ...t...t.........ta..a....a..........ga..a.g.....c.....tt....a..........a..t.........
H.neocaledonicus 5543        ...t...t.........ta..a....a..........ga..a.g.....c.....tt....a..........a..t.........
H.neocaledonicus 5544        ...t...t.........ta..a....a..........ga....g.....c.....tt..............a..t.........
H.neocaledonicus 5545        ...t...t.........ta..a....a..........ga..a.g.....c.....tt....a..........a..t.........
H.neocaledonicus 5546        ...t...t.........ta..a....a..........ga..a.g.....c.....tt....a..........a..t.........
H.neocaledonicus 5547        ...t...t.........ta..a....a..........ga..a.g.g....c.....tt..............a..t.........
H.neocaledonicus 5548        ...t...t.........ta..a....a..........ga..a.g.g....c.....tt..............a..t.........
H.neocaledonicus 6224        ...t...t.........ta..a....a..........ga..a.g.....c.....tt....a..........a..t.........
H.nyawaygi 6354              ...t...t..c......t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.papuanus 2718              ...t...t.........t...a....a..........aa..atgc....c.....tt.gt.a..........a..t.........
H.papuanus 2725              ...t...t..c......t...a....a........c..ga...ttc....c.....tt..t.a..........g..t.........
H.papuanus 2726              ...t...t..c......t...a....a..........ga..tt.c..a.......tt..t.a..............t.........
H.papuanus 2727              ...t...tt.c......t...a....a..........ga..tt.c..a.......tt..t.a..............t.........
H.penta 1817                 ...t...t.........t...a....a..........ga...tg.....c.....tt....a..........a..t.........
H.polisorum 1614             .a.t...t.........t...a....a..............a..atgc....c.....tt..t.a..........a..t..a.......
H.solomonensis 1818          ...t...t.........t...a....a..........ga...tgc..........tt.tt.a..........a..t.........
H.solomonensis 1819          ...t...t.........t...a....a..........ga...tgc..........tt.tt.a..........a..t.........
H.solomonensis 5549          ...t...t.........t...a....a..........ga...tgc..........tt.tt.a..........a..t.........
H.solomonensis 5550          ...t...t.........t...a....a..........ga...tgc.g........tt.tt.a..........a..t.........
H.solomonensis 5551          ...t...t.........t...a....a..........ga...tgc.g........tt.tt.a..........a..t.........
H.solomonensis 5552          ...t...t..c......t...a....a........c..ga...tgc.g........tt.tt.a..........a..t.........
H.solomonensis 5554          ...t...t.........t...a....a..........ga...tgc.g........tt.tt.a..........a..t.........
H.tagulae 3008               ...t...t.........t...a....a..........ga..atgc....c.....tt..t.a..........a..t.........
H.tjapukai 2184              ...t...t..c......t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.tjapukai 6641              ...t...t..c......t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.tytthognaphos 6346         ...t...t.........t.a.a....a..........ga...tg.....c.....tt..t.a.......t..a..t..a.......
H.tytthognaphos 6347         ...t...t.........t.a.a....a..........ga...tg.....c.....tt..t.a.......t..a..t..a.......
H.wallaman 6353              ...t...t.........t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.yelae 3007                 ...t...t.........t...a....a..........ga..atgc....c.....tt..t.a..........a..t.........
H.sp. WA 8017                ...t...t.........t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
H.sp. WA 8021                ...t...t.........t...a....a..........ga..atgc....c.....tt..t.a..........a..t..a.......
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2.5.3 Aligned molecular sequences. Mitochondrial large-subunit ribosomal DNA 16S gene, base-pairs 175–261. Dots indicate a match with the first taxon. (Continued)

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C.ochropus 2189              aaaaaagctaaaatttacttcagggacgagaagaccctatcaagctttacaaatga--aatt-atttctcttaaaat--aactaagt
C.ochropus 6894              ..................................................at--.t..-.............--......ac
C.ochropus 9069              ..................................................at--.t..-.............--......ac
I.nitidus 9827               ................t.........................a.t..t.t.--.tc.-....t......g..--.gact.aa
I.politus 1514               g..............tc.t.aa...a...........t........t...gagtg.t..-...a.........--..a.c.ac
I.politus 3256               g..............tc.t.aa...a...........t........t...gagtg.t..-...a.........--..a.c.ac
O.elatus 1837                g..............ctc.t.aa...a.....................atg--..c.-g..ct....t..gc--.gaa.ta.
O.laevipes 1835              .....g.tc......ctg..t......a.........g..............c.--.tc.-....a....g.t..--.ga...ag
O.lecomtei 1608              ..............a.tc.a.aa...a...........t......a.....at.--ttgcc...aa....tttg.--gg.a..t.
O.lecomtei 2194A             ..............a.tc.a.aa...a...........t...........at.--tcc.c...aa..c.ttt..--g.gg..t.
O.madagascariensis 2800      ........c......at...t.aa..............t............at--.t..-...ct.....g...--..aa..a.
O.madagascariensis 2811      .....g..c......at.....aa..............t...........cat--.t..-..cct......gg.--..aa..tc
O.madagascariensis 2812      ........c......at...t.aa..............t..............t--.t..-...ct......g..--..aa..a.
H.infulcra 2185              ......a.......ag.t..t.t.....................a.........t.--g.aa-t.a.t.tc.c....-a.gt.t.aa
L.australasiae 1854          ..............aa..c.t.aa...................a.........ctt--.g..-t.a.t.tc.g....ta..gcttaa
L.australasiae 2181          ..............ag..c.t.aa...................a.........ctt--gtcc-t.a.t.tc.g...cta.ggcttaa
L.australasiae 2182          ..............ag..c.t.aa...................a.........ctt--gtcc-t.a.t.tc.g...cta.ggcttaa
L.australasiae 2183          ..............ag..c.t.aa...................a.........ctt--gtcc-t.a.t.tc.g...cta.ggcttaa
L.australasiae 2729          ..............ag..c.t.aa...................a.........ctt--gtcc-t.a.t.tc.g...cta.ggcttaa
L.australasiae 2733          ..............ag..c.t.aa.............g....a.........ctt--gtcc-t.a.t.tc.g...cta.ggcttaa
L.australasiae 2996          ..............ag..c.t.aa...................a.........ctt--gtcc-t.a.t.tc.g...cta.ggcttaa
L.australasiae 3684          ..............aa..c.t.aa...................a.........tc--.g..-t.a.t.tc....t.-a.cacttag
L.australasiae 4764          ..............ag..c.t.aa...................a.........ctt--gtcc-t.a.t.tc.g...cta.ggcttaa
L.australasiae 5553          ..............ag..c.t.aa.............g....a.........ctt--gtcc-t.a.t.tc.g...ctagggcttaa
L.australasiae 8676          ..............ag..c.t.aa...................a.........ctt--gtcc-t.a.t.tc.g...cta.ggcttaa
L.australasiae 8677          ..............ag..c.t.aa...................a.........ctt--gtcc-t.a.t.tc.g...cta.ggcttaa
L.longimanus 6388            ..............gag.c.t.aa...................a.........ag--.gac-t.act.tc.t..t.-a.gt.ttaa
L.malaya 1909                ..............g.g.c...aa..............g....a.........ag--gga.-t.ac..tcc...t.-a..tctt.g
H.aethes 3002                ..............g..c.t.aa...................at..a......c.--..a.-t.a.t.tc....g.-a..g.ttaa
H.aethes 3005                ..............g..c.t.aa...................at..a......c.--..a.-t.a.t.tc....g.-a..g.ttaa
H.anekasankylis 6355         ................tc.t.aa...................a...a......c.--..aa-t.a.t.tcc.....-a..a.ttag
H.anekasankylis 6356         ..................c.t.aa...................a...a......c.--..aa-t.a.t.tcc.....-a..a.ttag
H.anekasankylis 6357         ................tc.t.aa...................a...a......c.--..aa-t.a.t.tcc.....-a..a.ttag
H.ankistros 4339             ..........g....a.tc.t.aa...................a...a......c.--..a.-t.g.t.tc...g..-a..g.ttaa
H.bandjin 5556               ................tc.t.aa...................a.........ca.--....-t.a.tctc......-a..a.ttta
H.bandjin 5557               ................tc.t.aa...................a.........ca.--....-t.a.tctc......-a..a.ttta
H.bandjin 5558               ................tc.t.aa...................a.........ca.--....-t.a.tctc......-a..t.ttta
H.caudicula 1502             ................t..t.aa...................a..........t.--g...-t.a.t.tcc...g.-a..a.ttta
H.caudicula 2339             ................a..t.aa...................a..........t.--g...-t.a.t.tcc...g.-a..a.ttta
H.caudicula 2340             ..................c.t.aa...................at.........a.--..a.t..a...tcc.....-a..a.ttta
H.caudicula 6360             ................t..t.aa...................a...a......t.--g...-t.a.t.tcc...g.-a..g.tttg
H.caudicula 6361             ................t..t.aa...................a..........t.--g...-t.a.t.tcc...g.-a..a.ttta
H.caudicula 6362             ................t..t.aa...................a..........t.--g...-t.a.t.tcc...g.-a..a.ttta
H.chthamalochoros 6350       ................tc.t.aa...................a...a.....ca.--....-t.a.t.tc......-a..t.ttta
H.chthamalochoros 6351       ................tc.t.aa...................a...a.....ca.--....-t.a.tctc......-a..t.ttta
H.chthamalochoros 6352       ................tc.t.aa...................a...a.....ca.--....-t.a.t.tc......-a..t.ttta
H.chthamalochoros 8023       ................tc.t.aa...................a...a.....ca.--....-t.a.t.tc......-a..t.ttta
H.chydaeostigmata 5560       ................tc.t.aa...................a...a...g..a.--..aatt.a.t.tcc...g.-a..a.ttaa
H.chydaeostigmata 8015       ................tc.t.aa...................a...a.....a.--..aatt.a.t.tcc...g.-a..a.t.aa
H.chydaeostigmata 8016       ................tc.t.aa...................a...a.....a.--..aatt.a.t.tcc...g.-a..a.t.aa
H.chydaeostigmata 8019       ................tc.t.aa...................a...a.....a.--..aatt.a.t.tcc...g.-a..a.ttaa
H.chydaeostigmata 8020       ................tc.t.aa...................a...a.....a.--..aatt.a.t.tcc...g.-a..a.ttaa
H.chydaeostigmata 8022       ................tc.t.aa...................a...a.....a.--..aatt.a.t.tcc...g.-a..a.t.aa
H.dechangei 7789             ................tc.t.aa...................a...g.....c.--gg..-t.a...tc......-a.ga.tcag
H.euktaenospatha 4340        ................tc.t.aa..............t....a.........t.--ggg.-t.a.t.tc...gg.-a.g..tcta
H.glaphyroscytos 6640        ................tc.t.aa...................a.........c.--..a.-t.a.t.tc..g...-a..a.ttag
H.hylaios 6358               ................tc.t.aa..............g....a...a.....c.--..a.-t.a.t.tc....g.-a..a.ttag
H.hylaios 6359               ................tc.t.aa...................a...a.....cc.--.ga.-t.a.t.tc....g.-a..a.ttag
H.hylaios 6363               ................tc.t.aa...................a...a.....c.--..a.-t.a.t.tc....g.-a..a.ttag
H.ischnoryctes 6639          ................tc.t.aa...................a.........c.--..ag-t.a.t.tc......-a..a.ttag
H.kukunyungkal 6341          ................tc.t.aa...................a.........t.--..a.-t.a.t.tcc.....-a..a.t.aa
H.kukunyungkal 6342          ................tc.t.aa...................a.........t.--..a.-t.a.t.tcc.....-a..a.t.aa
H.kukunyungkal 6343          ................tc.t.aa...................a.........t.--..a.-t.a.t.tcc.....-a..a.t.aa
H.laevitropis 6348           ................tc.t.a....................a.........t.--..a.-t.a.t.tcc.....-a..a.t.aa
H.leptochela 6344            ................tc.t.aa...................a...a.....c.--..aa-t.a.t.tcc.....-ag.a.ttaa
H.leptochela 6345            ................tc.t.aa...................a...a.....c.--..aa-t.a.t.tcc.....-ag.a.ttaa
H.litodactylus 5559          ..............g.tc.t.aa...................a...a.....a.--..aa-t.a.tctcc...g.-a..a.ttag
H.macrochela 5555            ................tc.t.aa...................a.........a.--g...-t.a.tctc......-a..g.ttta
H.neocaledonicus 4323        ................gtc.t.aa...................a.........t.--..a.-t.a.t.tc.ggg..-a..t.ctag
H.neocaledonicus 5542        ................gtc.t.aa...................a.........t.--..a.-t.a.t.tc.gg...-a..t.ctag
H.neocaledonicus 5543        ..............gtc.t.aa...................a.........t.--..a.-t.a.t.tc.gg...-a..t.ctag
H.neocaledonicus 5544        ................tc.t.aa...................a.........t.--..a.-t.a.t.tc.gg.g.-a.tt.ctag
H.neocaledonicus 5545        ..............gtc.t.aa...a...............a.........t.--..a.-t.a.t.tc.gg...-a..t.ctag
H.neocaledonicus 5546        ..............gtc.t.aa...................a.........t.--..a.-t.a.t.tc.gg...-a..t.ctag
H.neocaledonicus 5547        ................gtc.t.aa...................a.........t.--..aa-c.act.tc.gg.g.-a.tt.ctag
H.neocaledonicus 5548        ..............gtc.t.aa...................a.........t.--..aa-c.act.tc.gg.g.-a.tt.ctag
H.neocaledonicus 6224        ..............gtc.t.aa...a...............a.........t.--..a.-t.a.t.tc.gg...-a..t.ctag
H.nyawaygi 6354              ................tc.t.aa..............t....a...a.....a.--....-t.a.tctc......aa..a.ttta
H.papuanus 2718              ..............a.....t.aa...................a...g......c.--..a.-t.a.t.tc......-a..g.ttaa
H.papuanus 2725              ..............c..tc.t.aa...................a.........t.--..a.-t.a.t.tc......-a..a.tcaa
H.papuanus 2726              ................cttc.t.aa...................a...g......c.--..a.-t.a.t.tc......-a..actcaa
H.papuanus 2727              ................cttc.t.aa...................a...g......c.--..a.-t.a.t.tc......-a..actcaa
H.penta 1817                 ................tc.t.aa...................a.........tg--....-t.a.t.tc.gg.t.-a..t.tc.g
H.polisorum 1614             ..............ac.tc.t.aa...................a...a.t...cc.--..ag-t.a.t.tc......-a..t.ttaa
H.solomonensis 1818          .....g..........tc.t.aa...................a.........c.--..a.-c.ac..tc...gg.-ag.t.t.ag
H.solomonensis 1819          .....g..........tc.t.aa...................a.........c.--..a.-c..c..tc...gg.-ag.t.t.ag
H.solomonensis 5549          .....g..........tc.t.aa...................a.........c.--g.a.-t.a...tc...g..-a.gt.ttag
H.solomonensis 5550          .....g..........tc.t.aa...a...............a.........c.--..ac-c.a...tc.t.g..-a..t.ttag
H.solomonensis 5551          .....g..........tc.t.aa...a...............a.........c.--..a.-c.a...tc.t.g..-a..t.ttag
H.solomonensis 5552          .....g..........tc.t.aa...a...............a.........c.--..a.-c.a...tc.t.g..-a..t.ttag
H.solomonensis 5554          .....g..........tc.t.aa...a...............a.........c.--..a.-c.a...tc.t.g..-a..t.ttag
H.tagulae 3008               ................t..t.aa................t..a...a....g.c.--..c.-c.a.t.tc....t.-ag.g.ttaa
H.tjapukai 2184              ................tc.t.aa...................a...a.....c.--..aa-t.a.t.tcc.....-a..a.ttag
H.tjapukai 6641              ................tc.t.aa...................a...a.....c.--..aa-t.a.t.tcc.....-a..a.ttag
H.tytthognaphos 6346         ..................c.t.aa...................a.........cg--..aa-t.a.t.tcc...g.-a.ga.ttag
H.tytthognaphos 6347         ................tc.t.aa...................a.........cg--..aa-t.a.t.tcc.....-a.ga.ttag
H.wallaman 6353              ................tc.t.aa...................a...a.....a.--g...-t.a.tctc......-a..g.ttta
H.yelae 3007                 ..............gtc.t.aa...................a...a.....c.--..a.-t.a.t.tc....g.-ag.a.ttag
H.sp. WA 8017                ................tc.t.aa...................a...a.....a.--..agtt.a.t.tcc.....-a..a.ttaa
H.sp. WA 8021                ................tc.t.aa...................a...a.....a.--..agtt.a.t.tcc.....-a..a.ttaa
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2.5.3 Aligned molecular sequences. Mitochondrial large-subunit ribosomal DNA 16S gene, base-pairs 262–348. Dots indicate a match with the first taxon. (Continued)

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C.ochropus 2189              tttgtttttactggggcagtaggtaa---aa---aatactacttttttattatgaaat-tttctcttgtaagatcgaaaatttttcaa
C.ochropus 6894              .....................a....a--..---.....................g...-.............................
C.ochropus 9069              .....................a....a--..---.....................g...-.............................
I.nitidus 9827               a..a..cc...........gaa...---.tata...tt..t..g.a....g....tct..ag......ggt...............
I.politus 1514               ...a..a..............ac..a--.t---...tt.gt...aaa...g....t.-.aat....t...a...a.........t..
I.politus 3256               ...a..a..............ac..a--.t---...tt.gt...aaa...g....t.-.aat....t...a...a.........t..
O.elatus 1837                .......a...........t.a...a--.t---...tt..t..gaaa...ga.gt.a-..ca...a.a..t...a.g..a..c.t..
O.laevipes 1835              .......a...........t.a...---.t---...tt..t....a...........t.g.t.....ct.t...agg..a..cct..
O.lecomtei 1608              .......g...........aa...a-a.t---.c.tt..t..aaaa.c.g..gg.a-.acgc..g.a..a...a....g....t..
O.lecomtei 2194A             .......a...........a....ata.t---.t.tt..t....aa.......tga-.gga...a.a..a...a....g....t..
O.madagascariensis 2800      .....................aa...---gc---....t..t..aaa..a.....tt.-.aaa.....a..a........g.......
O.madagascariensis 2811      .....................aa...---.t---....t..t..aaac.a.....ct.-.aaa........a........g.......
O.madagascariensis 2812      .....................aa...---gc---....t..t..aaa..a.....tt.-.aaa.....a..a........g.......
H.infulcra 2185              ........gt.......a..aaa..a--.t---.t.tt.tt..aaaa...g..g.t.-.aat........a...a....a....t..
L.australasiae 1854          ...................t...gga-ttt---gg.t........ga...g....t.-.aat.....at.a...a.........t..
L.australasiae 2181          .......a...........t.a.gga-ttt---gg.t.c.t....ga...g....t.-.aat.....at.a...a.........t..
L.australasiae 2182          .......a...........t.a.gga-ttt---gg.t.c.t....ga...g....t.-.aat.....at.a...a.........t..
L.australasiae 2183          .......a...........t.a.gga-ttt---gg.t.c.t....ga...g....t.-.aat.....at.a...a.........t..
L.australasiae 2729          .......a...........t.a.gga-ttt---gg.t.c.t....ga........t.-.aat.....at.a...a.........t..
L.australasiae 2733          .......a...........t.a.gga-ttt---gg.t.c.t....ga...g....t.-.aat.....at.a...a.........t..
L.australasiae 2996          .......a...........t.acgga-ttt---gg.t.c.t....ga...g....t.-.aat.....at.a...a.........t..
L.australasiae 3684          ...................t...gga-ttt---gg.t.c.t...aaa...g....t.-.aat.....at.a...a.........t..
L.australasiae 4764          .......a...........t.a.gga-ttt---gg.t.c.t....ga...g....t.-.aat.....at.a...a.........t..
L.australasiae 5553          .......a...........t.a.gga-ttt---gg.t.c.t....ga...g....t.-.aat.....at.a...a.........t..
L.australasiae 8676          .......a...........t.a.gga-ttt---gg.t.c.t....ga...g..g.t.-.aat.....at.a...a.........t..
L.australasiae 8677          .......a...........t.a.gga-ttt---gg.t.c.t....ga...g..g.t.-.aat.....at.a...a.........t..
L.longimanus 6388            ........g...........aa...a--.t---....t..t....g....g..gtt.-.aag.....g..a...a....a....t..
L.malaya 1909                .....................a.g.a--tt---gg.tt..t....g....g..gtt.t.aga.....gg.a...a....g....t..
H.aethes 3002                .......a...........t.....a--.t---.t.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.aethes 3005                .......a...........t.....a--.t---.t.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.anekasankylis 6355         .......g...........taa...a--.t---gt.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.anekasankylis 6356         .......a...........t.a...a--.t---gt.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.anekasankylis 6357         .......g...........ta....a--.t---gt.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.ankistros 4339             .......a...........taa.g.a--.t---.t.ttc.t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.bandjin 5556               .......a...........taa.g.a--.t---.t.tt..t..ac.a...ga..tt.-..aa......t.a...a....a....t..
H.bandjin 5557               .......a...........taa.g.a--.t---.t.tt..t..ac.a...ga..tt.-..aa......t.a...a....a....t..
H.bandjin 5558               .......a...........taa.g.a--.t---gt.tt..t..ac.a...ga..tt.-..aa......t.a...a....a....t..
H.caudicula 1502             .......a...........taa...a--.t---.t.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.caudicula 2339             .......a...........ta..g.a--.t---.t.tt..t..a.ca...ga..tt.-..aa......t.a...a....ag...t..
H.caudicula 2340             .......a...........taa...a--.c---.t.tt..t..ac.a...ga..ct.-c.aa....a.c.a...a....a....t..
H.caudicula 6360             .......a...........taa.g.a--.t---gt.tt..t..g.aa...ga..tt.-..aa......t.a...a....ag...t..
H.caudicula 6361             .......a...........taa...a--.t---.t.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.caudicula 6362             .......a...........taa...a--.t---.t.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.chthamalochoros 6350       .......a...........taa...a--.t---gt.tt..t..ac.a...ga..tt.-..aa......c.a...a....g....t..
H.chthamalochoros 6351       .......a...........taa...a--.t---gt.tt..t..ac.a...ga..tt.-..aa......t.a...a....g....t..
H.chthamalochoros 6352       .......a...........taa...a--.t---gt.tt..t..a..a...ga..tt.-..aa......c.a...a....g....t..
H.chthamalochoros 8023       .......a...........taa...a--.t---gt.tt..t..ac.a...ga..tt.-..aa......c.a...a....g....t..
H.chydaeostigmata 5560       .......a...........taa...a--.t---gt.tt..t..a..a...ga..tt.-.caa......t.a...a....ag...t..
H.chydaeostigmata 8015       .......g...........taa...a--.t---gt.tt..t..a..a...ga..tt.-.caa......t.a...a....ag...t..
H.chydaeostigmata 8016       .......g...........taa...a--.t---gt.tt..t..a..a...ga..tt.-.caa......t.a...a....ag...t..
H.chydaeostigmata 8019       .......g...........taa...a--.t---gt.tt..t..a..a...ga..tt.-.caa......t.a...a....ag...t..
H.chydaeostigmata 8020       .......g...........taa...a--.t---gt.tt..t..a..a...ga..tt.-.caa......t.a...a....ag...t..
H.chydaeostigmata 8022       .......g...........taa...a--.t---.t.tt..t..a..a...ga..tt.-.caa......t.a...a....ag...t..
H.dechangei 7789             .c.....a.t.......a.t.....a--.t---.t.tt..t..g.aa...ga...t.-..aa......t.a...a....ag...t..
H.euktaenospatha 4340        .......a...........ta....a--.t---.t.tt..t..ac.g...gg.g...-.caac.....g.a...a....a....t..
H.glaphyroscytos 6640        .......a...........taa...a--.t---.t.tt..t..a..g...ga..ct.-.aag............a....a....t..
H.hylaios 6358               .......a...........t.a.g.a--.t---.t.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.hylaios 6359               .......a...........t.a...a--.t---.t.tt..t..g..a...ga..tt.-..aa......t.a...a....a....t..
H.hylaios 6363               .......a...........t.a.g.a--.t---.t.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.ischnoryctes 6639          .......a...........taa...a--.t---.t.tt..t..g..g...ga..tt.-..aaa.......ga...a.......t..
H.kukunyungkal 6341          .......a...........t.a.g.a--.t---.t.tt..t..a..a...ga..tt.-..aa......tga........ag...t..
H.kukunyungkal 6342          .......a...........t.a.g.a--.t---.t.tt.gt..a..a...ga..tt.-..aa......tga........ag...t..
H.kukunyungkal 6343          .......a...........t.a.g.a--.t---.t.tt.gt..a..a...ga..tt.-..aa......tga........ag...t..
H.laevitropis 6348           .......a...........t.a.g.a--.t---.t.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.leptochela 6344            .......a...........taa...a--.t---.t.tt..t..aaaa...ga..tt.-.aaa......t.a...a....ag...t..
H.leptochela 6345            .......a...........taa...a--.t---.t.tt..t..aaaa...ga..tt.-.aaa......t.a...a....ag...t..
H.litodactylus 5559          .......a...........taa...a--.t---.t.tt..t..aaaa...ga..tt.-..aa......t.a...a....ag...t..
H.macrochela 5555            .......a...........taa.g.a--.t---.t.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.neocaledonicus 4323        .......a...........taa..ga--.t---.t.t...t..a......ga..tt.g...a...a..g.a.c.a.........t..
H.neocaledonicus 5542        .......a...........taa..ga--.t---.t.t...t..a......ga..ttag.aaa...a..g.a.c.a.........t..
H.neocaledonicus 5543        .......a...........taa..ga--.t---.t.t...t..a......ga..ttag.aaa...a..g.a.c.a.........t..
H.neocaledonicus 5544        .......a...........taa..ga--.t---gt.t...t..g......ga..tt.g...a.........a...a.........t..
H.neocaledonicus 5545        .......a...........taa..ga--.t---.t.t...t..a......ga..tt.g..aa...a..g.a.c.a.........t..
H.neocaledonicus 5546        .......a...........taa..ga--.t---.t.t...t..a......ga..tt.g..aa...a..g.a.c.a.........t..
H.neocaledonicus 5547        .......a...........tat..ga--.t---gt.t...t..a......ga..tt.g.g.a......g.a.c.a....a....t..
H.neocaledonicus 5548        .......a...........tat..ga--.t---gt.t...t..a......ga..tt.g.g.a......g.a.c.a....a....t..
H.neocaledonicus 6224        .......a...........taa..ga--.t---.t.t...t..a......ga..tt.g..aa...a..g.a.c.a.........t..
H.nyawaygi 6354              .......a...........taa.g.a--.t---.t.tt.gt..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.papuanus 2718              c......a...........t.a...a--.t---.t.tt..t..g..a...ga..tta-c.aa......t.a...a....a....t..
H.papuanus 2725              .......a...........t.a...a--.t---gt.tt..t..aa.a...ga...t.-.caa......t.a...a....ag...t..
H.papuanus 2726              .......a...........t.a...a--.t---.c.tt..t..aaaa...ga..t..-.aaa......t.a.c.a.........t..
H.papuanus 2727              .......a...........t.a...a--.t---.c.tt..t..aaaa...ga..t..-.aaa......t.a.c.a.........t..
H.penta 1817                 .......a...........t...g.a--.t---gt.tt.....g......ga..tt.a...a..gc..t.a...a.t..a....t..
H.polisorum 1614             ...a...a...........taa.g.a--.t---.t.tt..t..a..a...ga..tt.-..aa......t.a...a.........t..
H.solomonensis 1818          .......a...........t.a.g.a--tt---.t.ttc.t..a..a...ga..gg.-.aaa.....a..a...a....a....t..
H.solomonensis 1819          .......a...........t.a.g.a--tt---.t.ttc....a..a...ga..gg.-.aaa.....a..a...a....a....t..
H.solomonensis 5549          .......a...........t.a.g.a--.t---.t.ttc.t..a..a...ga...g.-..aa.....a..a...ag.g.....t..
H.solomonensis 5550          .......a...........t...g.a--.t---.t.ttc.t..a..a...ga...g.-caaa........a.c.a....g....t..
H.solomonensis 5551          .......a...........t...g.a--.t---.t.ttc.t..a..g...ga...g.-..aa........a.c.a....a....t..
H.solomonensis 5552          .......a...........t.a.g.a--.t---.t.ttc.t..a..a...ga...g.-.aaa........a...a....a....t..
H.solomonensis 5554          .......a...........t...g.a--.t---.t.ttc.t..a..a...ga...g.-..aa........a...a....a....t..
H.tagulae 3008               .......a...........t.a...a--.t---.t.tt..t..g..a...ga..ttg-ccaa......t.a...a....ag...t..
H.tjapukai 2184              .......a.......t...taa.g.a--.t---gt.ttc.t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.tjapukai 6641              .......a...........taa.g.a--.t---gt.ttc.t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.tytthognaphos 6346         .......a...........taa...a--.t---.t.tt..t..aaaa...ga..tt.-..aa......t.a...a....ag...t..
H.tytthognaphos 6347         .......a...........taa...a--.t---.t.tt..t..aaaa...ga..tt.-..aa......t.a...a....ag...t..
H.wallaman 6353              .......a...........taa.g.a--.t---.t.tt..t..a..a...ga..tt.-..aa......t.a...a....ag...t..
H.yelae 3007                 .......a...........t.a.g.a--.t---.t.tt..t..g..a...ga..tt.-.aaa......t.a...a....ag...t..
H.sp. WA 8017                .......a...........taa...a--.t---gt.tt..t..a..a...ga..tt.-.caa......t.a...a....ag...t..
H.sp. WA 8021                .......a...........taa...a--.t---gt.tt..t..a..a...ga..tt.-.caa......t.a...a....ag...t..
```

2.5.3 Aligned molecular sequences. Mitochondrial large-subunit ribosomal DNA 16S gene, base-pairs 349–435. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              ataaaaataagttactgtagggataacagcgtaattttctttgaaagatcttattatcaagaaagtttgcgacctcgatgttggatt
C.ochropus 6894              ............................................................................................
C.ochropus 9069              ............................................................................................
I.nitidus 9827               .a..t...c.....................................a.g..t.....................................
I.politus 1514               ga..g..........a.....................ta.aa.g..t........a..ta.....................
I.politus 3256               ga..g..........a.....................ta.aa.g..t........a..ta.....................
O.elatus 1837                c.............................g.....ta.aa.g..t..a...c.g..ta.....................
O.laevipes 1835              .a..g...t........c...................c.....a.g..t...c..c.......g.....................
O.lecomtei 1608              ga..............a.....................ta.aa.g..t......c....ta.....................
O.lecomtei 2194A             ga..............a.....................ta.aa.g..t......cg...ta.....................
O.madagascariensis 2800      ........t.......a.........................a.g..t......c.....................
O.madagascariensis 2811      ....g...t.......a.........................a.g..t......c.....................
O.madagascariensis 2812      ........t.......a.........................a.g..t......c.....................
H.infulcra 2185              ta..g.........................a.t........aa.g..ta.a....g.............t.....
L.australasiae 1854          ta..g.........................a......t...a.g..t.......g..g.a.......t.....
L.australasiae 2181          t...g.........................a......t...a.g..t.......g..g.a.......t.....
L.australasiae 2182          t...g.........................a......t...a.g..t.......g..g.a.......t.....
L.australasiae 2183          t...g.........................a......t...a.g..t.......g..g.a.......t.....
L.australasiae 2729          t...g.........................a......t...a.g..t.......g..g.a.......t.....
L.australasiae 2733          t...g.........................a......t...a.g..t.......g..g.a.......t.....
L.australasiae 2996          t...g.........................a......t...a.g..t.......g..g.a.......t.....
L.australasiae 3684          ta..g......c..................a......t...a.g..t.......g....a.......t.....
L.australasiae 4764          t...g.........................a......t...a.g..t.......g..g.a.......t.....
L.australasiae 5553          t...g.........................a......t...a.g..t.......g..g.a.......t.....
L.australasiae 8676          t...g.........................a......t...a.g..t.......g..g.a.......t.....
L.australasiae 8677          t...g.........................a......t...a.g..t.......g..g.a.......t.....
L.longimanus 6388            ..............................a......t...a.g..ta..........a.......t.....
L.malaya 1909                t..gg...........c.............a......t...a.g..t.......g..g.a.......t.....
H.aethes 3002                .a.gg.........................a......t...a.g..t...........a.......t.....
H.aethes 3005                .a.gg.........................a......t...a.g..t...........a.......t.....
H.anekasankylis 6355         .a..g...t.....................a......t...a.g..t...........a...t....t.....
H.anekasankylis 6356         .a.gg...t.....................a......t...a.g..t...........a...t....t.....
H.anekasankylis 6357         .a..g...t.....................a......t...a.g..t...........a...t....t.....
H.ankistros 4339             .a...........................a......t..aa.g..t...........a.......t.....
H.bandjin 5556               .a..g.........................a......t...a.g..t...........a...t....t.....
H.bandjin 5557               .a..g.........................a......t...a.g..t...........a...t....t.....
H.bandjin 5558               .a..g.........................a......t...a.g..t...........a...t....t.....
H.caudicula 1502             .a.gg.........................a......t...a.g..t...........a...t....t.....
H.caudicula 2339             .a.gg.........................a......t...a.g..t...........a...t....t.....
H.caudicula 2340             .a.gg...t.a...................a......t...a....t...........a...t....t.....
H.caudicula 6360             .a.gg.........................a......t...a.g..t...........a...t....t.....
H.caudicula 6361             .a.gg.........................a......t...a.g..t...........a...t....t.....
H.caudicula 6362             .a.gg.........................a......t...a.g..t...........a...t....t.....
H.chthamalochoros 6350       .a...........................a......t...a....t...........a...t....t.....
H.chthamalochoros 6351       .a...........................a......t...a.g..t...........a...t....t.....
H.chthamalochoros 6352       .a...........................a......t...a....t...........a...t....t.....
H.chthamalochoros 8023       .a...........................a......t...a....t...........a...t....t.....
H.chydaeostigmata 5560       .a..g.........................a......t...a.g..t...........a...t....t.....
H.chydaeostigmata 8015       .a..g.........................a......t...a.g..t...........a...t....t.....
H.chydaeostigmata 8016       .a..g.........................a......t...a.g..t...........a...t....t.....
H.chydaeostigmata 8019       .a..g.........................a......t...a.g..t...........a...t....t.....
H.chydaeostigmata 8020       .a..g.........................a......t...a.g..t...........a...t....t.....
H.chydaeostigmata 8022       .a..g.........................a......t...a.g..t...........a...t....t.....
H.dechangei 7789             .a..g.........................a......t...a.g..t...........a.......t.....
H.euktaenospatha 4340        ga..g............a............a......t...a.g..t........g...a.......t.....
H.glaphyroscytos 6640        gg............................a......t...a.g..t..........g.a...t....t.....
H.hylaios 6358               .a............................a......t...a.g..t.......g....a...t....t.....
H.hylaios 6359               .a..g.........................a......t...a.g..t.......g....a...t....t.....
H.hylaios 6363               .a..g.........................a......t...a.g..t.......g....a...t....t.....
H.ischnoryctes 6639          gg............................a......t...a.g..t..........g.a...t....t.....
H.kukunyungkal 6341          ga............................a......t...a.g..t..........g.a...t....t.....
H.kukunyungkal 6342          ga............................a......t...a.g..t..........g.a...t....t.....
H.kukunyungkal 6343          ga............................a......t...a.g..t..........g.a...t....t.....
H.laevitropis 6348           ga............................a......t...a.g..t..........g.a...t....t.....
H.leptochela 6344            .a..g.........................a......t...a....t...........a...t....t.....
H.leptochela 6345            .a..g.........................a......t...a....t...........a...t....t.....
H.litodactylus 5559          .a..g.........................a......t...a....t...........a...t....t.....
H.macrochela 5555            .a..g.........................a......t...a.g..t...........a...t....t.....
H.neocaledonicus 4323        .a............................a......tc....g..ta.a....g...ga.......t.....
H.neocaledonicus 5542        .a............................a......tc....g..ta.a....g...ga.......t.....
H.neocaledonicus 5543        .a............................a......tc....g..ta.a....g...ga.......t.....
H.neocaledonicus 5544        tg............................a......tc....g..ta.a....g...ga.......t.....
H.neocaledonicus 5545        .a............................a......tc....g..ta.a....g...ga.......t.....
H.neocaledonicus 5546        .a............................a......tc....g..ta.a....g...ga.......t.....
H.neocaledonicus 5547        tg............................a......tc....g..ta.a....g...ga.......t.....
H.neocaledonicus 5548        tg............................a......tc....g..ta.a....g...ga.......t.....
H.neocaledonicus 6224        .a............................a......tc....g..ta.a....g...ga.......t.....
H.nyawaygi 6354              .a..g.........................a......t...a.g..t...........a...t....t.....
H.papuanus 2718              .a.g..........................a......t...a.g..t...........a.......t.....
H.papuanus 2725              gg............................a......t...a.g..t...........a.......t.....
H.papuanus 2726              ..............................a......t...a.g..t..........g.a.......t.....
H.papuanus 2727              ..............................a......t...a.g..t..........g.a.......t.....
H.penta 1817                 ta............................a......tc....g..ta.a....g...ga.......t.....
H.polisorum 1614             .a..g.........................a......t..ca.g..t.......gc...a...t....t.....
H.solomonensis 1818          .a.gg.........................a......t..a..g..t........a...a.......t.....
H.solomonensis 1819          .a.gg.........................a......t..a..g..t........a...a.......t.....
H.solomonensis 5549          .a.t..........................a......t..a..g..t........a...a.......t.....
H.solomonensis 5550          .a.gg.........................a......t..aa.g..t........a...a.......t.....
H.solomonensis 5551          .g.gg.........................a......t..a..g..t........a...a.......t.....
H.solomonensis 5552          .a.gg.gc......................a......t..a..g..t........a...a.......t.....
H.solomonensis 5554          .a.gg.gc......................a......t..a..g..t........a...a.......t.....
H.tagulae 3008               .a.gg.........................a......t...a.g..t..........g.a.......t.....
H.tjapukai 2184              .a.gg.........................a......t...a.g..t...........a...t....t.....
H.tjapukai 6641              .a.gg.........................a......t...a.g..t...........a...t....t.....
H.tytthognaphos 6346         .a..g.........................a......t...a....t...........a...t....t.....
H.tytthognaphos 6347         .a..g.........................a......t...a....t...........a...t....t.....
H.wallaman 6353              .a............................a......t...a.g..t...........a...t....t.....
H.yelae 3007                 .a.g..........................a......t...a.g..t...........a...a....t.....
H.sp. WA 8017                .a..g.........................a......t...a.g..t...........a...t....t.....
H.sp. WA 8021                .a..g.........................a......t...a.g..t...........a...t....t.....
```

2.5.3 Aligned molecular sequences. Mitochondrial large-subunit ribosomal DNA 16S gene, base-pairs 436–499. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              aaaattcctaatttccgcaata-ggaaata-gaggaagtctgtt-cgacttttaaaattttcca
C.ochropus 6894              ......................-.......-a...........-.....................
C.ochropus 9069              ......................-.......-a...........-.....................
I.nitidus 9827               ...t..................-.....at-...........-...........a.....
I.politus 1514               ............cgt...g..-.tg..a.-a...........-.....................
I.politus 3256               ............cgt...g..-.tg..a.-a...........-.....................
O.elatus 1837                ....ca.......ag.......-.cc..a.-a...........-.....................
O.laevipes 1835              ....gg....t..c........-..g..at-a...g........-.....................
O.lecomtei 1608              .......t.tt...at...ga.-.t...a.-..a.........-.....................
O.lecomtei 2194A             .......t.tt...at...ga.-.t...a.-a.a.........-.....................
O.madagascariensis 2800      .....a.......c........-..g..a.-a...........-..........t........
O.madagascariensis 2811      .....a.......c........-..g..g.-a...........-..........t........
O.madagascariensis 2812      .....a.......c........-..g..a.-a...........-..........t........
H.infulcra 2185              ....a.........gt...gc.-.c...ataa...g........-..t..c.....t.......
L.australasiae 1854          ..g.aa...gg...at...ga.-.t...ct-a...........-......a...tt.c.....
L.australasiae 2181          ..g.gat..g....a....ga.-.t....t-a...........-......a...tt.c.....
L.australasiae 2182          ..g.gat..g....a....ga.-.t....t-a...........-......a...tt.c.....
L.australasiae 2183          ..g.gat..g....a....ga.-.t....t-a...........-......a...tt.c.....
L.australasiae 2729          ..g.gat..g....a....ga.-.t.....a...........-......a...tt.c.....
L.australasiae 2733          ..g.gat..g....a....ga.-.t....t-a...........-......a...tt.c.....
L.australasiae 2996          ..g.gat..g....a....ga.-.t....t-a...........-......a...tt.c.....
L.australasiae 3684          ..g.ga...g....a.....a.-.t....t-a...........-......a...ct.c.....
L.australasiae 4764          ..g.gat..g....a....ga.-.t....t-a...........-......a...tt.c.....
L.australasiae 5553          ..g.gat..g....a....ga.-.t....t-a...........-......a...tt.c.....
L.australasiae 8676          ..g.gat..g....a....ga.-.t....t-a...........-......a...tt.c.....
L.australasiae 8677          ..g.gat..g....a....ga.-.t....t-a...........-......a...tt.c.....
L.longimanus 6388            ..g.ga........gt...g..-at....t-a...g........-........g..t.c.....
L.malaya 1909                ..g.ga........at.a.g..-.tg..at-a...g.........-...........t.c.....
H.aethes 3002                ..g.ga....t...gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.aethes 3005                ..g.ga....t...gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.anekasankylis 6355         ..g.ga...g....gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.anekasankylis 6356         ..g.ga........gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.anekasankylis 6357         ..g.ga...g....gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.ankistros 4339             ..g.aa........gt.t.gc.-.ct..at-a...gg.......-....c......t.c.....
H.bandjin 5556               ..g.ga........gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.bandjin 5557               ..g.ga........gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.bandjin 5558               ..g.ga........gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.caudicula 1502             ..g.ga........gt.t.gc.-.tt..at-a....g.......-....c......t.c.....
H.caudicula 2339             ..g.ga...g....gt.t.gc.-.ct...t-a....g.......-....c......t.c.....
H.caudicula 2340             ....ga........at.t.gc.-.tt..a.-a....g.......-....c......g.......
H.caudicula 6360             ..g.ga........gt.t.gc.-.ct.g.t-a...gg.......-....c......t.c.....
H.caudicula 6361             ..g.ga........gt.t.gc.-.tt..at-a...gg.......-....c......t.c.....
H.caudicula 6362             ..g.ga........gt.t.gc.-.tt..at-a....g.......-....c......t.c.....
H.chthamalochoros 6350       ..g.aa........gt.t.gc.-.tt..at-a....g.......-....c..a...t.c.....
H.chthamalochoros 6351       ..g.aa........gt.t.gc.-.tt..at-a....g.......-....c......t.c.....
H.chthamalochoros 6352       ..g.aa........gt.t.gc.-.tt..at-a....g.......-....c..a...t.c.....
H.chthamalochoros 8023       ..g.aa........gt.t.gc.-.tt..at-a....g.......-....c..a...t.c.....
H.chydaeostigmata 5560       ..g.ga........at.t.gc.-.t...at-a....g.......-....c......t.c.....
H.chydaeostigmata 8015       ..g.ga........at.t.gc.-.t...at-a....g.......-....c......t.c.....
H.chydaeostigmata 8016       ..g.ga........at.t.gc.-.t...at-a....g.......-....c......t.c.....
H.chydaeostigmata 8019       ..g.ga........at.t.gc.-.t...at-a....g.......-....c......t.c.....
H.chydaeostigmata 8020       ..g.ga........at.t.gc.-.t...at-a....g.......-....c......t.c.....
H.chydaeostigmata 8022       ..g.ga........at.t.gc.-.t...at-a....g.......-....c......t.c.....
H.dechangei 7789             ..g.aa........gt.t.gc.-.ct...t-a...gg.......-....c........c.....
H.euktaenospatha 4340        ..g.aa....g...gt.t.gc.-.ct..a.-a...gg.......-....c......t.c.....
H.glaphyroscytos 6640        ..g.ga........gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.hylaios 6358               ..g.ga........gt.t.gc.-.ct..ac-a....g.......-....c......t.c.....
H.hylaios 6359               ..g.ga........gt.t.gcg-.ct..at-a....g.......-....c......t.c.....
H.hylaios 6363               ..g.ga........gt.t.gc.-.ct..ac-a....g.......-....c......t.c.....
H.ischnoryctes 6639          ..g.ga........gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.kukunyungkal 6341          ..g.ga........gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.kukunyungkal 6342          ..g.ga........gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.kukunyungkal 6343          ..g.ga........gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.laevitropis 6348           ..g.aa........gt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.leptochela 6344            ..g.ga........gt.t.gc.-.tt..at-a....g.......-....c......t.c.....
H.leptochela 6345            ..g.ga........gt.t.gc.-.tt..at-a....g.......-....c......t.c.....
H.litodactylus 5559          ..g.ga........gt.t.gc.-.tt..at-a....g.......-....c......t.c.....
H.macrochela 5555            ..g.ga........gt.t.gc.-.tt..at-a....g.......-....c......t.c.....
H.neocaledonicus 4323        ..g..a........at...g..-.t....t-a...........-...........t.c.....
H.neocaledonicus 5542        ..g..a........at...g..-.t....t-a...........-...........t.c.....
H.neocaledonicus 5543        ..g..a........at...g..-.t....t-a...........-...........t.c.....
H.neocaledonicus 5544        ..g..a........at...ga.-.t....t-a...........-...........t.c.....
H.neocaledonicus 5545        ..g..a........at...g..-.t....t-a...........-...........t.c.....
H.neocaledonicus 5546        ..g..a........at...g..-.t....t-a...........-...........t.c.....
H.neocaledonicus 5547        ..g..a........at...gg.-.t....t-a...........-...........t.c.....
H.neocaledonicus 5548        ..g..a........at...gg.-.t....t-a...........-...........t.c.....
H.neocaledonicus 6224        ..g..a........at...g..-.t....t-a...........-...........t.c.....
H.nyawaygi 6354              ..g.aa....t..cgt.t.gc.-.ct..at-a....g.......-....c......t.c.....
H.papuanus 2718              ..g.aa....t...g....gc.-.ct..ct-a....g.......-....cc.....t.c.....
H.papuanus 2725              ..g.ga...gt...gt...g..-.ct..at-a...gg.......-....c......t.c.....
H.papuanus 2726              ..g.aa........at....c.-.tt..at-a...gg.......-....c......t.c.....
H.papuanus 2727              ..g.aa........at....c.-.tt..at-a...gg.......-....c......t.c.....
H.penta 1817                 ..g.ga........at...g..-.t...at-a...........-...........t.c.....
H.polisorum 1614             ..g.ga........g.......-.tt..gt-a....g.......-....c......t.c.....
H.solomonensis 1818          ..g.ga........g....gc.-.ct..a.-a...gg.......-....c...t..c.c.....
H.solomonensis 1819          ..g.ga........g....gc.-.ct..a.-a...gg.......-....c...t..c.c.....
H.solomonensis 5549          ..g.ga........gt...gc.-.cc..g.-....gg.......-....c......t.c.....
H.solomonensis 5550          ..g.ga........gt...gc.-.ct..a.-a...gg.......-....c......t.c.....
H.solomonensis 5551          ..g.ga........gt...gc.-.ct..a.-a...gg.......-....c......t.c.....
H.solomonensis 5552          ..g.ga........gt....c.-.ct..a.-a...gg.......-....c......t.c.....
H.solomonensis 5554          ..g.ga........gt....c.-.ct..a.-a...gg.......-....c......t.c.....
H.tagulae 3008               ..g.ga....t...g.....c.-.tt..at-....gg.......-....c......t.c.....
H.tjapukai 2184              ..g.ga........gt.t.gc.-.t...at-a....g.......-....c......t.c.....
H.tjapukai 6641              ..g.ga........gt.t.gc.-.t...at-a....g.......-....c......t.c.....
H.tytthognaphos 6346         ..g.ga........at.t.gc.-.tt..at-a...gg.......-....c......t.c.....
H.tytthognaphos 6347         ..g.ga........gt.t.gc.-.tt..at-a...gg.......-....c......t.c.....
H.wallaman 6353              ..g.aa....c...gt...gc.-.ct..gt-a....g.......-....c......t.c.....
H.yelae 3007                 ..g.ga........gt.t.gc.-.ct..at-a....g.......-....c.....tt.c.....
H.sp. WA 8017                ..g.ga........at.t.gc.-.t...at-a....g.......-....c......t.c.....
H.sp. WA 8021                ..g.ga........at.t.gc.-.t...at-a....g.......-....c......t.c.....
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 1–87. Dots indicate a match with the first taxon.

```
C.ochropus 2189              tcatatgcttgtctcaaagattaagccatgcatgtctaagtacaagccgaaataaggtgaaaccgcgaatggctcattaaatcagtt
C.ochropus 6984              ...............................................................................................
C.ochropus 9069              ...............................................................................................
I.nitidus 9827               ...............................................................................................
I.politus 1514               ...............................................................................................
I.politus 3256               ???????????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                ...............................................................................................
O.laevipes 1835              ..................................................a............................................
O.lecomtei 1608              ...............................................................................................
O.lecomtei 2194A             ...............................................................................................
O.madagascariensis 2800      ...............................................................................................
O.madagascariensis 2811      ...............................................................................................
O.madagascariensis 2812      ...............................................................................................
O.piceus 6260                ...............................................................................................
H.infulcra 2185              ..........................................ga.....................................................
L.australasiae 1854          ...............................................................................................
L.australasiae 2181          ...............................................................................................
L.australasiae 2182          ...............................................................................................
L.australasiae 2183          ...............................................................................................
L.australasiae 2729          ...............................................................................................
L.australasiae 2733          ...............................................................................................
L.australasiae 2996          ???????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ...............................................................................................
L.australasiae 4764          ...............................................................................................
L.australasiae 5553          ...............................................................................................
L.australasiae 8676          ...............................................................................................
L.australasiae 8677          ???????????????????????????????????????????????????????????????????????????????????????
L.longimanus 6388            ...............................................................................................
L.malaya 1909                ...............................................................................................
H.aethes 3002                ...............................................................................................
H.aethes 3005                ???????????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ...............................................................................................
H.anekasankylis 6356         ...............................................................................................
H.anekasankylis 6357         ...............................................................................................
H.ankistros 4339             ???????????????????????????????????????????????????????????????????????????????????????
H.bandjin 5556               ...............................................................................................
H.bandjin 5557               ...............................................................................................
H.bandjin 5558               ...............................................................................................
H.caudicula 1502             ...............................................................................................
H.caudicula 2339             ...............................................................................................
H.caudicula 2340             ...............................................................................................
H.caudicula 6360             ...............................................................................................
H.caudicula 6361             ...............................................................................................
H.caudicula 6362             ...............................................................................................
H.chthamalochoros 6350       ...............................................................................................
H.chthamalochoros 6351       ...............................................................................................
H.chthamalochoros 6352       ...............................................................................................
H.chthamalochoros 8023       ...............................................................................................
H.chydaeostigmata 5560       ...............................................................................................
H.chydaeostigmata 8015       ...............................................................................................
H.chydaeostigmata 8016       ...............................................................................................
H.chydaeostigmata 8019       ...............................................................................................
H.chydaeostigmata 8020       ...............................................................................................
H.chydaeostigmata 8022       ...............................................................................................
H.dechangei 7789             ..................................................a............................................
H.euktaenospatha 4340        ...............................................................................................
H.glaphyroscytos 6640        ...............................................................................................
H.hylaios 6358               ...............................................................................................
H.hylaios 6359               ...............................................................................................
H.hylaios 6363               ...............................................................................................
H.ischnoryctes 6639          ...............................................................................................
H.kukunyungkal 6341          ...............................................................................................
H.kukunyungkal 6342          ...............................................................................................
H.kukunyungkal 6343          ...............................................................................................
H.laevitropis 6348            ...............................................................................................
H.leptochela 6344            ...............................................................................................
H.leptochela 6345            ...............................................................................................
H.litodactylus 5559           ...............................................................................................
H.macrochela 5555            ...............................................................................................
H.neocaledonicus 4323        ...............................................................................................
H.neocaledonicus 5542        ...............................................................................................
H.neocaledonicus 5543        ...............................................................................................
H.neocaledonicus 5544        ...............................................................................................
H.neocaledonicus 5545        ...............................................................................................
H.neocaledonicus 5546        ...............................................................................................
H.neocaledonicus 5547        ...............................................................................................
H.neocaledonicus 5548        ...............................................................................................
H.neocaledonicus 6224        ???????????????????????????????????????????????????????????????????????????????????????
H.nyawaygi 6354              ???????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2718              ...............................................................................................
H.papuanus 2725              ????????????????????????????????????????????????????????????????...........................
H.papuanus 2726              ...............................................................................................
H.papuanus 2727              ...............................................................................................
H.penta 1817                 ???????????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ...............................................................................................
H.solomonensis 1818          ...............................................................................................
H.solomonensis 1819          ...............................................................................................
H.solomonensis 5549          ...............................................................................................
H.solomonensis 5550          ...............................................................................................
H.solomonensis 5551          ...............................................................................................
H.solomonensis 5552          ...............................................................................................
H.solomonensis 5554          ...............................................................................................
H.tjapukai 2184              ...............................................................................................
H.tjapukai 6641              ...............................................................................................
H.tytthognaphos 6346         ...............................................................................................
H.tytthognaphos 6347         ...............................................................................................
H.wallaman 6353              ...............................................................................................
H.yelae 3007                 ...............................................................................................
H.sp. WA 8017                ...............................................................................................
H.sp. WA 8021                ...............................................................................................
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 88–174. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              acggttccttagactatacttttttacttggataactgtggtaattctagagctaatacatgcatctgagctccgaccttcggggac
C.ochropus 6984              ....................................................................................
C.ochropus 9069              ....................................................................................
I.nitidus 9827               ....................................................................................
I.politus 1514               ......................cc............................................................
I.politus 3256               ????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                ......................cc............................................................
O.laevipes 1835              ....................................................................................
O.lecomtei 1608              ......................cc............................................................
O.lecomtei 2194A             ......................cc............................................................
O.madagascariensis 2800      ....................................................................................
O.madagascariensis 2811      ....................................................................................
O.madagascariensis 2812      ....................................................................................
O.piceus 6260                ....................................................................................
H.infulcra 2185              ......................cc............................................................
L.australasiae 1854          ......................cc............................................................
L.australasiae 2181          ......................cc............................................................
L.australasiae 2182          ......................cc............................................................
L.australasiae 2183          ......................cc............................................................
L.australasiae 2729          ......................cc............................................................
L.australasiae 2733          ......................cc............................................................
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ......................cc............................................................
L.australasiae 4764          ......................cc............................................................
L.australasiae 5553          ......................cc............................................................
L.australasiae 8676          ......................cc............................................................
L.australasiae 8677          ????????????????????????????????????????????????????????????????????????????????
L.longimanus 6388            ......................cc............................................................
L.malaya 1909                ......................cc............................................................
H.aethes 3002                ......................cc............................................................
H.aethes 3005                ????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ......................cc............................................................
H.anekasankylis 6356         ......................cc............................................................
H.anekasankylis 6357         ......................cc............................................................
H.ankistros 4339             ????????????????????????????????????????????????????????????????????????????????
H.bandjin 5556               ......................cc............................................................
H.bandjin 5557               ......................cc............................................................
H.bandjin 5558               ......................cc............................................................
H.caudicula 1502             ......................cc............................................................
H.caudicula 2339             ......................cc............................................................
H.caudicula 2340             ......................cc............................................................
H.caudicula 6360             ......................cc............................................................
H.caudicula 6361             ......................cc............................................................
H.caudicula 6362             ......................cc............................................................
H.chthamalochoros 6350       ......................cc............................................................
H.chthamalochoros 6351       ......................cc............................................................
H.chthamalochoros 6352       ......................cc............................................................
H.chthamalochoros 8023       ......................cc............................................................
H.chydaeostigmata 5560       ......................cc............................................................
H.chydaeostigmata 8015       ......................cc............................................................
H.chydaeostigmata 8016       ......................cc............................................................
H.chydaeostigmata 8019       ......................cc............................................................
H.chydaeostigmata 8020       ......................cc............................................................
H.chydaeostigmata 8022       ......................cc............................................................
H.dechangei 7789             ......................cc............................................................
H.euktaenospatha 4340        ......................cc............................................................
H.glaphyroscytos 6640        ......................cc............................................................
H.hylaios 6358               ......................cc............................................................
H.hylaios 6359               ......................cc............................................................
H.hylaios 6363               ......................cc............................................................
H.ischnoryctes 6639          ......................cc............................................................
H.kukunyungkal 6341          ......................cc............................................................
H.kukunyungkal 6342          ......................cc............................................................
H.kukunyungkal 6343          ......................cc............................................................
H.laevitropis 6348           ......................cc............................................................
H.leptochela 6344            ......................cc............................................................
H.leptochela 6345            ......................cc............................................................
H.litodactylus 5559           ......................cc............................................................
H.macrochela 5555            ......................cc............................................................
H.neocaledonicus 4323        ......................cc............................................................
H.neocaledonicus 5542        ......................cc............................................................
H.neocaledonicus 5543        ......................cc............................................................
H.neocaledonicus 5544        ......................cc............................................................
H.neocaledonicus 5545        ......................cc............................................................
H.neocaledonicus 5546        ......................cc............................................................
H.neocaledonicus 5547        ......................cc............................................................
H.neocaledonicus 5548        ......................cc............................................................
H.neocaledonicus 6224        ????????????????????????????????????????????????????????????????????????????????
H.nyawaygi 6354              ????????????????????????????????????????????????????????????????????????????????
H.papuanus 2718              ......................cc............................................................
H.papuanus 2725              ......................cc............................................................
H.papuanus 2726              ......................cc............................................................
H.papuanus 2727              ......................cc............................................................
H.penta 1817                 ????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ......................cc............................................................
H.solomonensis 1818          ......................cc............................................................
H.solomonensis 1819          ......................cc............................................................
H.solomonensis 5549          ......................cc............................................................
H.solomonensis 5550          ......................cc............................................................
H.solomonensis 5551          ......................cc............................................................
H.solomonensis 5552          ......................cc............................................................
H.solomonensis 5554          ......................cc............................................................
H.tjapukai 2184              ......................cc............................................................
H.tjapukai 6641              ......................cc............................................................
H.tytthognaphos 6346         ......................cc............................................................
H.tytthognaphos 6347         ......................cc............................................................
H.wallaman 6353              ......................cc............................................................
H.yelae 3007                 ......................cc............................................................
H.sp. WA 8017                ......................cc............................................................
H.sp. WA 8021                ......................cc............................................................
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 175–261. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              gagcgcttttattagaccaagaccaatcggactaaggtccgcaaaacgtggcgactctggataactttgggcggatcgcacggtcta
C.ochropus 6984              ...............................................................................................
C.ochropus 9069              ...............................................................................................
I.nitidus 9827               ...............................................................................................
I.politus 1514               ..................................c............t.....................................................
I.politus 3256               ???????????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                ..................................c............t.....................................................
O.laevipes 1835              ...............................................................................................
O.lecomtei 1608              ..................................c............t.....................c.......................
O.lecomtei 2194A             ..................................c............t.....................................................
O.madagascariensis 2800      ...............................................................................................
O.madagascariensis 2811      ...............................................................................................
O.madagascariensis 2812      ...............................................................................................
O.piceus 6260                ...............................................................................................
H.infulcra 2185              ..................................c.....................................aa..c.....................
L.australasiae 1854          ..................................t.....................................................c.....................
L.australasiae 2181          ..................................t.....................................................c.....................
L.australasiae 2182          ..................................t.....................................................c.....................
L.australasiae 2183          ..................................t.....................................................c.....................
L.australasiae 2729          ..................................t.....................................................c.....................
L.australasiae 2733          ..................................t.....................................................c.....................
L.australasiae 2996          ???????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ..................................t.....................................................c.....................
L.australasiae 4764          ..................................t.....................................................c.....................
L.australasiae 5553          ..................................t.....................................................c.....................
L.australasiae 8676          ..................................t.....................................................c.....................
L.australasiae 8677          ???????????????????????????????????????????????????????????????????????????????????????
L.longimanus 6388            ..................................ctc...................................................c.....................
L.malaya 1909                ..................................t.....................................................c.....................
H.aethes 3002                ..................................t.....................................................c.....................
H.aethes 3005                ???????????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ..................................ct....................................................c.....................
H.anekasankylis 6356         ..................................ct....................................................c.....................
H.anekasankylis 6357         ..................................ct....................................................c.....................
H.ankistros 4339             ???????????????????????????????????????????????????????????????????????????????????????
H.bandjin 5556               ..................................t.....................................................c.....................
H.bandjin 5557               ..................................t.....................................................c.....................
H.bandjin 5558               ..................................t.....................................................c.....................
H.caudicula 1502             ..................................t.....................................................c.....................
H.caudicula 2339             ..................................t.....................................................c.....................
H.caudicula 2340             ..................................t.....................................................c.....................
H.caudicula 6360             ..................................t.....................................................c.....................
H.caudicula 6361             ..................................t.....................................................c.....................
H.caudicula 6362             ..................................t.....................................................c.....................
H.chthamalochoros 6350       ..................................t.....................................................c.....................
H.chthamalochoros 6351       ..................................t.....................................................c.....................
H.chthamalochoros 6352       ..................................t.....................................................c.....................
H.chthamalochoros 8023       ..................................t.....................................................c.....................
H.chydaeostigmata 5560       ..................................t.....................................................c.....................
H.chydaeostigmata 8015       ..................................t.....................................................c.....................
H.chydaeostigmata 8016       ..................................t.....................................................c.....................
H.chydaeostigmata 8019       ..................................t.....................................................c.....................
H.chydaeostigmata 8020       ..................................t.....................................................c.....................
H.chydaeostigmata 8022       ..................................t.....................................................c.....................
H.dechangei 7789             ..................................t.....................................................c.....................
H.euktaenospatha 4340        ..................................t.....................................................c.....................
H.glaphyroscytos 6640        ..................................t.....................................................c.....................
H.hylaios 6358               ..................................t.....................................................c.....................
H.hylaios 6359               ..................................t.....................................................c.....................
H.hylaios 6363               ..................................t.....................................................c.....................
H.ischnoryctes 6639          ..................................t.....................................................c.....................
H.kukunyungkal 6341          ..................................t.....................................................c.....................
H.kukunyungkal 6342          ..................................t.....................................................c.....................
H.kukunyungkal 6343          ..................................t.....................................................c.....................
H.laevitropis 6348           ..................................t.....................................................c.....................
H.leptochela 6344            ..................................t.....................................................c.....................
H.leptochela 6345            ..................................t.....................................................c.....................
H.litodactylus 5559          ..................................t.....................................................c.....................
H.macrochela 5555            ..................................t.....................................................c.....................
H.neocaledonicus 4323        ..................................t.....................................................c.....................
H.neocaledonicus 5542        ..................................t.....................................................c.....................
H.neocaledonicus 5543        ..................................t.....................................................c.....................
H.neocaledonicus 5544        ..................................t.....................................................c.....................
H.neocaledonicus 5545        ..................................t.....................................................c.....................
H.neocaledonicus 5546        ..................................t.....................................................c.....................
H.neocaledonicus 5547        ..................................t.....................................................c.....................
H.neocaledonicus 5548        ..................................t.....................................................c.....................
H.neocaledonicus 6224        ???????????????????????????????????????????????????????????????????????????????????????
H.nyawaygi 6354              ???????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2718              ..................................t.....................................................c.....................
H.papuanus 2725              ..................................t.....................................................c.....................
H.papuanus 2726              ..................................t.....................................................c.....................
H.papuanus 2727              ..................................t.....................................................c.....................
H.penta 1817                 ???????????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ..................................c.....................................................c.....................
H.solomonensis 1818          ..................................t.....................................................c.....................
H.solomonensis 1819          ..................................t.....................................................c.....................
H.solomonensis 5549          ..................................t.....................................................c.....................
H.solomonensis 5550          ..................................t.....................................................c.....................
H.solomonensis 5551          ..................................t.....................................................c.....................
H.solomonensis 5552          ..................................t.....................................................c.....................
H.solomonensis 5554          ..................................t.....................................................c.....................
H.tjapukai 2184              ..................................ct....................................................c.....................
H.tjapukai 6641              ..................................ct....................................................c.....................
H.tytthognaphos 6346         ..................................t.....................................................c.....................
H.tytthognaphos 6347         ..................................t.....................................................c.....................
H.wallaman 6353              ..................................t.....................................................c.....................
H.yelae 3007                 ..................................t.....................................................c.....................
H.sp. WA 8017                ..................................t.....................................................c.....................
H.sp. WA 8021                ..................................t.....................................................c.....................
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 262–348. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              gcaccggcgacgtatctttcaagtgtctgccttatcaactttcgatggtaggttatgcgcctaccatggtcgttacgggtaacgggg
C.ochropus 6984              ................................................................................
C.ochropus 9069              ................................................................................
I.nitidus 9827               ................................................................................
I.politus 1514               ................................................................................
I.politus 3256               ????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                ................................................................................
O.laevipes 1835              ................................................................................
O.lecomtei 1608              ................................................................................
O.lecomtei 2194A             ................................................................................
O.madagascariensis 2800      ................................................................................
O.madagascariensis 2811      ................................................................................
O.madagascariensis 2812      ................................................................................
O.piceus 6260                ................................................................................
H.infulcra 2185              ...............................................................................a.
L.australasiae 1854          ...............................................................................a.
L.australasiae 2181          ...............................................................................a.
L.australasiae 2182          ...............................................................................a.
L.australasiae 2183          ...............................................................................a.
L.australasiae 2729          ...............................................................................a.
L.australasiae 2733          ...............................................................................a.
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ...............................................................................a.
L.australasiae 4764          ...............................................................................a.
L.australasiae 5553          ...............................................................................a.
L.australasiae 8676          ...............................................................................a.
L.australasiae 8677          ????????????????????????????????????????????????????????????????????????????????
L.longimanus 6388            ...............................................................................a.
L.malaya 1909                ...............................................................................a.
H.aethes 3002                ...............................................................................a.
H.aethes 3005                ????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ...............................................................................a.
H.anekasankylis 6356         ...............................................................................a.
H.anekasankylis 6357         ...............................................................................a.
H.ankistros 4339             ????????????????????????????????????????????????????????????????????????????????
H.bandjin 5556               ...............................................................................a.
H.bandjin 5557               ...............................................................................a.
H.bandjin 5558               ...............................................................................a.
H.caudicula 1502             ...............................................................................a.
H.caudicula 2339             ...............................................................................a.
H.caudicula 2340             ...............................................................................a.
H.caudicula 6360             ...............................................................................a.
H.caudicula 6361             ...............................................................................a.
H.caudicula 6362             ...............................................................................a.
H.chthamalochoros 6350       ...............................................................................a.
H.chthamalochoros 6351       ...............................................................................a.
H.chthamalochoros 6352       ...............................................................................a.
H.chthamalochoros 8023       ...............................................................................a.
H.chydaeostigmata 5560       ...............................................................................a.
H.chydaeostigmata 8015       ...............................................................................a.
H.chydaeostigmata 8016       ...............................................................................a.
H.chydaeostigmata 8019       ...............................................................................a.
H.chydaeostigmata 8020       ...............................................................................a.
H.chydaeostigmata 8022       ...............................................................................a.
H.dechangei 7789             ...............................................................................a.
H.euktaenospatha 4340        ...............................................................................a.
H.glaphyroscytos 6640        ...............................................................................a.
H.hylaios 6358               ...............................................................................a.
H.hylaios 6359               ...............................................................................a.
H.hylaios 6363               ...............................................................................a.
H.ischnoryctes 6639          ...............................................................................a.
H.kukunyungkal 6341          ...............................................................................a.
H.kukunyungkal 6342          ...............................................................................a.
H.kukunyungkal 6343          ...............................................................................a.
H.laevitropis 6348           ...............................................................................a.
H.leptochela 6344            ...............................................................................a.
H.leptochela 6345            ...............................................................................a.
H.litodactylus 5559           ...............................................................................a.
H.macrochela 5555            ...............................................................................a.
H.neocaledonicus 4323        ...............................................................................a.
H.neocaledonicus 5542        ...............................................................................a.
H.neocaledonicus 5543        ...............................................................................a.
H.neocaledonicus 5544        ...............................................................................a.
H.neocaledonicus 5545        ...............................................................................a.
H.neocaledonicus 5546        ...............................................................................a.
H.neocaledonicus 5547        ...............................................................................a.
H.neocaledonicus 5548        ...............................................................................a.
H.neocaledonicus 6224        ????????????????????????????????????????????????????????????????????????????????
H.nyawaygi 6354              ????????????????????????????????????????????????????????????????????????????????
H.papuanus 2718              ...............................................................................a.
H.papuanus 2725              ...............................................................................a.
H.papuanus 2726              ...............................................................................a.
H.papuanus 2727              ...............................................................................a.
H.penta 1817                 ????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ...............................................................................a.
H.solomonensis 1818          ...............................................................................a.
H.solomonensis 1819          ...............................................................................a.
H.solomonensis 5549          ...............................................................................a.
H.solomonensis 5550          ...............................................................................a.
H.solomonensis 5551          ...............................................................................a.
H.solomonensis 5552          ...............................................................................a.
H.solomonensis 5554          ...............................................................................a.
H.tjapukai 2184              ...............................................................................a.
H.tjapukai 6641              ...............................................................................a.
H.tytthognaphos 6346         ...............................................................................a.
H.tytthognaphos 6347         ...............................................................................a.
H.wallaman 6353              ...............................................................................a.
H.yelae 3007                 ...............................................................................a.
H.sp. WA 8017                ...............................................................................a.
H.sp. WA 8021                ...............................................................................a.
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 349–435. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              aatcagggttcgattccggagagggagcctgagaaacggctaccacatccaaggaaggcagcaggcgcgcaaattacccactcccgg
C.ochropus 6984              ...............................................................................................
C.ochropus 9069              ...............................................................................................
I.nitidus 9827               ...............................................................................................
I.politus 1514               ...............................................................................................
I.politus 3256               ?????..........................................................................................
O.elatus 1837                ...............................................................................................
O.laevipes 1835              ...............................................................................................
O.lecomtei 1608              ...............................................................................................
O.lecomtei 2194A             ...............................................................................................
O.madagascariensis 2800      ...............................................................................................
O.madagascariensis 2811      ...............................................................................................
O.madagascariensis 2812      ...............................................................................................
O.piceus 6260                ...............................................................................................
H.infulcra 2185              ...............................................................................................
L.australasiae 1854          ...............................................................................................
L.australasiae 2181          ...............................................................................................
L.australasiae 2182          ...............................................................................................
L.australasiae 2183          ...............................................................................................
L.australasiae 2729          ...............................................................................................
L.australasiae 2733          ...............................................................................................
L.australasiae 2996          ???????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ...............................................................................................
L.australasiae 4764          ...............................................................................................
L.australasiae 5553          ...............................................................................................
L.australasiae 8676          ...............................................................................................
L.australasiae 8677          ????????????????...............................................................................
L.longimanus 6388            ...............................................................................................
L.malaya 1909                ...............................................................................................
H.aethes 3002                ...............................................................................................
H.aethes 3005                ???????????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ...............................................................................................
H.anekasankylis 6356         ...............................................................................................
H.anekasankylis 6357         ...............................................................................................
H.ankistros 4339             ???????........................................................................................
H.bandjin 5556               ...............................................................................................
H.bandjin 5557               ...............................................................................................
H.bandjin 5558               ...............................................................................................
H.caudicula 1502             ...............................................................................................
H.caudicula 2339             ...............................................................................................
H.caudicula 2340             ...............................................................................................
H.caudicula 6360             ...............................................................................................
H.caudicula 6361             ...............................................................................................
H.caudicula 6362             ...............................................................................................
H.chthamalochoros 6350       ...............................................................................................
H.chthamalochoros 6351       ...............................................................................................
H.chthamalochoros 6352       ...............................................................................................
H.chthamalochoros 8023       ...............................................................................................
H.chydaeostigmata 5560       ...............................................................................................
H.chydaeostigmata 8015       ...............................................................................................
H.chydaeostigmata 8016       ...............................................................................................
H.chydaeostigmata 8019       ...............................................................................................
H.chydaeostigmata 8020       ...............................................................................................
H.chydaeostigmata 8022       ...............................................................................................
H.dechangei 7789             ...............................................................................................
H.euktaenospatha 4340        ...............................................................................................
H.glaphyroscytos 6640        ...............................................................................................
H.hylaios 6358               ...............................................................................................
H.hylaios 6359               ...............................................................................................
H.hylaios 6363               ...............................................................................................
H.ischnoryctes 6639          ...............................................................................................
H.kukunyungkal 6341          ...............................................................................................
H.kukunyungkal 6342          ...............................................................................................
H.kukunyungkal 6343          ...............................................................................................
H.laevitropis 6348            ...............................................................................................
H.leptochela 6344            ...............................................................................................
H.leptochela 6345            ...............................................................................................
H.litodactylus 5559           ...............................................................................................
H.macrochela 5555            ...............................................................................................
H.neocaledonicus 4323        ...............................................................................................
H.neocaledonicus 5542        ...............................................................................................
H.neocaledonicus 5543        ...............................................................................................
H.neocaledonicus 5544        ...............................................................................................
H.neocaledonicus 5545        ...............................................................................................
H.neocaledonicus 5546        ...............................................................................................
H.neocaledonicus 5547        ...............................................................................................
H.neocaledonicus 5548        ...............................................................................................
H.neocaledonicus 6224        ???????????????????????????????????????????????????????????????????????????????????....
H.nyawaygi 6354              ??????.........................................................................................
H.papuanus 2718              ...............................................................................................
H.papuanus 2725              ...............................................................................................
H.papuanus 2726              ...............................................................................................
H.papuanus 2727              ...............................................................................................
H.penta 1817                 ???????????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ...............................................................................................
H.solomonensis 1818          ...............................................................................................
H.solomonensis 1819          ...............................................................................................
H.solomonensis 5549          ...............................................................................................
H.solomonensis 5550          ...............................................................................................
H.solomonensis 5551          ...............................................................................................
H.solomonensis 5552          ...............................................................................................
H.solomonensis 5554          ...............................................................................................
H.tjapukai 2184              ...............................................................................................
H.tjapukai 6641              ...............................................................................................
H.tytthognaphos 6346         ...............................................................................................
H.tytthognaphos 6347         ...............................................................................................
H.wallaman 6353              ...............................................................................................
H.yelae 3007                 ...............................................................................................
H.sp. WA 8017                ...............................................................................................
H.sp. WA 8021                ...............................................................................................
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2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 436–522. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              cacggggaggtagtgacgaaaaataacaatacgggactctattgaggccccgtaattggaatgggtacactctaaaccctttaacga
C.ochropus 6984              ................................................................................
C.ochropus 9069              ................................................................................
I.nitidus 9827               ...............................................................c................
I.politus 1514               ................................................................................
I.politus 3256               ................................................................................
O.elatus 1837                ................................................................................
O.laevipes 1835              ................................................................................
O.lecomtei 1608              ................................................................................
O.lecomtei 2194A             ................................................................................
O.madagascariensis 2800      ................................................................................
O.madagascariensis 2811      ................................................................................
O.madagascariensis 2812      ................................................................................
O.piceus 6260                ................................................................................
H.infulcra 2185              ................................................................................
L.australasiae 1854          ................................................................................
L.australasiae 2181          ................................................................................
L.australasiae 2182          ................................................................................
L.australasiae 2183          ................................................................................
L.australasiae 2729          ................................................................................
L.australasiae 2733          ................................................................................
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ................................................................................
L.australasiae 4764          ................................................................................
L.australasiae 5553          ................................................................................
L.australasiae 8676          ................................................................................
L.australasiae 8677          ................................................................................
L.longimanus 6388            ................................................................................
L.malaya 1909                ................................................................................
H.aethes 3002                ................................................................................
H.aethes 3005                ????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ................................................................................
H.anekasankylis 6356         ................................................................................
H.anekasankylis 6357         ................................................................................
H.ankistros 4339             ................................................................................
H.bandjin 5556               ................................................................................
H.bandjin 5557               ................................................................................
H.bandjin 5558               ................................................................................
H.caudicula 1502             ................................................................................
H.caudicula 2339             ................................................................................
H.caudicula 2340             ................................................................................
H.caudicula 6360             ................................................................................
H.caudicula 6361             ................................................................................
H.caudicula 6362             ................................................................................
H.chthamalochoros 6350       ................................................................................
H.chthamalochoros 6351       ................................................................................
H.chthamalochoros 6352       ................................................................................
H.chthamalochoros 8023       ................................................................................
H.chydaeostigmata 5560       ................................................................................
H.chydaeostigmata 8015       ................................................................................
H.chydaeostigmata 8016       ................................................................................
H.chydaeostigmata 8019       ................................................................................
H.chydaeostigmata 8020       ................................................................................
H.chydaeostigmata 8022       ................................................................................
H.dechangei 7789             ................................................................................
H.euktaenospatha 4340        ................................................................................
H.glaphyroscytos 6640        ................................................................................
H.hylaios 6358               ................................................................................
H.hylaios 6359               ................................................................................
H.hylaios 6363               ................................................................................
H.ischnoryctes 6639          ................................................................................
H.kukunyungkal 6341          ................................................................................
H.kukunyungkal 6342          ................................................................................
H.kukunyungkal 6343          ................................................................................
H.laevitropis 6348            ................................................................................
H.leptochela 6344            ................................................................................
H.leptochela 6345            ................................................................................
H.litodactylus 5559           ................................................................................
H.macrochela 5555            ................................................................................
H.neocaledonicus 4323        ................................................................................
H.neocaledonicus 5542        ................................................................................
H.neocaledonicus 5543        ................................................................................
H.neocaledonicus 5544        ................................................................................
H.neocaledonicus 5545        ................................................................................
H.neocaledonicus 5546        ................................................................................
H.neocaledonicus 5547        ................................................................................
H.neocaledonicus 5548        ................................................................................
H.neocaledonicus 6224        ................................................................................
H.nyawaygi 6354              ................................................................................
H.papuanus 2718              ................................................................................
H.papuanus 2725              ................................................................................
H.papuanus 2726              ................................................................................
H.papuanus 2727              ................................................................................
H.penta 1817                 ????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ................................................................................
H.solomonensis 1818          ................................................................................
H.solomonensis 1819          ................................................................................
H.solomonensis 5549          ................................................................................
H.solomonensis 5550          ................................................................................
H.solomonensis 5551          ................................................................................
H.solomonensis 5552          ................................................................................
H.solomonensis 5554          ................................................................................
H.tjapukai 2184              ................................................................................
H.tjapukai 6641              ................................................................................
H.tytthognaphos 6346         ................................................................................
H.tytthognaphos 6347         ................................................................................
H.wallaman 6353              ................................................................................
H.yelae 3007                 ................................................................................
H.sp. WA 8017                ................................................................................
H.sp. WA 8021                ................................................................................
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2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 523–609. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              ggatctattggagggcaagtctggtgccagcagccgcggtaattccagctccaatagcgtatattaaagttgttgcggttaaaaagc
C.ochropus 6984              ..............................................................................................
C.ochropus 9069              ..............................................................................................
I.nitidus 9827               ..............................................................................................
I.politus 1514               ..............................................................................................
I.politus 3256               ..............................................................................................
O.elatus 1837                ..............................................................................................
O.laevipes 1835              ..............................................................................................
O.lecomtei 1608              ..............................................................................................
O.lecomtei 2194A             ..............................................................................................
O.madagascariensis 2800      ..............................................................................................
O.madagascariensis 2811      ..............................................................................................
O.madagascariensis 2812      ..............................................................................................
O.piceus 6260                ..............................................................................................
H.infulcra 2185              ..............................................................................................
L.australasiae 1854          ..............................................................................................
L.australasiae 2181          ..............................................................................................
L.australasiae 2182          ..............................................................................................
L.australasiae 2183          ..............................................................................................
L.australasiae 2729          ..............................................................................................
L.australasiae 2733          ..............................................................................................
L.australasiae 2996          ??????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ..............................................................................................
L.australasiae 4764          ..............................................................................................
L.australasiae 5553          ..............................................................................................
L.australasiae 8676          ..............................................................................................
L.australasiae 8677          ..............................................................................................
L.longimanus 6388            ..............................................................................................
L.malaya 1909                ..............................................................................................
H.aethes 3002                ..............................................................................................
H.aethes 3005                ??????????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ..............................................................................................
H.anekasankylis 6356         ..............................................................................................
H.anekasankylis 6357         ..............................................................................................
H.ankistros 4339             ..............................................................................................
H.bandjin 5556               ..............................................................................................
H.bandjin 5557               ..............................................................................................
H.bandjin 5558               ..............................................................................................
H.caudicula 1502             ..............................................................................................
H.caudicula 2339             ..............................................................................................
H.caudicula 2340             ..............................................................................................
H.caudicula 6360             ..............................................................................................
H.caudicula 6361             ..............................................................................................
H.caudicula 6362             ..............................................................................................
H.chthamalochoros 6350       ..............................................................................................
H.chthamalochoros 6351       ..............................................................................................
H.chthamalochoros 6352       ..............................................................................................
H.chthamalochoros 8023       ..............................................................................................
H.chydaeostigmata 5560       ..............................................................................................
H.chydaeostigmata 8015       ..............................................................................................
H.chydaeostigmata 8016       ..............................................................................................
H.chydaeostigmata 8019       ..............................................................................................
H.chydaeostigmata 8020       ..............................................................................................
H.chydaeostigmata 8022       ..............................................................................................
H.dechangei 7789             ..............................................................................................
H.euktaenospatha 4340        ..............................................................................................
H.glaphyroscytos 6640        ..............................................................................................
H.hylaios 6358               ..............................................................................................
H.hylaios 6359               ..............................................................................................
H.hylaios 6363               ..............................................................................................
H.ischnoryctes 6639          ..............................................................................................
H.kukunyungkal 6341          ..............................................................................................
H.kukunyungkal 6342          ..............................................................................................
H.kukunyungkal 6343          ..............................................................................................
H.laevitropis 6348            ..............................................................................................
H.leptochela 6344            ..............................................................................................
H.leptochela 6345            ..............................................................................................
H.litodactylus 5559           ..............................................................................................
H.macrochela 5555            ..............................................................................................
H.neocaledonicus 4323        ..............................................................................................
H.neocaledonicus 5542        ..............................................................................................
H.neocaledonicus 5543        ..............................................................................................
H.neocaledonicus 5544        ..............................................................................................
H.neocaledonicus 5545        ..............................................................................................
H.neocaledonicus 5546        ..............................................................................................
H.neocaledonicus 5547        ..............................................................................................
H.neocaledonicus 5548        ..............................................................................................
H.neocaledonicus 6224        ..............................................................................................
H.nyawaygi 6354              ..............................................................................................
H.papuanus 2718              ..............................................................................................
H.papuanus 2725              ..............................................................................................
H.papuanus 2726              ..............................................................................................
H.papuanus 2727              ..............................................................................................
H.penta 1817                 ??????????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ..............................................................................................
H.solomonensis 1818          ..............................................................................................
H.solomonensis 1819          ..............................................................................................
H.solomonensis 5549          ..............................................................................................
H.solomonensis 5550          ..............................................................................................
H.solomonensis 5551          ..............................................................................................
H.solomonensis 5552          ..............................................................................................
H.solomonensis 5554          ..............................................................................................
H.tjapukai 2184              ..............................................................................................
H.tjapukai 6641              ..............................................................................................
H.tytthognaphos 6346         ..............................................................................................
H.tytthognaphos 6347         ..............................................................................................
H.wallaman 6353              ..............................................................................................
H.yelae 3007                 ..............................................................................................
H.sp. WA 8017                ..............................................................................................
H.sp. WA 8021                ..............................................................................................
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2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 610–696. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              tcgtagttggatctcggttccggactgtcggtccgccgacaggcggttactggcaggaccggacgtctagccggcctccctcggtgc
C.ochropus 6984              ..............................................................................................
C.ochropus 9069              ..............................................................................................
I.nitidus 9827               ..............................................................................................
I.politus 1514               ..................................................t...........................................
I.politus 3256               ..................................................t...........................................
O.elatus 1837                ..................................................t...........................................
O.laevipes 1835              ..............................................................................................
O.lecomtei 1608              ..................................................t...........................................
O.lecomtei 2194A             ..................................................t...........................................
O.madagascariensis 2800      ..............................................................................................
O.madagascariensis 2811      ..............................................................................................
O.madagascariensis 2812      ..............................................................................................
O.piceus 6260                ..............................................................................................
H.infulcra 2185              ............................t.................................................................
L.australasiae 1854          ..............................................................................................
L.australasiae 2181          ..............................................................................................
L.australasiae 2182          ..............................................................................................
L.australasiae 2183          ..............................................................................................
L.australasiae 2729          ..............................................................................................
L.australasiae 2733          ..............................................................................................
L.australasiae 2996          ??????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ..............................................................................................
L.australasiae 4764          ..............................................................................................
L.australasiae 5553          ..............................................................................................
L.australasiae 8676          ..............................................................................................
L.australasiae 8677          ..............................................................................................
L.longimanus 6388            ..............................................................................................
L.malaya 1909                ..............................................................................................
H.aethes 3002                ..............................................................................................
H.aethes 3005                ??????????????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ..............................................................................................
H.anekasankylis 6356         ..............................................................................................
H.anekasankylis 6357         ..............................................................................................
H.ankistros 4339             ..............................................................................................
H.bandjin 5556               ..............................................................................................
H.bandjin 5557               ..............................................................................................
H.bandjin 5558               ..............................................................................................
H.caudicula 1502             ..............................................................................................
H.caudicula 2339             ..............................................................................................
H.caudicula 2340             ..............................................................................................
H.caudicula 6360             ..............................................................................................
H.caudicula 6361             ..............................................................................................
H.caudicula 6362             ..............................................................................................
H.chthamalochoros 6350       ..............................................................................................
H.chthamalochoros 6351       ..............................................................................................
H.chthamalochoros 6352       ..............................................................................................
H.chthamalochoros 8023       ..............................................................................................
H.chydaeostigmata 5560       ..............................................................................................
H.chydaeostigmata 8015       ..............................................................................................
H.chydaeostigmata 8016       ..............................................................................................
H.chydaeostigmata 8019       ..............................................................................................
H.chydaeostigmata 8020       ..............................................................................................
H.chydaeostigmata 8022       ..............................................................................................
H.dechangei 7789             ..............................................................................................
H.euktaenospatha 4340        ..............................................................................................
H.glaphyroscytos 6640        ..............................................................................................
H.hylaios 6358               ..............................................................................................
H.hylaios 6359               ..............................................................................................
H.hylaios 6363               ..............................................................................................
H.ischnoryctes 6639          ..............................................................................................
H.kukunyungkal 6341          ..............................................................................................
H.kukunyungkal 6342          ..............................................................................................
H.kukunyungkal 6343          ..............................................................................................
H.laevitropis 6348            ..............................................................................................
H.leptochela 6344            ..............................................................................................
H.leptochela 6345            ..............................................................................................
H.litodactylus 5559           ..............................................................................................
H.macrochela 5555            ..............................................................................................
H.neocaledonicus 4323        ..............................................................................................
H.neocaledonicus 5542        ..............................................................................................
H.neocaledonicus 5543        ..............................................................................................
H.neocaledonicus 5544        ..............................................................................................
H.neocaledonicus 5545        ..............................................................................................
H.neocaledonicus 5546        ..............................................................................................
H.neocaledonicus 5547        ..............................................................................................
H.neocaledonicus 5548        ..............................................................................................
H.neocaledonicus 6224        ..............................................................................................
H.nyawaygi 6354              ..............................................................................................
H.papuanus 2718              ..............................................................................................
H.papuanus 2725              ..............................................................................................
H.papuanus 2726              ..............................................................................................
H.papuanus 2727              ..............................................................................................
H.penta 1817                 ??????????????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ..............................................................................................
H.solomonensis 1818          ..............................................................................................
H.solomonensis 1819          ..............................................................................................
H.solomonensis 5549          ..............................................................................................
H.solomonensis 5550          ..............................................................................................
H.solomonensis 5551          ..............................................................................................
H.solomonensis 5552          ..............................................................................................
H.solomonensis 5554          ..............................................................................................
H.tjapukai 2184              ..............................................................................................
H.tjapukai 6641              ..............................................................................................
H.tytthognaphos 6346         ..............................................................................................
H.tytthognaphos 6347         ..............................................................................................
H.wallaman 6353              ..............................................................................................
H.yelae 3007                 ..............................................................................................
H.sp. WA 8017                ..............................................................................................
H.sp. WA 8021                ..............................................................................................
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2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 697–783. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              tcttcaccgggtgtcttgggtgtccggcacgtttactttgaaaaaattagagtgctcaaagcaggcgacctgcctgaataatggtgc
C.ochropus 6984              ..............................................................................................
C.ochropus 9069              ..............................................................................................
I.nitidus 9827               ..............................................................................................
I.politus 1514               ..............................................c...............................................
I.politus 3256               ..............................................c...............................................
O.elatus 1837                ....t.........................................c...............................................
O.laevipes 1835              ....t.........................................................................................
O.lecomtei 1608              ..............................................c...............................................
O.lecomtei 2194A             ..............................................c...............................................
O.madagascariensis 2800      ..............................................................................................
O.madagascariensis 2811      ..............................................................................................
O.madagascariensis 2812      ..............................................................................................
O.piceus 6260                ..............................................................................................
H.infulcra 2185              ..............................................g..c...............................
L.australasiae 1854          ..............................................g...............................................
L.australasiae 2181          ..............................................g...............................................
L.australasiae 2182          ..............................................g...............................................
L.australasiae 2183          ..............................................g...............................................
L.australasiae 2729          ..............................................g...............................................
L.australasiae 2733          ..............................................g...............................................
L.australasiae 2996          ??????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ..............................................g...............................................
L.australasiae 4764          ..............................................g...............................................
L.australasiae 5553          ..............................................g...............................................
L.australasiae 8676          ..............................................g...............................................
L.australasiae 8677          ..............................................g...............................................
L.longimanus 6388            ..............................................g...............................................
L.malaya 1909                ..............................................gt..............................................
H.aethes 3002                ..............................................gt..............................................
H.aethes 3005                ??????????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ..............................................gt..............................................
H.anekasankylis 6356         ..............................................gt..............................................
H.anekasankylis 6357         ..............................................gt..............................................
H.ankistros 4339             ..............................................gt..............................................
H.bandjin 5556               ..............................................gt..............................................
H.bandjin 5557               ..............................................gt..............................................
H.bandjin 5558               ..............................................gt..............................................
H.caudicula 1502             ..............................................gt..............................................
H.caudicula 2339             ..............................................gt..............................................
H.caudicula 2340             ..............................................gt..............................................
H.caudicula 6360             ..............................................gt..............................................
H.caudicula 6361             ..............................................gt..............................................
H.caudicula 6362             ..............................................gt..............................................
H.chthamalochoros 6350       ..............................................gt..............................................
H.chthamalochoros 6351       ..............................................gt..............................................
H.chthamalochoros 6352       ..............................................gt..............................................
H.chthamalochoros 8023       ..............................................gt..............................................
H.chydaeostigmata 5560       ..............................................gt..............................................
H.chydaeostigmata 8015       ..............................................gt..............................................
H.chydaeostigmata 8016       ..............................................gt..............................................
H.chydaeostigmata 8019       ..............................................gt..............................................
H.chydaeostigmata 8020       ..............................................gt..............................................
H.chydaeostigmata 8022       ..............................................gt..............................................
H.dechangei 7789             ..............................................gt..............................................
H.euktaenospatha 4340        ..............................................agt.............................................
H.glaphyroscytos 6640        ..............................................gt..............................................
H.hylaios 6358               ..............................................gt..............................................
H.hylaios 6359               ..............................................gt..............................................
H.hylaios 6363               ..............................................gt..............................................
H.ischnoryctes 6639          ..............................................gt..............................................
H.kukunyungkal 6341          ..............................................gt..............................................
H.kukunyungkal 6342          ..............................................gt..............................................
H.kukunyungkal 6343          ..............................................gt..............................................
H.laevitropis 6348           ..............................................gt..............................................
H.leptochela 6344            ..............................................gt..............................................
H.leptochela 6345            ..............................................gt..............................................
H.litodactylus 5559          ..............................................gt..............................................
H.macrochela 5555            ..............................................gt..............................................
H.neocaledonicus 4323        ..............................................gt..............................................
H.neocaledonicus 5542        ..............................................gt..............................................
H.neocaledonicus 5543        ..............................................gt..............................................
H.neocaledonicus 5544        ..............................................gt..............................................
H.neocaledonicus 5545        ..............................................gt..............................................
H.neocaledonicus 5546        ..............................................gt..............................................
H.neocaledonicus 5547        ..............................................gt..............................................
H.neocaledonicus 5548        ..............................................gt..............................................
H.neocaledonicus 6224        ..............................................gt..............................................
H.nyawaygi 6354              ..............................................gt..............................................
H.papuanus 2718              ..............................................gt..............................................
H.papuanus 2725              ..............................................gt..............................................
H.papuanus 2726              ..............................................gt..............................................
H.papuanus 2727              ..............................................gt..............................................
H.penta 1817                 ??????????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ..............................................gt..............................................
H.solomonensis 1818          ..............................................agt.............................................
H.solomonensis 1819          ..............................................agt.............................................
H.solomonensis 5549          ..............................................agt.............................................
H.solomonensis 5550          ..............................................agt.............................................
H.solomonensis 5551          ..............................................agt.............................................
H.solomonensis 5552          ..............................................agt.............................................
H.solomonensis 5554          ..............................................agt.............................................
H.tjapukai 2184              ..............................................gt..............................................
H.tjapukai 6641              ..............................................gt..............................................
H.tytthognaphos 6346         ..............................................gt..............................................
H.tytthognaphos 6347         ..............................................gt..............................................
H.wallaman 6353              ..............................................gt..............................................
H.yelae 3007                 ..............................................gt..............................................
H.sp. WA 8017                ..............................................gt..............................................
H.sp. WA 8021                ..............................................gt..............................................
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2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 784–870. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              atggaataatggaataggacctcggttctattttgttggttttcggaacacgaggaaatgattaagagggacagacgggggcattcg
C.ochropus 6984              ...............................................................................................
C.ochropus 9069              ...............................................................................................
I.nitidus 9827               ...............................................................................................
I.politus 1514               ...............................................................................................
I.politus 3256               ...............................................................................................
O.elatus 1837                ...............................................................................................
O.laevipes 1835              ...............................................................................................
O.lecomtei 1608              ...............................................................................................
O.lecomtei 2194A             ...............................................................................................
O.madagascariensis 2800      ...............................................................................................
O.madagascariensis 2811      ...............................................................................................
O.madagascariensis 2812      ...............................................................................................
O.piceus 6260                ...............................................................................................
H.infulcra 2185              ...............................................................................................
L.australasiae 1854          ...............................................................................................
L.australasiae 2181          ...............................................................................................
L.australasiae 2182          ...............................................................................................
L.australasiae 2183          ...............................................................................................
L.australasiae 2729          ...............................................................................................
L.australasiae 2733          ...............................................................................................
L.australasiae 2996          ???????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ...............................................................................................
L.australasiae 4764          ...............................................................................................
L.australasiae 5553          ...............................................................................................
L.australasiae 8676          ...............................................................................................
L.australasiae 8677          ...............................................................................................
L.longimanus 6388            ...............................................................................................
L.malaya 1909                ...............................................................................................
H.aethes 3002                ...............................................................................................
H.aethes 3005                ???????????????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ......................t........................................................................
H.anekasankylis 6356         ......................t........................................................................
H.anekasankylis 6357         ......................t........................................................................
H.ankistros 4339             ......................t........................................................................
H.bandjin 5556               ......................t........................................................................
H.bandjin 5557               ......................t........................................................................
H.bandjin 5558               ......................t........................................................................
H.caudicula 1502             ......................t........................................................................
H.caudicula 2339             ...............................................................................................
H.caudicula 2340             ...............................................................................................
H.caudicula 6360             ......................t........................................................................
H.caudicula 6361             ......................t........................................................................
H.caudicula 6362             ......................t........................................................................
H.chthamalochoros 6350       ......................t........................................................................
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H.chthamalochoros 6352       ......................t........................................................................
H.chthamalochoros 8023       ......................t........................................................................
H.chydaeostigmata 5560       ......................t........................................................................
H.chydaeostigmata 8015       ......................t........................................................................
H.chydaeostigmata 8016       ......................t........................................................................
H.chydaeostigmata 8019       ......................t........................................................................
H.chydaeostigmata 8020       ......................t........................................................................
H.chydaeostigmata 8022       ......................t........................................................................
H.dechangei 7789             ......................t........................................................................
H.euktaenospatha 4340        ......................t........................................................................
H.glaphyroscytos 6640        ...............................................................................................
H.hylaios 6358               ...............................................................................................
H.hylaios 6359               ...............................................................................................
H.hylaios 6363               ...............................................................................................
H.ischnoryctes 6639          ...............................................................................................
H.kukunyungkal 6341          ...............................................................................................
H.kukunyungkal 6342          ...............................................................................................
H.kukunyungkal 6343          ........................a......................................................................
H.laevitropis 6348           ...............................................................................................
H.leptochela 6344            ...............................................................................................
H.leptochela 6345            ...............................................................................................
H.litodactylus 5559           ...............................................................................................
H.macrochela 5555            ...............................................................................................
H.neocaledonicus 4323        ...............................................................................................
H.neocaledonicus 5542        ...............................................................................................
H.neocaledonicus 5543        ...............................................................................................
H.neocaledonicus 5544        ...............................................................................................
H.neocaledonicus 5545        ...............................................................................................
H.neocaledonicus 5546        ...............................................................................................
H.neocaledonicus 5547        ...............................................................................................
H.neocaledonicus 5548        ...............................................................................................
H.neocaledonicus 6224        ...............................................................................................
H.nyawaygi 6354              ...............................................................................................
H.papuanus 2718              ...............................................................................................
H.papuanus 2725              ......................t........................................................................
H.papuanus 2726              ......................t........................................................................
H.papuanus 2727              ......................t........................................................................
H.penta 1817                 ???????????????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ...............................................................................................
H.solomonensis 1818          ......................t........................................................................
H.solomonensis 1819          ......................t........................................................................
H.solomonensis 5549          ......................t........................................................................
H.solomonensis 5550          ......................t........................................................................
H.solomonensis 5551          ......................t........................................................................
H.solomonensis 5552          ......................t........................................................................
H.solomonensis 5554          ......................t........................................................................
H.tjapukai 2184              ...............................................................................................
H.tjapukai 6641              ...............................................................................................
H.tytthognaphos 6346         ...............................................................................................
H.tytthognaphos 6347         ...............................................................................................
H.wallaman 6353              ......................t........................................................................
H.yelae 3007                 ......................t........................................................................
H.sp. WA 8017                ......................t........................................................................
H.sp. WA 8021                ......................t........................................................................
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2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 871–957. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              tattgcgacgctagaggtgaaattcttggaccgtcgcaagacgaactactgcgaaagcatttgccaagaatgttttcattaatcaag
C.ochropus 6984              ................................................................................................
C.ochropus 9069              ................................................................................................
I.nitidus 9827               ................................................................................................
I.politus 1514               ................................................................................................
I.politus 3256               ................................................................................................
O.elatus 1837                ................................................................................................
O.laevipes 1835              ................................................................................................
O.lecomtei 1608              ................................................................................................
O.lecomtei 2194A             ................................................................................................
O.madagascariensis 2800      ................................................................................................
O.madagascariensis 2811      ................................................................................................
O.madagascariensis 2812      ................................................................................................
O.piceus 6260                ................................................................................................
H.infulcra 2185              ................................................................................................
L.australasiae 1854          ................................................................................................
L.australasiae 2181          ................................................................................................
L.australasiae 2182          ................................................................................................
L.australasiae 2183          ................................................................................................
L.australasiae 2729          ................................................................................................
L.australasiae 2733          ................................................................................................
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ...????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 4764          ................................................................................................
L.australasiae 5553          ................................................................................................
L.australasiae 8676          ................................................................................................
L.australasiae 8677          ................................................................................................
L.longimanus 6388            ................................................................................................
L.malaya 1909                ................................................................................................
H.aethes 3002                ................................................................................................
H.aethes 3005                ????????????????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ................................................................................................
H.anekasankylis 6356         ................................................................................................
H.anekasankylis 6357         ................................................................................................
H.ankistros 4339             ................................................................................................
H.bandjin 5556               ................................................................................................
H.bandjin 5557               ................................................................................................
H.bandjin 5558               ................................................................................................
H.caudicula 1502             .......???????.................................................................................
H.caudicula 2339             ................................................................................................
H.caudicula 2340             ................................................................................................
H.caudicula 6360             ................................................................................................
H.caudicula 6361             ................................................................................................
H.caudicula 6362             ................................................................................................
H.chthamalochoros 6350       ................................................................................................
H.chthamalochoros 6351       ................................................................................................
H.chthamalochoros 6352       ................................................................................................
H.chthamalochoros 8023       ................................................................................................
H.chydaeostigmata 5560       ................................................................................................
H.chydaeostigmata 8015       ................................................................................................
H.chydaeostigmata 8016       ................................................................................................
H.chydaeostigmata 8019       ................................................................................................
H.chydaeostigmata 8020       ................................................................................................
H.chydaeostigmata 8022       ................................................................................................
H.dechangei 7789             ................................................................................................
H.euktaenospatha 4340        ................................................................................................
H.glaphyroscytos 6640        ................................................................................................
H.hylaios 6358               ................................................................................................
H.hylaios 6359               ................................................................................................
H.hylaios 6363               ................................................................................................
H.ischnoryctes 6639          ................................................................................................
H.kukunyungkal 6341          ................................................................................................
H.kukunyungkal 6342          ................................................................................................
H.kukunyungkal 6343          ................................................................................................
H.laevitropis 6348            ................................................................................................
H.leptochela 6344            ................................................................................................
H.leptochela 6345            ................................................................................................
H.litodactylus 5559           ................................................................................................
H.macrochela 5555            ................................................................................................
H.neocaledonicus 4323        ................................................................................................
H.neocaledonicus 5542        ................................................................................................
H.neocaledonicus 5543        ................................................................................................
H.neocaledonicus 5544        ................................................................................................
H.neocaledonicus 5545        ................................................................................................
H.neocaledonicus 5546        ................................................................................................
H.neocaledonicus 5547        ................................................................................................
H.neocaledonicus 5548        ................................................................................................
H.neocaledonicus 6224        ................................................................................................
H.nyawaygi 6354              ................................................................................................
H.papuanus 2718              ................................................................................................
H.papuanus 2725              ................................................................................................
H.papuanus 2726              ................................................................................................
H.papuanus 2727              ................................................................................................
H.penta 1817                 ????????????????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ................................................................................................
H.solomonensis 1818          ................................................................................................
H.solomonensis 1819          ................................................................................................
H.solomonensis 5549          ................................................................................................
H.solomonensis 5550          ................................................................................................
H.solomonensis 5551          ................................................................................................
H.solomonensis 5552          ................................................................................................
H.solomonensis 5554          ................................................................................................
H.tjapukai 2184              ................................................................................................
H.tjapukai 6641              ................................................................................................
H.tytthognaphos 6346         ................................................................................................
H.tytthognaphos 6347         ................................................................................................
H.wallaman 6353              ................................................................................................
H.yelae 3007                 ................................................................................................
H.sp. WA 8017                ................................................................................................
H.sp. WA 8021                ................................................................................................
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 958–1044. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              aacgaaagttagaggttcgaaggcgatcagataccgccctagttctaaccataaacgatgccaaccagcgatccgcctgagttcctc
C.ochropus 6984              ........................................................................................
C.ochropus 9069              ........................................................................................
I.nitidus 9827               ........................................................................................
I.politus 1514               ........................................................................................
I.politus 3256               ........................................................................................
O.elatus 1837                ........................................................................................
O.laevipes 1835              ........................................................................................
O.lecomtei 1608              ........................................................................................
O.lecomtei 2194A             ........................................................................................
O.madagascariensis 2800      ........................................................................................
O.madagascariensis 2811      ........................................................................................
O.madagascariensis 2812      ........................................................................................
O.piceus 6260                ........................................................................................
H.infulcra 2185              ........................................................................................
L.australasiae 1854          ........................................................................................
L.australasiae 2181          ........................................................................................
L.australasiae 2182          ........................................................................................
L.australasiae 2183          ........................................................................................
L.australasiae 2729          ........................................................................................
L.australasiae 2733          ........................................................................................
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ????????????????????????????????????????????????????????????????????????????????
L.australasiae 4764          ........................................................................................
L.australasiae 5553          ........................................................................................
L.australasiae 8676          ........................................................................................
L.australasiae 8677          ........................................................................................
L.longimanus 6388            ........................................................................................
L.malaya 1909                ........................................................................................
H.aethes 3002                ........................................................................................
H.aethes 3005                ????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ........................................................................................
H.anekasankylis 6356         ........................................................................................
H.anekasankylis 6357         ........................................................................................
H.ankistros 4339             ........................................................................................
H.bandjin 5556               ........................................................................................
H.bandjin 5557               ........................................................................................
H.bandjin 5558               ........................................................................................
H.caudicula 1502             ........................................................................................
H.caudicula 2339             ........................................................................................
H.caudicula 2340             ........................................................................................
H.caudicula 6360             ........................................................................................
H.caudicula 6361             ........................................................................................
H.caudicula 6362             ........................................................................................
H.chthamalochoros 6350       ........................................................................................
H.chthamalochoros 6351       ........................................................................................
H.chthamalochoros 6352       ........................................................................................
H.chthamalochoros 8023       ........................................................................................
H.chydaeostigmata 5560       ........................................................................................
H.chydaeostigmata 8015       ........................................................................................
H.chydaeostigmata 8016       ........................................................................................
H.chydaeostigmata 8019       ........................................................................................
H.chydaeostigmata 8020       ........................................................................................
H.chydaeostigmata 8022       ........................................................................................
H.dechangei 7789             ........................................................................................
H.euktaenospatha 4340        ........................................................................................
H.glaphyroscytos 6640        ........................................................................................
H.hylaios 6358               ........................................................................................
H.hylaios 6359               ........................................................................................
H.hylaios 6363               ........................................................................................
H.ischnoryctes 6639          ........................................................................................
H.kukunyungkal 6341          ........................................................................................
H.kukunyungkal 6342          ........................................................................................
H.kukunyungkal 6343          ........................................................................................
H.laevitropis 6348            ........................................................................................
H.leptochela 6344            ........................................................................................
H.leptochela 6345            ........................................................................................
H.litodactylus 5559           ........................................................................................
H.macrochela 5555            ........................................................................................
H.neocaledonicus 4323        ........................................................................................
H.neocaledonicus 5542        ........................................................................................
H.neocaledonicus 5543        ........................................................................................
H.neocaledonicus 5544        ........................................................................................
H.neocaledonicus 5545        ........................................................................................
H.neocaledonicus 5546        ........................................................................................
H.neocaledonicus 5547        ........................................................................................
H.neocaledonicus 5548        ........................................................................................
H.neocaledonicus 6224        ........................................................................................
H.nyawaygi 6354              ........................................................................................
H.papuanus 2718              ........................................................................................
H.papuanus 2725              ........................................................................................
H.papuanus 2726              ........................................................................................
H.papuanus 2727              ........................................................................................
H.penta 1817                 ????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ........................................................................................
H.solomonensis 1818          ........................................................................................
H.solomonensis 1819          ........................................................................................
H.solomonensis 5549          ........................................................................................
H.solomonensis 5550          ........................................................................................
H.solomonensis 5551          ........................................................................................
H.solomonensis 5552          ........................................................................................
H.solomonensis 5554          ........................................................................................
H.tjapukai 2184              ........................................................................................
H.tjapukai 6641              ........................................................................................
H.tytthognaphos 6346         ........................................................................................
H.tytthognaphos 6347         ........................................................................................
H.wallaman 6353              ........................................................................................
H.yelae 3007                 ........................................................................................
H.sp. WA 8017                ........................................................................................
H.sp. WA 8021                ........................................................................................
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2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 1045–1131. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              aaatgactcggcgggcagcttccgggaaaccaaagtctctgggttccgggggaagtatggttgcaaagctgaaacttaaaggaattg
C.ochropus 6984              ....................................................................................
C.ochropus 9069              ....................................................................................
I.nitidus 9827               ....................................................................................
I.politus 1514               ....................................................................................
I.politus 3256               ....................................................................................
O.elatus 1837                ....................................................................................
O.laevipes 1835              ....................................................................................
O.lecomtei 1608              ....................................................................................
O.lecomtei 2194A             ....................................................................................
O.madagascariensis 2800      ....................................................................................
O.madagascariensis 2811      ....................................................................................
O.madagascariensis 2812      ....................................................................................
O.piceus 6260                ....................................................................................
H.infulcra 2185              ....................................................................................
L.australasiae 1854          ....................................................................................
L.australasiae 2181          ....................................................................................
L.australasiae 2182          ....................................................................................
L.australasiae 2183          ....................................................................................
L.australasiae 2729          ....................................................................................
L.australasiae 2733          ....................................................................................
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          ????????????????????????????????????????????????????????????????????????????????
L.australasiae 4764          ....................................................................................
L.australasiae 5553          ....................................................................................
L.australasiae 8676          ....................................................................................
L.australasiae 8677          ....................................................................................
L.longimanus 6388            ....................................................................................
L.malaya 1909                ....................................................................................
H.aethes 3002                ....................................................................................
H.aethes 3005                ????????????????????????????????????????????????????????????????????????????????
H.anekasankylis 6355         ....................................................................................
H.anekasankylis 6356         ....................................................................................
H.anekasankylis 6357         ....................................................................................
H.ankistros 4339             ....................................................................................
H.bandjin 5556               ....................................................................................
H.bandjin 5557               ....................................................................................
H.bandjin 5558               ....................................................................................
H.caudicula 1502             ....................................................................................
H.caudicula 2339             ....................................................................................
H.caudicula 2340             ....................................................................................
H.caudicula 6360             ....................................................................................
H.caudicula 6361             ....................................................................................
H.caudicula 6362             ....................................................................................
H.chthamalochoros 6350       ....................................................................................
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H.chthamalochoros 6352       ....................................................................................
H.chthamalochoros 8023       ....................................................................................
H.chydaeostigmata 5560       ....................................................................................
H.chydaeostigmata 8015       ....................................................................................
H.chydaeostigmata 8016       ....................................................................................
H.chydaeostigmata 8019       ....................................................................................
H.chydaeostigmata 8020       ....................................................................................
H.chydaeostigmata 8022       ....................................................................................
H.dechangei 7789             ....................................................................................
H.euktaenospatha 4340        ....................................................................................
H.glaphyroscytos 6640        ....................................................................................
H.hylaios 6358               ....................................................................................
H.hylaios 6359               ....................................................................................
H.hylaios 6363               ....................................................................................
H.ischnoryctes 6639          ....................................................................................
H.kukunyungkal 6341          ....................................................................................
H.kukunyungkal 6342          ....................................................................................
H.kukunyungkal 6343          ....................................................................................
H.laevitropis 6348            ....................................................................................
H.leptochela 6344            ....................................................................................
H.leptochela 6345            ....................................................................................
H.litodactylus 5559           ....................................................................................
H.macrochela 5555            ....................................................................................
H.neocaledonicus 4323        ....................................................................................
H.neocaledonicus 5542        ....................................................................................
H.neocaledonicus 5543        ....................................................................................
H.neocaledonicus 5544        ....................................................................................
H.neocaledonicus 5545        ....................................................................................
H.neocaledonicus 5546        ....................................................................................
H.neocaledonicus 5547        ....................................................................................
H.neocaledonicus 5548        ....................................................................................
H.neocaledonicus 6224        ....................................................................................
H.nyawaygi 6354              ....................................................................................
H.papuanus 2718              ....................................................................................
H.papuanus 2725              ....................................................................................
H.papuanus 2726              ....................................................................................
H.papuanus 2727              ....................................................................................
H.penta 1817                 ????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             ....................................................................................
H.solomonensis 1818          ....................................................................................
H.solomonensis 1819          ....................................................................................
H.solomonensis 5549          ....................................................................................
H.solomonensis 5550          ....................................................................................
H.solomonensis 5551          ....................................................................................
H.solomonensis 5552          ....................................................................................
H.solomonensis 5554          ....................................................................................
H.tjapukai 2184              ....................................................................................
H.tjapukai 6641              ....................................................................................
H.tytthognaphos 6346         ....................................................................................
H.tytthognaphos 6347         ....................................................................................
H.wallaman 6353              ....................................................................................
H.yelae 3007                 ....................................................................................
H.sp. WA 8017                ....................................................................................
H.sp. WA 8021                ....................................................................................
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 1132–1218. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              acggaagggcaccaccaggagtggagcctgcggcttaatttgactcaacacgggaaaacttacccggcccggacaccggaaggattg
C.ochropus 6984              ...............................................................................................
C.ochropus 9069              ...............................................................................................
I.nitidus 9827               ...............................................................................................
I.politus 1514               ...............................................................................................
I.politus 3256               ...............................................................................................
O.elatus 1837                ...............................................................................................
O.laevipes 1835              ...............................................................................................
O.lecomtei 1608              ...............................................................................................
O.lecomtei 2194A             ...............................................................................................
O.madagascariensis 2800      ...............................................................................................
O.madagascariensis 2811      ...............................................................................................
O.madagascariensis 2812      ...............................................................................................
O.piceus 6260                ...............................................................................................
H.infulcra 2185              ...............................................................................................
L.australasiae 1854          ...............................................................................................
L.australasiae 2181          ...............................................................................................
L.australasiae 2182          ...............................................................................................
L.australasiae 2183          ...............................................................................................
L.australasiae 2729          ...............................................................................................
L.australasiae 2733          ...............................................................................................
L.australasiae 2996          ...............................................................................................
L.australasiae 3684          ...............................................................................................
L.australasiae 4764          ...............................................................................................
L.australasiae 5553          ...............................................................................................
L.australasiae 8676          ...............................................................................................
L.australasiae 8677          ...............................................................................................
L.longimanus 6388           ...............................................................................................
L.malaya 1909               ...............................................................................................
H.aethes 3002               ...............................................................................................
H.aethes 3005               ...............................................................................................
H.anekasankylis 6355        ...............................................................................................
H.anekasankylis 6356        ...............................................................................................
H.anekasankylis 6357        ...............................................................................................
H.ankistros 4339            ...............................................................................................
H.bandjin 5556              ...............................................................................................
H.bandjin 5557              ...............................................................................................
H.bandjin 5558              ...............................................................................................
H.caudicula 1502            ...............................................................................................
H.caudicula 2339            ...............................................................................................
H.caudicula 2340            ...............................................................................................
H.caudicula 6360            ...............................................................................................
H.caudicula 6361            ...............................................................................................
H.caudicula 6362            ...............................................................................................
H.chthamalochoros 6350      ...............................................................................................
H.chthamalochoros 6351      ...............................................................................................
H.chthamalochoros 6352      ...............................................................................................
H.chthamalochoros 8023      ...............................................................................................
H.chydaeostigmata 5560      ...............................................................................................
H.chydaeostigmata 8015      ...............................................................................................
H.chydaeostigmata 8016      ...............................................................................................
H.chydaeostigmata 8019      ...............................................................................................
H.chydaeostigmata 8020      ...............................................................................................
H.chydaeostigmata 8022      ...............................................................................................
H.dechangei 7789            ...............................................................................................
H.euktaenospatha 4340       ...............................................................................................
H.glaphyroscytos 6640       ...............................................................................................
H.hylaios 6358              ...............................................................................................
H.hylaios 6359              ...............................................................................................
H.hylaios 6363              ...............................................................................................
H.ischnoryctes 6639         ...............................................................................................
H.kukunyungkal 6341         ...............................................................................................
H.kukunyungkal 6342         ...............................................................................................
H.kukunyungkal 6343         ...............................................................................................
H.laevitropis 6348           ...............................................................................................
H.leptochela 6344           ...............................................................................................
H.leptochela 6345           ...............................................................................................
H.litodactylus 5559          ...............................................................................................
H.macrochela 5555           ...............................................................................................
H.neocaledonicus 4323       ...............................................................................................
H.neocaledonicus 5542       ...............................................................................................
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H.neocaledonicus 5545       ...............................................................................................
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H.neocaledonicus 5548       ...............................................................................................
H.neocaledonicus 6224       ...............................................................................................
H.nyawaygi 6354             ...............................................................................................
H.papuanus 2718             ...............................................................................................
H.papuanus 2725             ...............................................................................................???
H.papuanus 2726             ...............................................................................................
H.papuanus 2727             ...............................................................................................
H.penta 1817                ...............................................................................................
H.polisorum 1614            ...............................................................................................
H.solomonensis 1818         ...............................................................................................
H.solomonensis 1819         ...............................................................................................
H.solomonensis 5549         ...............................................................................................
H.solomonensis 5550         ...............................................................................................
H.solomonensis 5551         ...............................................................................................
H.solomonensis 5552         ...............................................................................................
H.solomonensis 5554         ...............................................................................................
H.tjapukai 2184             ...............................................................c...............
H.tjapukai 6641             ...............................................................c...............
H.tytthognaphos 6346        ...............................................................................................
H.tytthognaphos 6347        ...............................................................................................
H.wallaman 6353             ...............................................................................................
H.yelae 3007                ...............................................................................................
H.sp. WA 8017               ...............................................................................................
H.sp. WA 8021               ...............................................................................................
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 1219–1305. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              acagattaatagctctttcttgattcggtgggtggtggtgcatggccgttcttagttggtggagcgatttgtctggttaattccgat
C.ochropus 6984              ...............................................................................................
C.ochropus 9069              ...............................................................................................
I.nitidus 9827               ...............................................................................................
I.politus 1514               ...............................................................................................
I.politus 3256               ..........t.....................................................t.....................
O.elatus 1837                ...............................................................................................
O.laevipes 1835              ...............................................................................................
O.lecomtei 1608              ...............................................................................................
O.lecomtei 2194A             ...............................................................................................
O.madagascariensis 2800      ...............................................................................................
O.madagascariensis 2811      ...............................................................................................
O.madagascariensis 2812      ...............................................................................................
O.piceus 6260                ...............................................................................................
H.infulcra 2185              ...............................................................................................
L.australasiae 1854          ...............................................................................................
L.australasiae 2181          ...............................................................................................
L.australasiae 2182          ...............................................................................................
L.australasiae 2183          ...............................................................................................
L.australasiae 2729          ...............................................................................................
L.australasiae 2733          ...............................................................................................
L.australasiae 2996          ...............................................................................................
L.australasiae 3684          ...............................................................................................
L.australasiae 4764          ...............................................................................................
L.australasiae 5553          ...............................................................................................
L.australasiae 8676          ...............................................................................................
L.australasiae 8677          ...............................................................................................
L.longimanus 6388           ...............................................................................................
L.malaya 1909               ...............................................................................................
H.aethes 3002               ...............................................................................................
H.aethes 3005               ...............................................................................................
H.anekasankylis 6355        ...............................................................................................
H.anekasankylis 6356        ...............................................................................................
H.anekasankylis 6357        ...............................................................................................
H.ankistros 4339            ...............................................................................................
H.bandjin 5556              ...............................................................................................
H.bandjin 5557              ...............................................................................................
H.bandjin 5558              ...............................................................................................
H.caudicula 1502            ...............................................................................................
H.caudicula 2339            ...............................................................................................
H.caudicula 2340            ...............................................................................................
H.caudicula 6360            ...............................................................................................
H.caudicula 6361            ...............................................................................................
H.caudicula 6362            ...............................................................................................
H.chthamalochoros 6350      ...............................................................................................
H.chthamalochoros 6351      ...............................................................................................
H.chthamalochoros 6352      ...............................................................................................
H.chthamalochoros 8023      ...............................................................................................
H.chydaeostigmata 5560      ...............................................................................................
H.chydaeostigmata 8015      ...............................................................................................
H.chydaeostigmata 8016      ...............................................................................................
H.chydaeostigmata 8019      ...............................................................................................
H.chydaeostigmata 8020      ...............................................................................................
H.chydaeostigmata 8022      ...............................................................................................
H.dechangei 7789            ...............................................................................................
H.euktaenospatha 4340       ...............................................................................................
H.glaphyroscytos 6640       ...............................................................................................
H.hylaios 6358              ...............................................................................................
H.hylaios 6359              ...............................................................................................
H.hylaios 6363              ...............................................................................................
H.ischnoryctes 6639         ...............................................................................................
H.kukunyungkal 6341         ...............................................................................................
H.kukunyungkal 6342         ...............................................................................................
H.kukunyungkal 6343         ...............................................................................................
H.laevitropis 6348           ...............................................................................................
H.leptochela 6344           ...............................................................................................
H.leptochela 6345           ...............................................................................................
H.litodactylus 5559          ...............................................................................................
H.macrochela 5555           ...............................................................................................
H.neocaledonicus 4323       ...............................................................................................
H.neocaledonicus 5542       ...............................................................................................
H.neocaledonicus 5543       ...............................................................................................
H.neocaledonicus 5544       ...............................................................................................
H.neocaledonicus 5545       ...............................................................................................
H.neocaledonicus 5546       ...............................................................................................
H.neocaledonicus 5547       ...............................................................................................
H.neocaledonicus 5548       ...............................................................................................
H.neocaledonicus 6224       ...............................................................................................
H.nyawaygi 6354             ...............................................................................................
H.papuanus 2718             ...............................................................................................
H.papuanus 2725             ???????????????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2726             ...............................................................................................
H.papuanus 2727             ...............................................................................................
H.penta 1817                ...............................................................................................
H.polisorum 1614            ...............................................................................................
H.solomonensis 1818         ...............................................................................................
H.solomonensis 1819         ...............................................................................................
H.solomonensis 5549         ...............................................................................................
H.solomonensis 5550         ...............................................................................................
H.solomonensis 5551         ...............................................................................................
H.solomonensis 5552         ...............................................................................................
H.solomonensis 5554         ...............................................................................................
H.tjapukai 2184             ...............................................................................................
H.tjapukai 6641             ...............................................................................................
H.tytthognaphos 6346        ...............................................................................................
H.tytthognaphos 6347        ...............................................................................................
H.wallaman 6353             ...............................................................................................
H.yelae 3007                ...............................................................................................
H.sp. WA 8017               ...............................................................................................
H.sp. WA 8021               ...............................................................................................
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 1306–1392. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              aacgaacgagactctagcctactaaatagacgagcgattaaccgagtcgctcggacttcttagagggacaggcggcttacagccgca
C.ochropus 6984              ....................................................................................
C.ochropus 9069              ....................................................................................
I.nitidus 9827               ..........................................t.........................................
I.politus 1514               ....................................................................................
I.politus 3256               ....................................................................................
O.elatus 1837                ....................................................................................
O.laevipes 1835              ....................................................................................
O.lecomtei 1608              ..........................................t.........................................
O.lecomtei 2194A             ..........................................t.........................................
O.madagascariensis 2800      ....................................................................................
O.madagascariensis 2811      ....................................................................................
O.madagascariensis 2812      ....................................................................................
O.piceus 6260                ....................................................................................
H.infulcra 2185              ..............................t...........a.........................................
L.australasiae 1854          ..........................................a.ag....t.................................
L.australasiae 2181          ..........................................a.ag....t.................................
L.australasiae 2182          ..........................................a.ag....t.................................
L.australasiae 2183          ..........................................a.ag....t.................................
L.australasiae 2729          ..........................................a.ag....t.................................
L.australasiae 2733          ..........................................a.ag....t.................................
L.australasiae 2996          ..........................................a.ag....t.................................
L.australasiae 3684          ..........................................a.ag....t.................................
L.australasiae 4764          ..........................................a.ag....t.................................
L.australasiae 5553          ..........................................a.ag....t.................................
L.australasiae 8676          ..........................................a.ag....t.................................
L.australasiae 8677          ..........................................a.ag....t.................................
L.longimanus 6388            ..........................................a.a.....................................
L.malaya 1909                ..........................................a.a.....................................
H.aethes 3002                ..........................................a.....................................
H.aethes 3005                ..........................................a.....................................
H.anekasankylis 6355         ..........................................a.....................................
H.anekasankylis 6356         ..........................................a.....................................
H.anekasankylis 6357         ..........................................a.....................................
H.ankistros 4339             ..........................................a.....................................
H.bandjin 5556               ..........................................a.....................................
H.bandjin 5557               ..........................................a.....................................
H.bandjin 5558               ..........................................a.....................................
H.caudicula 1502             ..............????????????????????????????????????????????????????????????????????
H.caudicula 2339             ..........................................a.....................................
H.caudicula 2340             ..........................................a.....................................
H.caudicula 6360             ..........................................a.....................................
H.caudicula 6361             ..........................................a.....................................
H.caudicula 6362             ..........................................a.....................................
H.chthamalochoros 6350       ..........................................a.....................................
H.chthamalochoros 6351       ..........................................a.....................................
H.chthamalochoros 6352       ..........................................a.....................................
H.chthamalochoros 8023       ..........................................a.....................................
H.chydaeostigmata 5560       ..........................................a.....................................
H.chydaeostigmata 8015       ..........................................a.....................................
H.chydaeostigmata 8016       ..........................................a.....................................
H.chydaeostigmata 8019       ..........................................a.....................................
H.chydaeostigmata 8020       ..........................................a.....................................
H.chydaeostigmata 8022       ..........................................a.....................................
H.dechangei 7789             ..........................................a.....................................
H.euktaenospatha 4340        ..........................................a.....................................
H.glaphyroscytos 6640        ..........................................a.....................................
H.hylaios 6358               ..........................................a.....................................
H.hylaios 6359               ..........................................a.....................................
H.hylaios 6363               ..........................................a.....................................
H.ischnoryctes 6639          ..........................................a.....................................
H.kukunyungkal 6341          ..........................................a.....................................
H.kukunyungkal 6342          ..........................................a.....................................
H.kukunyungkal 6343          ..........................................a.....................................
H.laevitropis 6348           ..........................................a.....................................
H.leptochela 6344            ..........................................a.....................................
H.leptochela 6345            ..........................................a.....................................
H.litodactylus 5559          ..........................................a.....................................
H.macrochela 5555            ..........................................a.....................................
H.neocaledonicus 4323        ..........................................a.....................................
H.neocaledonicus 5542        ..........................................a.....................................
H.neocaledonicus 5543        ..........................................a.....................................
H.neocaledonicus 5544        ..........................................a.....................................
H.neocaledonicus 5545        ..........................................a.....................................
H.neocaledonicus 5546        ..........................................a.....................................
H.neocaledonicus 5547        ..........................................a.....................................
H.neocaledonicus 5548        ..........................................a.....................................
H.neocaledonicus 6224        ..........................................a.....................................
H.nyawaygi 6354              ..........................................a.....................................
H.papuanus 2718              ..........................................a.....................................
H.papuanus 2725              ????????????????????????????????????????????????????????????????????????????????
H.papuanus 2726              ..........................................a.....................................
H.papuanus 2727              ..........................................a.....................................
H.penta 1817                 ..........................................a.....................................
H.polisorum 1614             ..........................................a.......g.............................
H.solomonensis 1818          ..........................................a.....................................
H.solomonensis 1819          ..........................................a.....................................
H.solomonensis 5549          ..........................................a.....................................
H.solomonensis 5550          ..........................................a.....................................
H.solomonensis 5551          ..........................................a.....................................
H.solomonensis 5552          ..........................................a.....................................
H.solomonensis 5554          ..........................................a.....................................
H.tjapukai 2184              ..........................................a.....................................
H.tjapukai 6641              ..........................................a.....................................
H.tytthognaphos 6346         ..........................................a.....................................
H.tytthognaphos 6347         ..........................................a.....................................
H.wallaman 6353              ..........................................a.....................................
H.yelae 3007                 ..........................................a.....................................
H.sp. WA 8017                ..........................................a.....................................
H.sp. WA 8021                ..........................................a.....................................
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 1393–1479. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              cgagacagagcaataacaggtctgtgatgcccttagatgtccggggccgcacgcgcgctacactgaaggatgcagcgtgcgtttacc
C.ochropus 6984              ....................................................................................
C.ochropus 9069              ....................................................................................
I.nitidus 9827               ....................................................................................
I.politus 1514               ....................................................................................
I.politus 3256               ....................................................................................
O.elatus 1837                ....................................................................................
O.laevipes 1835              ....................................................................................
O.lecomtei 1608              ....................................................................................
O.lecomtei 2194A             ....................................................................................
O.madagascariensis 2800      ....................................................................................
O.madagascariensis 2811      ....................................................................................
O.madagascariensis 2812      ....................................................................................
O.piceus 6260                ....................................................................................
H.infulcra 2185              ....................................................................................
L.australasiae 1854          ....................................................................................
L.australasiae 2181          ....................................................................................
L.australasiae 2182          ....................................................................................
L.australasiae 2183          ....................................................................................
L.australasiae 2729          ....................................................................................
L.australasiae 2733          ....................................................................................
L.australasiae 2996          ....................................................................................
L.australasiae 3684          ....................................................................................
L.australasiae 4764          ....................................................................................
L.australasiae 5553          ....................................................................................
L.australasiae 8676          ....................................................................................
L.australasiae 8677          ....................................................................................
L.longimanus6388            ....................................................................c...............
L.malaya 1909                ....................................................................................
H.aethes 3002                ....................................................................................
H.aethes 3005                ....................................................................................
H.anekasankylis 6355         ....................................................................................
H.anekasankylis 6356         ....................................................................................
H.anekasankylis 6357         ....................................................................................
H.ankistros 4339             ....................................................................................
H.bandjin 5556               ....................................................................................
H.bandjin 5557               ....................................................................................
H.bandjin 5558               ....................................................................................
H.caudicula 1502             ????????????????????????????????????????????????????????????????????????????????????????????????????
H.caudicula 2339             ....................................................................................
H.caudicula 2340             ....................................................................................
H.caudicula 6360             ....................................................................................
H.caudicula 6361             ....................................................................................
H.caudicula 6362             ....................................................................................
H.chthamalochoros 6350       ....................................................................................
H.chthamalochoros 6351       ....................................................................................
H.chthamalochoros 6352       ....................................................................................
H.chthamalochoros 8023       ....................................................................................
H.chydaeostigmata 5560       ....................................................................................
H.chydaeostigmata 8015       ....................................................................................
H.chydaeostigmata 8016       ....................................................................................
H.chydaeostigmata 8019       ....................................................................................
H.chydaeostigmata 8020       ....................................................................................
H.chydaeostigmata 8022       ....................................................................................
H.dechangei 7789             ....................................................................................
H.euktaenospatha 4340        ....................................................................................
H.glaphyroscytos 6640        ....................................................................c...............
H.hylaios 6358               ....................................................................................
H.hylaios 6359               ....................................................................................
H.hylaios 6363               ....................................................................................
H.ischnoryctes 6639          ....................................................................................
H.kukunyungkal 6341          ....................................................................................
H.kukunyungkal 6342          ....................................................................................
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H.laevitropis 6348            ....................................................................................
H.leptochela 6344            ....................................................................................
H.leptochela 6345            ....................................................................................
H.litodactylus 5559           ....................................................................................
H.macrochela 5555            ....................................................................................
H.neocaledonicus 4323        ....................................................................c...............
H.neocaledonicus 5542        ....................................................................c...............
H.neocaledonicus 5543        ....................................................................c...............
H.neocaledonicus 5544        ....................................................................c...............
H.neocaledonicus 5545        ....................................................................c...............
H.neocaledonicus 5546        ....................................................................c...............
H.neocaledonicus 5547        ....................................................................c...............
H.neocaledonicus 5548        ....................................................................c...............
H.neocaledonicus 6224        ....................................................................c...............
H.nyawaygi 6354              ....................................................................................
H.papuanus 2718              ....................................................................................
H.papuanus 2725              ????????????????????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2726              ....................................................................................
H.papuanus 2727              ....................................................................................
H.penta 1817                 ....................................................................c...............
H.polisorum 1614             ....................................................................c...............
H.solomonensis 1818          ....................................................................................
H.solomonensis 1819          ....................................................................................
H.solomonensis 5549          ....................................................................................
H.solomonensis 5550          ....................................................................................
H.solomonensis 5551          ....................................................................................
H.solomonensis 5552          ....................................................................................
H.solomonensis 5554          ....................................................................................
H.tjapukai 2184              ....................................................................................
H.tjapukai 6641              ....................................................................................
H.tytthognaphos 6346         ....................................................................................
H.tytthognaphos 6347         ....................................................................................
H.wallaman 6353              ....................................................................................
H.yelae 3007                 ....................................................................................
H.sp. WA 8017                ....................................................................................
H.sp. WA 8021                ....................................................................................
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 1480–1566. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              cctgtccggaaggactgggtaacccctcaacctccttcgtgatagggatagggattggaattattcccctcaacgaggaattcc
C.ochropus 6984              ...............................................................................................
C.ochropus 9069              ...............................................................................................
I.nitidus 9827               ...............................................................................................
I.politus 1514               ...............................................................................................
I.politus 3256               ...............................................................................................
O.elatus 1837                ...............................................................................................
O.laevipes 1835              ...............................................................................................
O.lecomtei 1608              ...............................................................................................
O.lecomtei 2194A             ...............................................................................................
O.madagascariensis 2800      ..............................................c.....................a.............
O.madagascariensis 2811      ..............................................c.....................a.............
O.madagascariensis 2812      ..............................................c.....................a.............
O.piceus 6260                ..............................................c.....................a.............
H.infulcra 2185              ...............................................................................................
L.australasiae 1854          ...............................................................................................
L.australasiae 2181          ...............................................................................................
L.australasiae 2182          ...............................................................................................
L.australasiae 2183          ...............................................................................................
L.australasiae 2729          ...............................................................................................
L.australasiae 2733          ...............................................................................................
L.australasiae 2996          ...............................................................................................
L.australasiae 3684          ...............................................................................................
L.australasiae 4764          ...............................................................................................
L.australasiae 5553          ...............................................................................................
L.australasiae 8676          ...............................................................................................
L.australasiae 8677          ...............................................................................................
L.longimanus6388            ...............................................................................................
L.malaya 1909                ...............................................................................................
H.aethes 3002                ...............................................................................................
H.aethes 3005                ...............................................................................................
H.anekasankylis 6355         ...............................................................................................
H.anekasankylis 6356         ...............................................................................................
H.anekasankylis 6357         ...............................................................................................
H.ankistros 4339             ...............................................................................................
H.bandjin 5556               ...............................................................................................
H.bandjin 5557               ...............................................................................................
H.bandjin 5558               ...............................................................................................
H.caudicula 1502             ???????????????????????????????????????????????????????????????????????????????????????????????
H.caudicula 2339             ...............................................................................................
H.caudicula 2340             ...............................................................................................
H.caudicula 6360             ...............................................................................................
H.caudicula 6361             ...............................................................................................
H.caudicula 6362             ...............................................................................................
H.chthamalochoros 6350       ...............................................................................................
H.chthamalochoros 6351       ...............................................................................................
H.chthamalochoros 6352       ...............................................................................................
H.chthamalochoros 8023       ...............................................................................................
H.chydaeostigmata 5560       ...............................................................................................
H.chydaeostigmata 8015       ...............................................................................................
H.chydaeostigmata 8016       ...............................................................................................
H.chydaeostigmata 8019       ...............................................................................................
H.chydaeostigmata 8020       ...............................................................................................
H.chydaeostigmata 8022       ...............................................................................................
H.dechangei 7789             ...............................................................................................
H.euktaenospatha 4340        ...............................................................................................
H.glaphyroscytos 6640        ...............................................................................................
H.hylaios 6358               ...............................................................................................
H.hylaios 6359               ...............................................................................................
H.hylaios 6363               ...............................................................................................
H.ischnoryctes 6639          ...............................................................................................
H.kukunyungkal 6341          ...............................................................................................
H.kukunyungkal 6342          ...............................................................................................
H.kukunyungkal 6343          ...............................................................................................
H.laevitropis 6348            ...............................................................................................
H.leptochela 6344            ...............................................................................................
H.leptochela 6345            ...............................................................................................
H.litodactylus 5559           ...............................................................................................
H.macrochela 5555            ...............................................................................................
H.neocaledonicus 4323        ...............................................................................................
H.neocaledonicus 5542        ...............................................................................................
H.neocaledonicus 5543        ...............................................................................................
H.neocaledonicus 5544        ...............................................................................................
H.neocaledonicus 5545        ...............................................................................................
H.neocaledonicus 5546        ...............................................................................................
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H.neocaledonicus 5548        ...............................................................................................
H.neocaledonicus 6224        ...............................................................................................
H.nyawaygi 6354              ...............................................................................................
H.papuanus 2718              ...............................................................................................
H.papuanus 2725              ???????????????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2726              ...............................................................................................
H.papuanus 2727              ...............................................................................................
H.penta 1817                 ...............................................................................................
H.polisorum 1614             ...............................................................................................
H.solomonensis 1818          ...............................................................................................
H.solomonensis 1819          ...............................................................................................
H.solomonensis 5549          ...............................................................................................
H.solomonensis 5550          ...............................................................................................
H.solomonensis 5551          ...............................................................................................
H.solomonensis 5552          ...............................................................................................
H.solomonensis 5554          ...............................................................................................
H.tjapukai 2184              ...............................................................g...............................
H.tjapukai 6641              ...............................................................g...............................
H.tytthognaphos 6346         ...............................................................................................
H.tytthognaphos 6347         ...............................................................................................
H.wallaman 6353              ...............................................................................................
H.yelae 3007                 ...............................................................................................
H.sp. WA 8017                ...............................................................................................
H.sp. WA 8021                ...............................................................................................
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 1567–1653. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              cagtaagcgcgagtcataagctcgcgttgattacgtccctgccctttgtacacaccgcccgtcgctactaccgattgaatgatttag
C.ochropus 6984              ....................................................................................
C.ochropus 9069              ....................................................................................
I.nitidus 9827               ....................................................................................
I.politus 1514               .........t..........................................................................
I.politus 3256               .........t..........................................................................
O.elatus 1837                .........t..........................................................................
O.laevipes 1835              ....................................................................................
O.lecomtei 1608              .........t..........................................................................
O.lecomtei 2194A             .........t..........................................................................
O.madagascariensis 2800      ....................................................................................
O.madagascariensis 2811      ....................................................................................
O.madagascariensis 2812      ....................................................................................
O.piceus 6260                ....................................................................................
H.infulcra 2185              .......t.................a..........................................................
L.australasiae 1854          ....................................................................................
L.australasiae 2181          ....................................................................................
L.australasiae 2182          ....................................................................................
L.australasiae 2183          ....................................................................................
L.australasiae 2729          ....................................................................................
L.australasiae 2733          ....................................................................................
L.australasiae 2996          ....................................................................................
L.australasiae 3684          ....................................................................................
L.australasiae 4764          ....................................................................................
L.australasiae 5553          ....................................................................................
L.australasiae 8676          ....................................................................................
L.australasiae 8677          ....................................................................................
L.longimanus6388            ....................................................................................
L.malaya 1909                ....................................................................................
H.aethes 3002                ....................................................................................
H.aethes 3005                ....................................................................................
H.anekasankylis 6355         ....................................................................................
H.anekasankylis 6356         ....................................................................................
H.anekasankylis 6357         ....................................................................................
H.ankistros 4339             ....................................................................................
H.bandjin 5556               ....................................................................................
H.bandjin 5557               ....................................................................................
H.bandjin 5558               ....................................................................................
H.caudicula 1502             ????????????????????????????????????????????????????????????????????????????????????????????????????
H.caudicula 2339             ....................................................................................
H.caudicula 2340             ....................................................................................
H.caudicula 6360             ....................................................................................
H.caudicula 6361             ....................................................................................
H.caudicula 6362             ....................................................................................
H.chthamalochoros 6350       ....................................................................................
H.chthamalochoros 6351       ....................................................................................
H.chthamalochoros 6352       ....................................................................................
H.chthamalochoros 8023       ....................................................................................
H.chydaeostigmata 5560       ....................................................................................
H.chydaeostigmata 8015       ....................................................................................
H.chydaeostigmata 8016       ....................................................................................
H.chydaeostigmata 8019       ....................................................................................
H.chydaeostigmata 8020       ....................................................................................
H.chydaeostigmata 8022       ....................................................................................
H.dechangei 7789             ....................................................................................
H.euktaenospatha 4340        ....................................................................................
H.glaphyroscytos 6640        ....................................................................................
H.hylaios 6358               ....................................................................................
H.hylaios 6359               ....................................................................................
H.hylaios 6363               ....................................................................................
H.ischnoryctes 6639          ....................................................................................
H.kukunyungkal 6341          ....................................................................................
H.kukunyungkal 6342          ....................................................................................
H.kukunyungkal 6343          ....................................................................................
H.laevitropis 6348            ....................................................................................
H.leptochela 6344            ....................................................................................
H.leptochela 6345            ....................................................................................
H.litodactylus 5559           ....................................................................................
H.macrochela 5555            ....................................................................................
H.neocaledonicus 4323        ....................................................................................
H.neocaledonicus 5542        ....................................................................................
H.neocaledonicus 5543        ....................................................................................
H.neocaledonicus 5544        ....................................................................................
H.neocaledonicus 5545        ....................................................................................
H.neocaledonicus 5546        ....................................................................................
H.neocaledonicus 5547        ....................................................................................
H.neocaledonicus 5548        ....................................................................................
H.neocaledonicus 6224        ....................................................................................
H.nyawaygi 6354              ....................................................................................
H.papuanus 2718              ....................................................................................
H.papuanus 2725              ????????????????????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2726              ....................................................................................
H.papuanus 2727              ....................................................................................
H.penta 1817                 ....................................................................................
H.polisorum 1614             ....................................................................................
H.solomonensis 1818          ....................................................................................
H.solomonensis 1819          ....................................................................................
H.solomonensis 5549          ....................................................................................
H.solomonensis 5550          ....................................................................................
H.solomonensis 5551          ....................................................................................
H.solomonensis 5552          ....................................................................................
H.solomonensis 5554          ....................................................................................
H.tjapukai 2184              ....................................................................................
H.tjapukai 6641              ....................................................................................
H.tytthognaphos 6346         ....................................................................................
H.tytthognaphos 6347         ....................................................................................
H.wallaman 6353              ....................................................................................
H.yelae 3007                 ....................................................................................
H.sp. WA 8017                ....................................................................................
H.sp. WA 8021                ....................................................................................
```

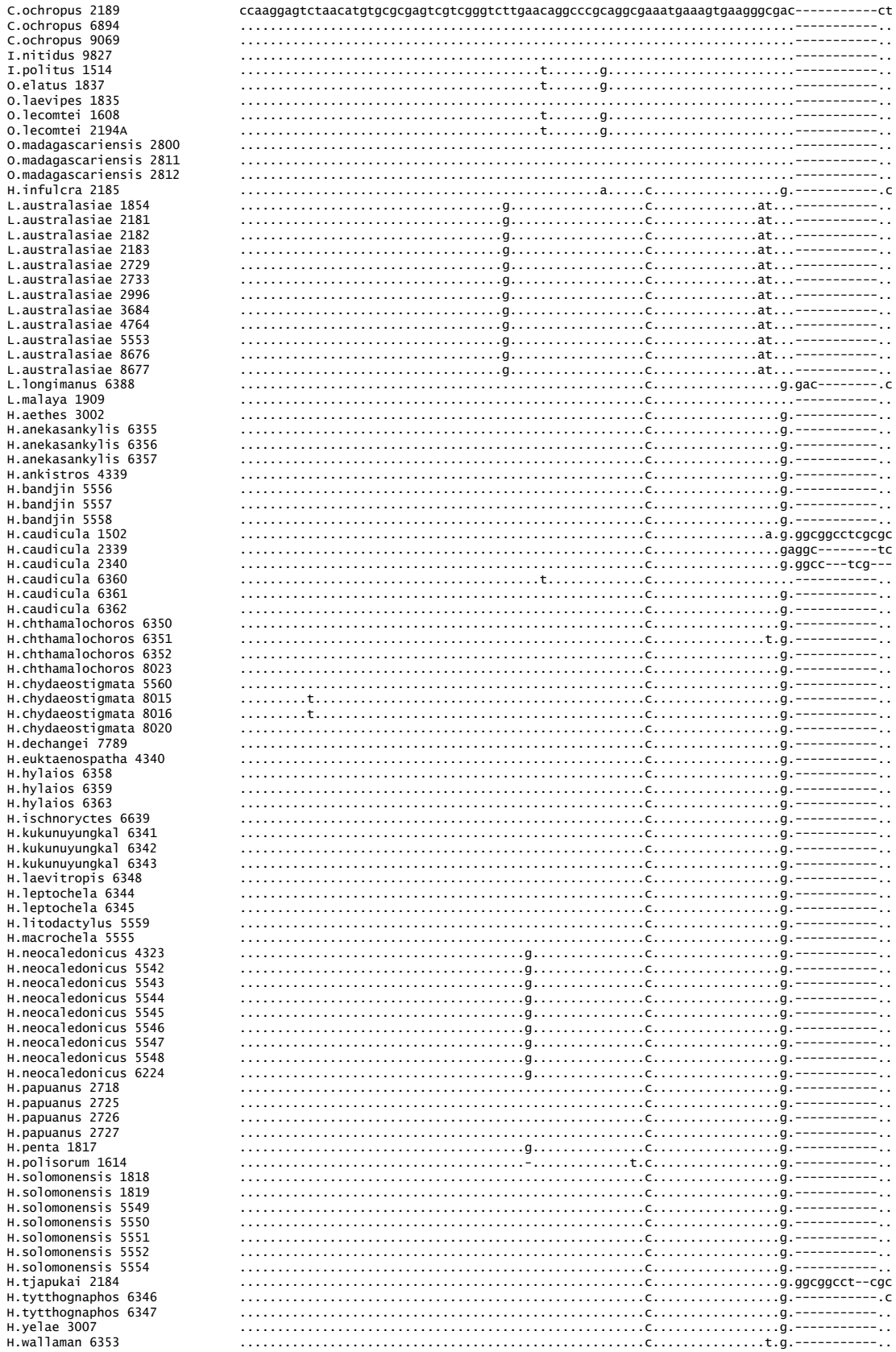
2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 1654–1740. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              tgaggtcttcggactggcgcccggagcggctcgcgggtcgcgccggcgtgccggaaagatgaccgaacttgattatttagaggaagt
C.ochropus 6984              ....................................................................................
C.ochropus 9069              ....................................................................................
I.nitidus 9827               ....................................................................................
I.politus 1514               ....................................................................................
I.politus 3256               ....................................................................................
O.elatus 1837                ............................tt....................................................
O.laevipes 1835              ....................................................................................
O.lecomtei 1608              ....................................................................................
O.lecomtei 2194A             ....................................................................................
O.madagascariensis 2800      ....................................................................................
O.madagascariensis 2811      ....................................................................................
O.madagascariensis 2812      ....................................................................................
O.piceus 6260                ....................................................................................
H.infulcra 2185              ............................a.............a.....................................
L.australasiae 1854          ...........................................t........................c...........
L.australasiae 2181          ...........................................t........................c...........
L.australasiae 2182          ...........................................t........................c...........
L.australasiae 2183          ...........................................t........................c...........
L.australasiae 2729          ...........................................t........................c...........
L.australasiae 2733          ...........................................t........................c...........
L.australasiae 2996          ...........................................t........................c...........
L.australasiae 3684          ...........................................t........................c...........
L.australasiae 4764          ...........................................t........................c...........
L.australasiae 5553          ...........................................t........................c...........
L.australasiae 8676          ...........................................t........................c...........
L.australasiae 8677          ...........................................t........................c...........
L.longimanus6388             ...........................................t........................c...........
L.malaya 1909                ...........................................t........................c...........
H.aethes 3002                ...........................................t........................c...........
H.aethes 3005                ...........................................t........................c...........
H.anekasankylis 6355         ...........................................t........................c...........
H.anekasankylis 6356         ...........................................t........................c...........
H.anekasankylis 6357         ...........................................t........................c...........
H.ankistros 4339             ...........................................t........................c...........
H.bandjin 5556               ...........................................t........................c...........
H.bandjin 5557               ...........................................t........................c...........
H.bandjin 5558               ...........................................t........................c...........
H.caudicula 1502             ????????????????????????????????????????????????????????????????????????????????
H.caudicula 2339             ...........................................t........................c...........
H.caudicula 2340             ...........................................t........................c...........
H.caudicula 6360             ...........................................t........................c...........
H.caudicula 6361             ...........................................t........................c...........
H.caudicula 6362             ...........................................t........................c...........
H.chthamalochoros 6350       ...........................................t........................c...........
H.chthamalochoros 6351       ...........................................t........................c...........
H.chthamalochoros 6352       ...........................................t........................c...........
H.chthamalochoros 8023       ...........................................t........................c...........
H.chydaeostigmata 5560       ...........................................t........................c...........
H.chydaeostigmata 8015       ...........................................t........................c...........
H.chydaeostigmata 8016       ...........................................t........................c...........
H.chydaeostigmata 8019       ...........................................t........................c...........
H.chydaeostigmata 8020       ...........................................t........................c...........
H.chydaeostigmata 8022       ...........................................t........................c...........
H.dechangei 7789             ...........................................t........................c...........
H.euktaenospatha 4340        ...........................................t........................c...........
H.glaphyroscytos 6640        ...........................................t........................c...........
H.hylaios 6358               ...........................................t........................c...........
H.hylaios 6359               ...........................................t........................c...........
H.hylaios 6363               ...........................................t........................c...........
H.ischnoryctes 6639          ...........................................t........................c...........
H.kukunyungkal 6341          ...........................................t........................c...........
H.kukunyungkal 6342          ...........................................t........................c...........
H.kukunyungkal 6343          ...........................................t........................c...........
H.laevitropis 6348           ...........................................t........................c...........
H.leptochela 6344            ...........................................t........................c...........
H.leptochela 6345            ...........................................t........................c...........
H.litodactylus 5559          ...........................................t........................c...........
H.macrochela 5555            ...........................................t........................c...........
H.neocaledonicus 4323        ...........................................t........................c...........
H.neocaledonicus 5542        ...........................................t........................c...........
H.neocaledonicus 5543        ...........................................t........................c...........
H.neocaledonicus 5544        ...........................................t........................c...........
H.neocaledonicus 5545        ...........................................t........................c...........
H.neocaledonicus 5546        ...........................................t........................c...........
H.neocaledonicus 5547        ...........................................t........................c...........
H.neocaledonicus 5548        ...........................................t........................c...........
H.neocaledonicus 6224        ...........................................t........................c...........
H.nyawaygi 6354              ...........................................t........................c...........
H.papuanus 2718              ...........................................t........................c...........
H.papuanus 2725              ????????????????????????????????????????????????????????????????????????????????
H.papuanus 2726              ...........................................t........................c...........
H.papuanus 2727              ...........................................t........................c...........
H.penta 1817                 ...........................................t........................c...........
H.polisorum 1614             ...........................................t........................c...........
H.solomonensis 1818          ...........................................t........................c...........
H.solomonensis 1819          ...........................................t........................c...........
H.solomonensis 5549          ...........................................t........................c...........
H.solomonensis 5550          ...........................................t........................c...........
H.solomonensis 5551          ...........................................t........................c...........
H.solomonensis 5552          ...........................................t........................c...........
H.solomonensis 5554          ...........................................t........................c...........
H.tjapukai 2184              ...........................................t........................c...........
H.tjapukai 6641              ...........................................t........................c...........
H.tytthognaphos 6346         ...........................................t........................c...........
H.tytthognaphos 6347         ...........................................t........................c...........
H.wallaman 6353              ...........................................t........................c...........
H.yelae 3007                 ...........................................t........................c...........
H.sp. WA 8017                ...........................................t........................c...........
H.sp. WA 8021                ...........................................t........................c...........
```

2.5.3 Aligned molecular sequences. Nuclear small-subunit ribosomal DNA 18S gene, base-pairs 1741–1761. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189               aaaagtcgtaacaaggtttcc
C.ochropus 6984               .....................
C.ochropus 9069               .....................
I.nitidus 9827                .....................
I.politus 1514                .....................
I.politus 3256                .....................
O.elatus 1837                 .....................
O.laevipes 1835               .....................
O.lecomtei 1608               .....................
O.lecomtei 2194A              .....................
O.madagascariensis 2800       .....................
O.madagascariensis 2811       .....................
O.madagascariensis 2812       .....................
O.piceus 6260                 .....................
H.infulcra 2185               .....................
L.australasiae 1854           .....................
L.australasiae 2181           .....................
L.australasiae 2182           .....................
L.australasiae 2183           .....................
L.australasiae 2729           .....................
L.australasiae 2733           .....................
L.australasiae 2996           .....................
L.australasiae 3684           .....................
L.australasiae 4764           .....................
L.australasiae 5553           .....................
L.australasiae 8676           .....................
L.australasiae 8677           .....................
L.longimanus 6388             .....................
L.malaya 1909                 .....................
H.aethes 3002                 .....................
H.aethes 3005                 .....................
H.anekasankylis 6355          .....................
H.anekasankylis 6356          .....................
H.anekasankylis 6357          .....................
H.ankistros 4339              .....................
H.bandjin 5556                .....................
H.bandjin 5557                .....................
H.bandjin 5558                .....................
H.caudicula 1502              ?????????????????????
H.caudicula 2339              .....................
H.caudicula 2340              .....................
H.caudicula 6360              .....................
H.caudicula 6361              .....................
H.caudicula 6362              .....................
H.chthamalochoros 6350        .....................
H.chthamalochoros 6351        .....................
H.chthamalochoros 6352        .....................
H.chthamalochoros 8023        .....................
H.chydaeostigmata 5560        .....................
H.chydaeostigmata 8015        .....................
H.chydaeostigmata 8016        .....................
H.chydaeostigmata 8019        .....................
H.chydaeostigmata 8020        .....................
H.chydaeostigmata 8022        .....................
H.dechangei 7789              .....................
H.euktaenospatha 4340         .....................
H.glaphyroscytos 6640         .....................
H.hylaios 6358                .....................
H.hylaios 6359                .....................
H.hylaios 6363                .....................
H.ischnoryctes 6639           .....................
H.kukunyungkal 6341           .....................
H.kukunyungkal 6342           .....................
H.kukunyungkal 6343           .....................
H.laevitropis 6348            .....................
H.leptochela 6344             .....................
H.leptochela 6345             .....................
H.litodactylus 5559           .....................
H.macrochela 5555             .....................
H.neocaledonicus 4323         .....................
H.neocaledonicus 5542         .....................
H.neocaledonicus 5543         .....................
H.neocaledonicus 5544         .....................
H.neocaledonicus 5545         .....................
H.neocaledonicus 5546         .....................
H.neocaledonicus 5547         .....................
H.neocaledonicus 5548         .....................
H.neocaledonicus 6224         .....................
H.nyawaygi 6354               .....................
H.papuanus 2718               .....................
H.papuanus 2725               ?????????????????????
H.papuanus 2726               .....................
H.papuanus 2727               .....................
H.penta 1817                  .....................
H.polisorum 1614              .....................
H.solomonensis 1818           .....................
H.solomonensis 1819           .....................
H.solomonensis 5549           .....................
H.solomonensis 5550           .....................
H.solomonensis 5551           .....................
H.solomonensis 5552           .....................
H.solomonensis 5554           .....................
H.tjapukai 2184               .....................
H.tjapukai 6641               .....................
H.tytthognaphos 6346          .....................
H.tytthognaphos 6347          .....................
H.wallaman 6353               .....................
H.yelae 3007                  .....................
H.sp. WA 8017                 .....................
H.sp. WA 8021                 .....................
```

2.5.3 Aligned molecular sequences. Nuclear large-subunit ribosomal DNA 28S gene, base-pairs 1–87. Dots indicate a match with the first taxon.


C.ochropus 2189
C.ochropus 6894
C.ochropus 9069
I.nitidus 9827
I.politus 1514
O.elatus 1837
O.laevipes 1835
O.lecomtei 1608
O.lecomtei 2194A
O.madagascariensis 2800
O.madagascariensis 2811
O.madagascariensis 2812
H.infulcra 2185
L.australasiae 1854
L.australasiae 2181
L.australasiae 2182
L.australasiae 2183
L.australasiae 2729
L.australasiae 2733
L.australasiae 2996
L.australasiae 3684
L.australasiae 4764
L.australasiae 5553
L.australasiae 8676
L.australasiae 8677
L.longimanus 6388
L.malaya 1909
H.aethes 3002
H.anekasankylis 6355
H.anekasankylis 6356
H.anekasankylis 6357
H.ankistros 4339
H.bandjin 5556
H.bandjin 5557
H.bandjin 5558
H.caudicula 1502
H.caudicula 2339
H.caudicula 2340
H.caudicula 6360
H.caudicula 6361
H.caudicula 6362
H.chthamalochoros 6350
H.chthamalochoros 6351
H.chthamalochoros 6352
H.chthamalochoros 8023
H.chydaeostigmata 5560
H.chydaeostigmata 8015
H.chydaeostigmata 8016
H.chydaeostigmata 8020
H.dechangei 7789
H.euktaenospatha 4340
H.hylaios 6358
H.hylaios 6359
H.hylaios 6363
H.ischnoryctes 6639
H.kukunuyungkal 6341
H.kukunuyungkal 6342
H.kukunuyungkal 6343
H.laevitropis 6348
H.leptochela 6344
H.leptochela 6345
H.litodactylus 5559
H.macrochela 5555
H.neocaledonicus 4323
H.neocaledonicus 5542
H.neocaledonicus 5543
H.neocaledonicus 5544
H.neocaledonicus 5545
H.neocaledonicus 5546
H.neocaledonicus 5547
H.neocaledonicus 5548
H.neocaledonicus 6224
H.papuanus 2718
H.papuanus 2725
H.papuanus 2726
H.papuanus 2727
H.penta 1817
H.polisorum 1614
H.solomonensis 1818
H.solomonensis 1819
H.solomonensis 5549
H.solomonensis 5550
H.solomonensis 5551
H.solomonensis 5552
H.solomonensis 5554
H.tjapukai 2184
H.tytthognaphos 6346
H.tytthognaphos 6347
H.yelae 3007
H.wallaman 6353

2.5.3 Aligned molecular sequences. Nuclear large-subunit ribosomal DNA 28S gene, base-pairs 88–174. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              cggcgtcgcctgcgttgggatccccggt-cccc-agggtccggggcgcaccaacggcccgtcccgtccgccacgtcggtgggacgga
C.ochropus 6894              ............................-....-............................................................
C.ochropus 9069              ............................-....-............................................................
I.nitidus 9827               ........................t..-....-....a.....................................g..............
I.politus 1514               ............................-tt..-.....................................t..............
O.elatus 1837                ........................t..-....-......g.............................t......a........
O.laevipes 1835              ............................-.g..-..a.g.....................t.......a..............
O.lecomtei 1608              ......t.....................-t...-....g.............................t......a........
O.lecomtei 2194A             ......t.....................-t...-....g.............................t......a........
O.madagascariensis 2800      ............................-....-............................................................
O.madagascariensis 2811      ............................-....-............................................................
O.madagascariensis 2812      ............................-....-............................................................
H.infulcra 2185              t.cg.c.....................ca..t.-t.c.........................c.....a...c...........
L.australasiae 1854          t.tt....t..................a..g.-t.c.........................t.....at..c...........
L.australasiae 2181          t.tt....t..................a..g.-t.c.........................t.....at..c...........
L.australasiae 2182          t.t.....t..................a..g.-t.c.........................a.....ac..c...........
L.australasiae 2183          t.tt....t..................a..g.-t.c.........................t.....at..c...........
L.australasiae 2729          t.tt....t..................a..g.-t.c.........................t.....at..c...........
L.australasiae 2733          t.tt....t..................a..g.-t.c.........................t.....at..c...........
L.australasiae 2996          t.tt....t..................a..g.-t.c.........................t.....at..c...........
L.australasiae 3684          t.tt....t..............t...a..g.-t.c.........................t.....ac..c...........
L.australasiae 4764          t.tt....t..................a..g.-t.c.........................t.....at..c...........
L.australasiae 5553          t.tt....t..................a..g.-t.c.........................t.....at..c...........
L.australasiae 8676          t.tt....t..................a..g.-t.c.........................t.....at..c...........
L.australasiae 8677          t.tt....t..................a..g.-t.c.........................t.....at..c...........
L.longimanus 6388            ..t.....t.c................a..g.a..a.........................t.....ac..c...c.......
L.malaya 1909                ..t.....t..................a..g.-t.c.........................t.....ac..c...........
H.aethes 3002                ..t........................a..g.-c.c.........................t.....ac..c...........
H.anekasankylis 6355         ..t........................a..g.-c.c.........................t.....ac..c...........
H.anekasankylis 6356         ..t........................a..g.-c.c.........................t.....ac..c...........
H.anekasankylis 6357         ..t........................a..g.-c.c.........................t.....ac..c...........
H.ankistros 4339             ..t........................a..g.-c.c.........................t.....ac..c...........
H.bandjin 5556               t.t........................a..g.-c.c.........................t.....ac..c...........
H.bandjin 5557               t.t........................a..g.-c.c.........................t.....ac..c...........
H.bandjin 5558               t.t........................a..g.-c.c.........................t.....ac..c...........
H.caudicula 1502             ..c..c....c................a..g.-c.c.........................ac..c...........
H.caudicula 2339             ..c..c....c................a..g.-c.c.........................ac..c...........
H.caudicula 2340             ..t..c.....................ca..g.-c.c.........................ac..c...........
H.caudicula 6360             ..t.....t..................a..-..ga-c.t...t.....................t......g.t.............
H.caudicula 6361             ..t........................ca..g.-c.c.........................t.....ac..c...........
H.caudicula 6362             ..t........................ca..g.-c.c.........................t.....ac..c...........
H.chthamalochoros 6350       ..t........................a..g.-c.c.........................t.....ac..c...........
H.chthamalochoros 6351       ..t........................a..g.-c.c.........................t.....ac..c...........
H.chthamalochoros 6352       ..t........................a..g.-c.c.........................t.....ac..c...........
H.chthamalochoros 8023       ..t........................a..g.-c.c.........................t.....ac..c...........
H.chydaeostigmata 5560       ..t........................ca..g.-c.c.........................t.....ac..c...........
H.chydaeostigmata 8015       ..t........................ca..g.-c.c.........................t.....ac..c...........
H.chydaeostigmata 8016       ..t........................ca..g.-c.c.........................t.....ac..c...........
H.chydaeostigmata 8020       ..t........................ca..g.-c.c.........................t.....ac..c...........
H.dechangei 7789             ..t........................ca..g.-c.c.........................t.....ac..c...........
H.euktaenospatha 4340        ..t........................a..g.-c.c.........................t.....ac..c...........
H.hylaios 6358               ..t........................a..g.-..c.........................t.....ac..c...........
H.hylaios 6359               ..t........................a..g.-..c.........................t.....ac..c...........
H.hylaios 6363               ..t........................a..g.-..c.........................t.....ac..c...........
H.ischnoryctes 6639          ..t......................c.ca..g.-c.c...g.....................t.....ac..c...........
H.kukunuyungkal 6341         ..t........................ca..g.-c.c.........................t.....ac..c...........
H.kukunuyungkal 6342         ..t........................ca..g.-c.c.........................t.....ac..c...........
H.kukunuyungkal 6343         ..t........................ca..g.-c.c.........................t.....ac..c...........
H.laevitropis 6348           ..t........................a..g.-c.c.........................t.....ac..c...c.......
H.leptochela 6344            ..t........................ca..g.-c.c.........................t.....ac..c...........
H.leptochela 6345            ..t........................ca..g.-c.c.........................t.....ac..c...........
H.litodactylus 5559          ..t........................a..g.-c.c.........................t.....ac..c...........
H.macrochela 5555            ..t........................a..g.-c.c.........................t.....ac..c...........
H.neocaledonicus 4323        ..t........................ca..g.-c.c.........................t.....ac..c...........
H.neocaledonicus 5542        ..t........................ca..g.-c.c.........................t.....ac..c...........
H.neocaledonicus 5543        ..t........................ca..g.-c.c.........................t.....ac..c...........
H.neocaledonicus 5544        ..t........................ca..g.-c.c.........................t.....ac..c...........
H.neocaledonicus 5545        ..t........................ca..g.-c.c.........................t.....ac..c...........
H.neocaledonicus 5546        ..t........................ca..g.-c.c.........................t.....ac..c...........
H.neocaledonicus 5547        ..t........................ca..g.-c.c.........................t.....ac..c...........
H.neocaledonicus 5548        ..t........................ca..g.-c.c.........................t.....ac..c...........
H.neocaledonicus 6224        ..t........................ca..g.-c.c.........................t.....ac..c...........
H.papuanus 2718              ..t........................ca..g.-c.c.........................t.....ac..c...........
H.papuanus 2725              ..t........................a..g.-c.c.........................t.....ac..c...........
H.papuanus 2726              ..t........................a..g.-c.c.........................t.....ac..c...........
H.papuanus 2727              ..t........................a..g.-c.c.........................t.....ac..c...........
H.penta 1817                 ..t........................ca..g.-c.c.........................t.....ac..c...........
H.polisorum 1614             ..tt...a.................t..ct..g.-c.c....a...t...........t.....t.....ac..ct....a......
H.solomonensis 1818          ..t........................a..g.-c.c.........................t.....ac..c...........
H.solomonensis 1819          ..t........................a..g.-c.c.........................t.....ac..c...........
H.solomonensis 5549          ..t........................a..g.-c.c.........................t.....ac..c...........
H.solomonensis 5550          ..t........................a..g.-c.c.........................t.....ac..c...........
H.solomonensis 5551          ..t........................a..g.-c.c.........................t.....ac..c...........
H.solomonensis 5552          ..t........................a..g.-c.c.........................t.....ac..c...........
H.solomonensis 5554          ..t........................a..g.-c.c.........................t.....ac..c...........
H.tjapukai 2184              ..t..c.....................a..g.-c.c.........................t.....ac..c...c.......
H.tytthognaphos 6346         ..t........................a..g.-c.c.........................t.....ac..c...........
H.tytthognaphos 6347         ..t........................a..g.-c.c.........................t.....ac..c...........
H.yelae 3007                 ..t........................a..g.-c.c.........................t.....ac..c...........
H.wallaman 6353              ..t........................a..g.-c.c.........................t.....ac..c...........
```

2.5.3 Aligned molecular sequences. Nuclear large-subunit ribosomal DNA 28S gene, base-pairs 175–261. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              gcgagagcgtacacgttgggacccgaaagatggtgaactatgcctgggcaggacgaggccagaggaaactctggtggaggtccgcag
C.ochropus 6894              ................................................................................
C.ochropus 9069              ................................................................................
I.nitidus 9827               ................................................................................
I.politus 1514               ................................................................................
O.elatus 1837                ................................................................................
O.laevipes 1835              ................................................................................
O.lecomtei 1608              ................................................................................
O.lecomtei 2194A             ................................................................................
O.madagascariensis 2800      ................................................................................
O.madagascariensis 2811      ................................................................................
O.madagascariensis 2812      ................................................................................
H.infulcra 2185              ................................................................................
L.australasiae 1854          ................................................................................
L.australasiae 2181          ................................................................................
L.australasiae 2182          ................................................................................
L.australasiae 2183          ................................................................................
L.australasiae 2729          ................................................................................
L.australasiae 2733          ................................................................................
L.australasiae 2996          ................................................................................
L.australasiae 3684          ................................................................................
L.australasiae 4764          ................................................................................
L.australasiae 5553          ................................................................................
L.australasiae 8676          ................................................................................
L.australasiae 8677          ................................................................................
L.longimanus 6388            ..........................................c.....................................
L.malaya 1909                ................................................................................
H.aethes 3002                ................................................................................
H.anekasankylis 6355         ................................................................................
H.anekasankylis 6356         ................................................................................
H.anekasankylis 6357         ................................................................................
H.ankistros 4339             ................................................................................
H.bandjin 5556               ................................................................................
H.bandjin 5557               ................................................................................
H.bandjin 5558               ................................................................................
H.caudicula 1502             ................................................................................
H.caudicula 2339             ................................................................................
H.caudicula 2340             ................................................................................
H.caudicula 6360             ................................................................................
H.caudicula 6361             ................................................................................
H.caudicula 6362             ................................................................................
H.chthamalochoros 6350       ................................................................................
H.chthamalochoros 6351       ................................................................................
H.chthamalochoros 6352       ................................................................................
H.chthamalochoros 8023       ................................................................................
H.chydaeostigmata 5560       ................................................................................
H.chydaeostigmata 8015       ................................................................................
H.chydaeostigmata 8016       ................................................................................
H.chydaeostigmata 8020       ................................................................................
H.dechangei 7789             ................................................................................
H.euktaenospatha 4340        ................................................................................
H.hylaios 6358               ................................................................................
H.hylaios 6359               ................................................................................
H.hylaios 6363               ................................................................................
H.ischnoryctes 6639          ................................................................................
H.kukunuyungkal 6341         ................................................................................
H.kukunuyungkal 6342         ................................................................................
H.kukunuyungkal 6343         ................................................................................
H.laevitropis 6348            ................................................................................
H.leptochela 6344            ................................................................................
H.leptochela 6345            ................................................................................
H.litodactylus 5559           ................................................................................
H.macrochela 5555            ................................................................................
H.neocaledonicus 4323        ................................................................................
H.neocaledonicus 5542        ................................................................................
H.neocaledonicus 5543        ................................................................................
H.neocaledonicus 5544        ................................................................................
H.neocaledonicus 5545        ................................................................................
H.neocaledonicus 5546        ................................................................................
H.neocaledonicus 5547        ................................................................................
H.neocaledonicus 5548        ................................................................................
H.neocaledonicus 6224        ................................................................................
H.papuanus 2718              ................................................................................
H.papuanus 2725              ................................................................................
H.papuanus 2726              ................................................................................
H.papuanus 2727              ................................................................................
H.penta 1817                 ................................................................................
H.polisorum 1614             .t.........t.........a.......................a.....................
H.solomonensis 1818          ................................................................................
H.solomonensis 1819          ................................................................................
H.solomonensis 5549          ................................................................................
H.solomonensis 5550          ................................................................................
H.solomonensis 5551          ................................................................................
H.solomonensis 5552          ................................................................................
H.solomonensis 5554          ................................................................................
H.tjapukai 2184              ................................................................................
H.tytthognaphos 6346         ................................................................................
H.tytthognaphos 6347         ................................................................................
H.yelae 3007                 ................................................................................
H.wallaman 6353              ................................................................................
```

2.5.3 Aligned molecular sequences. Nuclear large-subunit ribosomal DNA 28S gene, base-pairs 262–348. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              cgattctgacgtgcaaatcgatcgtcagacctgggtataggggcgaaagactaatcgaaccatctagttgctggttccctccgaagt
C.ochropus 6894              ..........................................................................................
C.ochropus 9069              ..........................................................................................
I.nitidus 9827               ..........................................................................................
I.politus 1514               ..........................................................................................
O.elatus 1837                ..........................................................................................
O.laevipes 1835              ..........................................................................................
O.lecomtei 1608              ..........................................................................................
O.lecomtei 2194A             ..........................................................................................
O.madagascariensis 2800      ..........................................................................................
O.madagascariensis 2811      ..........................................................................................
O.madagascariensis 2812      ..........................................................................................
H.infulcra 2185              ..........................................g.....a.....................................
L.australasiae 1854          ..........................................g.....a.....................................
L.australasiae 2181          ..........................................g.....a.....................................
L.australasiae 2182          ..........................................g.....a.....................................
L.australasiae 2183          ..........................................g.....a.....................................
L.australasiae 2729          ..........................................g.....a.....................................
L.australasiae 2733          ..........................................g.....a.....................................
L.australasiae 2996          ..........................................g.....a.....................................
L.australasiae 3684          ..........................................g.....a.....................................
L.australasiae 4764          ..........................................g.....a.....................................
L.australasiae 5553          ..........................................g.....a.....................................
L.australasiae 8676          ..........................................g.....a.....................................
L.australasiae 8677          ..........................................g.....a.....................................
L.longimanus 6388            ..........................................g.....a.....................................
L.malaya 1909                ..........................................g.....a.....................................
H.aethes 3002                ..........................................g.....a.....................................
H.anekasankylis 6355         ..........................................g.....a.....................................
H.anekasankylis 6356         ..........................................g.....a.....................................
H.anekasankylis 6357         ..........................................g.....a.....................................
H.ankistros 4339             ..........................................g.....a.....................................
H.bandjin 5556               ..........................................g.....a.....................................
H.bandjin 5557               ..........................................g.....a.....................................
H.bandjin 5558               ..........................................g.....a.....................................
H.caudicula 1502             ..........................................g.....a.....................................
H.caudicula 2339             ..........................................g.....a.....................................
H.caudicula 2340             ..........................................g.....a.....................................
H.caudicula 6360             ..........................................g.....a.....................................
H.caudicula 6361             ..........................................g.....a.....................................
H.caudicula 6362             ..........................................g.....a.....................................
H.chthamalochoros 6350       ..........................................g.....a.....................................
H.chthamalochoros 6351       ..........................................g.....a.....................................
H.chthamalochoros 6352       ..........................................g.....a.....................................
H.chthamalochoros 8023       ..........................................g.....a.....................................
H.chydaeostigmata 5560       ..........................................g.....a.....................................
H.chydaeostigmata 8015       ..........................................g.....a.....................................
H.chydaeostigmata 8016       ..........................................g.....a.....................................
H.chydaeostigmata 8020       ..........................................g.....a.....................................
H.dechangei 7789             ..........................................g.....a.....................................
H.euktaenospatha 4340        ..........................................g.....a.....................................
H.hylaios 6358               ..........................................g.....a.....................................
H.hylaios 6359               ..........................................g.....a.....................................
H.hylaios 6363               ..........................................g.....a.....................................
H.ischnoryctes 6639          ..........................................g.....a.....................................
H.kukunuyungkal 6341         ..........................................g.....a.....................................
H.kukunuyungkal 6342         ..........................................g.....a.....................................
H.kukunuyungkal 6343         ..........................................g.....a.....................................
H.laevitropis 6348           ..........................................g.....a.....................................
H.leptochela 6344            ..........................................g.....a.....................................
H.leptochela 6345            ..........................................g.....a.....................................
H.litodactylus 5559          ..........................................g.....a.....................................
H.macrochela 5555            ..........................................g.....a.....................................
H.neocaledonicus 4323        ..........................................g.....a.....................................
H.neocaledonicus 5542        ..........................................g.....a.....................................
H.neocaledonicus 5543        ..........................................g.....a.....................................
H.neocaledonicus 5544        ..........................................g.....a.....................................
H.neocaledonicus 5545        ..........................................g.....a.....................................
H.neocaledonicus 5546        ..........................................g.....a.....................................
H.neocaledonicus 5547        ..........................................g.....a.....................................
H.neocaledonicus 5548        ..........................................g.....a.....................................
H.neocaledonicus 6224        ..........................................g.....a.....................................
H.papuanus 2718              ..........................................g.....a.....................................
H.papuanus 2725              ..........................................g.....a.....................................
H.papuanus 2726              ..........................................g.....a.....................................
H.papuanus 2727              ..........................................g.....a.....................................
H.penta 1817                 ..........................................g.....a.....................................
H.polisorum 1614             ..........................................a....g.....a.....................................
H.solomonensis 1818          ..........................................g.....a.....................................
H.solomonensis 1819          ..........................................g.....a.....................................
H.solomonensis 5549          ..........................................g.....a.....................................
H.solomonensis 5550          ..........................................g.....a.....................................
H.solomonensis 5551          ..........................................g.....a.....................................
H.solomonensis 5552          ..........................................g.....a.....................................
H.solomonensis 5554          ..........................................g.....a.....................................
H.tjapukai 2184              ..........................................g.....a.....................................
H.tytthognaphos 6346         ..........................................g.....a.....................................
H.tytthognaphos 6347         ..........................................g.....a.....................................
H.yelae 3007                 ..........................................g.....a.....................................
H.wallaman 6353              ..........................................g.....a.....................................
```

2.5.3 Aligned molecular sequences. Nuclear large-subunit ribosomal DNA 28S gene, base-pairs 349–435. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              ttccctcaggatagctggtgctcgagggagtcagtctcatccggtaaagcgaatgattagaggccttggggccgaaacgacctcaac
C.ochropus 6894              ....................................................................................
C.ochropus 9069              ....................................................................................
I.nitidus 9827               ....................................................................................
I.politus 1514               ....................................................................................
O.elatus 1837                ....................................................................................
O.laevipes 1835              ....................................................................................
O.lecomtei 1608              ....................................................................................
O.lecomtei 2194A             ....................................................................................
O.madagascariensis 2800      ....................................................................................
O.madagascariensis 2811      ....................................................................................
O.madagascariensis 2812      ....................................................................................
H.infulcra 2185              ................c...................................................................
L.australasiae 1854          ................c...................................................................
L.australasiae 2181          ................c...................................................................
L.australasiae 2182          ................c...................................................................
L.australasiae 2183          ................c...................................................................
L.australasiae 2729          ................c...................................................................
L.australasiae 2733          ................c...................................................................
L.australasiae 2996          ................c...................................................................
L.australasiae 3684          ................c...................................................................
L.australasiae 4764          ................c...................................................................
L.australasiae 5553          ................c...................................................................
L.australasiae 8676          ................c...................................................................
L.australasiae 8677          ................c...................................................................
L.longimanus 6388            ................c...................................................................
L.malaya 1909                ................c...................................................................
H.aethes 3002                ................c...................................................................
H.anekasankylis 6355         ................c...................................................................
H.anekasankylis 6356         ................c...................................................................
H.anekasankylis 6357         ................c...................................................................
H.ankistros 4339             ................c...................................................................
H.bandjin 5556               ................c...................................................................
H.bandjin 5557               ................c...................................................................
H.bandjin 5558               ................c...................................................................
H.caudicula 1502             ................c...................................................................
H.caudicula 2339             ................c...................................................................
H.caudicula 2340             ................c...................................................................
H.caudicula 6360             ................c...................................................................
H.caudicula 6361             ................c...................................................................
H.caudicula 6362             ................c...................................................................
H.chthamalochoros 6350       ................c...................................................................
H.chthamalochoros 6351       ................c...................................................................
H.chthamalochoros 6352       ................c...................................................................
H.chthamalochoros 8023       ................c...................................................................
H.chydaeostigmata 5560       ................c...................................................................
H.chydaeostigmata 8015       ................c...................................................................
H.chydaeostigmata 8016       ................c...................................................................
H.chydaeostigmata 8020       ................c...................................................................
H.dechangei 7789             ................c...................................................................
H.euktaenospatha 4340        ................c...................................................................
H.hylaios 6358               ................c...................................................................
H.hylaios 6359               ................c...................................................................
H.hylaios 6363               ................c...................................................................
H.ischnoryctes 6639          ................c...................................................................
H.kukunuyungkal 6341         ................c...................................................................
H.kukunuyungkal 6342         ................c...................................................................
H.kukunuyungkal 6343         ................c...................................................................
H.laevitropis 6348           ................c...................................................................
H.leptochela 6344            ................c...................................................................
H.leptochela 6345            ................c...................................................................
H.litodactylus 5559          ................c...................................................................
H.macrochela 5555            ................c...................................................................
H.neocaledonicus 4323        ................c...................................................................
H.neocaledonicus 5542        ................c...................................................................
H.neocaledonicus 5543        ................c...................................................................
H.neocaledonicus 5544        ................c...................................................................
H.neocaledonicus 5545        ................c...................................................................
H.neocaledonicus 5546        ................c...................................................................
H.neocaledonicus 5547        ................c...................................................................
H.neocaledonicus 5548        ................c...................................................................
H.neocaledonicus 6224        ................c...................................................................
H.papuanus 2718              ................c...................................................................
H.papuanus 2725              ................c...................................................................
H.papuanus 2726              ................c...................................................................
H.papuanus 2727              ................c...................................................................
H.penta 1817                 ................c...................................................................
H.polisorum 1614             ................c...a................................................................
H.solomonensis 1818          ................c...................................................................
H.solomonensis 1819          ................c...................................................................
H.solomonensis 5549          ................c...................................................................
H.solomonensis 5550          ................c...................................................................
H.solomonensis 5551          ................c...................................................................
H.solomonensis 5552          ................c...................................................................
H.solomonensis 5554          ................c...................................................................
H.tjapukai 2184              ................c...................................................................
H.tytthognaphos 6346         ................c...................................................................
H.tytthognaphos 6347         ................c...................................................................
H.yelae 3007                 ................c...................................................................
H.wallaman 6353              ................c...................................................................
```

2.5.3 Aligned molecular sequences. Nuclear large-subunit ribosomal DNA 28S gene, base-pairs 436–522. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189              ctattctcaaactttcaatgggtgagaagtccggtttacgtgactgaagcccggacgattctcaggatgcgagtgcccagtgggcca
C.ochropus 6894              ....................................................................................
C.ochropus 9069              ....................................................................................
I.nitidus 9827               ....................................................................................
I.politus 1514               ....................a...............................................................
O.elatus 1837                ....................a...............................................................
O.laevipes 1835              ....................................................................................
O.lecomtei 1608              ....................a...............................................................
O.lecomtei 2194A             ....................a...............................................................
O.madagascariensis 2800      ....................................................................................
O.madagascariensis 2811      ....................................................................................
O.madagascariensis 2812      ....................................................................................
H.infulcra 2185              ....................a.............a.....................................................
L.australasiae 1854          ....................a.............a.....................................................
L.australasiae 2181          ....................a.............a.....................................................
L.australasiae 2182          ....................a.............a.....................................................
L.australasiae 2183          ....................a.............a.....................................................
L.australasiae 2729          ....................a.............a.....................................................
L.australasiae 2733          ....................a.............a.....................................................
L.australasiae 2996          ....................a.............a.....................................................
L.australasiae 3684          ....................a.............a.....................................................
L.australasiae 4764          ....................a.............a.....................................................
L.australasiae 5553          ....................a.............a.....................................................
L.australasiae 8676          ....................a.............a.....................................................
L.australasiae 8677          ....................a.............a.....................................................
L.longimanus 6388            ....................a.............a.....................................................
L.malaya 1909                ....................a.............a.....................................................
H.aethes 3002                ....................a.............a.....................................................
H.anekasankylis 6355         ....................a.............a.....................................................
H.anekasankylis 6356         ....................a.............a.....................................................
H.anekasankylis 6357         ....................a.............a.....................................................
H.ankistros 4339             ....................a.............a.....................................................
H.bandjin 5556               ....................a.............a.....................................................
H.bandjin 5557               ....................a.............a.....................................................
H.bandjin 5558               ....................a.............a.....................................................
H.caudicula 1502             ....................a.............a.....................................................
H.caudicula 2339             ....................a.............a.....................................................
H.caudicula 2340             ....................a.............a.....................................................
H.caudicula 6360             ....................a.............a.....................................................
H.caudicula 6361             ....................a..............t....................................................
H.caudicula 6362             ....................a..............t....................................................
H.chthamalochoros 6350       ....................a.............a.....................................................
H.chthamalochoros 6351       ....................a.............a.....................................................
H.chthamalochoros 6352       ....................a.............a.....................................................
H.chthamalochoros 8023       ....................a.............a.....................................................
H.chydaeostigmata 5560       ....................a..............t....................................................
H.chydaeostigmata 8015       ....................a..............t....................................................
H.chydaeostigmata 8016       ....................a..............t....................................................
H.chydaeostigmata 8020       ....................a.............t.....................................................
H.dechangei 7789             ....................a.............a.....................................................
H.euktaenospatha 4340        ....................a.............a.....................................................
H.hylaios 6358               ....................a.............a.....................................................
H.hylaios 6359               ....................a.............a.....................................................
H.hylaios 6363               ....................a.............a.....................................................
H.ischnoryctes 6639          ....................a..............t....................................................
H.kukunuyungkal 6341         ....................a..............t....................................................
H.kukunuyungkal 6342         ....................a..............t....................................................
H.kukunuyungkal 6343         ....................a..............t....................................................
H.laevitropis 6348            ....................a..............t....................................................
H.leptochela 6344            ....................a.............a.....................................................
H.leptochela 6345            ....................a.............a.....................................................
H.litodactylus 5559          ....................a.............a.....................................................
H.macrochela 5555            ....................a.............a.....................................................
H.neocaledonicus 4323        ....................a.............a.....................................................
H.neocaledonicus 5542        ....................a.............a.....................................................
H.neocaledonicus 5543        ....................a.............a.....................................................
H.neocaledonicus 5544        ....................a.............a.....................................................
H.neocaledonicus 5545        ....................a.............a.....................................................
H.neocaledonicus 5546        ....................a.............a.....................................................
H.neocaledonicus 5547        ....................a.............a.....................................................
H.neocaledonicus 5548        ....................a.............a.....................................................
H.neocaledonicus 6224        ....................a.............a.....................................................
H.papuanus 2718              ....................a.............a.....................................................
H.papuanus 2725              ....................a.............a.....................................................
H.papuanus 2726              ....................a.............a.....................................................
H.papuanus 2727              ....................a.............a.....................................................
H.penta 1817                 ....................a.............a.....................................................
H.polisorum 1614             ..........................a.....a...........a...a.....................................
H.solomonensis 1818          ....................a.............a.....................................................
H.solomonensis 1819          ....................a.............a.....................................................
H.solomonensis 5549          ....................a.............a.....................................................
H.solomonensis 5550          ....................a.............a.....................................................
H.solomonensis 5551          ....................a.............a.....................................................
H.solomonensis 5552          ....................a.............a.....................................................
H.solomonensis 5554          ....................a.............a.....................................................
H.tjapukai 2184              ....................a.............a.....................................................
H.tytthognaphos 6346         ....................a.............a.....................................................
H.tytthognaphos 6347         ....................a.............a.....................................................
H.yelae 3007                 ....................a.............a.....................................................
H.wallaman 6353              ....................a.............a.....................................................
```

2.5.3 Aligned molecular sequences. Nuclear large-subunit ribosomal DNA 28S gene, base-pairs 523–527. Dots indicate a match with the first taxon. (Continued)

```
C.ochropus 2189               ctttt
C.ochropus 6894               .....
C.ochropus 9069               .....
I.nitidus 9827                .....
I.politus 1514                .....
O.elatus 1837                 .....
O.laevipes 1835               .....
O.lecomtei 1608               .....
O.lecomtei 2194A              .....
O.madagascariensis 2800       .....
O.madagascariensis 2811       .....
O.madagascariensis 2812       .....
H.infulcra 2185               .....
L.australasiae 1854           .....
L.australasiae 2181           .....
L.australasiae 2182           .....
L.australasiae 2183           .....
L.australasiae 2729           .....
L.australasiae 2733           .....
L.australasiae 2996           .....
L.australasiae 3684           .....
L.australasiae 4764           .....
L.australasiae 5553           .....
L.australasiae 8676           .....
L.australasiae 8677           .....
L.longimanus 6388             .....
L.malaya 1909                 .....
H.aethes 3002                 .....
H.anekasankylis 6355          .....
H.anekasankylis 6356          .....
H.anekasankylis 6357          .....
H.ankistros 4339              .....
H.bandjin 5556                .....
H.bandjin 5557                .....
H.bandjin 5558                .....
H.caudicula 1502              .....
H.caudicula 2339              .....
H.caudicula 2340              .....
H.caudicula 6360              .....
H.caudicula 6361              .....
H.caudicula 6362              .....
H.chthamalochoros 6350        .....
H.chthamalochoros 6351        .....
H.chthamalochoros 6352        .....
H.chthamalochoros 8023        .....
H.chydaeostigmata 5560        .....
H.chydaeostigmata 8015        .....
H.chydaeostigmata 8016        .....
H.chydaeostigmata 8020        .....
H.dechangei 7789              .....
H.euktaenospatha 4340         .....
H.hylaios 6358                .....
H.hylaios 6359                .....
H.hylaios 6363                .....
H.ischnoryctes 6639           .....
H.kukunuyungkal 6341          .....
H.kukunuyungkal 6342          .....
H.kukunuyungkal 6343          .....
H.laevitropis 6348            .....
H.leptochela 6344             .....
H.leptochela 6345             .....
H.litodactylus 5559           .....
H.macrochela 5555             .....
H.neocaledonicus 4323         .....
H.neocaledonicus 5542         .....
H.neocaledonicus 5543         .....
H.neocaledonicus 5544         .....
H.neocaledonicus 5545         .....
H.neocaledonicus 5546         .....
H.neocaledonicus 5547         .....
H.neocaledonicus 5548         .....
H.neocaledonicus 6224         .....
H.papuanus 2718               .....
H.papuanus 2725               .....
H.papuanus 2726               .....
H.papuanus 2727               .....
H.penta 1817                  .....
H.polisorum 1614              .....
H.solomonensis 1818           .....
H.solomonensis 1819           .....
H.solomonensis 5549           .....
H.solomonensis 5550           .....
H.solomonensis 5551           .....
H.solomonensis 5552           .....
H.solomonensis 5554           .....
H.tjapukai 2184               .....
H.tytthognaphos 6346          .....
H.tytthognaphos 6347          .....
H.yelae 3007                  .....
H.wallaman 6353               .....
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 1–87. Dots indicate a match with the first taxon.

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O.laevipes 1835              gactatatatttaatttttaggggggtgagcttctatagttggaacggctttgagattgatgattcgggttgaggtagggagaccagg
C.ochropus 2189              t.................g..t..t........g....a..g..t..g.......a..a.....t.......g.......t..
C.ochropus 9069              t.................g..t..t........g....a..g..t..g..a.......a.....t.......g.......t..
I.nitidus 9827               ????????????????????????????????????????????????????????????????????????????????????
I.politus 1514               ......g....g....ag..a..t..g.......g.............a....at.......t..a....g..a..t..t..
I.politus 3256               ????????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                .....................a.................a..g..t.....................a.g......g.........
O.lecomtei 1608              t.....g.............a..a..........g.......t.......t..a.......a..g.....c.......t..
O.lecomtei 2194A             t.....................a.................g..t....a..t..a.......t.......t..a....g..
O.madagascariensis 2800      t.....g....g..........t.............a..t..t..g..a.....a..a.....t..c.....t.......t..
O.madagascariensis 2812      t.....g....g..........t.............a..t..t..g..a.....a..a.....t..c..a..t.......t..
O.madagascariensis 2811      t..g..g....g.......a..t.............a..t..t....a....a..a.....t..a....c..a....t..
O.piceus 6260A               t.....g.....g......t.....................g.t.....a..ta.a..a.....t.c...at....a..t.gt..
H.infulcra 2185              a...........g.......t..a..g...g....g.....t.tt........a....a.....a.c....t.g..a..t..t..
L.australasiae 1854          ......g.............a..t..g..gg....g........tt........a..........t.cg...t....a....t..
L.australasiae 2181          ......g.............a..t..g..gg..........t..tt....a...a.a..a......ca...t.g.......t..
L.australasiae 2182          a.....g..............t.....gg..........g..tt....a..ta.a..........cg...t.g..a.......
L.australasiae 2183          ......g.............a..t..g..gg..........t..tt....a...a.a..a.....a.ca...t.g.......t..
L.australasiae 2729          ......g.............a..t..g..gg..........t..tt....a...a.a..a......ca...t.g.......t..
L.australasiae 2733          ......g.............a..t..g..gg..........t..tt....a...a.a..a......ca...t.g.......t..
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          t..........g.....g..t..t.....ag....g.....g..tt....a..ta.a..........ca...t..........t..
L.australasiae 4764          ......g.............a..t..g..gg..........t..tt....a...a.a..a......ca...t.g....t...t..
L.australasiae 5553          ......g.............a..t..g..gg..........t..tt....a...a.a..a......ca...t.g.......t..
L.australasiae 8676          ......g.............a..t..g..gg....g.....t..tt....a...a.a..a......ca...t.g.......t..
L.australasiae 8677          ......g.............a..t..g..gg....g.....t..tt....a...a.a..a......ca...t.g.......t..
L.longimanus 6388            ????????????????????????????????????????????????????????????????????????????????????
L.malaya 1909                t.....g.....gg..........t......g.a..g.....g..tt....a...a..t..g.g....c....t.......c..c..
H.aethes 3002                c............g..cac..a..t....g.g.a.a..ag..g..tt....a...a..........a.c....t.g.....t..t..
H.aethes 3005                ......g.....gg....g..a..t....g.g.a.....g..g..tt....a...a..........a.c....t.g.....t..t..
H.anekasankylis 6355         ......g.....gg..........t....g.g.a..g..a..g..tt....a...a.a.......a.c...at.g..a..t..t..
H.anekasankylis 6356         a.-.g.......gg..........t....g.g.a..gt.g..g..tt....a...a.a.......a.c....t.......t..t..
H.anekasankylis 6357         ????????????????????????????????????????????????????????????????????????????????????
H.ankistros 4339             a..a..g.....gg.......a..t..g.g.g.....g..g..g..tt........a..........a.c...at.......t..t..
H.bandjin 5556               a...........g.....g..a..t....g.g.a..g..a.....tt........a.a........a.c...at.g..a..t..t..
H.bandjin 5557               a...........g.....g..a..t....g.g.a..g..g.....tt........a.a........a.c...at.g..a..t..t..
H.bandjin 5558               a...........gg....g..a..t....g.g.a..g..g.....tt........a.a........a.c...at.g..a..t..t..
H.caudicula 1502             a...........gg....g.....t....gag.a.....g..g..tt........a.a..a.....a.c....t.g.....t..t..
H.caudicula 2339             t...........g.....g.....t....g.g.a.....a..g..tt....a..ta.a..a.....a.c....t.......t..t..
H.caudicula 2340             a.....g..c..t........a..t..g.ggg.a..g..a..ggttt........a....a....a.....t.......t..t..
H.caudicula 6360             a.....g.....gg....g.....t....gag.a.....a..t..tt....a...a....a.....a.c....t.g.....t..t..
H.caudicula 6361             a...........gg....g.....t....gag.a.....g.....tt........a.a..a.....a.c....t.g.....t..t..
H.caudicula 6362             a...........gg....g.....t....gag.a.....g..g..tt........a.a..a.....a.c....t.g.....t..t..
H.chthamalochoros 6350       a.....g.....gg..........t....g.g.a..g..a.....tt........a.a........a.c...at.g.....t..t..
H.chthamalochoros 6351       a.....g.....gg...ag.....t....g.g.a..g..a.....tt........a.a........a.c...at.g.....t..t..
H.chthamalochoros 6352       a.....g.....gg..........t....g.g.a..g..a.....tt........a.a........a.c...at.g.....t..t..
H.chthamalochoros 8023       a.....g.....gg..........t....g.g.a..g..a.....tt........a.a........a.c...at.g.....t..t..
H.chydaeostigmata 5560       a.....g.....g..........t....gag.a..gt.....gttt........a.a..a.....a.c...at.......t..t..
H.chydaeostigmata 8015       a.....g.....g.......t..t....gag.a..g......gttt........a.a..a.......c...at.......t..t..
H.chydaeostigmata 8016       a.....g.....g.......t..t....gag.a..g......gttt........a.a..a.......c...at.......t..t..
H.chydaeostigmata 8019       a.....g.....g..........t....gag.a..g......gttt........a.a..a.....a.c...at.......t..t..
H.chydaeostigmata 8020       a.....g.....g..........t....gag.a..g......gttt........a.a..a.....a.c...at.......t..t..
H.chydaeostigmata 8022       a.....g.....g.......t..t....gag.a..g......gttt........a.a..a.......c...at.......t..t..
H.dechangei 7789             a.....g..............a..t....g.g.a..g..a.....tt....a...a.a..a.....t.c....t....a..t..t..
H.euktaenospatha 4340        ......g.....gg..........t....g.g.g..g.....t..tt....a...a.........a.c....t....a.....g..
H.glaphyroscytos 6640        a.....g.....g....g..a..t..g.g.g.a.....a..g..tt........a....a.....a.c....t.g.....t..t..
H.hylaios 6358               a...........ggg.........t....g.gtg..g..a..g..tt....a...a.a........a.c...at.......ttt...
H.hylaios 6359               a.....g....agg..........c....g.gt...g..a.....tt....a...a.a........a.c...at.......ttt...
H.hylaios 6363               a...........gg..........t....g.gtg..g..a..g..tt....a...a.a........a.c...at.......ttt...
H.ischnoryctes 6639          a.....g.....gg.......a..t..g.g.g.a.....g..g..tt.......a.a..a.....a.c....t.g.....t..t..
H.kukunyungkal 6341          a............g....g.....t....g.g.g..g..g..g..tt....a...a.a........a.c....t.g..a..t..t..
H.kukunyungkal 6342          ????????????????????????????????????????????????????????????????????????????????????
H.kukunyungkal 6343          a...........g....g.....c....g.g.g..g..g..g..tt....-...a.a.....c..a.c....t.g..a..t..t..
H.laevitropis6348            a.....g.....gg.a........t....g.g.a..g..a..g..tt........a.a..a.....a.c....t....a..t..t..
H.leptochela 6344            t.....g......g..........t....gag.g..g..a...gttt........a.a........a.c...at.g.....t..t..
H.leptochela 6345            t.....g......g..........t....gag.g..g..a...gttt........a.a........a.c...at.g.....t..t..
H.litodactylus 5559          a.....g.....g.....g.....t....g.g.g..g..a...gttt....a...a.a........a.c....t.g..t..t..t..
H.macrochela 5555            a...g......ag.....g.....t....g.g.a.....a...gttt....a...a.a........a.c...at.g.....t..t..
H.neocaledonicus 4323        c.....g......g..c.t..a..t.....g....g..a..g..ct........a.a..........ca..at....a....t..
H.neocaledonicus 5542        t.....g.....gg..c.t..a..t......g....g..a..g..ct........a.a..........ca..at....a....t..
H.neocaledonicus 5543        t.....g.....gg.cc.g..a..t......g....g..a..g..ct........a.a..........ca..at....a....t..
H.neocaledonicus 5544        t.....g.....gg..c.g..a..t.....gg....g..a..t..tt........a.a..........cg..at.g..a....t..
H.neocaledonicus 5545        ......g.....gg..c.g.....t......g....g..a..g..ct........a.a..........ca...t....a....t..
H.neocaledonicus 5546        t.....g.....g...c.t.....t......g....g..a..g..ct.c......a.a..........ca..at....a....t..
H.neocaledonicus 5547        t...........a.g..c.c..a..t..g..ag....g..a..g..tt........a.a..a.....a.cg..at.g.......t..
H.neocaledonicus 5548        t............g..c.c..a..t..g..ag....g..a..g..tt........a.a..a.....a.cg..at.g.......t..
H.neocaledonicus 6224        t.....g.....gg..c.t.....t......g....g..a..g..ct........a.a..........ca...t....a....t..
H.nyawaygi 6354              a...........gg....g..a..t....g.g.a.....g.....tt........a.a........a.c...at.......t..t..
H.papuanus 2718              ????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2725              a.....g.....gg....g.....t....g.g....g..a..g..tt....a...a.a........a.....ac.t.....t..t..
H.papuanus 2727              a............g....g.....t....g.g....g..a..g..tt....a...a.a..........c....t.g..t..t..t..
H.penta 1817                 ???.c.......gg.g.a...t..t.....gg..g....a..g..tt........a.a..a.....a.c...at....a....t..
H.polisorum 1614             t.....g......g....g..t..t....g.g.c..g..g..g..tt.......ta.a..a.......c....t.......t.....
H.solomonensis 1818          t.....g.....gg....g.....t....g.g.a..g........tt.........a....a.....a.c....t....a..t..t..
H.solomonensis 1819          t.....g.....gg....g.....t....g.g.a..g........tt.c......a....a.....a.c....t....a..c..t..
H.solomonensis 5549          a...........gg..........t....g.g.g..g.....g..tt........a....a.....a.c....t.......t..t..
H.solomonensis 5550          a.....g.....gg....g.....t....g.g.a..g.....g..tt........a....a.....a.c...at.g.....t..t..
H.solomonensis 5551          ............gg....c.....t....g.g.ag.g.....g..tt........a....a.....a.c...at.g.....t..t..
H.solomonensis 5552          a...g.......gg....c.....t....g.g.ag.g.....g..tt........a....a.....a.c...at.g.....t..t..
H.solomonensis 5554          a.....g.....gg..........t....g.g.a..g.....g..tt........a....a.....a.c...at.g.....t..t..
H.tjapukai 2184              ......g.....gg.a........t....g.g.a..g..a.....tt....a...a.a.......a.c....t.g..a..t..t..
H.tjapukai 6641              a.....g.....gg.a........t....g.g.a..g..a.....tt....a...a.a........a.c....t.g..a..t..t..
H.tytthognaphos 6346         a.....g.....gg....g.....t....g.g.g..g..a...gttt....a...a.a........a.c....t....t..t..t..
H.tytthognaphos 6347         a.....g.....gg....g..a..t....g.g.g..g..a...gttt....a...a.a........a.c....c....t..t..c..
H.wallaman 6353              a.....g.....gg....g..a..t....g.g.c.....g..g..tt........a.a..a.......c...at.g..a..t..t..
H.yelae 3007                 ??????????????????????????????????????ag..g..tt........a.a..........c...at.......t..g..
H. sp. WA 8017               ......g..c..gg..............gag.a..g......gttt........a.a..........c...at.......t..t..
H. sp. WA 8021               ......g..c..gg..............gag.a..g......gttt........a.a..........c...at.......t..t..
```

2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 88–174. Dots indicate a match with the first taxon. (Continued)

```
O.laevipes 1835              ttctttcattggggatgatcagttgtataatgtggtagtaactgctcatgcttttgtaataatttttttttatggtcatgcctattat
C.ochropus 2189              ......t....t.....................a..t..t....a...........t..g.............a..........
C.ochropus 9069              ......t....t.....................a..t..t....a...........t..g.............a..........
I.nitidus 9827               ????????????????????????????????????????????????????????????????????????????????????????????????
I.politus 1514               ......t..............a.t........t..g..t....t...........g..g.............g..a.......
I.politus 3256               ????????????????????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                ......t..c..t.........g.t..c........g..g....g..........t..g.............t..........
O.lecomtei 1608              gg....t.....t.........a.t........t..t..t................t...........c.....g.....g.....
O.lecomtei 2194A             ag....t.....a.........a.t........t..t..t................c.............a..g..........
O.madagascariensis 2800      ......t.....t.....................a..g..t..a.............g...........a..a..a.......
O.madagascariensis 2812      ......t.....t.........c..........a..g..t..a.............g..g...........a..a..a..c.....
O.madagascariensis 2811      ......t.....t........a..a........a..g..t..g.............t.............a..a..........
O.piceus 6260A               a.....t.....t.......aa.t..........t..t.....g..........g...............t......g....
H.infulcra 2185              ......t.....t.........a.t.t........a.t........c...........g.....c...........a.....ag.g..
L.australasiae 1854          g..a..t..............aa.t..............t........c........g..g.............t......g.g..
L.australasiae 2181          a.....t..............aa.t........t.....t.................g..............t......g.g..
L.australasiae 2182          ......t..............a.t........t.....t.................t..g.............t.....gg.a..
L.australasiae 2183          a.....t..............aa.t........t..g..t..c..............................t......g.g..
L.australasiae 2729          a.....t..............aa.t........t..g..t.....................................t......g.g..
L.australasiae 2733          a.....t..............aa.t........t..g..t.....................................t......g.g..
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          g.....t..............a.t........t.....t.................t..............a..t..a...g.a..
L.australasiae 4764          a.....t..............aa.t........t..g..t...................g.............t......g.g..
L.australasiae 5553          a.....t..............aa.t........t..g..t.....................................t......g.g..
L.australasiae 8676          a.....t..............aa.t........t..g..t.....................................t......g.g..
L.australasiae 8677          a.....t..............aa.t........t..g..t.....................................t......g.g..
L.longimanus 6388            ????????????????????????????????????????????????????????????????????????????????????????????????
L.malaya 1909                g..g..t.....t.........a.t........aa.t..g.....................g...........a..t..a...g.g..
H.aethes 3002                c..a..t..............aa.t........t..t..t..a..c..c........g..............t..a..cg.g..
H.aethes 3005                c..a..t..............aa.t........t..t..t..a..c..c........g..............t..a..cg.g..
H.anekasankylis 6355         ...g..t.....t.......aa.t........t..t..g..a.............g..g...........t......g.g..
H.anekasankylis 6356         c..g..t.....t.........a.t........t..t..g..a.............t..............t......g.a..
H.anekasankylis 6357         ????????????????????????????????????????????????????????????????????????????????????????????????
H.ankistros 4339             ...a..t.....t........aa.t........t..t..t..g..c.....................................a......g.g..
H.bandjin 5556               ...g..t.....t..c.....aa.t........t..t.....g.........................a..a..a...g.a..
H.bandjin 5557               ...g..t.....t..c.....aa.t........t..t.....g.........................a..a..a...g.a..
H.bandjin 5558               ...g..t.....t..c.....aa.t........t..t.....g.........................a..a..a...g.a..
H.caudicula 1502             ......t.....t........aa.t........t..t.....g..g.....................a.........g.g..
H.caudicula 2339             ...g..t.....t........aa.t........t..t.....g.....................................t..a..cg.a..
H.caudicula 2340             ...g..t.....t........aa.t........t..t.....gt....................................a..t......g.a..
H.caudicula 6360             ...g..t.....t........aa.t........t..t..g..g..a..c.....................................t..a...g.a..
H.caudicula 6361             ...g..t.....t........aa.t........t..t.....a..a.....................................a..t..a...g.g..
H.caudicula 6362             ...g..t.....t........aa.t........t..t.....g..a.....................................a.....a...g.g..
H.chthamalochoros 6350       ...g..t.....t........aa.t........t..t.....a.....................................t..a...g.a..
H.chthamalochoros 6351       ...g..t.....t........aa.t........t..t.....a.....................................t..a..ag.a..
H.chthamalochoros 6352       ...g..t.....t........aa.t........t..t.....a.....................................t..a...g.a..
H.chthamalochoros 8023       ...g..t.....t........aa.t........t..t.....a.....................................t..a...g.a..
H.chydaeostigmata 5560       ...g..t.....t.........a.t........t..t.....g.............g...............t......g....
H.chydaeostigmata 8015       ...g..t.....t.........a.t........t..t.....g.............g...............t......g....
H.chydaeostigmata 8016       ...g..t.....t.........a.t........t..t.....g.............g...............t......g....
H.chydaeostigmata 8019       ...g..t.....t.........a.t........t..t.....g.............g...............t......g....
H.chydaeostigmata 8020       ...g..t.....t.........a.t........t..t.....g.............g...............t......g....
H.chydaeostigmata 8022       ...g..t.....t.........a.t........t..t.....g.............g...............t......g....
H.dechangei 7789             ......t.....t........aa.t..........g..c.....g..........g.............a..a......g.a..
H.euktaenospatha 4340        ...g..t.....t........a.t........t..t..g..a..g.....................................t......g.g..
H.glaphyroscytos 6640        ...g..t.....t........aa.t........t..t..g..g..g...........g..g.............t......g.a..
H.hylaios 6358               ...g..t..............aa.t........t..t.....g.............t..............a..t......g.g..
H.hylaios 6359               ...a..t.....a........aa.t........t..t.....................c.............t......g.g..
H.hylaios 6363               ...g..t..............aa.t........t..t.....g.............t..............a..t......g.g..
H.ischnoryctes 6639          ...g..t.....t........aa.t........t..t..g..g..g.......c..g..g.............t......g.g..
H.kukunyungkal 6341          ......t.....a........aa.t........t..t..g..g.............g..g...........a..t..a...g.g..
H.kukunyungkal 6342          ??????t...........a..ag.t...........t..g..g.............g..g...........a..t..a...g.g..
H.kukunyungkal 6343          c.....t..............aa.t........t..t..g..g.............g..g...........a..t..a...g.g..
H.laevitropis6348            ......t.....t........aa.t........t..t..g..a.............t..g...........t..a...g.g..
H.leptochela 6344            ...g..t..............aa.t........t..t..g..g.............g..g.............t......g.a..
H.leptochela 6345            ...g..t..............aa.t........t..t..g..g.............g..g.............t......g.a..
H.litodactylus 5559          ...g..t...........c..aa.t........t..t..t..g.....................................t......g....
H.macrochela 5555            ...g..t.....t........aa.t........t..t.....g.............g..g.............t......g.g..
H.neocaledonicus 4323        ......t.....t.........a.t........ta.t.....a..a.................t..............a......g.g..
H.neocaledonicus 5542        c.....t.....t.........a.t........ta.t.....a..a.....................a..a......g.g..
H.neocaledonicus 5543        c.....t.....t.........a.t........ta.t.....a..a.....................a..a......g.g..
H.neocaledonicus 5544        c.....t.....t.........a.t........t..t.....a.....................a..g......g.g..
H.neocaledonicus 5545        ......t.....t.........a.t........ta.t.....a..a.....................a..a......g.g..
H.neocaledonicus 5546        ......t.....t.........a.t........ta.t.....a..a.....................a..a......g.g..
H.neocaledonicus 5547        ......t..............a.t........t..t.....a.....................t..............g..a...g.a..
H.neocaledonicus 5548        ......t..............a.t........t..t.....a.....................t..............g..a...g.a..
H.neocaledonicus 6224        ......t.....t.........a.t........ta.t.....a..a.....................a..a......g.g..
H.nyawaygi 6354              ...g..t.....t.........a.t........t..t.....g.....................g..............a..t..a...g.a..
H.papuanus 2718              ????????????????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2725              ...g..t..............a.t........ta.t..g..g.............t..................t......g.g..
H.papuanus 2727              ...g..t.....a........a.t..c......a.t.....g.....c........t..g.............t..a...g.g..
H.penta 1817                 ......t.....t.........a.t........ta.t..t..g.............t..............a..a..a...g....
H.polisorum 1614             g.....t..............g.t........t..t..t..g.....................g..............t..a...g.g..
H.solomonensis 1818          ...g..t.....t.........a.t........t..t.....a.....c........t..................t......g.g..
H.solomonensis 1819          ...g..t.....t.........a.t........t..t.....a.....c........t..................t......g.g..
H.solomonensis 5549          ...g..t..............a.t.....c..t..t.....g.............t..g..............t..a...g.a..
H.solomonensis 5550          ...g..t..............a.t........t..t..g..a.............t..g..............t......g.g..
H.solomonensis 5551          ...g..t..............a.t........t..t..g..a.............t..g..............t......g.g..
H.solomonensis 5552          ...g..t..............a.t........t..t..t..g.............t..g..............t......g.g..
H.solomonensis 5554          ...g..t..............a.t........t..t..t..g.............t..g..............t......g.g..
H.tjapukai 2184              ...g..t.....t........aa.t........t..t.....a.............g..............t......g.g..
H.tjapukai 6641              ...g..t.....t........aa.t........t..t.....a.............g..............t......g.g..
H.tytthognaphos 6346         ...g..t..............aa.t........t..t..g..g.............g..g............t......g.a..
H.tytthognaphos 6347         ...g..t..............aa.t........t..t..g..g.............g..g............t......g.a..
H.wallaman 6353              ...g..t.....t........aa.t........t..t.....a.....................................t......g.a..
H.yelae 3007                 c..a..t..............a.t........t..t..t..g.............t..g..............a......g.g..
H. sp. WA 8017               ...g..t.....t..c.....a.t........t..t.....g.............g..g..............t......g.g..
H. sp. WA 8021               ...g..t.....t..c.....a.t........t..t.....g.............g..g..............t......g.g..
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 175–261. Dots indicate a match with the first taxon. (Continued)

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O.laevipes 1835              gattggaggttttggaaattggctagttcctttaatgttgggggcgcctgatatggcttttccacgtttgaataatatgagattttg
C.ochropus 2189              a....g..a..........at.g..........a.......t.................t..a.....................
C.ochropus 9069              a....g.............at.g..........a.......t.......a.......t..a.....................
I.nitidus 9827               ????????????????????????????????????????????????????????????????????????????????????????
I.politus 1514               a....t..g..c.........t.g.......g....a....t..g....a..g....t..g.............c.....
I.politus 3256               ????????????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                a..a..t..g....g.....t.g..c..c..g.........t.................t....a..........t.....
O.lecomtei 1608              ......t.......g.....t.g....g.......a..a..t.......a.......t..g...................
O.lecomtei 2194A             a....t.......t....at.g....g.......a....t.......a.......t..g...................
O.madagascariensis 2800      ....................t.........g..a....a..a.......a.......t..g..........a.......
O.madagascariensis 2812      ......g.............t.........g.......a..a.......a.......t..g..........a.......
O.madagascariensis 2811      ......g.......t.....t.g.......g..........a.......a.......t..g...................
O.piceus 6260A               a....t..g.......c...t........c.t.......t..t.................t....a..........t.....
H.infulcra 2185              a....g.......g....at.g.......g....a....t.................g..g...................
L.australasiae 1854          ......g.......g.....t...a.............c.................g..g..a.......a.......
L.australasiae 2181          a.......g....t....at.........g..ac.....t.................g..........a.......
L.australasiae 2182          a....g.......g.....t.........g...c....a..t..g.............t..g...................
L.australasiae 2183          a.......g....t....at.........g..ac.a....t.................g..........a.......
L.australasiae 2729          a.......a....t....at.........g..ac.a....t.................g.......c..a.......
L.australasiae 2733          a.......g....t....at.........g..ac.a....t.................g..........a.......
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          .....g..g....g....at.........g..........t..g.............g..g...................
L.australasiae 4764          a.......g....t....at.........g..ac.....t.................g..........a.......
L.australasiae 5553          a.......g....t....a..........g..ac.a....t.................g..........a.......
L.australasiae 8676          a.......g....t....at.........g..ac.a....t.................g..........a.......
L.australasiae 8677          a.......g....t....at.........g..ac.a....t.................g..........a.......
L.longimanus 6388            ????????????????????????????????????????????????????????????????????????????????????????
L.malaya 1909                .....g..g....g.....t.g.............a....t.................t.....................
H.aethes 3002                a....g.......g....at...g....g..........t..g....a.......t..a..a.......a.......
H.aethes 3005                a....g.......g....at...g....g..........t..g....a.......t..a..a.......a.......
H.anekasankylis 6355         a....g..a....g.....t.g..a....g..a..a....t.................t.............a..t.....
H.anekasankylis 6356         a....g..a....g....at.g..g....g.......t..c..........a....t.................t.....
H.anekasankylis 6357         ????????????????????????????????????????????????????????????????????????????????????????
H.ankistros 4339             a....t.......g....at...a.......a..a....t.......a.......t....a..............
H.bandjin 5556               a.......a....g....at...g....g..........t.................t....a.......a..t.....
H.bandjin 5557               a.......a....g....at...g....g..........t.................t....a.......a..t.....
H.bandjin 5558               a.......a....g....at...g....g..........t.................t....a.......a..t.....
H.caudicula 1502             ......g..g....t....at...a.......a....a..a.......a.......t.................t.....
H.caudicula 2339             ...c..g..a....t....at...a....g..a..a....t.................t....a.......a..t.....
H.caudicula 2340             ......g..g....t.....t...a....g.......a..t..c.............t.................t.....
H.caudicula 6360             a.......g....t....at...g..c..........a..t.......a.......t....a.......a..t.....
H.caudicula 6361             ......g..g....t..c..at...a.......a....a..a.......a.......t.......c.......t.....
H.caudicula 6362             ......g..g....t....at...a.......a....a..a.......a.......t.................t.....
H.chthamalochoros 6350       ...c..g..g....g.....t...a....g.......a..t.................t....a.......a..t.....
H.chthamalochoros 6351       ........g....g....at...g....g..........t.................t....a.......a..t.....
H.chthamalochoros 6352       ...c..g..g....g.....t...a....g.......a..t.................t....a.......a..t.....
H.chthamalochoros 8023       ...c..g..g....g.....t...a....g.......a..t.................t....a.......a..t.....
H.chydaeostigmata 5560       ........g....g....at...a....g..........t....c..........t.................t.....
H.chydaeostigmata 8015       ........g....g.....t...a....g..........t....c..........t.................t.....
H.chydaeostigmata 8016       ........g....g.....t...a....g..........t....c..........t.................t.....
H.chydaeostigmata 8019       ........g....g....at...a....g..........t....c..........t.................t.....
H.chydaeostigmata 8020       ........g....g....at...a....g..........t....c..........t.................t.....
H.chydaeostigmata 8022       ........g....g.....t...a....g..........t....c..........t.................t.....
H.dechangei 7789             a............g....at.g..g.................t..g....a.......t.............c.....
H.euktaenospatha 4340        a....g..g...........t...a..g..g....a..t..t..g..........c..t.............a.......
H.glaphyroscytos 6640        ..............g.....t...a....g..........t.......a.......g...................
H.hylaios 6358               a....g..g....t.....t.........g..a..a..a..t.......a.......t....a.......a.......
H.hylaios 6359               a....t..g....t.....t.........g....a....t.......a.......t....a.......a.......
H.hylaios 6363               a....g..g....t.....t.........g..a..a..a..t.......a.......t....a.......a.......
H.ischnoryctes 6639          ......g.......g.....t...a....g....a..a..t.......a.......g...................
H.kukunyungkal 6341          ......g..g..........at...a....g..........t.......a.......t..a.........a.......
H.kukunyungkal 6342          ......g..g..........a....a....g..........t.......a.......t..a.........a.......
H.kukunyungkal 6343          ......g..g..........a....a....g..........t.......a.......t..a.........a.......
H.laevitropis6348            ......g..g....g.....t.g..g.................t.......a.......t.....................
H.leptochela 6344            a....g..g..........at...g....g..a....a..t.......a.......t.....................
H.leptochela 6345            a....g..g..........at...g....g..a....a..t.......a.......t.....................
H.litodactylus 5559          a....g..a....g.....t...g....g....a....a.......a.......t.....................
H.macrochela 5555            ......g..g..........at.g..a....g....a....t.......a....c..t....a..........t.....
H.neocaledonicus 4323        a.............t.....t.g..a....g..........t.......a.......t..g...................
H.neocaledonicus 5542        a.............t.....t.g.......g.......a..t.......a.......t..a...................
H.neocaledonicus 5543        a.............t.....t.g.......g.......c..t.......a.......t..a...................
H.neocaledonicus 5544        a.................at.g..........a....a..t.......a.......t..g..a................
H.neocaledonicus 5545        a.............t.....t.g.......g.......a..t.......a.......t..g...................
H.neocaledonicus 5546        a.............t.....t.g.......g.......a..t.......a.......t..a...................
H.neocaledonicus 5547        a....g.............t.........g....a..a..t.......a.......t..g...................
H.neocaledonicus 5548        a....g.............t.........g....a..a..t.......a.......t..g...................
H.neocaledonicus 6224        a.............t.....t.g.......g.......a..t.......a.......t..g...................
H.nyawaygi 6354              .....g..g....g.....t...a....g..a....a..t.............t....a.......a..t.....
H.papuanus 2718              ????????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2725              ......g..g..........at.........g..........t..g..c..a.......c.....a...............
H.papuanus 2727              a....g..a..........t.......a..........a..t..g....a.......t....a.......a.......
H.penta 1817                 .........a...........t.g.................t....c..........t..g..a...............
H.polisorum 1614             ......t..a..........at.g..a....g..a....a..t.................g..a.......a.......
H.solomonensis 1818          a.............t.....t.g.................c..a.......g....t....a..........t.....
H.solomonensis 1819          a.............t.....t.g.................c..a.......g....t....a..........c.....
H.solomonensis 5549          ......g.......t.....at...a....g..........t..g.............t....a..........t.....
H.solomonensis 5550          ......g.......t....at.g..a..g.......a....t..a....a.......t....a..........t.....
H.solomonensis 5551          ......g.......t....at.g..g..a.......a....t..a....a.......t....a..........t.....
H.solomonensis 5552          ..................at.g..g..g.............t..a....a.......t....a..........t.....
H.solomonensis 5554          ..................at.g..g..g.............t..a....a.......t....a..........t.....
H.tjapukai 2184              ......g..a..........t.g..c.......a..a..a..t.................t....a.......a..t.....
H.tjapukai 6641              ......g..a..........t.g..c.......a..a..a..t.................t....a.......a..t.....
H.tytthognaphos 6346         a....g..g..........at.g..g....g....a....t.......a.......t.....................
H.tytthognaphos 6347         a....g..a..........at...g....g....a....t.......a.......t.....................
H.wallaman 6353              a....g..a....g....at....c..c..g..a.......t.......a..a....t....a.......a..t.....
H.yelae 3007                 ......g..g....t.....t.g..g....g..a..a..a..t.g.............t.....................
H. sp. WA 8017               ......g..a..........at...g....g..........t.................t....a..........t.....
H. sp. WA 8021               ......g..a..........at...g....g..........t.................t....a..........t.....
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 262–348. Dots indicate a match with the first taxon. (Continued)

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O.laevipes 1835              gttgttgcctcctgctttttttctttttattaggatctgcttctttggaaagaggggctggaacggggtggactgtatatcctcctttt
C.ochropus 2189              a..ac.t..........c..........ga.t.....................a.....t..t.....a.....t.....a..g..
C.ochropus 9069              a..ac.t..........c..........ga.t..........a.............t..t.....a.....t.....a..g..
I.nitidus 9827               ????????????????????????????????????????????????????????????????????????????????????????
I.politus 1514               ...a.......a..g......t.........g..catg..g..a..g.......g..t..t..t.....a..g...........
I.politus 3256               ????????????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                ....c.t..a..g.......c...c.t..g..g..aatgg....a..g.......g..g..a..........c..c..g..cc.
O.lecomtei 1608              ....c.t......t..c.....t..c.t..g..g...ata.g.......................a.......g.....a..g..
O.lecomtei 2194A             ...a..a......t..c.....t..c.t.........atg.g...a.............g..t..t..a..........g.....
O.madagascariensis 2800      ......a.....c.....................g......g.....................t.......g..t..c.......
O.madagascariensis 2812      ...a..a.....c.....................g......g.....................t.......g..t...........
O.madagascariensis 2811      a.....a..................c.t..g..g......g.....................g..t..a.....g..t...........
O.piceus 6260A               a.....a..............c.............a..a.....a.......t.....g..t..a..a..........g.....
H.infulcra 2185              a..a........a.........t.a..g.....t.....a.a.....................t..t...........t...........
L.australasiae 1854          ...a................c.t.g..g..g..........g......g..t........t..t..t..a.....t...........
L.australasiae 2181          a..a................c.t.g.......g......g.....g.........t..t.....t..t.....t...........
L.australasiae 2182          a...................c.t.a.......t......g.....g..t........t..t..t..a.....t...........
L.australasiae 2183          a..a................c.t.g..g.....g......g.....g.........t..t.....t..t.....t...........
L.australasiae 2729          a..a................c.t.g..g.....g......g.....g.........t..t.....t..t.....t...........
L.australasiae 2733          a..a................c.t.g..g.....g......g.....g.........t..t.....t..t.....t...........
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          a..a..a..g..a......c.t.g..g.....t......g.....g..t..........t.....................a..
L.australasiae 4764          a..a................c.t.g.......g.a.....g.....t..........t..t.....t...........
L.australasiae 5553          a..a................c.t.g..g.....g......g.....g.........t..t.....t..t.....t...........
L.australasiae 8676          a..a................c.t.g..g.....g......g.....g.........t..t.....t..t.....t...........
L.australasiae 8677          a..a................c.t.g..g.....g......g.....g.........t..t.....t..t.....t...........
L.longimanus 6388            ????????????????????????????????????????????????????????????????????????????????????????
L.malaya 1909                ....................t.g..g..g..t......g.a.t..g.....t.....g..t..t..a..a..t.....a.....
H.aethes 3002                a...................t.g..g..g..g..a...a.........t..a..a..........a.....t...........
H.aethes 3005                a...................t.g..g..g..g..a...a.........t..a..a..........a.....t...........
H.anekasankylis 6355         ....................t.g.....g..g..a...a......g..t.....g.....a..t..a.....t.......g..
H.anekasankylis 6356         ...a..a.............t.g..g........a...a......g..t.............t..a.....g........g..
H.anekasankylis 6357         ????????????????????????????????????????????????????????????????????????????????????????
H.ankistros 4339             a..a..a..g.....a.....t.g...c....t.......a......g..t.....a.....a..t..a..g.............
H.bandjin 5556               ...a..a.....c.........t.g..g..g..g..g...a.........t.....g..g..a..t..a..a........a..g..
H.bandjin 5557               ...a..a.....c.........t.g..g..g..g..g...a.........t.....g..g..a..t..a..a........a..g..
H.bandjin 5558               ...a..a.....c.........t.g.....g..g..g...a.........t..a..g..g..a..t..a..a........a..g..
H.caudicula 1502             a..a..a.............t.g.....g..t..g...a.........t..a..g.....a..t..a.....t........a..
H.caudicula 2339             a..a..a.............t.g...c.g..g..g...a......g..t..a..g.....a..t..a.....c........a..
H.caudicula 2340             ...a................t.g..g........g.t..g.a...g..t..a..g.....a..t..a.....t........a..
H.caudicula 6360             ...a................t.a..........g...a.........t..a..g..g.....t..a.....t........a..
H.caudicula 6361             a..a..a.............t.g.....g..t..g...a.........t..a..g.....a..t..a.....t........ac.
H.caudicula 6362             a..a..a.............t.g.....g..t..g...a.........t..a..g.....a..t..a.....t........a..
H.chthamalochoros 6350       a..a........c.........t.g..g.....g..a...a.........t..a..g.....a..t.....a........g..g..
H.chthamalochoros 6351       ...a..a.....c.........t.g..g.....g..g...a.........t..a..g..g..a..t.....a........a..a..
H.chthamalochoros 6352       a..a........c.........t.g..g.....g..a...a.........t..a..g.....a..t.....a........g..g..
H.chthamalochoros 8023       a..a........c.........t.g..g.....g..a...a.........t..a..g.....a..t.....a........g..g..
H.chydaeostigmata 5560       ...a.....c..g.........t.g.......g..g...a......g..t..a..g..g.....t.......t........a..
H.chydaeostigmata 8015       ...a........g.........t.a.......g..g...a......g..t..a..g..g.....t.......t........a..
H.chydaeostigmata 8016       ...a........g.........t.a.......g..g...a......g..t..a..g..g.....t.......t........a..
H.chydaeostigmata 8019       ...a.....c..g.........t.g.......g..g...a.........t..a..g..g.....t.......t........a..
H.chydaeostigmata 8020       ...a.....c..g.........t.g.......g..g...a.........t..a..g..g.....t.......t........a..
H.chydaeostigmata 8022       ...a........g.........t.a.......g..g...a......g..t..a..g..g.....t.......t........a..
H.dechangei 7789             ......a.............t.g..g..g..t..g...a......g..t..t..a.......t..a..g..g.......g..
H.euktaenospatha 4340        ......a.............t.g.....g..c..a...a.........t..t.....g........a.....t.....c..g..
H.glaphyroscytos 6640        ...a..a.....a.........t.a..g........g...a...a..g..t.....a........t.......t........g..
H.hylaios 6358               ac..................t.a..........g...a.........c..a..g..g..a..t..a.....t........a..
H.hylaios 6359               a.....a.............t.a........g..g...a.........c..a.....g..a..t..a.....t........g..
H.hylaios 6363               ac..................t.a..........g...a......g..c..a..g..g..a..t..a.....t........a..
H.ischnoryctes 6639          ...a..a.....a.........t.a..g..g.....g...a...a..g..t.....a.......t.......t........g..
H.kukunyungkal 6341          a...c.a.............t.g..g.....g..g...a.........t.....a..g..a..t.......t........a..
H.kukunyungkal 6342          a.....a.............t.g..g.....g..g...a.........t.....a.....a..t.......t.....c..g..
H.kukunyungkal 6343          a.....a.............t.g..g.....g..g...a.........t.....a.....a..t.......t.....c..g..
H.laevitropis6348            a.....a.............t.a..g.....g..g...a.c.a.....t.....a.....a..t..a.....t........a..
H.leptochela 6344            ...a................t.a.....g..g..g...a......g..t.....a.....a..t..a..g..t........g..
H.leptochela 6345            ...a................t.a.....g..g..g...a......g..t.....a.....a..t..a..g..t........g..
H.litodactylus 5559          ...ac.a.............t.a..g..g.....g....a...a..g..t.....g..g..a..t..a.....t........
H.macrochela 5555            .........c..........t.g..g..g..g..g...a...a.....t..a..g........t..a.....t........ac.
H.neocaledonicus 4323        a...................t.g..g.....t..g....a.........t..t........t..a.....................
H.neocaledonicus 5542        a...................t.g........t..g...a.........t..t........t..a..a.....g...........
H.neocaledonicus 5543        a...................t.g........t..g...a.........t..t........t..a..a.....g...........
H.neocaledonicus 5544        a.....a.............t.g..g.....t..g....a.........t..t..c..t..t..a..a.....g...........
H.neocaledonicus 5545        a...................t.g........t..g...a.........t..t.....g..t..a..a.....g...........
H.neocaledonicus 5546        a..a................t.g........t..g...a.........t..t.....g..t..a..a.....g........cc.
H.neocaledonicus 5547        a.....a.............t.a........t..g....a.........t..t.....t..t..a..a.....g........cc.
H.neocaledonicus 5548        a.....a..a..........t.a........t..g...a.........t..t.....t..t..a..a.....g........cc.
H.neocaledonicus 6224        a...................t.g........t..g...a.........t..t.....g..t..a..a.....g...........
H.nyawaygi 6354              ...a.......a.........t.g.....g.....a....a.........t..a..g.........a..a.....t.......ac.
H.papuanus 2718              ????????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2725              a..a..a.............t.g..g..g..t..g...a......g..t..a..g........t........t...........
H.papuanus 2727              a.....a.............t.g..g.....t..a....a......g..t.....a.....a..t..a.....t...........
H.penta 1817                 a..a..a.................a..g..g..t..g...a......g..t.................a...............
H.polisorum 1614             ...a..a.............t.g..g.....t.......gg.....g.....a..g..g.....t........t...........
H.solomonensis 1818          a.....a.............t.g..g..g..t..g....a......g..t.....g..g..t..a...................
H.solomonensis 1819          a.....a.............t.g..g..g..t..g....a......g..t.....g..g..t..a...................
H.solomonensis 5549          ......a.............t.g..g..g..g..g...a......g..t..a..g..g..t..a.....g..t..c........
H.solomonensis 5550          ....................t.g..g..g.....g....a......g..t..a..g.....t..a.....t.....g.....
H.solomonensis 5551          ....................t.a..g..g..g..g...a......g..t..a..g..g..t..a.....t.....g.....
H.solomonensis 5552          a...................t.g..g..g.....g...a......g..t..a..g..g..t..a..a.....t...........
H.solomonensis 5554          a...................t.g..g..g.....g...a......g..t..a..g..g..t..a..a.....t...........
H.tjapukai 2184              ......a.............t.g..g..g.....g...a...a..g..t.....a.....a..t.....g........a..
H.tjapukai 6641              ......a.............t.g..g..g.....g...a...a..g..t.....a.....a..t.....g........a..
H.tytthognaphos 6346         a..a..a.............t.a..g..g..g..g...a...a..g..t.....a.....a..t..a.....t.....g..g..
H.tytthognaphos 6347         a..a..a.............t.a..g..g.....g...a...a..g..t.....a.....a..t..a.....t.....g..a..
H.wallaman 6353              ...a........c.........t.g.....g.....g...a.........t..t..g.....t..t.................g..
H.yelae 3007                 a.....a..c..........t.g..g..g..g..g...a..a.......a..a..g.....t..a.....t........c..
H. sp. WA 8017               a..a.....c..g.........t.g..g.....g..g...ac.....g..t..a..a..g.....t..a.....t........g..
H. sp. WA 8021               a..a.....c..g.........t.g..g.....g..g...ac.....g..t..a..a..g.....t..a.....t........g..
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 349–435. Dots indicate a match with the first taxon. (Continued)

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O.laevipes 1835              gtcttcttacatgtttcattcaggggttcagtagatatgactatttttttctttgcatttggctggggtttcatctattttgggggc
C.ochropus 2189              .........t.............t..g..t..g....a.............a............a....t..........t..
C.ochropus 9069              .........t..a..........t..g..t..g....a.............a............a....t..........t..
I.nitidus 9827               ????????????????????????????????????????????????????????????????????????????????????????
I.politus 1514               a......aga..a.......t..t....t..t....t..a.....................t....t..a.......t..
I.politus 3256               ????????????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                c.....c..tg.........g..a..g..t....c..a.............a..........t..g..t.......a....
O.lecomtei 1608              ........ct..a..........t..ag.t..t....t.....................a....a....t.......a....
O.lecomtei 2194A             a.......ct..a........g..t..ag.c..t....t.........................c..t.............
O.madagascariensis 2800      ......a..t..a.............g..t..t....a.............a....a......a....t..c.....a....
O.madagascariensis 2812      ......a..t.................g..t..t....a.............a....a.....a....t.......a....
O.madagascariensis 2811      a....a..t..............a..g..c..t....a.............a....a..........t.............
O.piceus 6260A               ...c.....t..a..............ag.g.......a..........a..a...........ta....t.......a..a..
H.infulcra 2185              .......ggg..a........t........t..g....a.............a.............g..t.......a....
L.australasiae 1854          .......gggt.a........t..t..g..t..t...................a...........t..g..t.......a..t..
L.australasiae 2181          .......gggt..........t..t.....t..t....a.............a..............t.......t..
L.australasiae 2182          .......gggt.a........t..c..g..t..t....a.............................t.......a..t..
L.australasiae 2183          .......gggt..........t..t.....t..t....a.............a.............a..t..........c..
L.australasiae 2729          .......gggt..........t..t.....t..t....a.............a.............a..t..........t..
L.australasiae 2733          .......gggt..........t..t.....t..t....a.............a.............a..t..........t..
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          a......ggg...........t..t..g..c..t....a.............a.............g..t.......a....
L.australasiae 4764          .....t.gggt.........gt..a.....t.gt....a.............a.........a....a..t.g.........t..
L.australasiae 5553          .......gggt..........t..t.....t..t....a.............a.............a..t..........t..
L.australasiae 8676          .......gggt..........t..t.....t..t....a.............a.............a..t..........t..
L.australasiae 8677          .......gggt..........t..t.....t..t....a.............a.............a..t..........t..
L.longimanus 6388            ????????????????????????????????????????????????????????????????????????????????????????
L.malaya 1909                a......ggg...........t.....a.....t.....................a.......g...c...c..g.....a....
H.aethes 3002                .......gga...........t........g..t....a...........g..a....a....a..g..t..a..........
H.aethes 3005                .......gga...........t........g..t....a...........g..a....a....a..g..t..a..........
H.anekasankylis 6355         .......gga..a........t..t.....t.....................................a....a..t..g.........
H.anekasankylis 6356         .......ggg..a........t..t..c..g..t.....................a..c.....g..a..g..t..a..........
H.anekasankylis 6357         ????????????????????????????????????????????????????????????????????????????????????????
H.ankistros 4339             a......gga..a...........c.....g..t.....................a..c.....g.....a..t..a........a..
H.bandjin 5556               .......gga...........t..t........t.....................a.......a....a..t..a........a..
H.bandjin 5557               .......gga...........t..t........t.....................a.......a....a..t..a........a..
H.bandjin 5558               .......gga...........t..t........t.....................a.......a....a..t..a........a..
H.caudicula 1502             a......gga..a........t..t.....g..t....a.............a...........a..a..t..g..........
H.caudicula 2339             .......ggg...........t..t.....g..t....a.............a.........g..a.....t..g.......a..
H.caudicula 2340             ......agga..a........t..t.....g..t......gt.....................c.....g..t..g........t.g
H.caudicula 6360             .......gga...........t..t.....g..t....a.............a.............g..t..g..........
H.caudicula 6361             a......gga..a........t..t.....g..t....a.............a...........a..a..t..g..........
H.caudicula 6362             a......gga..a........t..t.....g..t....a.............a...........a..a..t..g..........
H.chthamalochoros 6350       .......ggt..a........t..t........g...................a.......a....a..t..a........a..
H.chthamalochoros 6351       .......gga..a........t..t........t.....................a.....a..a....a..t..g..........
H.chthamalochoros 6352       .......ggt..a........t..t........g...................a.......a....a..t..a........a..
H.chthamalochoros 8023       .......ggt..a........t..t........g...................a.......a....a..t..a........a..
H.chydaeostigmata 5560       .......gga...........t..t.....g..t...................a.............a..t........a....
H.chydaeostigmata 8015       .......gga..a........t..t.....g..t....a.............a.............a..t........a....
H.chydaeostigmata 8016       .......gga..a........t..t.....g..t...................a.............a..t........a....
H.chydaeostigmata 8019       .......gga...........t..t.....g..t...................a.............a..t........a....
H.chydaeostigmata 8020       .......gga...........t..t.....g..t....a.............a.............a..t........a....
H.chydaeostigmata 8022       .......gga..a........t..t.....g..t...................a.............a..t........a....
H.dechangei 7789             .......gga...........t..a.......t.....a...........g..a.....a..g..a..a..t..a.....a..
H.euktaenospatha 4340        a....ggga.....c.............g..t.....a..a........g..a.....a..g..a..g..t........a..a..
H.glaphyroscytes 6640        .......ggg...........t..t.....t..t...................a.......g....g..t..g....a.....
H.hylaios 6358               a......ggg..a........t..t........t.....a.............a..c.....c........t..g.......a..
H.hylaios 6359               a......ggg...........t..t.......t.....a.............a.........a.....t..a........a..
H.hylaios 6363               a......ggg..a........t..t.......t.....a.............a..c.....c........t..g.......a..
H.ischnoryctes 6639          .......ggg...........t..t.....t..t...................a...c....g.....a..t..g....a.....
H.kukunyungkal 6341          a......gga...........t..........t.....................a....a....a..a..t..g..........
H.kukunyungkal 6342          a......gga...........t..........t.....................a...c.......a..a..t..g..........
H.kukunyungkal 6343          a......gga...........t..........t.....................a...c.......a..a..t..g..........
H.laevitropis6348            .......gga..a........t........g..t.................c.....c..a........g..t..a........
H.leptochela 6344            .......ggg...........t..t........t.............................a..a..t..a..........
H.leptochela 6345            .......ggg...........t..t........t.............................a..a..t..a..........
H.litodactylus 5559          .......gga...........t..a....g..t....a..c.......a..........g....g..t..g..........
H.macrochela 5555            .......gga..a........t........g..t....a.............a..c....g....g..t..a..........
H.neocaledonicus 4323        .......ggt..a........t..t........t....a.....................a.........t..g.....a..a..
H.neocaledonicus 5542        .......ggt...........t..t........t....a.............a....a..........t..g....a.....
H.neocaledonicus 5543        .......ggt...........t..t........t....a.............a....a..........t..g....a.....
H.neocaledonicus 5544        .......ggt..a........t..a........t.....................a.....................t..a.....a..
H.neocaledonicus 5545        .......ggt...........t..t........t....a.............a....a..........t..g....a.....
H.neocaledonicus 5546        .......ggt..a........t..t........t....a.............a....a..........t..g....a.....
H.neocaledonicus 5547        .......ggt..a........t..t........t....a.............a.....................t..g.....
H.neocaledonicus 5548        .......ggt..a........t..t........t....a.............a.....................t..g.....
H.neocaledonicus 6224        .......ggt...........t..t........t....a.............a....a..........t..g....a.....
H.nyawaygi 6354              a......gga...........t..t.....g..t....a.....................g.....g..g..a.....
H.papuanus 2718              ????????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2725              .......ggg...........g..c........t....a.....................g..a..g..t..a.....a..a..
H.papuanus 2727              ...g...gga...........g..........g.....................a.......g.....g..t..a..........
H.penta 1817                 .......gga...........t..t..c...........a............c.a.......g........t..a........a..
H.polisorum 1614             a......gga..a........t..t.....g..t....a.............a.......a.....g..t..............
H.solomonensis 1818          .......ggg..a........t.........g..t....a.....................g..a..g..t..a........a..
H.solomonensis 1819          .......ggg..a........t........g..t....a.....................g..a..g..t..a........a..
H.solomonensis 5549          .......gggg..........t...........t....a...........c..........g..a..g..t..a..........
H.solomonensis 5550          .......ggt...........t..a.....t..t....a.....................a.....g..t..a..........
H.solomonensis 5551          .......ggt...........t..a.....t..t.....................g........t..a........a..
H.solomonensis 5552          .......ggt...........t..a.....t..t....a.....................g..a..g..t..a..........
H.solomonensis 5554          .......ggt...........t..a.....t..t....a.....................g..a..g..t..a..........
H.tjapukai 2184              .......aga.....c.....t..t.....g..t...................a.......a.....g..t..g..........
H.tjapukai 6641              .......aga.....c.....t..t.....g..t...................a.......a.....g..t..g..........
H.tytthognaphos 6346         .......ggg...........t........g..t.................a.....c...........a..t..g..........
H.tytthognaphos 6347         .......ggg...........t........g..t.................a...............a..t..g........a..
H.wallaman 6353              a......gga..a........t..t.....g..t...................a.......a..a..g..t..a..........
H.yelae 3007                 .......gga...........t..t.....g..t.....................t......g.....a..t..a..........
H. sp. WA 8017               .......ggg...........t..t.....g..t.....................................a..g..t..........
H. sp. WA 8021               .......ggg...........t..t.....g..t.....................................a..g..t..........
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 436–522. Dots indicate a match with the first taxon. (Continued)

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O.laevipes 1835              tattaattttattactactattttaaatatgcgtagagaggggatgattttggatcgtgtacctctgtttgtttgatctgtaaaggt
C.ochropus 2189              .........................g........a....a..a..ag..........g..g...t..........g.....t.g...
C.ochropus 9069              .........................g........a....a..a..ag............g...t..........g..c..t.g...
I.nitidus 9827               ????????????????????????????????????????????????????????????????????????????????????
I.politus 1514               ...............a......g.g........g.....t......g.......g..g..t...t..........g.....t.t.a.
I.politus 3256               ????????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                .........................g.....a..a........a...cg.....g.....t...t..........g.....t.....
O.lecomtei 1608              .........................g.....a..............cc.a....g.....t...t.......g........ttt.a.
O.lecomtei 2194A             a.............................................tc.a...g.....t...t.......a..g.....ttt.a.
O.madagascariensis 2800      .........................g.................a........a........t...t.a.....g..g.....g..aa.
O.madagascariensis 2812      .........................g.........................a........t...t.a.....g..g.....g..aa.
O.madagascariensis 2811      .........................g.................a..........c.....t...t.a.....g..g.......g.a.
O.piceus 6260A               ...................a.................t........at.gc.t..a...a.....t.a.....a..g.......g...
H.infulcra 2185              ...................g...a.t........g.....t..a...cag........aa.t...t.......g........tgg...
L.australasiae 1854          ............c.........g.t.....a...g.g..a..a..ag.g.........a.t...t.a........g.....t.tt..
L.australasiae 2181          .......................a.t.....a...g.g.....a..a.............a.t...t.a........g.....tgct..
L.australasiae 2182          a.................a...a.t.........g.g.....a..ag.a.........a.t..at.......a..g.....tgct..
L.australasiae 2183          .......................a.t.........g.g.....a..a.............a.t...t.a........g.....tgct..
L.australasiae 2729          .......................a.t.....a...g.g.....a..a.............a.t...t.a........g.....tgct..
L.australasiae 2733          .......................a.t.....a...g.g.....a..a.............a.t...t.a........g.....tgct..
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          .......................g.t.........g.g..a..a..ag.g..a.....ga.t...t.a........g.....tgct..
L.australasiae 4764          .......................a.t.....a...g.g.....a..a.............a.t...t.a........g.....tgtt..
L.australasiae 5553          .......................a.t.....a...g.g.....a..a.............a.t...t.a........g.....tgct..
L.australasiae 8676          .......................a.t.....a...g.g..a..a..a.............a.t...t.a........g.....tgct..
L.australasiae 8677          .......................a.t.....a...g.g..a..a..a.............a.t...t.a........g.....tgct..
L.longimanus 6388            ????????????????????????????????????????????????????????????????????????????????????
L.malaya 1909                .........................g.g.....a........t..a..a...........g..t...t..........g.......tt..
H.aethes 3002                ...............a......g..........a.....a.....at.g.........a.t..gt.......a........tggaa.
H.aethes 3005                ...............a......g..........a.....a.....at.g.........a.t..gt.......a........tggaa.
H.anekasankylis 6355         .g.............g......g.g..c..a..a.....a.....t.g..........t...t.a.....a..g......gg.a.
H.anekasankylis 6356         .g.............g......g.g.....a..g..t........at.ac.a........t...t.......a........ggg.a.
H.anekasankylis 6357         ????????????????????????????????????????????????????????????????????????????????????
H.ankistros 4339             .........................g....c..a..a.....a......t.g..a......a.t..gt.......a..g.....gggaa.
H.bandjin 5556               a..............g......g.g........a............t.a........g..t..gt.......a..g......gg.a.
H.bandjin 5557               a..............g......g.g........a............t.a........g..t..gt.......a..g......gg.a.
H.bandjin 5558               a..............g......g.g........a............t.a........g..t..gt.......a..g......gg.a.
H.caudicula 1502             ...............g......g..........g........a..at.a..a......a.t..gt.......g........ggaa.
H.caudicula 2339             g...............g......g.t.....a..g........a...t.a..a......a.t..at.......g........ggg.a.
H.caudicula 2340             a..............g......g.g........g...........t.a..........t..gt.......g..g......gg.a.
H.caudicula 6360             a..............g......g.t........a........a...t.a.........a.t..at.......g........ggg.a.
H.caudicula 6361             ...............g......g.g........g........a..at.a..a......a.t..gt.......g........ggaa.
H.caudicula 6362             ...............g......g.g........g........a..at.a..a......a.t..gt.......g........ggaa.
H.chthamalochoros 6350       a..............g......g.g..c.....a........a..at.g...........t..gt.......g..g.....ggg.a.
H.chthamalochoros 6351       a..............g......g.g..c.....a...........ac.g...........t..gt.......g.......ggg.a.
H.chthamalochoros 6352       a..............g......g.g..c.....a........a..at.g...........t..gt.......g..g.....ggg.a.
H.chthamalochoros 8023       a..............r......g.g..c.....a........a..at.g...........t..gt.......g..g.....ggg.a.
H.chydaeostigmata 5560       g.....................g.g........ag....a..a...t.g..a........t..gt.......g..g..a...gg...
H.chydaeostigmata 8015       g.....................g.g........ag.......a...t.g..a........t..gt.......g..g......gg...
H.chydaeostigmata 8016       g.....................g.g........ag.......a...t.g..a........t..gt.......g..g......gg...
H.chydaeostigmata 8019       g.....................g.g........ag....a..a...t.g..a........t..gt.......g..g..a...gg...
H.chydaeostigmata 8020       g.....................g.g........ag....a..a...t.g..a........t..gt.......g..g..a...gg...
H.chydaeostigmata 8022       g.....................g.g........ag.......a...t.g..a........t..gt.......g..g......gg...
H.dechangei 7789             ...............g..g...g.g........a........a..at.a..a.....aa.t...t..............tgg.a.
H.euktaenospatha 4340        ...............g..g...g..........a............t.g........a.t..gt.a.....g..g.....tgg.a.
H.glaphyroscytos 6640        ...............g......g.t........a.....a..a...t.a.........a.t..at.a.....g..g.....tggaa.
H.hylaios 6358               ...............a......g.t........a...........at.gc.a......a.t...t.a.....g........tgg.a.
H.hylaios 6359               ...c...........a......g.t........a........a..at.g..a......a.t...t.a.....g........tgg.a.
H.hylaios 6363               ...............a......g.t........a...........at.gc.a......a.t...t.a.....g........tgg.a.
H.ischnoryctes 6639          ...............a......g.g........a.....a..a...t.a.........a.t..gt.a.....g..g.....tggaa.
H.kukunyungkal 6341          ...............g......g.......a..g...........at.g.........a.t..gt.......g........tgg.a.
H.kukunyungkal 6342          ...............g......g.......a..g...........at.g.........a.t..gt.......a........tgg.a.
H.kukunyungkal 6343          ...............g......g.......a..g...........at.g.........a.t..gt.......a........tgg.a.
H.laevitropis6348            ...c...........a......g..........g.....a......t.a.........a.t..gt.......a..g.....tgg.a.
H.leptochela 6344            ...............g......g.......a..a............t.g..a......a.t..gt.a........g.....tggaa.
H.leptochela 6345            ...............g......g.......a..a............t.g..a......a.t..gt.a........g.....tggaa.
H.litodactylus 5559          ...c...........g......g.......a..a....g......at.g...........t..gt.a.....a.........gg.a.
H.macrochela 5555            g..............a......g.g........a........a..at.a..a........c..gt.......g........ggg.a.
H.neocaledonicus 4323        a..............a......a.t.....................at.g.........a.t..at..........g.....ggga..
H.neocaledonicus 5542        ...............a......a.t.................a..at.g.........a.t..at................gga..
H.neocaledonicus 5543        ...............a......a.t.................a..at.g.........a.t..at................gga..
H.neocaledonicus 5544        ...............a......a.t.....a..a.....a..at.g.........a.c..at.a..............tgg...
H.neocaledonicus 5545        ...............a......a.t.....................at.g.........a.t..at..........g......gga..
H.neocaledonicus 5546        ...............a......a.t.....................at.g.........a.t..at..........g......gga..
H.neocaledonicus 5547        ...............a......a.t.....a...........a..at.a........aa.t..gt..........g......gga..
H.neocaledonicus 5548        ...............a......a.t.....a...........a..at.a........aa.t..gt..........g......gga..
H.neocaledonicus 6224        ...............a......a.t.....................at.g.........a.t..at..........g......gga..
H.nyawaygi 6354              a..............g......g.t........a.............t.g..............gt.......g.........ggaa.
H.papuanus 2718              ????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2725              ...c.....c.....a......g.t.....a..g............t.a..a......a.t..gt.a.....a..g......gg.a.
H.papuanus 2727              ...............a......g.g.......g.....a.....at.g........aa.t..gt.......a........tggaa.
H.penta 1817                 ...............a......a.t.....a..a........a...t.g.........a.t..gt.a.....a..g.....ggga..
H.polisorum 1614             ...............g..a...g.g........a........t...t.g..t.....ga.c..gt..........g.....ggg.a.
H.solomonensis 1818          ...............g..g...g.g........g.........a..at.a..a.....a.t..gt..................tggaa.
H.solomonensis 1819          ...............g..g...g.g........g........a..at.a.........a.t..gt..................tggaa.
H.solomonensis 5549          ...............a..g...g.g.....a..g............at.g..a......a.t..at.......g..g.....tgg.a.
H.solomonensis 5550          ...................a...g.c........g....g.......t.a..a.....aa.c..at.......g..g.....tggaa.
H.solomonensis 5551          ...............g..g...g.c........g....g.......t.a..a.....aa.t..ct.......g..g.....tggaa.
H.solomonensis 5552          ...............g..a...g.t........g............t.g..a.....aa.c..at.......g..g.....tggaa.
H.solomonensis 5554          ...............g..a...g.t........g............t.g..a.....aa.t..at.......g..g.....tggaa.
H.tjapukai 2184              ...............a......g.t........a............t.g..a........t..gt.......a..g.....tgg.a.
H.tjapukai 6641              ...............a......g.t........a............t.g..a........t..gt.......a..g.....tgg.a.
H.tytthognaphos 6346         ...............g......g.......a..g.....t.....at.a..........a.t..gt.a.....a..g.....tgg.a.
H.tytthognaphos 6347         ...............g......g.......a..g.....t.....at.a..........t..gt.a.....a..g.....tgg.a.
H.wallaman 6353              a..............g......g.......a..a............t.a..........t..gt.......g........ggg.a.
H.yelae 3007                 ...............a......g.........a.........a...t.g..a......a.t..gt.a.....g........tggaa.
H. sp. WA 8017               a.....................g.g........ag.......a..at.g..a........t..gt.......g..g.....ggga..
H. sp. WA 8021               a.....................g.g........ag.......a..at.g..a........t..gt.......g..g.....ggga..
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 523–609. Dots indicate a match with the first taxon. (Continued)

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O.laevipes 1835              tactgctattttgttgttgttgtctcttcctgttttagctggggctattactatattattgactgatcgaaatttttaatacttctttt
C.ochropus 2189              ............a....a.............g....g..t..........g..g..........g.................
C.ochropus 9069              ............a..a..a.............g....g..t..........g..g..........g.................
I.nitidus 9827               ????????????????????????????????????????????????????????????????????????????????????????????????
I.politus 1514               ...g...g.g..ac.t.........t.a.....g.....................c.t..a.......t.................
I.politus 3256               ????????????????????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                g.....................g.........g....g.............g..gc.........g.................
O.lecomtei 1608              ......a....a..a....a.......g....g...................g..........t..........a.....
O.lecomtei 2194A             ..............a..a..a.......g....g...................g..a.......g.................
O.madagascariensis 2800      ............c.t..a.....t.a.........a.........g....g....a.....................g..
O.madagascariensis 2812      ............c.t..a.....t.g..........a..t.......g....g....a.....................g..
O.madagascariensis 2811      ............c.t..a.....t.g.......g....a..........g..g..a..a....g.................
O.piceus 6260A               .......g.a..a..a..a..a...t.g..a..a.......t.............gc.t..g....t.................
H.infulcra 2185              g..g...g..c.t.....a..a...t.g.............a....c...................g.................
L.australasiae 1854          .......g..c.t..ac.t.................g..g.................g.......................a.....
L.australasiae 2181          g..a...g..c.c..ac.t..a.............g.................g..g....a.............c.......
L.australasiae 2182          g..g......c.t...c.t........c.....g..g.................g.......a....t..........a.....
L.australasiae 2183          g..a...g..c.c..ac.t..a.............g..........c....g..g....a.............c.......
L.australasiae 2729          g..a...g..c.a..ac.t..a.............g.................g..g....a.............c.......
L.australasiae 2733          g..a...g..c.c..ac.t..a.............g.................g..g....a.............c.......
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          a..g...g..c.t..ac.t.............g...................g..g..a..g....t..........a.....
L.australasiae 4764          g..a...g..c.c..ac.t..a.............g.................g..g....a.....................
L.australasiae 5553          g..a...g..c.c..ac.t..a.............g.................g..g....a.............c.......
L.australasiae 8676          g..a...g..c.c..ac.t..a.............g.................g..g....a.............c.......
L.australasiae 8677          g..a...g..c.c..ac.t..a.............g.................g..g....a.............c.......
L.longimanus 6388            ????????????????????????????????????????????????????????????????????????????????????????????????
L.malaya 1909                g.....g..c.t....a....gt.a....c..g..a.............gc.g..a.......g..........c.....
H.aethes 3002                .......g.gc.t..a.................g..g.................g..g....g.....................
H.aethes 3005                .......g.gc.t..a.................g..g.................g..g....g.....................
H.anekasankylis 6355         .........c.t.....................................g..g....a....g.....................
H.anekasankylis 6356         .........c.t..a..a.........................a..........g..g..a..a.....t.............
H.anekasankylis 6357         ????????????????????????????????????????????????????????????????????????????????????????????????
H.ankistros 4339             .........c.t.................c....g....a...................a....g.................
H.bandjin 5556               .......g..c.t....a.................g.................g....a..g.....................
H.bandjin 5557               .......g..c.t.....a................g.................g....a..g.....................
H.bandjin 5558               c......g..c.t....a.................g.................g....a..g.....................
H.caudicula 1502             .......g..c.t....a.................g....a....c.......g..a..a.............c.......
H.caudicula 2339             .......g..c.t.....a................g.................g..g..a..a....g....c...........
H.caudicula 2340             .........c.t....a..a...............g.................g..g....g.....................
H.caudicula 6360             .......g..c.t.......a..............g.................g..g..a..a....g.................
H.caudicula 6361             .......g..c.t....a.................g....a....c.......g..a..a.............c.......
H.caudicula 6362             .......g..c.t....a.................g....a....c.......g..a..a.............c.......
H.chthamalochoros 6350       .......g..c.t....a.................ga...a.................a..g.....................
H.chthamalochoros 6351       .......g..c.t..a..a................g....a.................a..g.....................
H.chthamalochoros 6352       .......g..c.t....a.................g....a.................a..g.....................
H.chthamalochoros 8023       .......g..c.t....a.................ga...a.................a..g.....................
H.chydaeostigmata 5560       .......g.cc.t..a..................g..a..a.........g..g..a..g....t.................
H.chydaeostigmata 8015       .......g.cc.t..a..................g....a.........g..g..a..g....t.................
H.chydaeostigmata 8016       .......g.cc.t..a..................g....a.........g..g..a..g....t.................
H.chydaeostigmata 8019       .......g..c.t..a..................g..a..a.........g..g..a..g....t..c.............
H.chydaeostigmata 8020       .......g..c.t..a..................g..a..a.........g..g..a..g....t.................
H.chydaeostigmata 8022       .......g.cc.t..a..................g....a.........g....a..g....t.................
H.dechangei 7789             .........c.t..a....a..............g.................g...c.a..g.....................
H.euktaenospatha 4340        .......g..c.t....a.....................................g..a..a....t.................
H.glaphyroscytos 6640        ......cg..c.t..a....a.............g....a....c....g..g....a.....................
H.hylaios 6358               .......g..c.t..a..a..a..........g..g.........c.............a.....................
H.hylaios 6359               .......g..c.t..a..a..a..........g.......a....c.............g.....................
H.hylaios 6363               .......g..c.t..a..a..a..........g..g.........c.............a.....................
H.ischnoryctes 6639          .......g..c.t.......a..................a....c....g..g....g.....................
H.kukunyungkal 6341          ......cg..c.t.......a.............g....a....c.............a....g.................
H.kukunyungkal 6342          .......g..c.t.......a.............g....a....c.............a....g.................
H.kukunyungkal 6343          .......g..c.t.......a.............g....a....c.............a....g.................
H.laevitropis6348            .......g..c.t..a....a.............g.................g..g..a..a....g.................
H.leptochela 6344            .......g..c.t..a..a..a.................g..a.................a..g....g.......c.......
H.leptochela 6345            .......g..c.t..a..a..a.................g..a.................a..g....g.......c.......
H.litodactylus 5559          .......g..c.t.......a.............g..a..a.................a..g....g.....................
H.macrochela 5555            ......a...c.t..a..a................g..g.............g..g....g.............c.......
H.neocaledonicus 4323        .........c.t.....................g..a.................g..a..g....t.................
H.neocaledonicus 5542        .........c.t.......a.............g..a.................a..g....t.....................
H.neocaledonicus 5543        .........c.t.......a.............g..a.................a..g....t.....................
H.neocaledonicus 5544        .........c.t.......a.............a.............g..g....g....t.........g....
H.neocaledonicus 5545        .........c.t.......a.............g..a.................a..g....t.....................
H.neocaledonicus 5546        .........c.t.......a.............g..g.................a..g....t.........c.....
H.neocaledonicus 5547        .........c.t..a..a..a.............g.............g..g....g....t.........a.....
H.neocaledonicus 5548        .........c.t..a..a..a.............g.............g..g....g....t.........a.....
H.neocaledonicus 6224        .........c.t.......a.............g..a.................a..g....t.....................
H.nyawaygi 6354              .......g..c.t..a..a..............g....a.........g....a..g....g.....................
H.papuanus 2718              ????????????????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2725              .......g..c.t.....................g.................ga.a..c.....t....c...c.........
H.papuanus 2727              .......g..c.t..a..a.............c..g....a.........g..gc....g.....c.....c...........
H.penta 1817                 .......g.gc.t.....a..a.............g.................g..g....g....t.....................
H.polisorum 1614             ......ag..c.t.....a..a..at.g.......g.................c....a.......g.....................
H.solomonensis 1818          .......g..c.t..a...c.a.................c.............g..g....g....t....c...........
H.solomonensis 1819          .......g..c.t..a....a.................c.............g..g....g....t.....c...........
H.solomonensis 5549          ...a...g..c.t..a..a.............................c.............a....g.................
H.solomonensis 5550          .......g..c.t..a..a.....................................g.......a.....................
H.solomonensis 5551          .......g..c.t..a..a.....................................g.......a.....................
H.solomonensis 5552          .......g..c.t..a..a.................................gc.......a.....................
H.solomonensis 5554          .......g..c.t..a..a.....................c.....gc.......a.....................
H.tjapukai 2184              .......g..c.t..a..a..a...t.a.......g.................g..g..a..g....g.................
H.tjapukai 6641              .......g..c.t..a..a..a...t.a.......g.................g..g..a..g....g.................
H.tytthognaphos 6346         .......g..c.t.....................g..g.................a..g....g.....................
H.tytthognaphos 6347         .......g..c.t.....................g..g.................a..g....g.....................
H.wallaman 6353              ......cg..c.t.................c....g.......a....t...g..g..a..g....g.....................
H.yelae 3007                 .......g..c.t.......a.............????????????????????????????????????????????????????
H. sp. WA 8017               .......g..c.t..a..................g..........c.......g..a..g.....t..c.....................
H. sp. WA 8021               .......g..c.t..a..................g..........c.......g..a..g.....t..c.....................
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 610–696. Dots indicate a match with the first taxon. (Continued)

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O.laevipes 1835              ttttgatccggctgggggaggggatcccattttgtaccagcatctgttctggtttttggtcatccggaggtatatattttgatttt
C.ochropus 2189              .........t....a..g..a..c..a........t......t.a..t??????????????????????????????????????
C.ochropus 9069              .........t....a..g..a....a........t..a...t.a..t..............t....g...........c.
I.nitidus 9827               ????????????????????????????????????????????????????????????????????????????????????
I.politus 1514               ............................t........t......t.a..t??????????????????????????????????
I.politus 3256               ????????????????????????????????????????????????????????????????????????????????????
O.elatus 1837                .........t..g..t..g..a..c..t....a....a...t....t.............c..t....t...........c.
O.lecomtei 1608              .........t..g..a..g........t........t......t.a..t..a...................t........a.....
O.lecomtei 2194A             .........t..g........t....t........t......t....t..a..........c..t..a..t........a.....
O.madagascariensis 2800      .........t..a....t.......t....a..t......t....t??????????????????????????????????????
O.madagascariensis 2812      .........t..a....t.......t....a..t......t....t??????????????????????????????????????
O.madagascariensis 2811      .........t..g....t.......t....a..t..a.......t??????????????????????????????????????
O.piceus 6260A               .........a..a..a..t.......t........t..a...t.a..t..........a.....t..a..g...........c.
H.infulcra 2185              .........t.............a..t...c.t..t..a...t.a..t..a.c...a........t..a..t........a.....
L.australasiae 1854          .........t.gg..t..t..a....t....a..t..a...t....t.................t....t.............
L.australasiae 2181          .........t.gg..t..t.......t....a..t..a...t.a..t.................t..a..t........a.....
L.australasiae 2182          .........t.g...t..t..t..........a..t..a...t....t..a.............t..a..t........a.....
L.australasiae 2183          .........t.gg..t..t.............a..t......t.a..t.................t..a..t........a.....
L.australasiae 2729          .........t.gg..t..t.......t....a..t......t.a..t??????????????????????????????????????
L.australasiae 2733          .........t.gg..t..t.......t....a..t......t....t??????????????????????????????????????
L.australasiae 2996          ????????????????????????????????????????????????????????????????????????????????????
L.australasiae 3684          c........t.g...t..t.......t.......t..a...t.a..t..a.............t....t.............
L.australasiae 4764          .........t.gg..t..t.......t....a..t......t.a..t.................t..a..t.............
L.australasiae 5553          .........t.gg..t..t.......t....a..t......t....t.................t..a..t.............
L.australasiae 8676          .........t.gg..t..t.......t....a..t......t.a..t.................t..a..t.............
L.australasiae 8677          .........t.gg..t..t.......t....a..t......t.a..t.................t..a..t.............
L.longimanus 6388            ????????????????????????????????????????????????????????????????????????????????????
L.malaya 1909                .........t..g..t..t.......t....a....a...t....t..a..........c..t....t.............
H.aethes 3002                .........t.................a....a..t..a...t....t.aa...a..........t..a..t.............
H.aethes 3005                .........t..........t....a....a.t.......t....t..a.............t....t.............
H.anekasankylis 6355         .........t....a..g....c..a....a..t..a...t.a..t..a.............t..a..t........a.....
H.anekasankylis 6356         ......c..t........t.......a........t..a...t....t..a.............t..a..t........a.....
H.anekasankylis 6357         ????????????????????????????????????????????????????????????????????????????????????
H.ankistros 4339             .........t....a..t..a....t....a..t......t....t.............c..t..a..t........a.....
H.bandjin 5556               .........t.......g..a....a........t..a...t.a..t.................t..a..t........a.....
H.bandjin 5557               .........t.......g..a....a........t..a...t.a..t.................t..a..t........a.....
H.bandjin 5558               .........t....a..g..a....a........t..a...t.a..t.................t..a..t........a.....
H.caudicula 1502             c........t....a..g..a....a........t..a...t.a..t.................t..a..t........a.....
H.caudicula 2339             .........t....a....a....a........t..a...t.a..t..a...........c..t..a..t........a.....
H.caudicula 2340             .........t........t..a....a........t..a...t....t..a...........c..t..a..t........a.....
H.caudicula 6360             .........t....a....a..c..a..........a...t.a..t.................t..a..t........a.....
H.caudicula 6361             c........t....a..g..a....a........t..a...t.a..t.................t..a..t........a.....
H.caudicula 6362             .........t....a..g..a....a........t..a...t.a..t.................t..a..t........a.....
H.chthamalochoros 6350       .........t.......g..a..c..a........t..a...t.a..t.................t..a..t..c.....a.....
H.chthamalochoros 6351       .........t.......g..a....a..........a...t.a..t.................t..a..t........a.....
H.chthamalochoros 6352       .........t.......g..a..c..a........t..a...t.a..t.................t..a..t..c.....a.....
H.chthamalochoros 8023       .........t.......g..a..c..a........t..a...t.a..t.................t..a..t..c.....a.....
H.chydaeostigmata 5560       .........t.......t.......t.......t..a...t.a..t.................t..a..t.............
H.chydaeostigmata 8015       ......c..t.......t.......t.......t..a...t.a..t.................t..a..t.............
H.chydaeostigmata 8016       ......c..t.......t.......t.......t..a...t.a..t.................t..a..t.............
H.chydaeostigmata 8019       .........t.......t.......t.......t..a...t.a..t.................t..a..t.............
H.chydaeostigmata 8020       .........t.......t.......t.......t..a...t.a..t.................t..a..t.............
H.chydaeostigmata 8022       .........t.......t.......t.......t..a...t.a..t.................t..a..t...g.........
H.dechangei 7789             .........t....a..........t.......t.....t...t..a.........a....t.....................
H.euktaenospatha 4340        .........c..........a....t....a..t..a...t....t..a...........t....g.............
H.glaphyroscytos 6640        ................g..a....g.......t......t...t.................t..a..t........a.....
H.hylaios 6358               .........t.......g..a....t....a..t..a...t....t.................t....t........a.....
H.hylaios 6359               .........a..........a..........a..t..a...t....t..a...........c..t..a..t.....c..a.....
H.hylaios 6363               .........t.......g..a....t....a..t..a...t.a..t.................t....t........a.....
H.ischnoryctes 6639          ................g..a....g..............t....t..a.............t..a..t........a.....
H.kukunyungkal 6341          .........t..a..t..g..a....a........t..a...t....t.................t..a..t........a.....
H.kukunyungkal 6342          .........t..a..t..g........a........t..a...t....t.................t..a..t........a.....
H.kukunyungkal 6343          .........t..a..t..g........a........t..a...t....t.................t..a..t........a.....
H.laevitropis6348            .........t..a..a....a....g....a..t..a...t....t..a...............t..a..t........a.....
H.leptochela 6344            .........t................a........t..a...t.a..t..a.............t..a..t........a.....
H.leptochela 6345            .........t................a........t..a...t.a..t..a.............t..a..t........a.....
H.litodactylus 5559          .........c..g........a..c..a........t......t....t..a...........t..a..t.....c..a.....
H.macrochela 5555            .........t.............c..a....a....a...t.a..t..a.............t..a..t..c.....a.....
H.neocaledonicus 4323        .........t....a..g.......t..c..a..t..a...t....t.............c..t....g.............
H.neocaledonicus 5542        .........t....a..........t....a..t..a...t....t..a...........c..t....g.............
H.neocaledonicus 5543        .........t....a..g....c..t....a..t..a...t....t..a...........c..t....g.............
H.neocaledonicus 5544        .........t....a..g..a..c..a....a..t..a...t....t.................t..a..g.............
H.neocaledonicus 5545        .........t....a..g........t....a..t..a...t....t..a.............t..a.......c.......
H.neocaledonicus 5546        .........t....a..g........t....a..t..a...t....t..a.............t....g....c.......
H.neocaledonicus 5547        .........t....a....a....t....a..t......t.a..t..........g..c..t..................
H.neocaledonicus 5548        .........t....a....a....t....a..t......t.a..t..........g..c..t..................
H.neocaledonicus 6224        .........t....a..g........t....a..t..a...t....t..a.............t..a.......c.......
H.nyawaygi 6354              .........t..........a....a........t..a...t.a..t..a.............a..a..t........a.....
H.papuanus 2718              ????????????????????????????????????????????????????????????????????????????????????
H.papuanus 2725              .........t..c..a..g........a........t..a...t....t??????????????????????????????????????
H.papuanus 2727              .........t..............c..a.....a..t..a...t.a..t..........g.....t..a..t.............
H.penta 1817                 .........t....a..g..t..c..a.....a..t......t.a..t..a........g.....t.....t.....c.......
H.polisorum 1614             .........t....a....a....a....a........t..a...t.a..t..a.............t.....t........a.....
H.solomonensis 1818          .........t........g..t..c..........t.....t....t..a........g.....t..a..t.............
H.solomonensis 1819          .........t........g..t..c..........t.....t....t..a........g.....t..a..t.............
H.solomonensis 5549          .........t....a..g..t.....t..............t....t..a.............t.....t.............
H.solomonensis 5550          .........t........g..t..............t.....t....t..............c..t.....t.............
H.solomonensis 5551          .........t....t....t....a........t......t....t..a.............t.....t.............
H.solomonensis 5552          .........t........g..c.....t........t.....t....t..a.............t.....t.............
H.solomonensis 5554          .........t........g..c.....t........t.....t....t..........a.....t.....t.............
H.tjapukai 2184              ......c..t.....t..g........a..........a...t.a..t.............a..t..a..t........a.....
H.tjapukai 6641              ......c..t.....t..g........a..........a...t.a..t.................t..a..t........a.....
H.tytthognaphos 6346         .........t.....a..g........a........t..a...t.a..t..a.............t..a..t........a.....
H.tytthognaphos 6347         .........c..c..............a........t..a...t.a..t..a.............t..a..t........a.....
H.wallaman 6353              .........t........g..a....a........t..a...t.a..t..a.............t..a..t........a.....
H.yelae 3007                 ????????????????????????????????????????????????????????????????????????????????????
H. sp. WA 8017               .........t..c.....t........t.......t..a...t.a..t..a.............c..a..t.............
H. sp. WA 8021               .........t..c.....t........t.......t..a...t.a..t..a.............c..a..t.............
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 697–783. Dots indicate a match with the first taxon. (Continued)

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O.laevipes 1835              accgggggtttggtatagtatctcatattattagacgtcatactggaaagaaggagccttttggggctttgggtatggtttatgctat
C.ochropus 2189              ????????????????????????????????????????????????????????????????????????????????????????????????????
C.ochropus 9069              t..t..a....g..g..t..g..........t.......g......g...a.......c.....a..a..a..a.......
I.nitidus 9827               ??????a....a....t..g..c.......t..a.......g.............a.....................
I.politus 1514               ??????a....g..ga.t.............t..........t...g...a.............a..a...a.........
I.politus 3256               ??????a....g..ga.t.............t..........t...g...a.............a..a...a.........
O.elatus 1837                t..t.......g..g..t.......c....c...t..........g.....................a.....................
O.lecomtei 1608              ...t..t....g....g.................a.......t.................a....a..g..aa......g..
O.lecomtei 2194A             ...t..t....g..g..g.................a.........g..g...a..c..........a..a..aa.........
O.madagascariensis 2800      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.madagascariensis 2812      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.madagascariensis 2811      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.piceus 6260A               t..a..t....c....t......g.a....t.a.......??????????????????????????????????????????????
H.infulcra 2185              ...t..c.....a...a.t......g..t.g..t.a.....ta.....a.g............t.t...a..a...........a..
L.australasiae 1854          g..t.......a..ga.t..g...g.gt.a..t.a...c.tg..t..a.....a..c.......t......a.............
L.australasiae 2181          ...t.......a...a.t......g.gt.a..t.a.....ta..g..a.g.............t...a..a..a.........
L.australasiae 2182          ...t.....c..g...a.t..g...g.at.a..t.a.....ta..g....g...a.........t......a.............
L.australasiae 2183          ...t.......a...a.t......g.gt.a..t.a.....ta..g..a.g...a.........t...a..a.............
L.australasiae 2729          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 2733          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 2996          ??????.....a...a.t......g.gt.a..t.a.....ta..g..a.g.............t...a..a..a.........
L.australasiae 3684          ...t..a....g..ga.t......g.at.a..c.a.....ta..g....g...a.........t.........a.........
L.australasiae 4764          ...t.......a...a.t......g.gt.a..t.a.....ta..g..a.g.............t...a..a..a.........
L.australasiae 5553          ...t.......a...a.t......g.gt.a..t.a.....ta..g..a.g.............t...a..a..a.........
L.australasiae 8676          ...t.......a...a.t......g.gt.a..t.a.....ta..g..a.g.............t...a..a..a.........
L.australasiae 8677          ...t.......a...a.t......g.gt.a..t.a.....ta..g..a.g....??????????????????????????????
L.longimanus 6388            ??????...c......a.t......g..t......a...c.tg..g.g..g.....g......tg..a.....a..g......t.
L.malaya 1909                g..t..a....a..ga.t......g..t....t.a.....ta....g.....a.........tg.....g..a.........
H.aethes 3002                ..at..a....g..ga.t..a......t.a..t...a...tg.....a..............tg..............a..
H.aethes 3005                ...t..a....g..ga.t..a......t.a..t...a...tg.....a..............tg..............a..
H.anekasankylis 6355         ...t..a....g...a.t.........t.a..t...a...tg..g..a.....a.........tg.....g...........
H.anekasankylis 6356         ...t.......g..ga.t.........t.g..c...a...tg..g..a.....a.......a.tg..a..g.....c.......
H.anekasankylis 6357         ??????a....g...a.t.........t.a..t...a...tg..g..a.....a..c.....tg.....g...........
H.ankistros 4339             g..t..a.........a.t.........t.g..t.a.a...ta..g..a.....a.........ta..a..a...........
H.bandjin 5556               ...t..a....g...a.t..c......t.g..t...a...tg......g...a.......a.ta.....g.....a.......
H.bandjin 5557               ...t..a....g...a.t..c......t.g..t...a...tg......g...a.......a.ta.....g.....a.......
H.bandjin 5558               ...t..a....g...a.t.........t.g..t...a...tg......g...a.......a.ta.....g.....a.......
H.caudicula 1502             ...t.....c..g..ga.t.........t.g..t...a...tg..g..a.....a.........tg.....a...........
H.caudicula 2339             ...t........g...a.t.........t.a..t...a...ta..g..a.....a..c.....a.tg.....g...........
H.caudicula 2340             ...t........g..ga.t.........t.g..t...ag..tg..g..a.....a.........tg.....a...........
H.caudicula 6360             g.....a.....a..ga.t.........t.g..t...a...tg..g..a..............tg.....g..a.........
H.caudicula 6361             ............g..ga.t.........t.g..t...a...tg..g..a.....a.........tg.....a...........
H.caudicula 6362             .........c..g..ga.t.........t.g..t...a...tg..g..a.....a.........tg.....a...........
H.chthamalochoros 6350       ...t..a....g...a.t.........t.g..t...a...ta..g..a.....a.........ta.....a..a..g.......
H.chthamalochoros 6351       ...t..a....g...a.t.........t.g..t...a...tg.....a.....a.......a.ta.....a..a..g.......
H.chthamalochoros 6352       ...t..a....g...a.t.........t.g..t...a...ta..g..a.....a.........ta.....a..a..g.......
H.chthamalochoros 8023       ...t..a....g...a.t.........t.g..t...a...ta..g..a.....a.........ta.....a..a..g.......
H.chydaeostigmata 5560       g..t........g...a.t.........t.g..t...a...tg..g..a..............a.tg.....a...........
H.chydaeostigmata 8015       g..t........g...a.t.........t.g..t...a...tg..g..a..............a.tgc....a...........
H.chydaeostigmata 8016       g..t........g...a.t.........t.g..t...a...tg..g..a..............a.tgc....a...........
H.chydaeostigmata 8019       g..t........g...a.t.........t.g..t...a...tg..g..a..............a.tgc....a...........
H.chydaeostigmata 8020       g..t........g...a.t.........t.g..t...a...tg..g..a......??????????????????????????????
H.chydaeostigmata 8022       g..t........g...a.t.........t.g..t...a...tg..g..a..............a.tg.....a...........
H.dechangei 7789             g.....a.....a..ga.t.........t.g..t.a.a...ta.....a........g..c..a.tg.....a...........
H.euktaenospatha 4340        g..........a..ga.t.........ct.g....a.a...tg..g...........c......tg..a.............a..
H.glaphyroscytos 6640        g..t........a...a.t.........t.g..t.a.a...ta..g..................tg.....a.....g.......
H.hylaios 6358               g..c..a.....a..ga.t.........t.g..t.a.a...tg..t..................tg..a...............
H.hylaios 6359               g..t........g..ga.t.........t.g..t.a.a...tg..t..a..............a.tg..................
H.hylaios 6363               g..........a..ga.t.........t.g..t.a.a...tg..t...........c.......tg..a...............
H.ischnoryctes 6639          g..t........a...a.t.........t.g..t.a.a...tg..g..................tg..a..a.....g..c.....
H.kukunyungkal 6341          ...t..a.....a..ga.t.........t.a..t.a.a...ta..g..a..............ta.....a.....g.......
H.kukunyungkal 6342          ...t..a.....a..ga.t.........t.a..t.a.a...ta..g..a..............ta.....a.....g.......
H.kukunyungkal 6343          ...t..a.....a..ga.t.........t.a..t.a.a...ta..g..a..............ta.....a.....g.......
H.laevitropis6348            g..t..a.....a...a.t.........t.a....a.a...tg..g..a........c.....a.ta..a..a..a.........
H.leptochela 6344            ...t..a.....a..ga.t.........t.g..c.a.a...ta.....a..............ta..a..g.............
H.leptochela 6345            ...t..a.....a..ga.t.........t.g..c.a.a...ta.....a..............ta..a..g.............
H.litodactylus 5559          g..t..a.....g...a.t.........t.g..t.a.a...tg..g..a..............tg.....a.............
H.macrochela 5555            g..t..a.....a...a.t.........t.g..t...a...tg..g..a..............a.tg.....g..a.........
H.neocaledonicus 4323        g..a.......a..ga.t.........t.a..t.a.a...tg..g....g...a.......a.ta.....g.............
H.neocaledonicus 5542        g..a..a.....a..ga.t.........t.a..t.a.a...tg......g...a..c.....a.ta.....g.............
H.neocaledonicus 5543        g..a..a.....a..ga.t.........t.a..t.a.a...tg......g...a..c.....a.ta.....g.............
H.neocaledonicus 5544        g.....a.....a..ga.t.........t.g..t.a.a...tg..................a.ta..a..a.............
H.neocaledonicus 5545        g..a..a.....a..ga.t.........t.a..t.a.a...tg..........a.......a.ta.....g.............
H.neocaledonicus 5546        g..a..a.....a..ga.t.........t.a..t.a.a...tg......g...a..c.....a.ta.....g.............
H.neocaledonicus 5547        ...a.......g...a.t.........t.g..t.a.a...ta..............c.......t...a..g..a.........
H.neocaledonicus 5548        ...a.......g...a.t.........t.g..t.a.a...ta..............c.......t...a..g..a.........
H.neocaledonicus 6224        g..a..a.....a..ga.t.........t.a..t.a.a...tg...........a.??????????????????????????????
H.nyawaygi 6354              ...t..a.....a...a.t.........t.g..t...a...tg..g..a.....a.........a.ta.....g.............
H.papuanus 2718              ??????a.....a..ga.t.........t.g..t.a.a...tg..g..a..............ta..a.............g..
H.papuanus 2725              ??????......a..ga.t.........t.a..t.a.a...tg..g....g...a.......a.ta.....g.............
H.papuanus 2727              g..t..a.....a...a.t.........t.g..c.a.a...tg..g.......a.........tg.....g.............
H.penta 1817                 g..a..a........ga.t..c......t.g....a.a...tg.....................ta.....a..a...........
H.polisorum 1614             g..t..a.....a..ga.t.........t.g..t...a...tg..t..a..............tg..a..a..a...........
H.solomonensis 1818          ............a..ga.t.........t.a..t.a.a...tg..g....g.............tac.................
H.solomonensis 1819          ............a..ga.t.........t.a..t.a.a...tg..g....g.............tac.................
H.solomonensis 5549          g..............ga.t.........t.g..t.a.a...tg..t....g............a.tg.............c.....
H.solomonensis 5550          g............a..ga.t.........t.a..t.a.a...ta..........................t.................
H.solomonensis 5551          g..........a..ga.t.........t.a....a.a...tg..g....g..............t...a.................
H.solomonensis 5552          g..a........a..ga.t.........t.a..t.a.a...tg.....................t...a.....a...........
H.solomonensis 5554          g..a........a..ga.t.........t.a..t.a.a...tg.....................t...a.................
H.tjapukai 2184              ...t..a.....a..ga.t.........t.g..t...a...tg..g..................a.tg.....a...........c..
H.tjapukai 6641              ...t..a.....a..ga.t.........t.g..t...a...tg..g..................a.tg.....a...........c..
H.tytthognaphos 6346         g..t........a..ga.t.........t.g....a.a...ta..g..a..............a.tg..a..g........c.....
H.tytthognaphos 6347         g..t..a.....a..ga.t.........t.g....a.a...ta..g..a..............a.tg..a..g........c.....
H.wallaman 6353              g..t........a.....t..c......t.g..t...a...tg...........a..........tg.....g..a...........
H.yelae 3007                 ????????????????????????????????????????????????????????????????????????????????????????????????????
H. sp. WA 8017               ...t..a.....g...a.t..g......t.g..t...a...ta..g..a..............a.tg.....g.............
H. sp. WA 8021               ...t..a.....g...a.t..g......t.g..t...a...ta..g..a..............a.tg.....g.............
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 784–870. Dots indicate a match with the first taxon. (Continued)

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O.laevipes 1835              ggtggctattgggtttttgggattcgttgtgtgggctcatcatatgtttactgttggtatggatgttgatactcgggcttattttac
C.ochropus 2189              ????????????????????????????????????????????????????????????????????????????????????????????????????
C.ochropus 9069              ...........a..........t..g.......................g..a.....................................
I.nitidus 9827               aa.t.......a....a..g..t....a...........a.......a.........g.......t..........
I.politus 1514               .a....g....a....a..g..t..g..t..........c.............g.................a..........
I.politus 3256               .a....g....a....a..g..t..g..t..........c.............g.................a..........
O.elatus 1837                a..a..a....a.....a.......g..t..g..t....g.......a.........a.......a.......a.........
O.lecomtei 1608              aa.................a..g..t..g..t.............a.......c..a.......g.....................
O.lecomtei 2194A             .a.........a.......g..t..g..t..a.........a.........a..a....g.....................
O.madagascariensis 2800      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.madagascariensis 2812      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.madagascariensis 2811      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.piceus 6260A               ????????????????????????????????????????????????????????????????????????????????????????????????????
H.infulcra 2185              ...t.........g.g........t.....t..a.....................a.................a..........
L.australasiae 1854          ...t........a..a..a..g..t....a..a..........a..........g.....................g..c.....
L.australasiae 2181          a..t........a..a..a..g..t.....t.....................g.......g.......a..g.......
L.australasiae 2182          a..t...........g....t..t....a.............a..........g..a.............a..a.......
L.australasiae 2183          a..t........a..a..a..g..t.....t.....................g.......g.......a..g.......
L.australasiae 2729          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 2733          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 2996          a..t........a..a..a..g..t.....t.....................g.......g.......a..g.......
L.australasiae 3684          ...t........a.?????????????????????????????????????????????????????????????????????????????????????
L.australasiae 4764          a..t........a..a..a..g..t.....t.....................g.......g.......a..g.......
L.australasiae 5553          a..t........a..a..a..g..t.....t.....................g.......g.......a..g.......
L.australasiae 8676          a..t........a..a..a..g..t.....t.....................g.......g.......a..g.......
L.australasiae 8677          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.longimanus 6388            ..............g..a..g..t.....t..a..........a..........a..a.....................................
L.malaya 1909                ...t..........g....g..t.....a..a.....................a..........a..........c........
H.aethes 3002                ............aa....a..g..t........a........c..a..........g..a.....g.......a..........
H.aethes 3005                ............aa.......g..t........a........c..a..........g..a.....g.......a..........
H.anekasankylis 6355         .........c..aa....a....t.....a.............................a.....g.......a..........
H.anekasankylis 6356         a....a....aa..........t.....................................g.......a..........
H.anekasankylis 6357         ............aa.c..a.....t.....................................a.....g.......a..........
H.ankistros 4339             .............a....a..g..t.....a..a.............................g.....................
H.bandjin 5556               ............aa.......g..t..g.....a..........a.....................a.......a..........
H.bandjin 5557               ............aa.......g..t..g.....a..........a.....................a.......a..........
H.bandjin 5558               ............aa.......g..t..g.....a..........a.....................a.......a..........
H.caudicula 1502             ............aa....a..g..t..a.....a..........a..c.................g.......a..........
H.caudicula 2339             ............aa.......g..t..a.....................a.....................g.....c..a..........
H.caudicula 2340             ...a.........a....a..g..ta.g..a..a.............................a.....g.......a..........
H.caudicula 6360             ...a.........a....a..g..t..a.....a..........a.....................g.....................
H.caudicula 6361             .........c..aa....a..g..t..a.....a..........a.....................g.......a..........
H.caudicula 6362             ............aa....a..g..t..a.....a..........a.....................g.......a..........
H.chthamalochoros 6350       ............aa....a..g..t..g.....a..c.......a.............a.....a.......a..........
H.chthamalochoros 6351       ............aa....a..g..t..g..a..a..c..c.....a.............a.....a.......a..........
H.chthamalochoros 6352       ............aa....a..g..t..g.....a..c.......a.............a.....a.......a..........
H.chthamalochoros 8023       ............aa....a..g..t..g.....a..c.......a.............a.....a.......a..........
H.chydaeostigmata 5560       ............aa.......g..t..g..a.......c.......c.......a..a.............a..........
H.chydaeostigmata 8015       ............aa.......g..t..g..a.................c.......a..a.............a..........
H.chydaeostigmata 8016       ............aa.......g..t..g..a.................c.......a..a.............a..........
H.chydaeostigmata 8019       ............aa.......g..t..g..a.................c.......a..a.............a..........
H.chydaeostigmata 8020       ????????????????????????????????????????????????????????????????????????????????????????????????????
H.chydaeostigmata 8022       ............aa.......g..t..g..a.................c.......a..a.............a..........
H.dechangei 7789             ...a.........ag....a.....t.......a..a.....................g.......g.......a.......c..
H.euktaenospatha 4340        a....a....aa.......g..........a..c..c.....a....a?????????????????????????????????
H.glaphyroscytos 6640        ......c....aa.......t..t.............................g..a.............a.....c.....
H.hylaios 6358               ............aa.......g..t.....a..a.........c.....................g.....................
H.hylaios 6359               ............aa.......g..t.....a..a.....................c..g.......g.....................
H.hylaios 6363               ............aa.......g..t.....a..a.........c.....................g.....................
H.ischnoryctes 6639          ......c....aa.......g..t.....................................g..a.............a.....c.....
H.kukunyungkal 6341          a..........aa....a..g..t.....a.....c.....................a.............a.....c.....
H.kukunyungkal 6342          a..........aa....a..g..t.....a.....c.....................a.............a.....c.....
H.kukunyungkal 6343          a..........aa....a..g..t.....a.....c.....................a.............a.....c.....
H.laevitropis6348            ............aa....a.....t.....a.....c.....................a.............a.....c.....
H.leptochela 6344            ...a........aa.......g..t........a.....................a.....a.....g.......a..........
H.leptochela 6345            ...a........aa.......g..t........a.....................a.....a.....g.......a..........
H.litodactylus 5559          ...a........ag..........t.....................................g.......a..........
H.macrochela 5555            .............a....a.....t..a.....a.....................g.......a..........
H.neocaledonicus 4323        ...t........aa.......t........t..a.................g...ta.......a..........tc.......
H.neocaledonicus 5542        ...t........aa.......c........t..a.................g..g..g...........c..............
H.neocaledonicus 5543        ...t........aa.......c........t..a.................g..g..g.....................................
H.neocaledonicus 5544        ...t........aa.......t........t..a.................g..a..g.......a.......ca..........
H.neocaledonicus 5545        ...t........aa.......t........t..a..........a.....g..g..g..a.....a.....................
H.neocaledonicus 5546        ...t........aa....a..........t..a.................g..a..g..a.....a.......a..........
H.neocaledonicus 5547        a..t........aa.......t........t.................a.....g..a..a.......a.......a..........
H.neocaledonicus 5548        a..t........aa.......t........t..............a.....g..a..a.......a.......a..........
H.neocaledonicus 6224        ????????????????????????????????????????????????????????????????????????????????????????????????????
H.nyawaygi 6354              ...........ta....a.....t..a.....a.....................a.....................a..........
H.papuanus 2718              ...a........aa.......g..t..........a.....c.....................g.......t..........
H.papuanus 2725              ...a.........a....a.....t.....a.....................g.....................................
H.papuanus 2727              ...a........ta..........t.....t..a.....................g.....................................
H.penta 1817                 ...t........aa....a..g........t.aa..............c..a.?????????????????????????????????
H.polisorum 1614             ............aa..........t.....a..a........c..a.....................g........a..........
H.solomonensis 1818          ????????????????????????????????????????????????????????????????????????????????????????????????????
H.solomonensis 1819          a...........aa.c..a..g..t.....t.?????????????????????????????????????????????????????
H.solomonensis 5549          a...........aa....a..g..t.....t.....................g.......a.....g.....g..............
H.solomonensis 5550          ............aa....a.....t.....t.....................g.g.....a.....a.....c..a..........
H.solomonensis 5551          ..........ccaa....a.....t.....t.....................g.......a.....g.....g..a..........
H.solomonensis 5552          .............a....a..g..t.....t.....................g.............g.......a..........
H.solomonensis 5554          ............a....a..g..t.....t.....................g.............g.......a..........
H.tjapukai 2184              ............aa....a.....t........a.................g.......a.....g.....................
H.tjapukai 6641              ............aa....a.....t........a.................g.......a.....g.....................
H.tytthognaphos 6346         ............ag.......g..t.....a..a.....c.........c.................g.......a..........
H.tytthognaphos 6347         ............ag.......g..t.....a..a.................c.................g.......a..........
H.wallaman 6353              ............aa....a..t..t..a.....a.....................................a.....g.......a..........
H.yelae 3007                 ????????????????????????????????????????????????????????????????????????????????????????????????????
H. sp. WA 8017               ...a........aa.......g..t..a.....a.............c........a..a.....g.......a..........
H. sp. WA 8021               ...a........aa.......g..t..a.....a.............c........a..a.....g.......a..........
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 871–957. Dots indicate a match with the first taxon. (Continued)

```
O.laevipes 1835              ggctgcaactatagtaattgctgtgcctacagggattaaaatttttagatgaatagcaactttatatggttcttattttgtttttac
C.ochropus 2189              ????????????????????????????????????????????????????????????????????????????????????????????????????
C.ochropus 9069              t..a..t.......c.......t.....t..a....g.....c.......g..g..........a...............
I.nitidus 9827               ......t..a..g..........t.......t..c.....................t.......c.............aa.....
I.politus 1514               t..a..t......a.t........t..g..t..a.................g..g..c.............g......tc..a.gt
I.politus 3256               t..a..t......a.t........t..g..t..a.................g..g..c.............g......tc..a.gt
O.elatus 1837                t..g..t..g.....g.....a.....................t.......t.....g.......c...........t.
O.lecomtei 1608              a.....t.....................t........gg..........gt....t.....g.....a..........a.....
O.lecomtei 2194A             a.....t.....g..g........t.....t..a....ggg...........t.g..t.....g.....a..........g.....
O.madagascariensis 2800      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.madagascariensis 2812      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.madagascariensis 2811      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.piceus 6260A               ????????????????????????????????????????????????????????????????????????????????????????????????????
H.infulcra 2185              ...g..t..a..ga.t........a.....t..a....gg..............g..t..ga...................aa....
L.australasiae 1854          t.....t.....ga.t........t.....g.......gg...........g..g..t...a.g.....a..........aaa..t.
L.australasiae 2181          t.....t.....a.t.............g.......g..........g..g..t...a.......a..........aga..t.
L.australasiae 2182          t.....t......a.t........t.....t..a..c..g...........g.........a.g.....g..........aaa..t.
L.australasiae 2183          t.....t......a.t.............g.....................g..g..t...a......a..........aga..t.
L.australasiae 2729          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 2733          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 2996          t.....t......a.t.............g.......g..........g.....t...a.......g..........aga..t.
L.australasiae 3684          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 4764          t.....t......a.t.............g.......g..........g..g..t...a.......a..........aga..t.
L.australasiae 5553          t.....t......a.t.............g.......g..........g.....t...a.......a..........aga..t.
L.australasiae 8676          t.....t......a.t.............g.......g..........g.....t...a.......a..........aga..t.
L.australasiae 8677          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.longimanus 6388            a.....t.....ga.t........t.....t..a....gg...........g..g..t...a.g..c..g..g.......a.g.a..
L.malaya 1909                t.....t.....ga.t........t.....t........gg............g..t...a.......ag.gc......a.a.a..
H.aethes 3002                t.....t..a..ga.t........t.....t..a.....g........t.....g..t...a.g...............aag.a..
H.aethes 3005                t.....t..a..ga.t........t.....t..a.....g........t.....g..t...a.g...............aag.a..
H.anekasankylis 6355         t.....t.....ga.t........t.....t........g........t.....g..t...a.....c............aaa.....
H.anekasankylis 6356         t.....t.....ga.t........c.....t........g........t.....g..c...a.g...............agg.....
H.anekasankylis 6357         t.....t.....ga.t........t.....t........g........t.....g..t...a.................aaa.....
H.ankistros 4339             t.....t..a..ga.t........t.....t..a....gg........t.....g..c...a.g...............aga.....
H.bandjin 5556               t.....t.....ga.t........t.....t..a....gg........t........t...a.................aga.....
H.bandjin 5557               t.....t.....ga.t........t.....t..a....gg........t........t...a.................aga.....
H.bandjin 5558               t.....t.....ga.t........t.....t..a....gg........t........t...a.................aaa.....
H.caudicula 1502             t.....t.....ga.t........t.....t........g........t.....g..t...a.................aag.....
H.caudicula 2339             t.....g.....ga.t........t.....t........g........t.....g..t...a.................agg.....
H.caudicula 2340             t.....t.....ga.t........t.....t..a......g.......t........t...a.g...............agg.....
H.caudicula 6360             t.....t.....ga.t........t.....g........g........t.....g..t...a.................agg.....
H.caudicula 6361             t.....t.....ga.t........t.....t........g........t.....g..t...a.................aag.c..
H.caudicula 6362             t.....t.....ga.t........t.....t........g........t.....g..t...a.................agg.....
H.chthamalochoros 6350       t.....t......a.t........t.....t..a.....g........t.....g..t...a.g...............aga.....
H.chthamalochoros 6351       t.....c..c...a.t........t.....t..a.....g........t.....g..t...a.................aga.....
H.chthamalochoros 6352       t.....t......a.t........t.....t..a.....g........t.....g..t...a.g...............aga.....
H.chthamalochoros 8023       t.....t......a.t........t.....t..a.....g........t.....g..t...a.g...............aga.....
H.chydaeostigmata 5560       t.....t.....ga.t........c.....t........g........t.....g..t...a.g...............aaa.....
H.chydaeostigmata 8015       t.....t.....ga.t........c.....t........g........t.....g..t...a.g...............aaa.....
H.chydaeostigmata 8016       t.....t.....ga.t........c.....t........g........t.....g..t...a.g...............aaa.....
H.chydaeostigmata 8019       t.....t.....ga.t........c.....t........g........t.....g..t...a.g...............aaa.....
H.chydaeostigmata 8020       ????????????????????????????????????????????????????????????????????????????????????????????????????
H.chydaeostigmata 8022       t.....t.....ga.t........c.....t........g........t.....g..t...a.g...............aaa.....
H.dechangei 7789             t..g..t..a..ga.t........t.....t..a..........c..t.....g..t...a.g...............agg.....
H.euktaenospatha 4340        ????????????????????????????????????????????????????????????????????????????????????????????????????
H.glaphyroscytos 6640        t.....t.....ga.t........t.....t........g........t.....g..c...a.g...............aaa.....
H.hylaios 6358               t.....t......a.t........t..g..t..a.....................t........t...a.................aaa.....
H.hylaios 6359               t.....t......a.t........t..a..t..a.....g........t........t...a.g...............aag.....
H.hylaios 6363               t.....t......a.t........t..a..t..a.....................t........t...a.................aaa.....
H.ischnoryctes 6639          t.....t.....ga.t........t.....t........g........t.....g..c...a.g...............aaa.....
H.kukunyungkal 6341          t.....t.....ga.t........t.....t..a....gg........c.....g..c...a.g...............aag.....
H.kukunyungkal 6342          t.....t.....ga.t........t.....t..a....gg........c.....g..c...a.g...............aag.....
H.kukunyungkal 6343          t.....t.....ga.t........t.....t..a....gg........c.....g..c...a.g...............aag.....
H.laevitropis6348            t.....t.....ga.t........t.....t........g........t.....g..c...a.g...............aag.....
H.leptochela 6344            t.....t.....ga.t..............t.......gg........t.....g..c...a.g...............agg.....
H.leptochela 6345            t.....t.....ga.t..............t.......gg........t.....g..c...a.g...............agg.....
H.litodactylus 5559          t.....t......a.t........t.....t........g........t.....g..t...a.g.....g..........agg.....
H.macrochela 5555            t.....c.....ga.t........t.....t..t.....g........t........t...a.g.....g..........aaa.....
H.neocaledonicus 4323        t.....t..g...a.t........t..c..t.....................t.....g..t...a.g.....a..........aga..t.
H.neocaledonicus 5542        t.....t..g...a.t........c.....t.....................t.....g..t...a.g.....a..........aga..t.
H.neocaledonicus 5543        t.....t..g...a.t........c.....t.....................t.....g..t...a.g.....a..........aga..t.
H.neocaledonicus 5544        ......t..a...a.t........t.....t.....................t........t...aa.g...............aga..t.
H.neocaledonicus 5545        t.....t..g...a.t........c.....t.....................t.....g..t...a.g.....a..........aga..t.
H.neocaledonicus 5546        t.....t..c..ga.t........t.....t..ag.c...........t.....ga....aa.g.....a..........aaa..t.
H.neocaledonicus 5547        t.....t..g...a.t........t.....t..a..............t........t..ga.g.....a..........aaa.ct.
H.neocaledonicus 5548        t.....t..g...a.t........t.....t..a..............t........t..ga.g.....a..........aaa.ct.
H.neocaledonicus 6224        ????????????????????????????????????????????????????????????????????????????????????????????????????
H.nyawaygi 6354              t.....t......a.t........t.....t.......gg........t...........a.g...............agg.....
H.papuanus 2718              t.....t......a.t........t.....t.....................t........t...a.................aag.....
H.papuanus 2725              t.....c.....ga.t........t.....t........g........t.....g......a....c..c...........aag.....
H.papuanus 2727              t..g..t..a..ga.t........a.....t..a..............t.....g..g...a.g.....a..........aag.a..
H.penta 1817                 ????????????????????????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             a.....t......a.t........t..a..t.....................t........t...a.g..c.............aaa.....
H.solomonensis 1818          ????????????????????????????????????????????????????????????????????????????????????????????????????
H.solomonensis 1819          ????????????????????????????????????????????????????????????????????????????????????????????????????
H.solomonensis 5549          t........g...a.t........t.....t.......gg........t.....g.....ca.g...............agg..t.
H.solomonensis 5550          t.....g..a..ga.t........t.....t.....c..g.........t.....g..t...a....c.............agg.g..
H.solomonensis 5551          t.....g..a..ga.t........t.....t..a....gg........t.....g..t...a.......c..........agg.a..
H.solomonensis 5552          t.....g..a...a.t........c.....t.......gg........t.....g..t...a.................agg.a..
H.solomonensis 5554          t.....g..a...a.t........c.....t.......gg........t.....g..t...a.................agg.a..
H.tjapukai 2184              t.....t......a.t........t.....t........g........t.....g..t...a.g...............agg.....
H.tjapukai 6641              t.....t......a.t........t.....t........g........t.....g..t...a.g...............agg.....
H.tytthognaphos 6346         t.....t.....ga.t........t.....t.....................t.....g..t...a.g...............agg.....
H.tytthognaphos 6347         t.....t.....ga.t........c.....t.....................t.....g..t...a.g...............agg.....
H.wallaman 6353              t..a..t......a.t........t.....t........g........t.....g..t...a.................aaa.....
H.yelae 3007                 ????????????????????????????????????????????????????????????????????????????????????????????????????
H. sp. WA 8017               t.....t.....ga.t........c.....t........g........t.....g..t...a.g...............aag.....
H. sp. WA 8021               t.....t.....ga.t........c.....t........g........t.....g..t...a.g...............aag.....
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 958–1044. Dots indicate a match with the first taxon. (Continued)

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O.laevipes 1835              tcctcctttgttgtgagctttgggttttgtatttttgtttactgttggaggtttaactggggtgattttggctaattcttcgttgga
C.ochropus 2189              ????????????????????????????????????????????????????????????????????????????????????????????????????
C.ochropus 9069              ...........a..g....a..g....g....a.......a.......g....a..a....a..........t.....
I.nitidus 9827               g..a..............a..g..................g..g.............t..............t..a..
I.politus 1514               ....t.g..aa....g...a.a..g..........a.....ca......a..g.............a..............
I.politus 3256               ....t.g..aa....g...a.a..g..........a.....ca......a..g.............a..............
O.elatus 1837                g.....................g....g.............a..g..a....a....a....a..........t..a..
O.lecomtei 1608              ....t....aa.t.....gg.t..g....g....a.......g..g..........a..a.............a..t.....
O.lecomtei 2194A             ....t....aa.t.....gg.t..g....g....a.......a..g.......a..a..a.............g..t.....
O.madagascariensis 2800      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.madagascariensis 2812      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.madagascariensis 2811      ????????????????????????????????????????????????????????????????????????????????????????????????????
O.piceus 6260A               ????????????????????????????????????????????????????????????????????????????????????????????????????
H.infulcra 2185              ......cc.t.........g.t..g.....t.....c.....a.....g..a...........tg....a........g..t....t
L.australasiae 1854          ......ac.t.........g.t..g.....c.....t.................g..g..t...g....a...........t.....
L.australasiae 2181          .......c.t..a..g...g.t..g...........t........g..t..g..g.....t...g.gc............t.....
L.australasiae 2182          .......c.t.....g...g.t..g...........c........g..g..c..g.....t..tg.a.............t..a..
L.australasiae 2183          .......c.t..a..g...g.t..g...........t........g..t..g..g.....t...g.g.............t.....
L.australasiae 2729          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 2733          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 2996          .......c.t..a..g...g.t..g...........t........g..t..g..g.....t...g.g.............t.....
L.australasiae 3684          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.australasiae 4764          .......c.t..a..g...g.t..g...........t........g..t..g..g.....t...g.gc............t.....
L.australasiae 5553          .......c.t..a..g...g.t..g...........t........g..t..g..g.....t...g.g.............t.....
L.australasiae 8676          .......c.t..a..g...g.t..g.....g.....t........g..t..g..g.....t...g.g.............t.....
L.australasiae 8677          ????????????????????????????????????????????????????????????????????????????????????????????????????
L.longimanus 6388            .........a.........g.t..g...........t........g..g..c..g.........g.......c........t.....
L.malaya 1909                ......g..a..a..g...g.t..g...........t.........g..a..g.....c...g....a...........t..a..
H.aethes 3002                .......a.t.....g..gg.t..a.....g.....t........a..g..c..g.........g..............tt.....
H.aethes 3005                .......a.t.....g..gg.t..a.....g.....t........a..g..c..g.........g..............t.....
H.anekasankylis 6355         .......g.t..a.....gg.t..g.....t.....t......t.g..g.....g.....a...g.......a.......t..a..
H.anekasankylis 6356         .......g.a..a..g..gg.t..g.....t.....t......t.g..g..g..g.....a...g..........c.....ta.a..
H.anekasankylis 6357         .......g.t..a..g..gg.t..g.....t.....t......t.g..g.....g.....a...g.......a..c.....t..aa.
H.ankistros 4339             .......a.t........ag.t..g.....g.....t........g..t..a..g.....a...g.gc.a.....c.....tc....
H.bandjin 5556               .......g.t.......tgg.t..g.....c.....t......t.a..g...........a..ag....a...........t..a..
H.bandjin 5557               .......g.t.......tgg.t..g.....c.....t......t.a..g...........a..ag....a...........t..a..
H.bandjin 5558               .......g.t.......tgg.t..g.....c.....t......t.a..............a...g....a...........t..a..
H.caudicula 1502             .......g.t........gg.t..g.....t.....t......t.a..g........a..a...g....a...........t.....
H.caudicula 2339             .......g.t.......gg....a.....t.....t......t.g..g.....g..a..a...g....a...........t..aa.
H.caudicula 2340             .t..t..g.t.......taa.a..g.....t..c..t......t.g..............a...g..............t..a..
H.caudicula 6360             .......g.t..a.....gg.t..g.....t.....t......t.a........g..g..a...g....a...........t.....
H.caudicula 6361             .......g.t........gg.t..g.....t.....t......t.a..g........a..a...g....a..c.........t.....
H.caudicula 6362             .......g.t........gg.t..g.....t.....t......t.a..g........a..a...g....a...........t.....
H.chthamalochoros 6350       .......g.t.......tgg.t..g.....t.....t......t.a..............a..ag................t..a..
H.chthamalochoros 6351       .......g.t.......tgg.c..g.....t.....t.....ct.a..g...........a..ag................t..a..
H.chthamalochoros 6352       .......g.t.......tgg.t..g.....t.....t......t.a..............a..ag................t..a..
H.chthamalochoros 8023       .......g.t.......tgg.t..g.....t.....t......t.a..............a..ag................t..a..
H.chydaeostigmata 5560       ...c...g.t..a.....gg.t..a.....t.....t......t.g........g.....a...g................t..aa.
H.chydaeostigmata 8015       ...c...g.t..a.....gg.t..a.....t.....t......t.g........g.....a...g................t..aa.
H.chydaeostigmata 8016       ...c...g.t..a.....gg.t..a.....t.....t......t.g........g.....a...g................t..a..
H.chydaeostigmata 8019       ...c...g.t..a.....gg.t..a.....t.....t......t.g........g.....a...g................t..a..
H.chydaeostigmata 8020       ????????????????????????????????????????????????????????????????????????????????????????????????????
H.chydaeostigmata 8022       ...c...g.t..a.....gg.t..a.....t.....t......t.g........g.....a...g................t..aa.
H.dechangei 7789             .......a.t.........g.t..a..........t.....................a..a...g....a...........t.....
H.euktaenospatha 4340        ????????????????????????????????????????????????????????????????????????????????????????????????????
H.glaphyroscytos 6640        ...c...a.t..a.....gg.t..a.....t.....t................g.....a...g................t..aa.
H.hylaios 6358               .......a.t.....g..ag.t..a..........t........a..............a...g..............c..t.....
H.hylaios 6359               .......a.t.....g..ag.t..g..........t........a.....g.....c..a..ag..............t.....
H.hylaios 6363               .......a.t.....g..ag.t..a..........t........a..............a...g..............c..t.....
H.ischnoryctes 6639          ...c...a.t..a.....gg.t..a.....t.....t.....a..........g.....a...g..........c.....t..a..
H.kukunyungkal 6341          ...c...a.t..a.....gg.t..g.....t.....t........c........g.....a...g................t..aa.
H.kukunyungkal 6342          ...c...a.t..a.....gg.t..g.....t.....t........c........g.....a...g................t..a..
H.kukunyungkal 6343          ...c...a.t..a.....gg.t..g.....t.....t........c........g.....a...g................t..a..
H.laevitropis6348            ...c...a.t..a.....gg.t..g.....t.....t........g........g.....a...g................t..a..
H.leptochela 6344            .......g.t........gg.t..g.....t.....t........g..g.....g.....a...g................t..a..
H.leptochela 6345            .......g.t........gg.t..g.....t.....t........g..g.....g.....a...g................t..a..
H.litodactylus 5559          .......g.t........gg.t..g.....t.....t................g.....a...g....a...........t..a..
H.macrochela 5555            .......g.t.....g..gg.t..g.....t.....t......t.g..................g....a...........t..a..
H.neocaledonicus 4323        ....t..g.t..a..g...g.a..a.....c.....t.................g........g...............t.....
H.neocaledonicus 5542        ....t..g.t..a..g...g.a..g.....c.....t........a.....c..g........g...............t.....
H.neocaledonicus 5543        ....t..g.t..a..g...g.a..g.....c.....t........a.....c..g........g...............t.....
H.neocaledonicus 5544        ....t..g.t..a......gcaa.a.....c.....t..........t..........a.??????????????????????????
H.neocaledonicus 5545        ....t..g.t..a..g...g.a..g.....c.....t..............c..g........g...............t.....
H.neocaledonicus 5546        ....t..g.t..a......g.c..a.......c.c.t...........g..c..g.....a...g....a..........at.....
H.neocaledonicus 5547        c...t..g.t..a..g...g.a..g.....t.....c........g..t..........a...g...............t.....
H.neocaledonicus 5548        c...t..g.t..a..g...g.a..g.....t.....c........g..t..........a...g...............t.....
H.neocaledonicus 6224        ????????????????????????????????????????????????????????????????????????????????????????????????????
H.nyawaygi 6354              ...a...g.t.....g..gg.t.......t.....t.....t.....t.a..............a...g....a...........t..a..
H.papuanus 2718              ......cg.t........g.c..g.....g.....t.....a..g.....g........a..ag....a...........t.....
H.papuanus 2725              g..a..cg.t..a.....gg.t..g.....t.....t........a..............a..tg.g..............t.....
H.papuanus 2727              .......g.t.......ag....g...........t........g.....a..g.....a...g.................t.....
H.penta 1817                 ????????????????????????????????????????????????????????????????????????????????????????????????????
H.polisorum 1614             .......a.t.....g.tgg.c..g.....t.....t...........g..g.....c..a...g................t.....
H.solomonensis 1818          ????????????????????????????????????????????????????????????????????????????????????????????????????
H.solomonensis 1819          ????????????????????????????????????????????????????????????????????????????????????????????????????
H.solomonensis 5549          .......a.t..a..g...g.a........gg....t.........................g................t.....
H.solomonensis 5550          .......g.t.....g...g.a.......t.....t.....t.a..g.......ac..a...g.....t.........t.....
H.solomonensis 5551          ...c...g.t.....g...g.a........g.....t......t.g..g...........a...g................t.....
H.solomonensis 5552          .......g.t.....g...g.a........g.....t......t.g..g.....g.....a..tg................t.....
H.solomonensis 5554          .......g.t.....g...g.a.......g.....t.....t.g..g.....g.....a..tg.........c......t...t.
H.tjapukai 2184              .......g.t........gg.t..g.....t.....t......t.a..g.....g.........g...............t..a..
H.tjapukai 6641              .......g.t........gg.t..g.....t.....t......t.a..g.....g.........g...............t..a..
H.tytthognaphos 6346         .......g.t.......gg.t..g.....t.....t.......g..g.....g.....a...g................t..a..
H.tytthognaphos 6347         .......g.t........gg.t..g.....t.....t........g..g.....g.....a...g................t..aa.
H.wallaman 6353              .......g.t.....g.tgg.t.........t.....t......t.a..............a...g....a...........t.....
H.yelae 3007                 ????????????????????????????????????????????????????????????????????????????????????????????????????
H. sp. WA 8017               .......g.t..a.....gg.t..a.....t.....t......t.g........g.....a...g................t..a..
H. sp. WA 8021               .......g.t..a.....gg.t..a.....t.....t......t.g........g.....a...g................t..a..
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2.5.3 Aligned molecular sequences. Mitochondrial Cytochrome C oxidase subunit I gene, base-pairs 1045–1078. Dots indicate a match with the first taxon. (Continued)

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O.laevipes 1835              tattgttcttcatgatacttattatgtagtggct
C.ochropus 2189              ???????????????????????????????????
C.ochropus 9069              ......................c.....g..t...
I.nitidus 9827               c......t.g.................g......
I.politus 1514               .g.a..............g........t..t...
I.politus 3256               .g.a..............g........t..t...
O.elatus 1837                ......gt.a.................g......
O.lecomtei 1608              .g.....t.a........c........t.gt...
O.lecomtei 2194A             .g.....t.g.................t..t...
O.madagascariensis 2800      ???????????????????????????????????
O.madagascariensis 2812      ???????????????????????????????????
O.madagascariensis 2811      ???????????????????????????????????
O.piceus 6260A               ???????????????????????????????????
H.infulcra 2185              ..a....t.g.....a..a..cc....taac.t.
L.australasiae 1854          ......at.g........a........t..a...
L.australasiae 2181          ......at.g.....c..a........t..a..c
L.australasiae 2182          ...c..at.g........a........t..a...
L.australasiae 2183          ......at.g........a........t..a..c
L.australasiae 2729          ???????????????????????????????????
L.australasiae 2733          ???????????????????????????????????
L.australasiae 2996          ......at.g........a........t..a..c
L.australasiae 3684          ???????????????????????????????????
L.australasiae 4764          ......at.g.....c..a........t..a..c
L.australasiae 5553          ......at.g........a........t..a...
L.australasiae 8676          ......at.g........a........t..a..c
L.australasiae 8677          ???????????????????????????????????
L.longimanus 6388            ......gt.a.................g..t...
L.malaya 1909                c......t.a........g..........t...
H.aethes 3002                a......t.g........g........t..t...
H.aethes 3005                .......t.g........g........t..t...
H.anekasankylis 6355         .......t.g........g..c.....t..t...
H.anekasankylis 6356         .........g........g..c..c..tt.ttt.
H.anekasankylis 6357         .......t.g........g........t..t...
H.ankistros 4339             .......t.a........g........t......
H.bandjin 5556               ......ct.g........c........t..t...
H.bandjin 5557               ......ct.g........c........t..t...
H.bandjin 5558               ......ct.g........c........t..t...
H.caudicula 1502             .......t.g........a..c.....t..t...
H.caudicula 2339             .......t.g........c........t..t...
H.caudicula 2340             .......t.a........g........t..t...
H.caudicula 6360             .......t.a........g........t..t...
H.caudicula 6361             .......t.a........a........t..t...
H.caudicula 6362             .......t.g........a........t..t...
H.chthamalochoros 6350       .......t.g........a..c.....t..t...
H.chthamalochoros 6351       .......t.g........a..c.....t..c...
H.chthamalochoros 6352       .......t.g........a..c.....t..t...
H.chthamalochoros 8023       .......t.g........a..c.....t..t...
H.chydaeostigmata 5560       .......t.g.....c..g........t..t...
H.chydaeostigmata 8015       .......t.g.....c..g........t..t...
H.chydaeostigmata 8016       .......t.g.....c..g........t..t...
H.chydaeostigmata 8019       .......t.g.....c..g........t..t...
H.chydaeostigmata 8020       ???????????????????????????????????
H.chydaeostigmata 8022       .......t.g.....c..g........t..t...
H.dechangei 7789             .......t.g........g........t..t...
H.euktaenospatha 4340        ???????????????????????????????????
H.glaphyroscytos 6640        .......t.g........g..c.....t..t...
H.hylaios 6358               ......gt.a.....c..a........t..t...
H.hylaios 6359               ......gt.g........g........t..t...
H.hylaios 6363               ......gt.a.....c..a........t..t...
H.ischnoryctes 6639          .......t.g........a........t..t...
H.kukunyungkal 6341          .......t.g........a........t..t...
H.kukunyungkal 6342          .......t.g........a........t..t...
H.kukunyungkal 6343          .......t.g........a........t..t...
H.laevitropis6348            .......t.g........g........t..t...
H.leptochela 6344            .......t.g........g........t..t...
H.leptochela 6345            .......t.g........g........t..t...
H.litodactylus 5559          .......t.g........g........t..t...
H.macrochela 5555            .......t.a........a........t..t...
H.neocaledonicus 4323        .......t.a.....c..a........t..t...
H.neocaledonicus 5542        .......t.a........a........t..t...
H.neocaledonicus 5543        .......t.a........a........t..t...
H.neocaledonicus 5544        ???????????????????????????????????
H.neocaledonicus 5545        .......t.a........g........t..t...
H.neocaledonicus 5546        .......t.g........g........t..t..-
H.neocaledonicus 5547        .......t.g........a........t..t...
H.neocaledonicus 5548        .......t.g........a........t..t...
H.neocaledonicus 6224        ???????????????????????????????????
H.nyawaygi 6354              .......t.g........g........t..t...
H.papuanus 2718              .......t.g........c........t..t...
H.papuanus 2725              .......t.a..................t..t...
H.papuanus 2727              .......t.g..................t..t...
H.penta 1817                 ???????????????????????????????????
H.polisorum 1614             .......t.g..c.....g........t..c...
H.solomonensis 1818          ???????????????????????????????????
H.solomonensis 1819          ???????????????????????????????????
H.solomonensis 5549          .......t.a.....c..a........t..t...
H.solomonensis 5550          .....g.t.g..a..a..a.t......t..t...
H.solomonensis 5551          .......t.g.....c..a........t..t...
H.solomonensis 5552          .......t.g........g........t..t...
H.solomonensis 5554          c..c.c.tcg......ctg....t.t.t..t...
H.tjapukai 2184              ..a....t.g........g..cc....tagt...
H.tjapukai 6641              .......t.g........g........t..t...
H.tytthognaphos 6346         .......t.g.....c..g........t..t...
H.tytthognaphos 6347         .......t.g.....c..g........t..t...
H.wallaman 6353              .......t.g........g..c.....t..t..g
H.yelae 3007                 ???????????????????????????????????
H. sp. WA 8017               .......t.g.....c..g........t..t...
H. sp. WA 8021               .......t.g.....c..g........t..t...
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2.5.4 Unambiguous morphological character changes (synapomorphies and parallel derivations of apomorphic states) supporting each node and terminal taxa on the optimal tree of the simultaneous analysis of morphological and molecular data (IW with *K* = *9* and gaps included).

Chiromachus ochropus: 1: 8.000 > 9.000; 2: 3.000-4.000 > 10.000; 3: 4.000 > 12.000; 4: 3.000-4.000 > 10.000; 5: 4.000 > 12.000; 6: 3.000-4.000 > 10.000; 7: 4.000-5.000 > 12.000; 8: 3.000-4.000 > 10.000; 9: 4.000-5.000 > 12.000; 13: 0 > 1; 14: 0 > 1; 17: 0 > 1; 28: 0 > 2; 30: 0 > 1; 32: 0 > 1; 36: 0 > 1; 68: 1 > 0; 74: 0 > 1; 77: 0 > 1; 79: 0 > 1; 88: 1 > 0; 109: 0 > 1; 110: 0 > 1; 117: 0 > 1; 146: 1 > 2; 147: 0 > 2; 150: 0 > 1; 152: 0 > 1; 154: 0 > 1; 170: 0 > 1; 185: 0 > 1; 187: 0 > 1; 189: 0 > 1; 210: 1 > 0; 223: 0 > 1; 224: 0 > 1; 225: 1 > 2; 226: 1 > 2; 227: 2 > 3; 263: T > A; 271: T > G; 285: G > A; 291: A > G; 293: T > A; 328: A > G; 351: A > T; 405: T > A; 436: A > G; 451: A > T; 455: A > T; 504: - > T; 513: A > T; 515: A > C; 516: C > G; 518: G > A; 530: T > A; 539: T > A; 541: A > C; 546: G > A; 566: T > A; 596: A > -; 620: A > T; 653: A > C; 674: A > T; 700: T > A; 704: T > C; 714: T > G; 718: A > G; 739: A > G; 759: A > T; 773: T > A; 851: T > C; 865: A > C; 892: A > G; 900: T > A; 908: T > C; 911: T > C; 916: A > T; 931: A > T; 932: A > C; 941: A > G; 1000: A > G; 1002: G > A; 1005: T > A; 1073: A > T; 3415: A > G; 3430: T > G; 3445: T > G; 3529: T > A; 3544: A > G; 3592: G > A; 3607: G > A; 3637: GT > A; 3661: G > A; 3662: T > C; 3676: T > C; 3688: A > G; 3689: G > A; 3739: T > A; 3742: T > G; 3778: AT > G; 3829: G > T; 3865: T > A; 3871: G > A; 3878: A > G; 3892: AT > G; 3952: T > G; 3958: T > G; 3973: A > G; 4027: G > A; 4033: T > A.

Hormiops infulcra: 0: 8.000 > 6.000; 5: 4.000 > 5.000; 15: 0 > 1; 17: 0 > 1; 20: 0 > 3; 21: 0 > 2; 76: 0 > 1; 81: 0 > 2; 93: 1 > 0; 106: 1 > 0; 116: 0 > 1; 122: 1 > 0; 127: 0 > 1; 128: 1 > 0; 132: 1 > 0; 135: 1 > 0; 151: 0 > 1; 153: 0 > 1; 156: 0 > 1; 168: 2 > 1; 172: 1 > 0; 187: 0 > 1; 202: 2 > 1; 203: 2 > 1; 288: A > T; 289: A > T; 321: G > A; 342: C > T; 359: A > T; 378: T > A; 379: T > C; 389: T > C; 405: T > G; 412: A > T; 418: T > G; 428: A > G; 438: T > A; 452: T > A; 479: A > G; 483: T > G; 486: T > C; 491: G > A; 500: A > G; 503: T > A; 508: T > A; 514: A > T; 522: A > T; 527: A > T; 530: T > G; 537: A > G; 578: A > T; 605: C > T; 643: T > C; 650: T > G;

653: A > T; 661: T > A; 716: G > A; 729: T > A; 742: T > C; 756: A > G; 766: T > C; 767: G > A; 777: T > A; 790: G > A; 799: T > G; 806: A > T; 842: A > G; 845: T > A; 856: A > C; 879: A > G; 880: C > T; 888: G > A; 893: T > A; 910: A > T; 924: A > G; 932: A > T; 990: A > T; 1006: T > A; 1008: T > A; 1065: T > C; 1075: - > A; 1092: A > T; 1095: T > C; 1153: A > G; 1154: G > A; 1351: G > A; 1352: G > A; 1746: C > T; 2444: C > T; 2682: C > T; 2700: G > A; 2794: G > A; 2918: C > A; 2956: T > C; 2957: C > T; 2960: C > G; 2962: T > C; 3421: T > A; 3424: A > G; 3439: G > T; 3441: C > T; 3478: A > T; 3510: A > T; 3518: G > A; 3523: T > A; 3529: T > C; 3541: T > G; 3547: T > C; 3565: T > A; 3592: G > A; 3610: G > A; 3634: T > G; 3661: G > A; 3670: T > A; 3697: T > A; 3757: G > A; 3850: T > G; 3865: T > G; 3878: A > C; 3879: T > A; 3889: T > A; 3904: T > G; 3907: G > A; 3922: T > G; 3944: C > T; 3946: T > G; 3961: G > A; 3967: T > C; 3976: G > A; 4030: T > A; 4037: T > C; 4059: T > C; 4063: T > A; 4075: G > A; 4087: G > A; 4099: A > C; 4141: G > A; 4156: G > T; 4177: T > A; 4192: A > G; 4193: T > G; 4267: T > G; 4270: T > G; 4291: T > A; 4305: A > G; 4327: T > G; 4360: T > C; 4396: T > A; 4432: T > G; 4440: A > T; 4443: T > A; 4456: T > A; 4462: T > C; 4463: T > C; 4469: G > A; 4470: T > A; 4471: T > C.

Hormurus: 42: 1 > 2; 94: 0 > 1; 132: 1 > 2; 140: 0 > 1; 146: 0 > 1; 147: 0 > 1; 148: 0 > 1; 149: 0 > 1; 165: 1 > 2; 174: 1 > 0; 214: 0 > 1; 256: 0 > 1; 263: T > A; 645: A > T; 747: T > C; 754: A > T; 922: T > A; 1873: C > T; 2991: T > C; 3436: T > A; 3664: G > A; 3694: T > G; 3754: G > A; 3820: T > A; 3878: A > T; 3982: T > G; 4130: C > A; 4143: G > A; 4193: T > A; 4315: A > T; 4414: G > A.

Iomachus nitidus: 0: 8.000 > 5.000; 1: 7.000-8.000 > 4.000-5.000; 3: 4.000 > 3.000; 5: 4.000 > 3.000; 7: 4.000 > 3.000; 9: 4.000 > 3.000; 12: 0 > 1; 20: 0 > 1; 21: 0 > 1; 79: 0 > 1; 105: 1 > 0; 107: 1 > 0; 110: 0 > 1; 127: 0 > 1; 135: 1 > 0; 142: 1 > 0; 143: 1 > 0; 144: 1 > 0; 174: 1 > 0; 178: 0 > 1; 179: 0 > 1; 214: 0 > 1; 216: 1 > 2; 243: 0 > 1; 244: 0 > 1; 281: G > A; 288: A > T; 304: C > T; 333: T > C; 348: T > A; 366: T > G; 374: T > A; 383: - > G; 408: A > G; 411: C > T; 435: A > G; 438: T > G; 455: A > G; 474: A > G; 476: A > C; 483: T > G; 503: T > A; 504: - > A; 505: - > G; 510: T > C; 527: A > C; 530: T > G; 537: A > T; 558: A > G; 571: - > G; 583: T > C; 587: A > G; 651: - > A; 662: A > T; 674: A > T; 706: T > C; 757: A > G; 831: T > A; 833: C > T; 836:

A > T; 866: T > C; 867: A > T; 871: T > A; 874: G > A; 877: T > C; 901: - > A; 902: - > T; 903: - > A; 914: T > G; 927: T > C; 940: A > G; 1048: A > T; 1076: A > G; 1102: T > A; 1609: T > C; 2455: C > T; 2981: C > T; 4114: T > G; 4117: T > C; 4129: T > A; 4138: A > G; 4156: G > A; 4180: G > A; 4181: G > A; 4183: G > T; 4198: G > A; 4210: G > A; 4225: G > A; 4234: T > A; 4246: T > G; 4255: G > T; 4276: T > A; 4279: A > G; 4303: T > C; 4333: T > C; 4347: T > A; 4348: T > A; 4354: T > G; 4357: T > A; 4438: G > A; 4441: T > C.

Iomachus politus: 2: 4.000 > 6.000; 15: 0 > 1; 46: 1 > 0; 60: 0 > 1; 79: 0 > 1; 81: 0 > 2; 93: 1 > 0; 96: 1 > 0; 100: 0 > 1; 105: 1 > 0; 106: 1 > 0; 114: 1 > 0; 116: 0 > 1; 127: 0 > 1; 128: 1 > 0; 132: 1 > 0; 133: 1 > 0; 134: 1 > 0; 135: 1 > 0; 136: 1 > 0; 138: 2 > 0; 139: 3 > 0; 142: 1 > 0; 143: 1 > 0; 144: 1 > 0; 156: 0 > 1; 176: 1 > 0; 205: 1 > 0; 213: 0 > 1; 274: A > T; 293: T > A; 298: T > G; 359: A > T; 381: T > C; 412: A > G; 418: T > A; 433: A > T; 435: A > T; 454: A > T; 483: T > A; 514: A > G; 542: A > T; 587: A > T; 592: T > G; 597: A > T; 604: A > G; 650: T > A; 653: A > G; 673: T > A; 684: A > T; 714: T > G; 716: G > A; 729: T > A; 763: T > A; 770: T > C; 833: C > T; 837: A > G; 838: T > A; 840: - > T; 841: - > G; 844: C > T; 867: A > C; 870: T > C; 874: G > A; 877: T > A; 893: T > C; 910: A > G; 932: A > T; 937: G > T; 1014: T > A; 1058: T > C; 1070: A > G; 4109: G > A; 4186: T > G; 4222: T > C; 4237: A > G; 4270: T > A; 4280: G > A; 4294: T > G; 4324: T > C; 4339: T > G; 4346: G > T; 4347: T > C; 4350: T > A; 4352: A > G; 4353: C > T; 4360: T > G; 4369: A > G; 4396: T > C; 4397: G > A; 4402: G > A; 4408: A > G; 4435: T > G; 4444: T > A; 4448: T > C; 4459: T > G.

Liocheles: 138: 2 > 1; 139: 3 > 2; 191: 0 > 1; 208: 0 > 1; 247: 1 > 2; 292: A > T; 333: T > C; 368: A > T; 455: A > T; 459: A > G; 524: - > A; 541: A > T; 558: A > G; 801: T > C; 843: A > G; 905: T > G; 2455: C > A; 2965: C > T; 3448: G > A; 3463: A > G; 3484: T > G; 3559: A > T; 3571: A > G; 3699: A > G; 3916: G > T; 4024: A > T; 4408: A > G.

Opisthacanthus (*Monodopisthacanthus*): 3: 4.000 > 3.000; 5: 4.000 > 3.000; 7: 4.000-5.000 > 3.000; 9: 4.000-5.000 > 3.000; 37: 0 > 1; 50: 2 > 1; 111: 0 > 1; 112: 0 > 1; 113: 0 > 1; 125: 1 > 0; 126: 2 > 1; 151: 0 > 1; 153: 0 > 1; 172: 1 > 0; 232: 3 > 2; 243: 0 > 2; 249: 0 > 2; 268:

T > C; 288: A > T; 310: A > G; 326: A > G; 333: T > C; 347: A > T; 357: T > C; 379: T > A; 381: T > G; 389: T > A; 435: A > T; 484: T > A; 486: T > A; 503: T > -; 508: T > A; 529: A > C; 531: G > T; 537: A > T; 558: A > G; 568: T > G; 574: T > C; 600: T > C; 2638: A > C; 2661: C > A; 3403: A > G; 3898: G > A; 3944: C > T; 3946: T > G; 4018: T > A.

Opisthacanthus (*Opisthacanthus*) *lecomtei*: 0: 8.000 > 11.000; 1: 8.000 > 10.000; 2: 4.000 > 3.000; 4: 4.000 > 3.000; 6: 4.000 > 3.000; 8: 4.000 > 3.000; 47: 1 > 0; 74: 0 > 1; 77: 0 > 1; 85: 0 > 1; 103: 0 > 1; 157: 0 > 1; 162: 1 > 0; 164: 1 > 0; 234: 0 > 1; 273: T > A; 292: A > T; 411: C > T; 423: A > G; 429: G > A; 434: A > T; 442: A > G; 523: T > C; 524: T > -; 525: A > G; 530: T > A; 560: A > G; 580: A > T; 593: A > T; 596: A > T; 609: C > T; 734: A > G; 799: T > A; 804: T > A; 842: A > T; 846: - > C; 857: A > T; 858: A > T; 863: A > G; 869: A > T; 898: - > A; 1052: C > T; 1054: A > T; 1055: A > T; 1059: G > A; 1065: T > A; 1078: G > A; 2454: A > T; 2963: C > T; 2995: T > G; 3421: T > A; 3451: A > T; 3485: T > G; 3601: T > G; 3604: G > A; 3671: G > T; 3674: T > C; 3699: C > G; 3772: T > A; 3773: T > G; 3881: T > A; 3914: A > T; 3940: G > A; 3949: T > G; 3955: A > G; 4099: A > T; 4111: T > G; 4126: T > A; 4129: T > A; 4168: G > A; 4246: T > G; 4255: A > G; 4267: T > A; 4307: A > G; 4319: A > T; 4336: T > A; 4366: G > T; 4372: T > G; 4414: G > A; 4423: A > G.

Opisthacanthus (*Opisthacanthus*) *elatus*: 5: 4.000 > 6.000; 6: 4.000 > 5.000; 7: 4.000-5.000 > 7.000; 8: 4.000 > 5.000; 9: 4.000-5.000 > 7.000; 16: 12 > 0; 28: 0 > 2; 32: 0 > 1; 36: 0 > 1; 48: 0 > 1; 49: 0 > 1; 59: 0 > 1; 68: 1 > 2; 85: 0 > 2; 94: 0 > 1; 96: 1 > 2; 110: 0 > 1; 126: 2 > 1; 129: 0 > 1; 132: 1 > 2; 137: 0 > 1; 141: 01 > 2; 146: 0 > 2; 147: 0 > 1; 150: 0 > 1; 153: 0 > 1; 154: 0 > 1; 165: 1 > 2; 170: 0 > 1; 267: A > G; 268: T > C; 271: T > A; 285: G > A; 292: A > C; 293: T > C; 298: T > C; 312: T > C; 325: T > C; 350: T > G; 379: T > A; 398: G > A; 404: T > C; 406: T > C; 427: T > G; 435: A > G; 440: A > G; 442: A > T; 443: A > T; 446: T > C; 447: T > C; 448: T > C; 479: A > T; 486: T > C; 503: T > -; 514: A > C; 515: A > T; 517: G > T; 527: A > C; 545: T > C; 565: A > G; 583: T > A; 588: T > C; 593: A > C; 601: A > G; 616: T > C; 628: A > G; 645: A > T; 707: T > C; 729: T > C; 732: T > C; 747: T > C; 748: T > C; 755: T > A; 758: T > A; 759: A > G; 763: T > C; 765: T > C; 800: A > C; 847: A > G; 859: A > G; 860: T > C; 868: A > T;

914: T > G; 922: T > A; 924: A > G; 941: A > T; 947: A > G; 953: T > C; 959: A > T; 990: A > G; 1008: T > A; 1014: T > G; 1049: T > C; 1050: T > A; 1058: T > A; 1070: A > C; 1809: C > T; 2492: A > C; 2794: G > T; 2795: C > T; 2982: G > T; 2997: C > G; 3421: T > G; 3436: T > A; 3465: T > G; 3481: T > A; 3493: T > C; 3506: A > G; 3511: T > C; 3523: T > G; 3529: T > G; 3574: T > A; 3598: T > C; 3601: T > C; 3640: G > A; 3652: A > T; 3662: T > C; 3667: T > A; 3670: T > G; 3679: T > C; 3688: A > G; 3694: T > A; 3698: T > G; 3721: T > A; 3736: T > C; 3742: T > C; 3743: T > C; 3751: T > C; 3755: A > G; 3772: T > G; 3781: T > C; 3862: G > A; 3865: T > A; 3941: T > G; 3958: T > G; 3973: A > G; 3977: T > C; 4021: G > T; 4024: A > G; 4027: G > A; 4030: T > C; 4042: T > C; 4091: T > C; 4093: A > T; 4099: A > G; 4120: T > C; 4126: T > C; 4130: C > T; 4180: G > A; 4183: G > A; 4186: T > A; 4216: T > G; 4246: T > A; 4270: T > G; 4276: T > G; 4288: T > A; 4291: T > G; 4297: T > A; 4315: A > T; 4321: G > A; 4339: T > C; 4352: A > T; 4354: T > G; 4375: AT > G; 4411: T > A; 4438: G > A; 4447: T > G; 4471: T > G.

Node 1: 132: 0 > 1; 133: 0 > 1; 134: 0 > 1; 139: 2 > 3; 156: 1 > 0; 234: 1 > 0; 381: A > T; 418: G > T; 443: T > A; 452: A > T; 502: G > A; 516: A > C; 572: G > A; 574: A > T; 705: T > C; 770: A > T; 928: T > -; 941: T > A; 4143: A > G; 4165: T > A; 4237: T > A; 4267: G > T; 4297: A > T; 4321: A > G; 4423: G > A; 4471: G > T.

Node 2 (MOC): 15: 0 > 1; 26: 12 > 0; 27: 12 > 0; 35: 0 > 1; 93: 1 > 0; 146: 0 > 1; 148: 0 > 1; 209: 1 > 0; 433: A > T; 434: A > G; 450: A > C; 507: T > A; 540: T > A; 567: T > A; 652: A > T; 736: A > T; 801: T > C; 838: T > A; 844: C > T; 864: G > A; 907: T > A; 959: A > T; 3772: T > G; 3812: G > A; 3961: G > T; 4091: T > C; 4093: A > T.

Node 3 (OPH): 235: 0 > 1; 236: 0 > 1; 272: - > AT; 274: T > A; 354: C > T; 365: G > A; 406: AG > T; 449: C > A; 626: A > T; 668: G > A; 684: T > A; 896: - > A; 917: T > A; 1059: C > G; 1069: G > CT; 1218: T > C; 1219: T > C; 1316: A > C; 3344: G > A; 3506: T > A; 3508: G > T; 3586: A > G; 4210: G > T; 4255: G > A.

Node 4 (OPI): 14: 0 > 1; 30: 0 > 1; 50: 2 > 1; 88: 1 > 0; 97: 0 > 1; 174: 1 > 0; 178: 0 >

1; 179: 0 > 1; 238: 0 > 12; 239: 1 > 0; 242: 0 > 2; 245: 1 > 0; 246: 1 > 0; 260: 0 > 1; 309: G > A; 357: T > A; 410: A > T; 734: T > A; 811: G > A; 837: T > A; 997: T > A; 1017: A > T; 1329: C > T; 1769: G > T; 2684: C > T; 2910: C > T; 2918: C > G; 3028: A > T; 3577: G > T; 3695: G > A; 3696: C > T; 3697: T > G; 3703: G > A; 3886: T > G.

NODE 5 (CAF): 17: 0 > 1; 22: 0 > 1; 23: 0 > 1; 24: 0 > 1; 68: 1 > 0; 107: 1 > 0; 232: 3 > 1; 263: T > A; 327: A > T; 330: A > T; 331: A > T; 369: T > A; 417: T > C; 420: A > G; 422: A > G; 522: A > T; 567: T > A; 568: T > A; 574: T > A; 652: A > T; 715: G > A; 739: A > G; 746: T > A; 824: C > T; 974: G > A; 2986: C > T; 3517: G > T; 3610: G > A; 3625: G > A; 3724: G > T; 3757: G > A; 3784: A > T; 3799: A > G; 3874: A > G; 3917: G > A; 4045: A > G; 4169: G > A; 4181: G > A; 4358: C > T; 4363: G > A; 4364: T > A; 4442: A > G.

NODE 6 (HHL): 42: 0 > 1; 46: 1 > 0; 47: 1 > 0; 88: 1 > 2; 111: 0 > 1; 112: 0 > 1; 113: 0 > 1; 126: 2 > 3; 159: 0 > 1; 160: 0 > 1; 161: 0 > 1; 182: 1 > 0; 183: 1 > 0; 189: 0 > 1; 196: 0 > 2; 197: 0 > 2; 207: 0 > 1; 244: 0 > 1; 247: 0 > 1; 249: 0 > 1; 250: 0 > 1; 255: 1 > 0; 358: A > G; 375: A > T; 411: C > T; 429: G > A; 524: T > -; 566: T > A; 587: A > T; 620: A > T; 637: G > A; 740: A > T; 827: G > A; 844: C > A; 847: A > T; 849: T > A; 853: C > T; 854: T > C; 862: - > A; 867: A > T; 905: A > T; 988: G > A; 1013: A > G; 1027: C > T; 1101: A > T; 1355: G > C; 1455: G > A; 1872: A > G; 2457: G > A; 2924: A > C; 2985: - > A; 2991: A > T; 2993: G > C; 3031: T > C; 3192: A > G; 3199: T > A; 3236: T > C; 3361: G > A; 3410: A > G; 3428: T > G; 3452: T > A; 3465: T > C; 3470: G > T; 3566: A > G; 3568: T > G; 3699: C > A; 3752: T > G; 3754: T > G; 3890: G > A; 3914: A > G; 3926: A > G; 3929: T > C; 3931: AG > T; 4109: G > A; 4121: A > T; 4128: G > A; 4134: C > T; 4135: T > A; 4158: C > T; 4183: G > T; 4213: G > A; 4279: A > G; 4280: G > A; 4328: T > A; 4349: T > A; 4363: G > T; 4418: A > G; 4459: T > A.

NODE 7 (HOL): 32: 0 > 1; 79: 0 > 1; 83: 0 > 1; 154: 0 > 1; 192: 0 > 1; 234: 0 > 1; 271: T > A; 427: T > C; 445: T > A; 449: A > T; 521: A > T; 770: T > A; 868: A > T; 1047: A > G; 1050: T > A; 1103: T > C; 1316: C > T; 2835: T > C; 3028: A > C; 3409: A > G; 3443: G > T; 3517: G > T; 3556: G > A; 3727: G > A; 3955: A > G; 3973: A > G; 4347: T > A.

NODE 8 (*HORMURUS*, PIA): 0: 8.000 > 9.000; 11: 1 > 0; 28: 0 > 1; 121: 0 > 1; 150: 0 > 1; 168: 2 > 0; 856: A > G; 857: A > G; 917: A > T; 925: A > T; 931: A > T; 962: G > A; 997: T > C; 1000: A > G; 1006: T > A; 1008: T > A; 1017: A > G; 2583: T > C; 2908: A > G; 3469: G > A; 3916: G > A; 4204: T > C.

NODE 9 (*HORMURUS*, excluding PIA): 42: 2 > 3; 156: 0 > 1; 177: 1 > 0; 189: 1 > 0; 190: 1 > 0; 577: A > T; 637: A > G; 653: A > T; 757: A > T; 838: T > C; 958: T > A; 1013: G > A; 1062: C > T; 1065: T > C; 1070: A > T; 1081: A > G; 1094: T > C; 1914: C > T; 3426: C > G; 3478: A > T; 3592: G > A; 3619: T > G; 3883: G > A; 3917: G > A; 4210: T > G; 4349: A > G.

NODE 10 (*HORMURUS*, excluding PIA and *Hormurus dechangei*): 8: 4.000 > 5.000; 38: 0 > 1; 48: 0 > 1; 49: 0 > 1; 50: 2 > 1; 71: 0 > 1; 196: 2 > 1; 197: 2 > 01; 3487: T > G; 3556: A > G; 3559: A > T; 3595: G > A; 3775: A > G; 3874: A > G; 3904: T > G; 4138: A > G.

NODE 11 (*HORMURUS*, AU): 199: 0 > 1; 200: 0 > 1; 202: 2 > 1; 203: 2 > 1; 292: A > T; 375: T > A; 776: T > A; 1022: G > T; 1914: T > C; 3619: G > T; 3808: G > T; 4087: G > A; 4276: A > T.

The Liochelidae Fet & Bechly, 2001 (Scorpiones) of the Indo-Pacific Region

systematics and biogeography

by

LIONEL MONOD

Volume II

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DISCLAIMER

All nomina followed by the acronym “n. sp.” designate new species that were discovered in the course of the present study but have not been formally described and named yet. These manuscript names will be made available in forthcoming publications.

CHAPTER III
-
BIOGEOGRAPHY

3.1 INTRODUCTION

Scorpions of the family Liochelidae are only found in southern continents with no representatives in Nearctic and Palearctic regions. This distribution is currently considered to be the result of vicariance induced by Gondwanaland fragmentation (Francke, 1974; Lamoral, 1980; Lourenço, 1984, 1985, 1995, 1996a, 1998, 2001; Sissom, 1990; Nenilin & Fet, 1992; Soleglad *et al.*, 2005). The phylogeny of Indo-Pacific liochelids inferred in the present work with morphological and molecular data (see chapter 2) confirms that these scorpions have an ancient Gondwana origin, the older taxa all occurring in parts of the former supercontinent, i.e. India, Madagascar, Seychelles, and South Africa. However, the cladogram differed significantly from Prendini's (2000) in the placement of the Indian *Chiromachetes* and *Iomachus*. These taxa are not retrieved here as closely related to *Liocheles sensu lato* but appear to be more basal, and are probably related to the Malagasy and Seychelles species, whereas the Afrotropical *Iomachus politus* and the Neotropical *Opisthacanthus* (*Opisthacanthus*) form the sister group to (*Hormiops* (*Hormurus* + *Liocheles*)). These phylogenetic relationships refute the "out-of-India" origin of Asian liochelids (Sissom, 1990; Soleglad *et al.*, 2005) which implies the survival of ancient Gondwana lineages on the Indian plate during its northward drift (fig. 7) and subsequent colonisation of Southeast Asia when the subcontinent finally collided with the Eurasian plate in the Late Cretaceous/Early Paleocene (fig. 8; Beck *et al.*, 1995; Jaeger *et al.*, 1989). Evolutionary affinity between the Afrotropics-Neotropics and Australasian biotas cannot be explained by Gondwana vicariance alone and thus dispersal or extinction must have played an important role in the establishment of the current distribution of these scorpions. Biogeographical patterns of several invertebrate groups (See appendix 3.5.2; Matthews, 1979; Moran, 1989; Monge-Najera, 1995; Archibald *et al.*, 2005; Archibald & Makarkin, 2006; Boyer *et al.*, 2007; Svenson & Whiting, 2009) suggest Laurasian biotic connections between Africa, Meso-South America and Asia in the Cretaceous and Early Cenozoic. Although liochelids are absent from the Nearctic and Palearctic provinces and fossils remain thus far unknown from Laurasia, it is plausible that they were more widely distributed in the Northern Hemisphere before decreasing global temperatures during the last 45 Mya (Raven & Axelrod, 1974; Haq *et al.*, 1987; Miller *et al.*, 1999; Morley, 2000; Miller *et al.*, 2005) forced them to migrate southward. Alternatively, they

may have dispersed via these northern land connections.

In addition, the present phylogeny does not support the “eastern Gondwana origin” hypothesis (Monod & Volschenk, 2004) but confirms the colonisation of the Australo-Papuan Archipelago by liochelid ancestors from Southeast Asia (fig. 8; Sissom, 1990; Koch, 1977, 1981). The distribution pattern and considerable species diversity of *Hormurus* in Australia suggest that the genus was present on the continent before the Neogene and diversified in response to the onset of aridification and contraction of rainforest habitats (Bowler, 1982; Kershaw *et al*., 1994; White, 1998; Morley, 2000). Although there are currently no absolute geological constraints on the timing of dispersal between Australasia and Sundaland, Metcalfe (2001) suggested that biotic exchanges between the Australo-Papuan Archipelago and Sundaland were established at least since the Mid Oligocene (30 Mya) when the Australian Craton drifted in close proximity to the Asian plate (Hall, 1998, 2001, 2002). However, the two geological provinces were probably connected before the Eocene by volcanic island arcs maybe as early as the Lower Paleocene when north-south sea floor spreading began in the rift between Australia and Antarctica (fig. 7; Kroenke, 1996; Hall, 1998; Müller *et al.*, 2000). By then, the Australian plate started to drift northward and subduction of its northern margins beneath the Asian and Pacific plates was initiated (Hamilton, 1988; Polhemus, 1996). Although there is currently no geological evidence that the volcanic island arcs in the nascent Australo-Papuan Archipelago were emergent in the Early Cenozoic, the present study strongly suggests that these island chains constituted suitable dispersal corridors for liochelids and that their geological dynamics were preponderant in the diversification of these scorpions. Distribution patterns of Melanesian *Hormurus* apparently result from speciation along island arcs followed by accretion of these islands onto other landmasses, a process considered to be the major shaping force of distribution patterns in the south-western Pacific (see appendix 3.5.1.2; Polhemus, 1996). Molecular clocks and statistical methods will be used here to determine whether the temporal sequence of diversification of Indo-Pacific Liochelidae is congruent with the present assumptions inferred from the phylogeny and with the geological history of the region.

3.2 MATERIAL & METHODS

Molecular clocks and phylogenetic biogeography. As emphasized by Posadas *et al.* (2006), historical biogeography needs to consider not only the distributional patterns of taxa but also their temporal patterns. Ignoring the timing of lineage diversification obscures the connection between biogeographical patterns and their possible underlying causes, i.e. dispersal and vicariance events. Currently, the fossil record, molecular clocks and major geological events are the three main sources of temporal information for dating nodes on a cladogram. The age of the earliest fossil for a group or allied group is commonly used for initial calibration for molecular clock analyses. Earlier molecular clock methods (Zuckerhandl & Pauling, 1962; 1965) assumed constant mutation rates in order to infer divergence dates. However, it was later demonstrated that constant mutation rate is an unrealistic assumption because the evolution of DNA sequences is not clock-like (Britten, 1986; Ayala, 1997; Hasegawa & Kishino, 1989; Ho & Jerwiin, 2004). Bayesian relaxed-clock methods (Thorne *et al.*, 1998; Aris-Brosou & Yang, 2002) address this issue by allowing substitution rates to vary among the branches of a cladogram. However, these earlier methods require the user to specify the tree topology a priori. The recent "relaxed phylogenetics" approach allows both the phylogeny and the divergence dates to be estimated simultaneously under a relaxed clock (Cranston & Rannala, 2005). Although important theoretical and computational advances have been made, molecular clocks remain highly conjectural because they are based on statistical inference and not on direct evidence. However, they are the only way to infer the timing of speciation events and can nevertheless provide important evidence when evaluating different biogeographical hypotheses. Relaxed phylogenetics algorithms implemented in BEAST (Drummond *et al.*, 2006; Drummond & Rambaut, 2007) are used in the present study to evaluate the absolute timing of cladogenesis events within the Indo-Pacific Liochelidae.

Historical (phylogenetic) biogeography consists of deriving cladograms for geographical regions based on the phylogenies of the organisms inhabiting these areas (Wiley, 1988; Page, 1994; Morrone & Crisci, 1995; Humphries & Parenti, 1999). Cracraft (2001) pointed out that historical biogeography and the recognition of generalized patterns is pivotal in assessing biogeographic hypotheses. Dismissing the significance of congruence and conflicts between

phylogenetic relationships of many groups and earth history, and relying solely on paleontological data and molecular clocks can potentially lead to erroneous conclusions. Several sources of error pertaining to fossil calibrations of molecular clocks can result in an underestimation of cladogenesis event ages and thus support inaccurate conjectures (Hedges & Kumar, 2004; Donoghue & Benton, 2007): (1) fossils may not represent the oldest representatives of a lineage; (2) fossils may be misplaced within phylogenies (Lee, 1999); (3) the age of the rocks in which the fossils were discovered may be incorrectly evaluated (Marshall, 1990; VanTuinen & Hadly, 2004). Thus, evidence from historical biogeography should always be used to corroborate results derived from the fossil record and molecular clocks. Most recent biogeographical studies are based on a solid phylogenetic framework, however very few evaluate congruence and conflicts with phylogeny and biogeography of other groups (Sharma & Giribet, 2009). In the present study, phylogenies and biogeographical patterns of various invertebrate groups were therefore compared to those of the Liochelidae in order to corroborate or reject the alternative hypotheses considered.

Molecular dating of divergence times without fossils. As mentioned above, the use of genetic data to estimate ages of divergence across evolutionary lineages is subject to many pitfalls (Arbogast *et al.*, 2002; Donoghue & Benton, 2007), some directly associated with the complexity of DNA sequence evolution (rate heterogeneity), other inherent to the current methods and their limitations, for example the need for a reliable fossil record. There are no fossils known for many organisms, and the few available for others cannot be unambiguously placed within a phylogeny because of the lack of diagnosable synapomorphic characters. However this does not preclude the use of a molecular clock to evaluate divergence times. Several authors (Murienne *et al.*, 2005; Ribas *et al.*, 2007) overcame the problem of an inadequate or non-existent fossil record by testing the consistency of age estimates across several independent analyses using different strategies, e.g. use of a ‘standard’ substitution rate, use of geological calibration points and/or of calibration points determined from other datasets. Like fossil calibration, calibrating molecular clocks with selected geological and/or climatic events can potentially lead to considerable errors because (1) the dates of many geological events and the details of

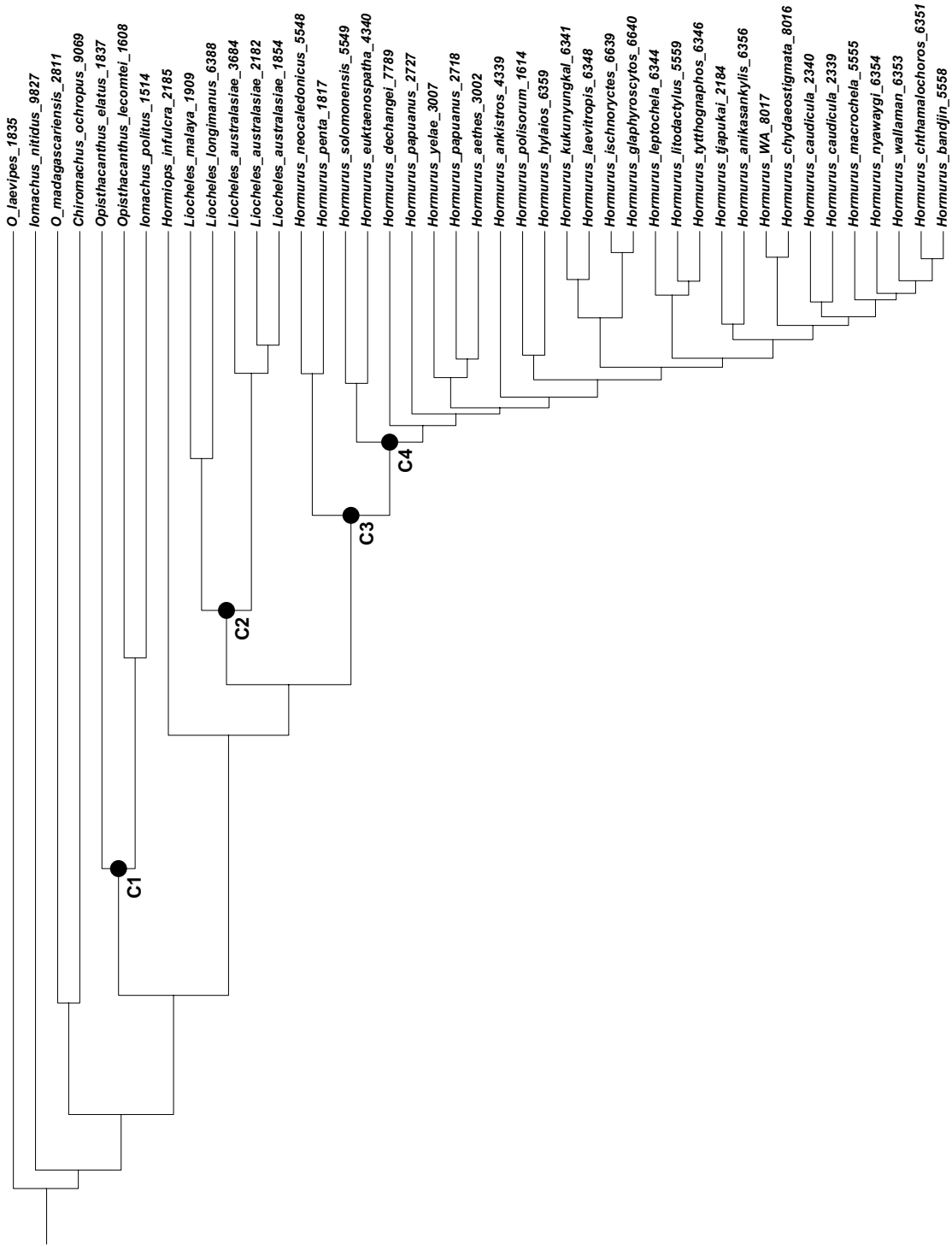
paleocoastline and climate are still poorly understood despite the reliable constraints of Gondwanan continents past positions, and (2) bias towards a preferred biogeographical scenario is likely to influence the choice of events and dates used as calibration points. Divergence times are then not empirically estimated but rather 'manufactured' to fit the author's opinion (Yoder & Nowak, 2006; Upchurch, 2008). Methods for evaluating discrepancies between nodal age estimates derived from independent calibration sets and for minimizing the impact of calibration errors have recently been an active field of research and several cross-validation strategies (Near & Sanderson, 2004; Near *et al.*, 2005; Rutschmann *et al.*, 2007; Pyron 2010; Ruane *et al.*, 2011) have been proposed thus far.

Calibration points in the Indo-Pacific Liochelidae. The main limitation to this biogeographic analysis is the absence of potential fossil calibrations. The only known liochelid fossil cannot be unambiguously placed in any of the extant taxa (see paragraph 0.2). Based on the phylogeny of Indo-Pacific Liochelidae, the biogeographical patterns observed in other terrestrial invertebrate groups inhabiting the same region and sharing similar ecological characteristics (refer to appendix 3.5.2 for details), and the alleged sequence of formation of the Indo-Pacific Region (refer to appendix 3.5.1.2 for details), four geotectonic/paleoclimatic events were identified as potential causes of vicariance and thus selected as calibration points in the present study (fig. 60):

(**C1**) **98 Mya (± 8)**: Divergence between Afrotropical *I. politus* and *O.* (*O.*) *lecomtei* and Neotropical *Opisthacanthus* is here assumed to be the result of vicariance driven by Gondwana continental drift in the Mid Cretaceous (Albian-Cenomanian). The final rifting between South America and Africa, which corresponds to the opening of the Central and Equatorial Atlantic Ocean, is estimated between 95 and 118 Mya (Nürnberg & Müller, 1991; Pitman *et al.*, 1993; Storey, 1995; McLoughlin, 2001; Pletsch *et al.*, 2001; Moulin *et al.*, 2010). At 85 Mya, the two southern landmasses were separated by wide seaways (Goldblatt, 1993; Burnham & Graham, 1999) and biotic isolation between them was completely effective. Origin of the Afrotropical and Neotropical liochelids is probably a direct outcome of this geotectonic event.

(**C2**) **53 (± 10)**: Divergence between *Liocheles* from Malaysian/northern Sumatra and

Fig. 60. Cladogram of the Indo-Pacific Liochelidae Fet & Bechly, 2001 with C1, C2, C3 and C4 calibration points indicated.


O_laevipes_1835
Iomachus_nitidus_9827
O_madagascariensis_2811
Chiromachus_ochropus_9069
Opisthacanthus_elatus_1837
Opisthacanthus_lecomtei_1608
Iomachus_politus_1514
Hormiops_infulcra_2185
Liocheles_malaya_1909
Liocheles_longimanus_6388
Liocheles_australasiae_3684
Liocheles_australasiae_2182
Liocheles_australasiae_1854
Hormurus_neocaledonicus_5548
Hormurus_penta_1817
Hormurus_solomonensis_5549
Hormurus_euktaenospatha_4340
Hormurus_dechangei_7789
Hormurus_papuanus_2727
Hormurus_yelae_3007
Hormurus_papuanus_2718
Hormurus_aethes_3002
Hormurus_ankistros_4339
Hormurus_polisorum_1614
Hormurus_hylaios_6359
Hormurus_kukunyungkal_6341
Hormurus_laevitropis_6348
Hormurus_ischnoryctes_6639
Hormurus_glaphyroscytos_6640
Hormurus_leptochela_6344
Hormurus_litodactylus_5559
Hormurus_tytthognaphos_6346
Hormurus_tjapukai_2184
Hormurus_anikasankylis_6356
Hormurus_WA_8017
Hormurus_chydaeostigmata_8016
Hormurus_caudicula_2340
Hormurus_caudicula_2339
Hormurus_macrochela_5555
Hormurus_nyawaygi_6354
Hormurus_wallaman_6353
Hormurus_chthamalochoros_6351
Hormurus_bandjin_5558
C1
C2
C3
C4

from continental Indochina is hypothesized to be the result of vicariance driven by sea level rises in the Paleocene-Early Eocene. Peninsular Malaysia and North Sumatra are faunistically and floristically closely related and distinct from the nearby Indochinese region. Woodruff (2003) identified the Isthmus linking the Thai-Malay peninsula with mainland Southeast Asia as a biogeographical transition between Sundaic and Indochinese subregions. However, could not find any climatological and geological evidence to account for this biotic cleavage. Woodruff (2003) postulated that parts of the Isthmus were probably flooded during Neogene marine transgressions and thus acted as biogeographical barriers. Sea levels were at their highest during the Paleocene-Eocene Thermal Maxima, ca. 65–45 Mya (Haq *et al.*, 1987; Keller, 2001; Miller *et al.*, 1999; Abramovich *et al.*, 2002; Miller *et al.*, 2005). They probably fluctuated between +50 and +100 m (relative to the present day) for most of that period and probably reached a record +150 m at ca. 53 Mya (Miller *et al.*, 1999, 2005). This dramatic paleoenvironmental change is here considered as the determinant factor of faunistic differences observed in the genus *Liocheles* on either side of the Thai-Malay Isthmus.

(**C3**) **35 Mya (± 5)**: Divergence between the PIA clade (eastern tip of Papua New Guinea, New Caledonia, Rennell and Solomon Island) and the rest of the genus *Hormurus* is considered to be correlated with the development of the Australasian volcanic arc system in the Eocene-Oligocene. Emergence of the Melanesian Arc, extending from New Britain through New Ireland, the Solomons, Fiji and a proto Kermadec-Tonga Arc system, was probably initiated at 85–80 Mya when expansion and spreading of the South Loyalty-Santa Cruz-Pocklington back-arc basin started along the north-east Australia-Pacific subduction zone (see appendix 3.5.1.2, fig. 84A; Schellart *et al.*, 2006). It had completely rifted from the Australian margin when the Solomon Sea started to develop as a back-arc basin along the north-dipping Pocklington subduction zone in the late Eocene, ca. 40–35 Mya (see appendix 3.5.1.2, fig. 84B; Hall, 2001, 2002; Hill & Hall, 2003; Schellart *et al.*, 2006). Spreading of the Solomon basin lasted during the Oligocene until about 28 Mya and induced the formation of the New Guinea arc (see appendix 3.5.1.2, figs 84C, D; Schellart *et al.*, 2006). This arc may have potentially carried *Hormurus* ancestors onto eastern New Guinea and New Caledonia away from their stem lineage located on the Melanesian arc.

(**C4**) **25 Mya (± 5)**: Divergence between Solomons-New Britain *Hormurus* and New Guinea-Australian *Hormurus* was probably associated with significant tectonic shifts that occurred in the West Pacific the Oligocene. Around 25 Mya, collisions between the Australian continental crust and Southeast Asia, between the East Philippines-Halmahera-South Caroline Arc and the northern New Guinea margin, and between the Ontong Java Plateau and the Melanesian Arc induced a major reorganisation of plate boundaries in the Australasian region (figs 74–75; Hall, 2001, 2002; Hill & Hall, 203): the Halmahera-Philippines arc and New Guinea terranes at the southern Caroline margin became effectively coupled with the Pacific plate while the marginal basins separating the Melanesian Arc from passive margins of north-eastern Australasia were further widened. It is hypothesized here that *Hormurus* present on islands of the Melanesian arc were isolated from counterparts located on the islands of the Halmahera-Philippines.

Cross-validation tests of age estimates. The sequence and temporal framework of Gondwana fragmentation is for the most part well constrained. However, given its complexity and the difficulty of assessing the extent of emergent and submerged land through time in the region, the geology of the Australasian archipelago can hardly be summarized by a series of unambiguous and well dated vicariance events. Thus, contrary to the Gondwana calibration point (C1) considered here as reliable, the Australasian calibration points (C2–4) are deemed more speculative and thus require more scrutiny. Two series of cross-validation analyses were performed in order to assess whether the initial assumptions used to select the calibration points were plausible:

(1) A 'keep-one approach' (Near *et al.*, 2005) was first implemented to ascertain that Gondwanan vicariance between Afrotropical and Neotropical taxa is congruent with Cenozoic dispersal of *Hormurus* ancestors from southeast Asia onto the nascent Australasian archipelago. Four analyses (A1, A2, A3 and A4) were conducted; each was based only on a single geological calibration point (C1, C2, C3 or C4 respectively) and constrained at the root by a maximum upper bound of **163 Mya (± 5),** the estimated age of rifting between East and West Gondwana which is considered as the cause of cladogenesis between the South African *O.* (*N.*) *laevipes* and the remaining liochelids. Comparison of the mean dates for all nodes that resul-

ted from the A1, A2, A3 and A4 analyses was subsequently performed using a Kruskal-Wallis ANOVA-by-Ranks test in the statistical package R (R development Core Team, 2010). The four age estimates for each calibration node were compared using ANOVA tests implemented in R. This sensitivity analysis determined whether the dates estimated with each calibration set were compatible with each other.

(2) In a second approach, a 'leave-one' procedure (Near & Sanderson, 2004), consisting of five analyses (A5, A6, A7, A8, A9), permitted an assessment of whether one of the calibration points strongly disagrees with the others and should be discarded. The first analysis **A5** uses all four calibration points (C1 + C2 + C3 + C4) whereas the following four analyses employ combinations of three constraints, each of these combinations excluding a different calibration node: **A6** (C2 + C3 + C4), **A7** (C1 + C3 + C4), **A8** (C1 + C2 + C4) and **A9** (C1 + C2 + C3). This method helps detect potential incongruence in the calibration set and to select more appropriate combination of constraints. As for the 'keep-one' analysis, comparison of the mean ages for all nodes obtained with A5, A6, A7, A8 and A9 was computed with the Kruskal-Wallis ANOVA-by-Ranks test and age estimates calculated for each calibration node were compared across all analyses with a series of ANOVA tests.

Genetic markers and bayesian inference. Mitochondrial DNA sequences are not a reliable source of data to determine the ages of deep phylogenetic nodes because of the saturation of nucleotide substitutions and are therefore only appropriate to time divergence between populations and/or closely related species (Jansa *et al.*, 2006; Roelants *et al.*, 2007; Kumar, 2009). On the other hand, clocks based on nuclear DNA are more suitable to establish the timing of older divergences. The origin of most liochelids probably dates back to the Gondwana break-up and dispersion, thus speciation events to be estimated in the present study putatively took place during the last 180 Mya. Three fast-evolving mitochondrial genes (12S rDNA, 16S rDNA and COI) and two highly conserved nuclear gene (18S rDNA and 28S rDNA) constitute the present dataset providing resolution for both ancient and more recent nodes. Tree topology, branch length and divergence dates were estimated for the combined dataset with BEAST version 1.6.1 (Drummond & Rambaut, 2007), which employs a Bayesian Markov Chain Monte

Carlo (MCMC). The data were partitioned by genes and best-fit substitution models were identified for each data partition with jModeltest version 0.1.1 (Posada, 2008; Guidon & Gascuel, 2003) using the Bayesian information criterion (BIC). Model parameters were unlinked across partitions because different models were selected for each partition. The HKY model (Hasegawa, Kishino & Yano, 1985) with variation rate (4 gamma categories) was implemented for the 12S rDNA, 16S rDNA and 28S rDNA partitions, the HKY model with invariant site parameter for the 18S rDNA partition and the HKY model with variation rate (4 gamma categories) and invariant site parameters for the COI partition. Molecular clock models were unlinked across partitions because all genes were assumed to evolve with different substitution rates. All analyses assumed a birth/death branching rate prior, with rate variation across branches assumed to be uncorrelated and lognormally distributed (Drummond *et al.*, 2006). Each calibration prior was assumed to be normally distributed to accommodate the potential inaccuracy of geological age estimates and the possibility that lineage divergences may postdate the formation of biogeographic barriers (Ho & Phillips, 2009). Each MCMC chain was run for 100'000'000 generations (burn-in 10'000'000 generations), with parameters sampled every 10'000 steps. All analyses were computed on the BIOPORTAL of the University of Olso, Norway (Kumar, Skjaeveland *et al.*, 2009). The results of each analysis were analysed with Tracer version 1.5 (Rambaut & Drummond, 2009). Finally, Tree Annotator version 1.6.1 (Drummond & Rambaut, 2007) was used to produce a maximum clade credibility chronogram from the post-burn-in trees and to determine the 95% probability density of ages for all nodes in the tree. The consensus tree was subsequently edited in FigTree version 1.3.1 (Rambaut, 2009).

Diversification rates through time. The study of variation in speciation and extinction rates over time has led to the development of several sophisticated statistical methods to address temporal variation in diversification rates. The APE (Paradis *et al.*, 2004) and LASER (Rabosky, 2006B) packages implemented for the R environment were used in the present study to infer change of diversification rates within the Indo-Pacific Liochelidae. The gamma-statistic (Pybus & Harvey, 2000) was first computed for the Indo-Pacific liochelids chronogram. Then, a birth-death likelihood test (Rabosky, 2006A) was performed. Both of these statistical tests

can provide evidence for abrupt shifts of diversification rates that may be indicative of adaptive radiation. The gamma-statistic determines whether the per-lineage speciation and extinction rates have remained constant through time. Because it tests the distribution of internal nodes in a molecular phylogeny for departure from the pure-birth process (Yule, 1924) and thus does not consider extinction rate, it can only emphasize temporal decrease in diversification but not temporal increase (Rabosky, 2006A). On the other hand, the birth-death likelihood test (Rabosky, 2006A) incorporates both speciation and extinction in the null hypothesis of rate-constancy and is, in that regard, a more powerful approach because it can distinguish between a temporal increase in diversification rate and a rate-constant model with nonzero extinction. The BDL-statistic test considers various rate-constant and rate-variable models of diversification and, by comparing their respective Akaike information criterium (AIC; Akaike, 1973) scores, determines the model that best approximates the phylogenetic data.

3.3 RESULTS

The nine MCMC searches converged on the same topology (fig. 61) that is also strongly congruent with the phylogenies inferred from the parsimony analysis of the molecular data presented in Chapter 2. Examination of MCMC samples suggested that each chain was adequately sampling the probability distribution: effective sampling sizes for all parameters were greater than 400, indicating that the sampled generations were uncorrelated and that the posterior distribution of the parameters were long and accurate. Age estimates obtained with the various sets of calibration points are given in table 22 and the chronogram obtained when all calibration points were included is presented in figure 61.

Mean age estimates for all nodes obtained with the four analyses of the "keep-one" procedure are not significantly different (Kruskal-Wallis chi-squared = 0.5642, df = 3, p-value = 0.9046; fig. 62). C1 age estimates obtained with the different analyses were not statistically different. However, ANOVA tests yielded significant differences between C2 age estimates from A2/A3/A4 and those from A1 (tab. 23). The marginal density plots from BEAST for both nodes (fig. 63B, E) do not indicate any major incongruence between the four analyses. On the other

Fig. 61. Maximum clade credibility chronogram of the Indo-Pacific Liochelidae Fet & Bechly, 2001 derived from BEAST (Drummond *et al*., 2006) analysis of molecular data using C1, C2, C3 and C4 calibration points (A5). Blue bars indicate the 95% highest probability density (HPD) for node ages and numbers above nodes are means of HPD.

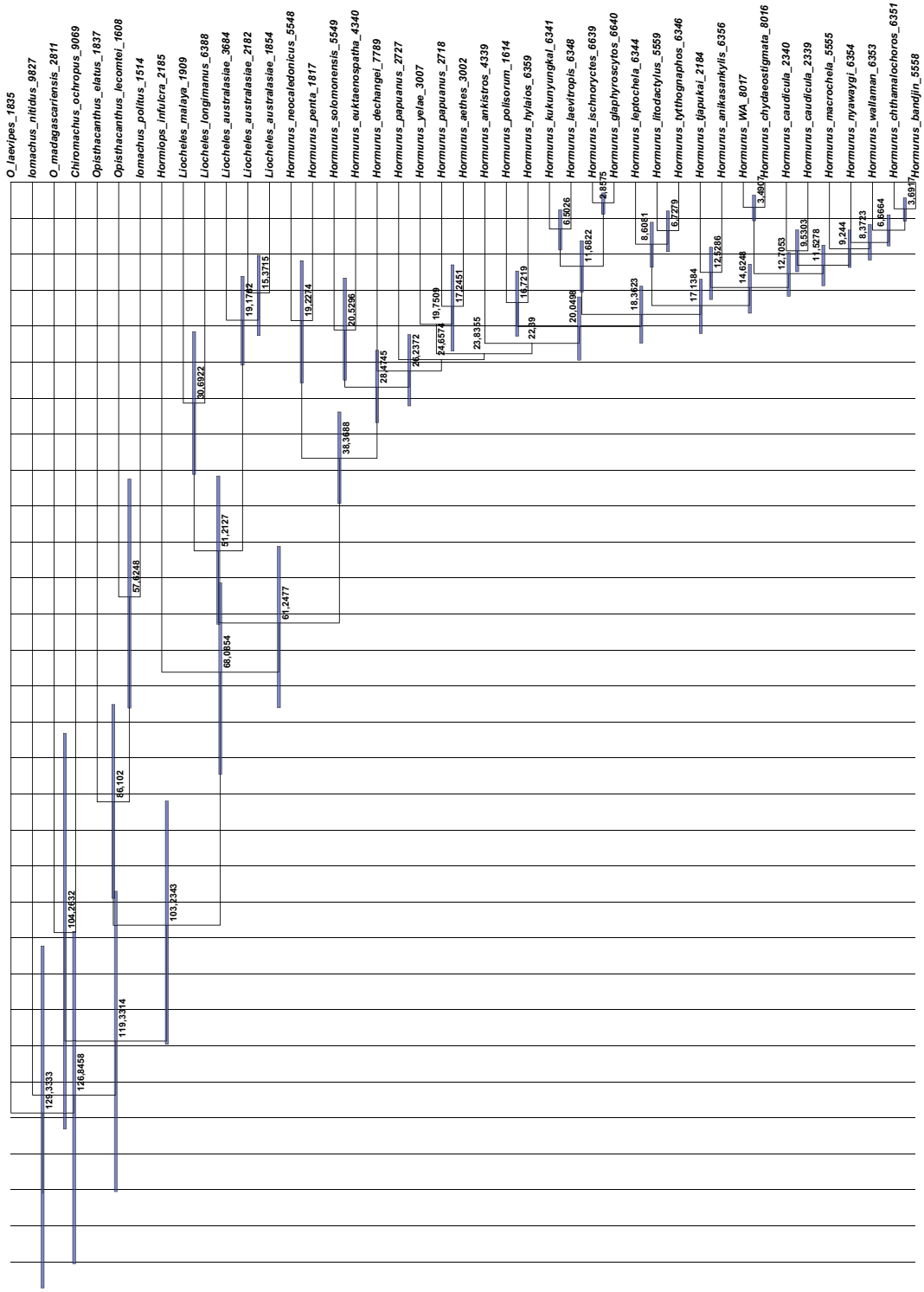

O_laevipes_1835
Iomachus_nitidus_9827
O_madagascariensis_2811
Chiromachus_ochropus_9069
Opisthacanthus_elatus_1837
Opisthacanthus_lecomtei_1608
Iomachus_politus_1514
Hormiops_infulcra_2185
Liocheles_malaya_1909
Liocheles_longimanus_6388
Liocheles_australasiae_3684
Liocheles_australasiae_2182
Liocheles_australasiae_1854
Hormurus_neocaledonicus_5548
Hormurus_penta_1817
Hormurus_solomonensis_5549
Hormurus_euktaenospatha_4340
Hormurus_dechangei_7789
Hormurus_papuanus_2727
Hormurus_yelae_3007
Hormurus_papuanus_2718
Hormurus_aethes_3002
Hormurus_ankistros_4339
Hormurus_polisorum_1614
Hormurus_hylaios_6359
Hormurus_kukunyungkal_6341
Hormurus_laevitropis_6348
Hormurus_ischnocyctes_6639
Hormurus_glaphyroscytos_6640
Hormurus_leptochela_6344
Hormurus_litodactylus_5559
Hormurus_tytthognaphos_6346
Hormurus_tjapukai_2184
Hormurus_anikasankylis_6356
Hormurus_WA_8017
Hormurus_chydaeostigmata_8016
Hormurus_caudicula_2340
Hormurus_caudicula_2339
Hormurus_macrochela_5555
Hormurus_nyawaygi_6354
Hormurus_wallaman_6353
Hormurus_chthamalochoros_6351
Hormurus_bandjin_5558
126,3333
104,2532
126,8458
119,3314
66,102
57,6248
103,2343
68,0854
51,2127
61,2477
30,6922
19,1762
15,3715
19,2214
38,3688
20,5296
28,4745
24,2372
24,6574
19,7509
17,2451
23,8355
22,39
16,7219
20,0498
6,5926
11,6822
8,875
18,3623
8,6081
6,7279
17,1384
12,5286
14,6248
3,4907
12,7053
9,5303
11,5278
9,244
8,3723
6,6664
3,6917
0,0
25,0
50,0
75,0
100,0
125,0
150,0
20,0

Table 22. Cladogenesis age estimates for the phylogeny of Indo-Pacific Liochelidae Fet & Bechly, 2001 calculated with the different sets of calibration. Expressed in Mya, 95% high probability density (HPD) indicated in parentheses. Taxonomic groups: HHL = *Hormiops* + *Hormurus* + *Liocheles sensu lato*; HOL = *Hormurus* + *Liocheles*; HOR = *Hormurus*; LIO = *Liocheles*; nonPIA = *Hormurus* except species of the PIA clade; OPH = OPI + HHL; OPI = *I. politus* + *Opisthacanthus* (*Opisthacanthus*); PIA = Pacific island arc *Hormurus*.

	A1 (C1)	**A2 (C2)**	**A3 (C3)**	**A4 (C4)**	**A5 (C1/C2/C3/ C4)**	**A6 (C2/C3/C4)**	**A7 (C1/C3/C4)**	**A8 (C1/C2/C4)**	**A9 (C1/C2/C3)**
O. (*N.*) *laevipes*-Remaining taxa	161.8 (152.2-171.1)	161.1 (151.8-170.7)	159.7 (150.2-169.5)	160.2 (150.7-169.7)	129.3 (106.1-153.6)	101.7 (73.6-130.2)	129.3 (104.1-154.3)	133.9 (108.3-161.1)	132.4 (109.1-158.8)
Outgroups - OPH	158.3 (147.2-169.5)	157.4 (146.2-169.3)	155.4 (142.9-167.4)	156.219 (144.2-167.7)	126.8 (104.1-150.3)	99.6 (72.2-127.4)	126.9 (102.4-151.5)	131.4 (106.0-157.0)	129.9 (105.9-154.2)
OPH	125.9 (112.5-140.0)	124.2 (109.1-139.9)	120.8 (104.7-136.0)	121.9 (106.3-137.8)	103.2 (86.0-119.8)	80.1 (59.0-102.8)	103.1 (84.2-121.1)	106.5 (88.4-126.4)	105.6 (87.4-123.0)
OPI	98.2 (86.6-110.8)	96.9 (78.2-115.1)	93.9 (75.5-112.9)	94.7 (75.5-113.2)	86.1 (72.6-99.5)	62.7 (43.5-81.9)	86.0 (71.7-99.8)	88.1 (74.1-102.6)	87.528 (74.2-101.3)
Hormiops-HOL	85.0 (71.9-99.9)	82.7 (69.0-96.5)	79.4 (65.1-93.3)	80.7 (67.0-95.4)	68.1 (55.7-82.3)	54.8 (40.2-70.3)	67.9 (53.8-82.8)	70.8 (56.8-85.7)	69.8 (56.0-83.6)
HOL	77.4 (64.3-90.2)	74.3 (62.4-86.8)	71.2 (58.9-84.2)	72.9 (60.3-86.6)	61.5 (50.4-73.0)	50.3 (37.2-63.4)	61.1 (48.5-74.1)	64.1 (51.6-76.9)	63.1 (51.7-75.5)
LIO	64.0 (50.6-77.3)	60.2 (48.8-70.6)	59.0 (46.2-71.6)	60.2 (47.2-73.2)	51.2 (40.8-61.4)	42.3 (30.7-53.8)	50.7 (38.6-62.6)	53.0 (41.9-64.0)	52.4 (41.9-63.5)
PIA - nonPIA	51.5 (40.7-62.3)	50.3 (40.1-60.9)	42.9 (36.4-49.8)	46.8 (36.9-56.7)	38.7 (31.9-44.6)	33.3 (25.8-41.1)	38.2 (31.6-45.1)	41.7 (32.6-51.6)	39.5 (32.4-46.1)
nonPIA	37.8 (30.1-45.9)	37.0 (29.2-44.6)	33.1 (26.8-39.0)	32.9 (27.0-38.4)	28.5 (23.4-33.4)	24.4 (18.4-30.2)	28.3 (23.3-33.8)	29.9 (24.2-36.1)	29.9 (24.0-36.3)

Fig. 62. Box-and-whisker plots of the mean divergence time estimates for all nodes obtained with the nine BEAST (Drummond *et al*., 2006) analyses using different calibration sets.

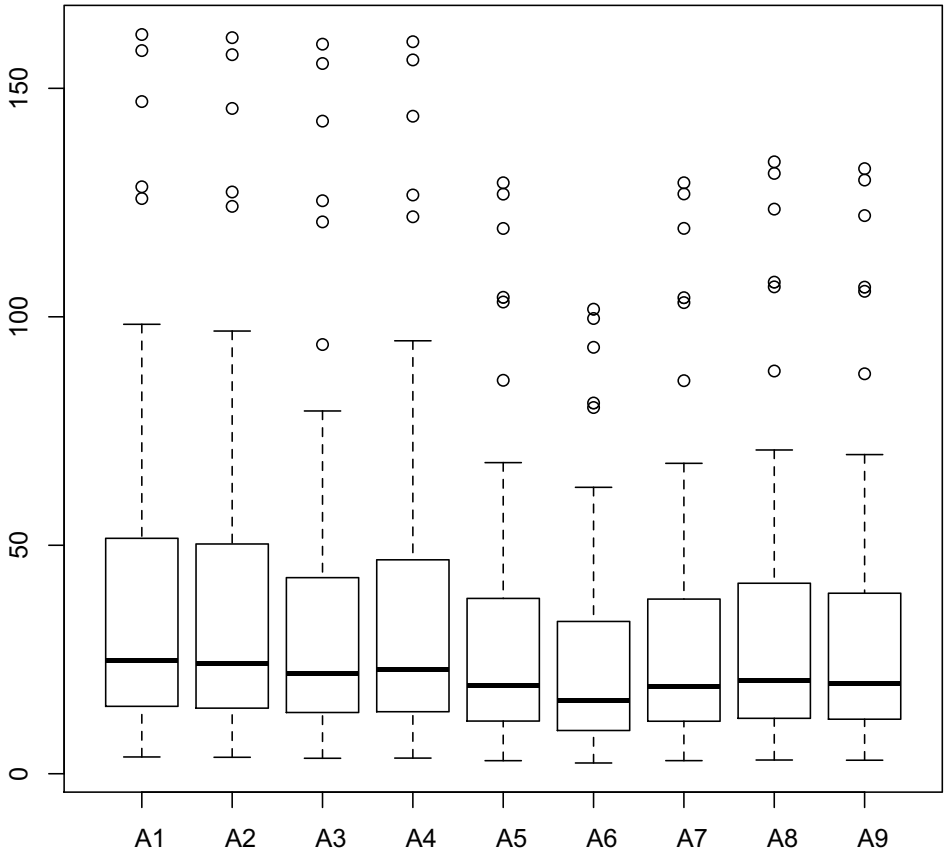
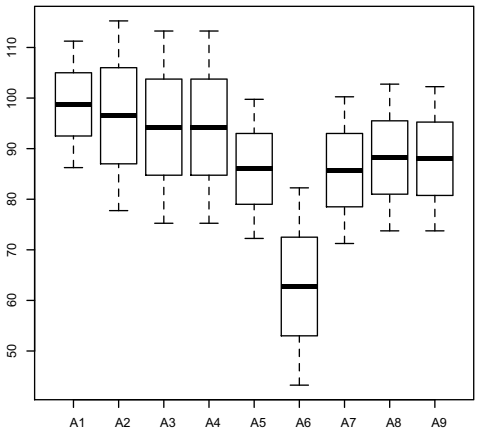

150
100
50
0
A1
A2
A3
A4
A5
A6
A7
A8
A9

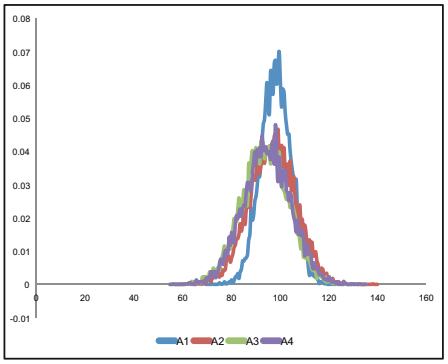
Table 23. Results (p values) of the ANOVA tests conducted between the estimates of divergence ages for C1, C2, C3 and C4 nodes obtained with the nine BEAST (Drummond *et al*., 2006) analyses using different sets of calibration. Significant differences are highlighted.

	C1	C2	C3	C4
A1-4	0.05768	0.001142 **	< 2.2e-16 ***	< 2.2e-16 ***
A2-4	-	0.5602	6.196e-12 ***	1.192e-11 ***
A1/2	-	-	0.2979	0.1757
A3/4	-	-	0.0001238 ***	0.8055
A5-9	< 2.2e-16 ***	< 2.2e-16 ***	< 2.2e-16 ***	< 2.2e-16 ***
A5/7/8/9	0.2456	0.04438 *	3.376e-07 ***	0.001332 **
A5/8/9	-	0.1117	6.28e-06 ***	0.002709 **
A5/7/9		-	0.3163	0.005781 **
A5/7	-	-	-	0.6901

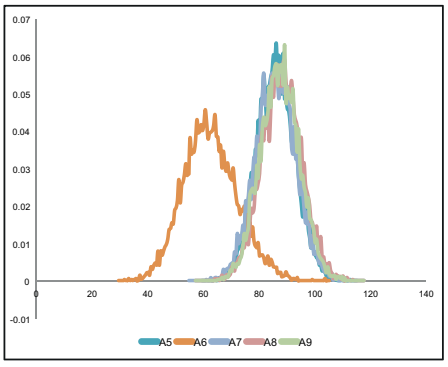
Fig. 63. Divergence time estimates for C1 node. A, box-and-whisker plots of values from the nine BEAST (Drummond *et al*., 2006) analyses using different calibration sets. B, marginal densities from BEAST analyses A1, A2, A3 and A4. C, marginal densities from BEAST analyses A5, A6, A7, A8 and A9. Divergence time estimates for C2 node. D, box-and-whisker plots of values from the nine BEAST analyses using different calibration sets. E, marginal densities from BEAST analyses A1, A2, A3 and A4. F, marginal densities from BEAST analyses A5, A6, A7, A8 and A9.


110
100
90
80
70
60
50
A1
A2
A3
A4
A5
A6
A7
A8
A9

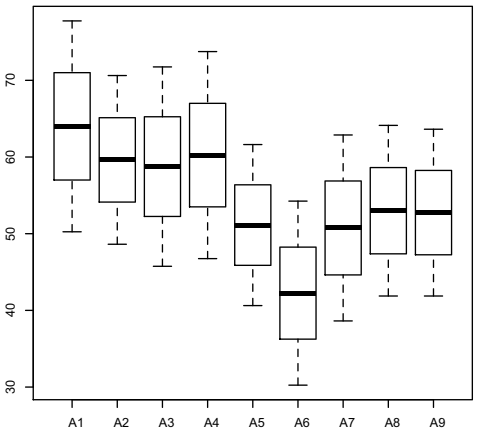
A


0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
-0.01
0
20
40
60
80
100
120
140
160
A1
A2
A3
A4

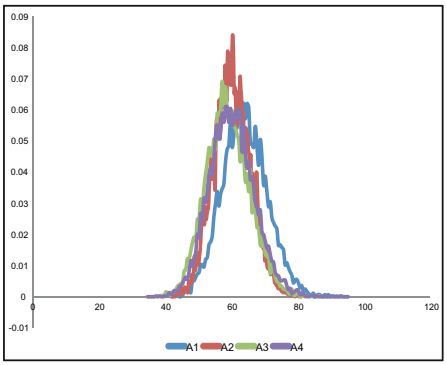
B


0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
-0.01
0
20
40
60
80
100
120
140
A5
A6
A7
A8
A9

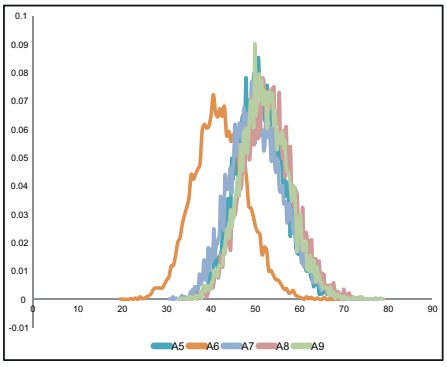
C


70
60
50
40
30
A1
A2
A3
A4
A5
A6
A7
A8
A9

D


0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
-0.01
0
20
40
60
80
100
120
A1
A2
A3
A4

E


0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
-0.01
0
10
20
30
40
50
60
70
80
90
A5
A6
A7
A8
A9

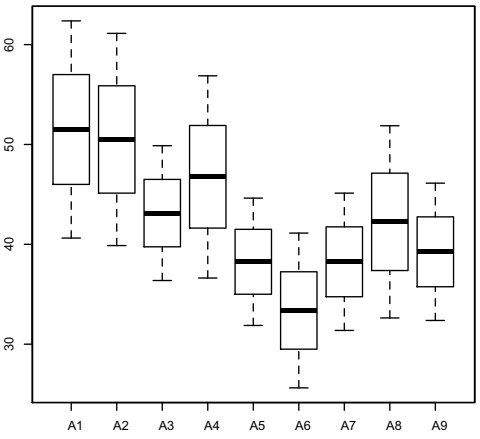
F

hand, age estimates for C3 and C4 retrieved from A1 and A2 are mutually congruent but significantly different from those obtained with A3 and A4. Additionally, C3 age estimates from A3 and A4 analyses are different from each other. The marginal plots overlap but suggest clear differences between the means (fig. 64B, E). Furhermore, time estimates for C3 and C4 determined with all “keep-one” analyses are 10–15 Mya older than the proposed calibration values for these nodes (tab. 23), contrary to the estimates for C1 and C2 which are congruent with the calibration intervals, suggesting that the dates use to calibrate C3 and C4 nodes may be slightly too recent.

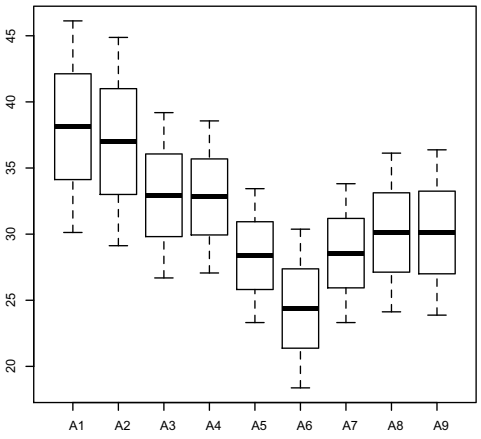
Mean estimates for all divergence events obtained with the five analyses of the “leave-one” procedure are not significantly different (Kruskal-Wallis chi-squared = 2.3423, df = 4, p-value = 0.6731; fig. 62). However, age estimates for all four calibration nodes are significantly under-estimated when C1 is excluded from the calibration set (A6 analysis; see tab. 23, fig. 63A, C, D, F, 64A, C, D, F). Underestimation of observed divergence times is a known effect when events to be estimated fall beyond the calibration point(s) (extrapolation) (Wilke *et al.*, 2009). Uncertainties increase with the distance between the calibration points and the estimated event because of mutational saturation (observed mutations are lower than expected mutations) between distantly related taxa (Arbogast *et al.* 2002; Bromham & Penny 2003). Thus, by excluding the oldest calibration node C1 from the analysis, the divergence time estimates, especially those of the deeper nodes, are estimated to be more recent than when C1 is included in the calibration set. Excluding C3 and C4 from the calibration set has the opposite effect. Analyses A8 and A9 yielded slightly older divergence estimates compared to other analyses (tab. 22). Significant differences with other date estimates was reported for C3 with the A8 calibration set (tab. 23, fig. 64A, C, D, F), and for C4 with both the A8 and A9 calibration sets (tab. 23, fig. 64D/F). This confirms the results from the ‘keep-one’ approach indicating that C3 an C4 events are probably slightly older than the proposed calibration dates.

The gamma statistics calculated for the chronogram obtained with A5 analysis (gammaStat= 0.9653816; p value=0.8328231) indicates that the internal nodes of the phylogeny are closer to its tips than expected by the pure birth process but that the null hypothesis of constant diversification rate cannot be rejected (fig. 65). The birth-death likelihood test yielded similar

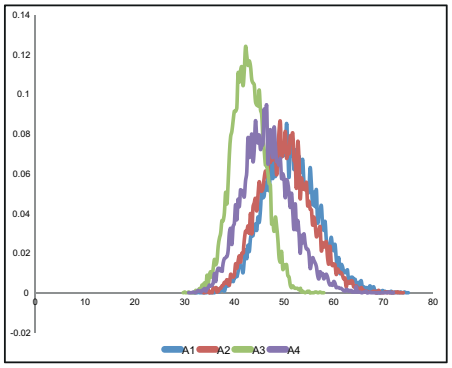
Fig. 64. Divergence time estimates for C3 node. A, box-and-whisker plots of values from the nine BEAST analyses using different calibration sets. B, marginal densities from BEAST analyses A1, A2, A3 and A4. C, marginal densities from BEAST (Drummond *et al*., 2006) analyses A5, A6, A7, A8 and A9. Divergence time estimates for C4 node. D, box-and-whisker plots of values from the nine BEAST analyses using different calibration sets. E, marginal densities from BEAST analyses A1, A2, A3 and A4. F, marginal densities from BEAST analyses A5, A6, A7, A8 and A9.


60
50
40
30
A1
A2
A3
A4
A5
A6
A7
A8
A9

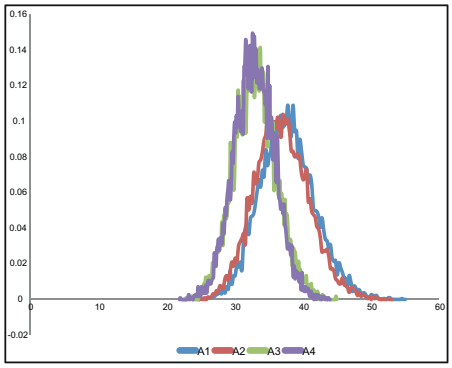
A


45
40
35
30
25
20
A1
A2
A3
A4
A5
A6
A7
A8
A9

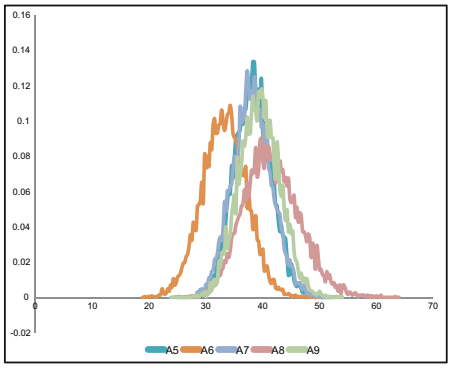
D


0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
0
10
20
30
40
50
60
70
80
A1
A2
A3
A4

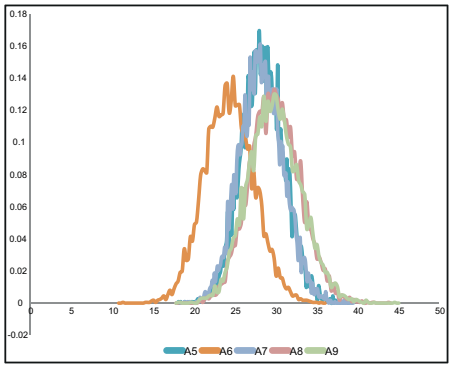
B


0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
0
10
20
30
40
50
60
A1
A2
A3
A4

E


0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
0
10
20
30
40
50
60
70
A5
A6
A7
A8
A9

C


0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
0
5
10
15
20
25
30
35
40
45
50
A5
A6
A7
A8
A9

F

Fig. 65. Lineage diversification through time in the Indo-Pacific Liochelidae Fet & Bechly, 2001.

log(N)
1
2
5
10
20
Time
0
-20
-40
-60
-80
-100
-120

results. The yule2rate model has the lowest AIC score (143.7475). This model assumes that the initial speciation rate changes once. For the present chronogram, the shift is evaluated to have taken place at about 30.7 Mya. The second lowest AIC score is retrieved for the pureBirth model (145.9770). The difference between the AIC scores for the two models is not sufficient to select one over the other. Therefore, constant birth and death rates over time is regarded as the most logical conclusion, the data not allowing an unequivocal choice.

3.4 PROPOSED BIOGEOGRAPHICAL HYPOTHESIS

Dispersal and pseudo-vicariance. Geological and climatic changes not only induce the formation of geographical barriers but can also cause such barriers to fall, allowing many taxa to expand their territory, a phenomenon referred to as geo-dispersal (Lieberman & Eldredge, 1996; Lieberman, 1997, 2000, 2005). Lieberman (2005) pointed out that the effects of geo-dispersal are overlooked by many authors who consider vicariance as the only valid mechanism that affected biotic distributions, usually evoking low vagility and dispersal ability of the organisms studied (Nelson & Platnick, 1981; Humphries & Parenti, 1986). However, the biogeographical importance of geo-dispersal and extinction is confirmed for numerous organisms (McKenna, 1975, 1983; Beard, 1998; Bossuyt & Milinkovitch, 2001; SanMartin *et al.*, 2001; Conti *et al.*, 2002; Karanth, 2006), including some with putatively low dispersal capacities (Gower *et al.*, 2002; Wilkinson *et al.*, 2002; Klaus *et al.*, 2010). Likewise, the colonisation by plants and animals of rafting microplates or emergent volcanic island arcs from nearby landmasses followed by subsequent speciation of these biotas induced by genetic isolation, founder effect, genetic drift and ecological interaction, a biogeographical process referred to as “pseudo-vicariance” (VanWelzen *et al.*, 2003), is considered as the main cause of current faunal and floral distributions in Australasia (Polhemus, 1996; VanWelzen *et al.*, 2003). The biogeographical hypothesis proposed here for the liochelids suggests that vicariance, geo-dispersal and pseudo-vicariance are not mutually exclusive and that all three mechanisms played a significant role in the development of the Indo-Pacific scorpion fauna.

Dispersal ability of liochelid scorpions. The parthenogenetic nature of *L. australasiae*

is probably a decisive factor in its tremendous capacity to disperse to remote islands and to establish new colonies if the areas colonized have appropriate habitats. Parthenogenetic species are usually good colonists because only one individual is theoretically needed to found an entire new population. In contrast, colonization is a major problem for plants and animals that reproduce sexually, because reproduction normally requires the participation of two mature individuals of different sexes. For these animals, the establishment of a durable breeding colony requires an initial dispersing unit of a specific size and composition. Non-parthenogenetic *Hormurus* species were nonetheless able to colonize the entire Australasian Archipelago. Adjacent islands of volcanic arcs are usually only separated by small stretches of water that are easily crossed on rafting logs. Therefore, repeated colonisation from neighbouring islands allowed a rapid expansion of the distributional range of the genus. Moreover, the long life span of liochelids (3–30 years) also increased the probability that potential mates arrive sufficiently close to each other in space and time to find each other and reproduce. The presence on Western Samoan Islands of the undescribed *H. samoa* n. sp., closely related to *H. penta* from the Solomon Islands, demonstrates the ability of liochelids to colonise remote new territories. The Samoa Archipelago is composed of volcanic islands that started to emerge around 13.5 Mya (see appendix 3.5.1.2). These islands have never been in contact with any continental landmasses and lie in the middle of the SW Pacific Ocean, around 9500 km from mainland Southeast Asia. Therefore, only dispersal can account for the biotic composition of these islands.

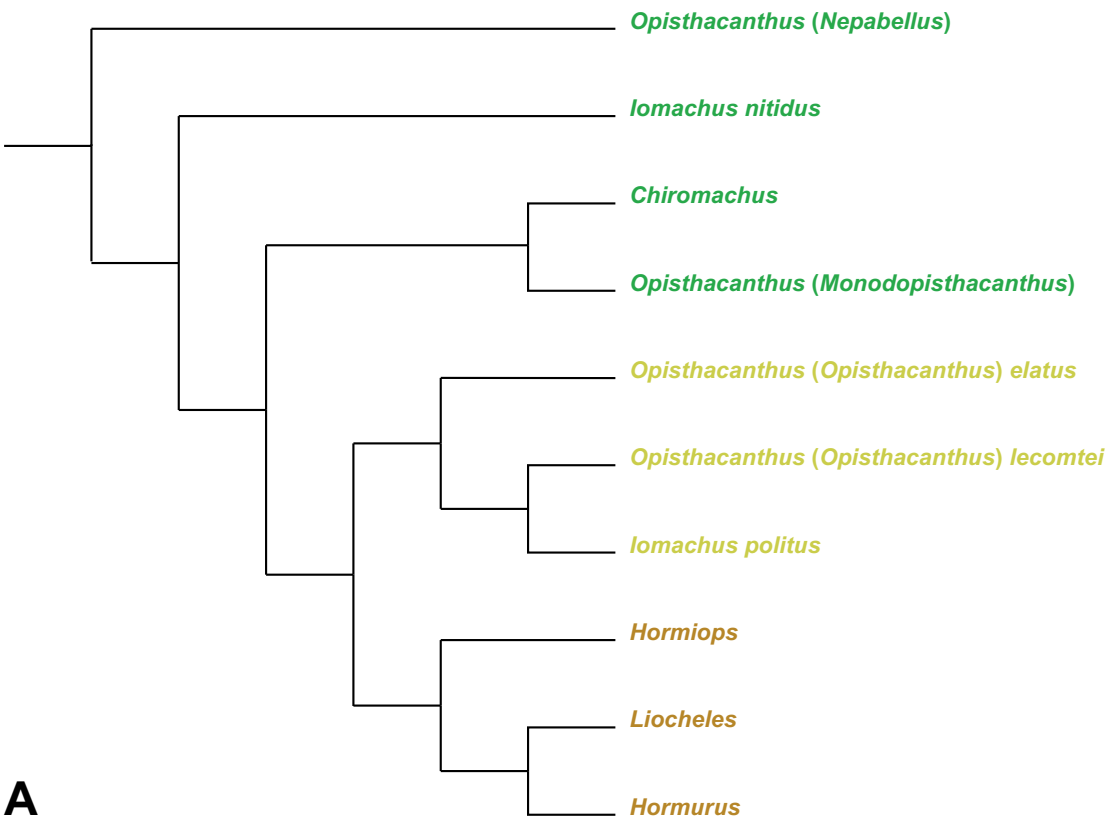
Congruence between fossils and geological calibration. The oldest scorpion fossil is recorded from the Middle Silurian (ca. 420–430 Mya) (Laurie, 1899; Kjellesvig-Waering, 1986; Dunlop *et al.*, 2008; Dunlop, 2010). However, all extant scorpions belong to the more recent lineage Orthosterni Pocock, 1911 (Jeram, 1994a, 1994b, 1998; Stockwell, 1989; Dunlop *et al.*, 2007), the origin of which goes back to the late Carboniferous (ca. 305–310 Mya) (Vogel & Durden, 1966; Jeram, 1994b). The oldest representatives of modern families are from the early Cretaceous of Myanmar and Brazil (100–115 Mya) (Santiago-Blay *et al.*, 2004; Menon *et al.*, 2007). Lourenço & Gall (2004) described an extinct family from the early Triassic of France (ca. 243–250 Mya) within the superfamily Buthoidea, but its affiliation to a modern group was

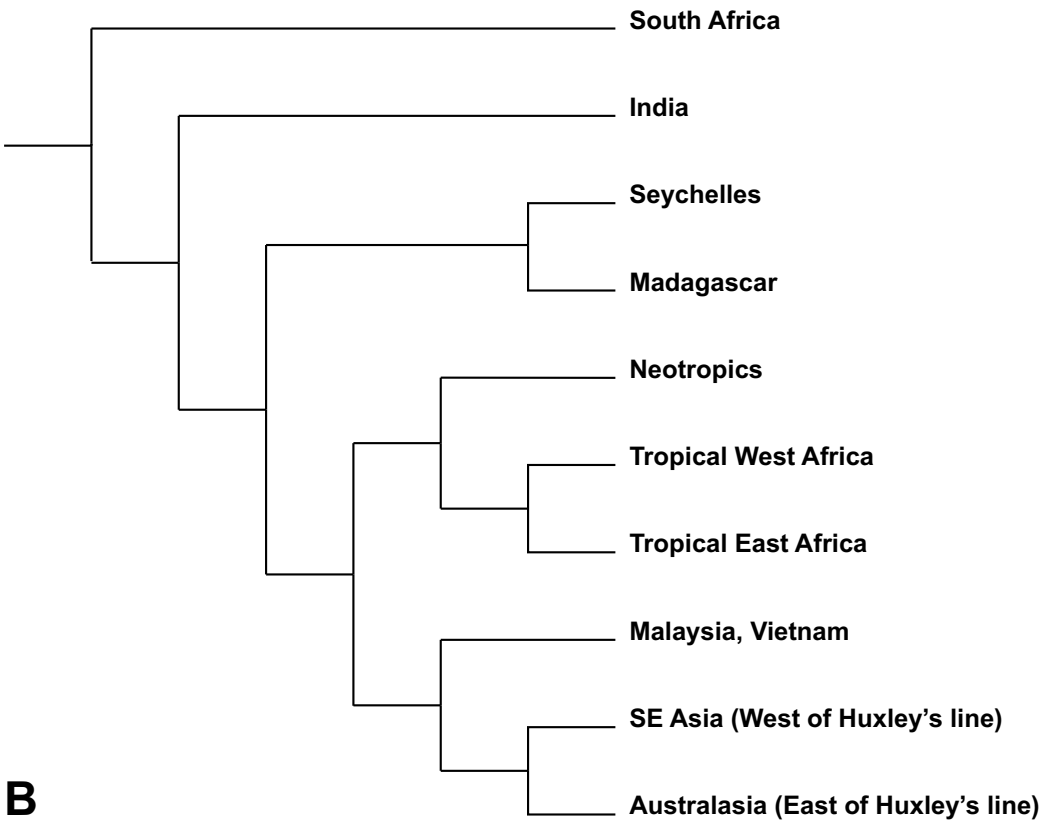
questioned by Baptista *et al.* (2006). Thus the diversification of modern scorpions appears to be relatively recent despite their arguably ancient origin. Therefore, it is not unreasonable to postulate that the evolution and diversification within Liochelidae most likely took place during and after the Gondwana fragmentation. Although *Protoischnurus axelrodorum* Carvalho & Lourenço, 2001 cannot be placed unambiguously into any of the extant genera, it nonetheless confirms the occurrence of liochelid scorpions in Brazil ca. 110 Mya and thus strongly suggests that the Africa/South America rifting 95–118 Mya (Nürnberg & Müller, 1991; Pitman *et al*., 1993; Storey, 1995; McLoughlin, 2001; Pletsch *et al.*, 2001; Moulin *et al*., 2010) was of paramount importance for the diversification of Afrotropical and Neotropical liochelids.

Indo-Pacific Liochelidae area cladogram (figs 66, 87A). Three clusters were retrieved consistently in the present phylogenetic analysis of the Indo-Pacific Liochelidae: (1) a basal Gondwana group with representatives in South Africa (*Opisthacanthus* (*Nepabellus*) spp.), Madagascar (*Opisthacanthus* (*Monodopisthacanthus*) spp.), India (*Chiromachetes*, Indian *Iomachus* spp.) and a relictual species in Northern Queensland (*Opisthacanthus* (*Monodopisthacanthus*) *apios*), and two more derived sister clades: (2) a West-Gondwana clade with most species in the Neotropics (*Opisthacanthus* (*Opisthacanthus*) spp.) and two relict species in tropical Africa (*Iomachus politus*, *Opisthacanthus* (*Opisthacanthus*) *lecomtei*), and (3) a Southeast Asian clade with a distributional range that extends to the Australo-Papuan archipelago and the Western Pacific (*Hormiops*, *Hormurus*, *Liocheles*). Phylogenetic patterns with a similar geographical structure were observed in several invertebrate groups (mostly from the soil and leaf-litter) restricted to tropical forests and with assumed poor dispersal ability, i.e. velvet worms (Monge-Najera, 1995), cyphophthalmid harvestmen (Boyer *et al.*, 2007; Clouse & Giribet, 2010) and forest damselflies (VanTol *et al.*, 2009) (see appendix 3.5.2 for details). In addition, biogeographical patterns of boid snakes (Noonan & Chippindale, 2006A) which are arguably better dispersers than the above-mentionned invertebrates, also show some similarities with that of the liochelid scorpions (see appendix 3.5.2).

Basal Gondwanan taxa. *Chiromachetes*, *C. ochropus*, Indian *Iomachus*, *Opisthacan-*

Fig. 66. A, Phylogenetic relationships within the Indo-Pacific Liochelidae. B, area cladogram.


Opisthacanthus (Nepabellus)
Iomachus nitidus
Chiromachus
Opisthacanthus (Monodopisthacanthus)
Opisthacanthus (Opisthacanthus) elatus
Opisthacanthus (Opisthacanthus) lecomtei
Iomachus politus
Hormiops
Liocheles
Hormurus
A


South Africa
India
Seychelles
Madagascar
Neotropics
Tropical West Africa
Tropical East Africa
Malaysia, Vietnam
SE Asia (West of Huxley's line)
Australasia (East of Huxley's line)
B

thus (*Monodopisthacanthus*), and *Palaeocheloctonus* were always placed basally in the phylogenies. They form a monophyletic clade (MIC) only in the morphological analysis. However, constraining the monophyly of this group in the molecular and combined analyses required only few additional steps and a minor loss in fitness (see chapter II for details), suggesting that the incomplete sampling of Indian taxa in the DNA dataset probably yielded the low topological resolution of the trees. Adding DNA samples for *Chiromachetes* and *Iomachus* will probably help to retrieve the MIC clade and reconcile the two conflicting topologies. In any case, these taxa and the South African outgroup species, *Opisthacanthus* (*Nepabellus*) *laevipes*, form a Gondwana element whose current distributional range can be explained solely by Gondwana vicariance. All Indian taxa, *Iomachus* and *Chiromachetes*, are more closely related to the Seychelles and Malagasy taxa than to members of the Southeast Asian clade HHL, despite the occurrence of the genus *Liocheles* (HHL clade) in India and Bangladesh. Phylogeny and biogeographical patterns of cyphophthalmid opilions share numerous similarities with those of liochelid scorpions and provide strong evidence for a Laurasian ancestry of the Far East elements (Boyer *et al.*, 2007; Clouse & Giribet, 2010; see appendix 3.5.2). The southeast Asian stylocellids are only distantly related to the basal temperate Gondwana (circum-Antarctic) pettalids despite the contiguity of their distribution areas. However, stylocellids are more closely related to the Laurasian sironids.

Afrotropical and Neotropical Clades. Africa separated from South America 95–118 Mya (McLoughlin, 2001), but marine barriers between the two West Gondwanan landmasses arguably remained narrow and shallow until 90 Mya. Moreover, the Walvis Ridge-Rio Grande Rise (O'Connor & Duncan, 1990) probably acted as a dispersal causeway through the nascent Atlantic Ocean until the early Tertiary (Morley, 2000). The OPI clade comprises species in Meso- and Northern South America and in Central Tropical Africa. Cladogenesis between the Neotropical (NEO) and Afrotropical (CAF) clades of OPI is attributed to Gondwana vicariance with the biotic isolation between Africa and South America (fig. 68). Divergence between Eastern and Western Afrotropical lineages is estimated at ca. 57 Mya (41–73 Mya) (fig. 61) when the complete calibration set (A5) is used in the molecular clock. Significant marine regressions

reported in the Late Cretaceous–Early Tertiary at ca. 71 Mya, 67–66 Mya, 61 Mya and 57 Mya (Haq *et al.*, 1987; Keller, 2001; Miller *et al.*, 1999; Abramovich *et al.*, 2002; Miller *et al.*, 2005) probably induced a decrease of global temperatures, an extensive aridification, and thus the fragmentation of the moist forest block of the Equatorial African Belt and the isolation of *I. politus* and *O.* (*O.*) *lecomtei* on mountainous rainforest refugias on either sides of Central Africa.

AFFINITIES AND ORIGIN OF THE HHL CLADE. According to the present phylogenetic study, the closest allied taxa of the HHL clade (*Hormiops* (*Hormurus* + *Liocheles*)) appear to be Afrotropical and Neotropical, i.e. *I. politus* and *Opisthacanthus* (*Opisthacanthus*) (OPI clade), whereas *Chiromachetes* and the Indian *Iomachus* species are consistently retrieved as more distantly related, contrary to previous studies (Prendini, 2000). Although the position of the Indian taxa is not fully resolved here probably due to the limited availability of DNA samples (only one sample for *Iomachus* and none for *Chiromachetes*), the position of OPI as sister to HHL is unambiguous. In order to explain the occurrence of liochelids in Asia as a result of Gondwana vicariance, it is necessary to assume the survival of an ancestral lineage on the Indian subcontinent during its northward drift and subsequent dispersal onto the Eurasian plate. Given the phylogenetic affinity between the Australasian HHL and the West Gondwana OPI, the two clades must have differentiated about 163 Mya with the rifting between East and West Gondwana. However, the age of cladogenesis between HHL and OPI is estimated in the present analysis at ca. 103 Mya (86–129 Mya) (fig. 61, tab. 22), at least 34 Mya after the isolation of the India-Madagascar-Seychelles block from Africa. The Gondwana vicariance and “out-of-India” origin hypothesis is thus rejected in favour of an alternative scenario implying dispersal, extinction or both.

Similar relationships between Afrotropical/Neotropical and Southeast Asian taxa are observed in several other tropical forest organisms (Monge-Najera, 1995; Noonan & Chippindale, 2006A; Boyer *et al.*, 2007; VanTol *et al.*, 2009; Clouse & Giribet, 2010; see appendix 3.5.2), and strongly suggest the past occurrence in northern latitudes of a common ancestor that was eradicated by the gradual decrease of global temperatures and the receding of boreotropical habitats after the Paleocene-Eocene thermal maximum (see appendix 3.5.1.2). Thus, liochelid scorpions may have been present in Laurasia before the Pangea breakup (fig. 67).

Alternatively, they may have colonised Southeast Asia from the Africa-south America block by using the northern migration pathways, either through Europa and the Middle East or through the island arcs of the Pacific Ring of fire and Beringia (appendix 3.5.1.2, fig. 67). The Cretaceous thermal maxima (ca. 120–80 Mya) (Clark & Jenkins, 1999; Bralower *et al.*, 2002; Huber *et al.*, 2002) and the resulting sea level rise, known as the Cenomanian marine transgression, may have disrupted the remaining land connections between Laurasian and Gondwanan landmasses leading to the isolation and divergence of the HHL and OPH lineages on each fragment of Pangea. Finally, climatic changes in the Mid-Late Eocene (45 Mya), i.e. decrease of the temperature, aridification and the ensuing sea level drops, resulted in the reduction and fragmentation of boreotropical habitats, leading to the extinction of tropical taxa in the Nearctic and Palearctic regions.

An alternative scenario can be proposed for the colonisation of Southeast Asia by liochelids, assuming that the OPH lineage was absent on Laurasia before the Gondwana breakup and that floral and faunal exchanges between Central America, the Afrotropics and India occured punctually until the late Paleocene/Early Eocene (Sahni, 1984; Krutzsch, 1987; Krause *et al.*, 1997, 1999; Sampson *et al.*, 1998; Buckley *et al.*, 2000; Morley, 2000, 2003; Vences *et al.*, 2001; Carrano *et al.*, 2002; Mehrotra, 2003; Moyle, 2004; VanBocxlaer *et al.*, 2006; Bossuyt *et al.*, 2006; fig. 70, see also appendix 3.5.1.1). In the Paleocene, ancestors of the HHL clade dispersed from East Africa onto the Indian subcontinent during its northward drift. These taxa were then carried to Laurasia. They finally colonized Southeast Asia when India collided with the Eurasian plate. However, both HHL species that may have been present on the rafting terrane, i.e. *Liocheles nigripes* from northern India and *Liocheles suspectus* from Bangladesh, are not placed basally within the clade, suggesting colonization of India from the Far East rather than the other way around. The discovery of an unknown Indian liochelid taxon linking the African *I. politus* with *Hormiops* which confirms the “out-of Africa/onto India” hypothesis in the Palaeocene cannot be completely ruled out, given the poor taxonomic knowledge of the arachnid fauna of India, but the “Laurasian origin” hypothesis is preferred in the present work. Besides, the distributional range of the family Hemiscorpiidae, currently recognized as the sister family to Liochelidae (Prendini, 2000), with species occuring in Djibouti, Ethiopia, Eritrea, Somalia, So-

Fig. 67. Paleogeographic reconstruction of the Earth for the Late Jurassic (146–166 Mya). Rifting of the East Gondwana block (Antarctica-Australia-India-Madagascar-Seychelles) from Africa continued, severing the connections between the MIC and OPH (= HHL + OPI) lineages. Genetic connections between HHL and OPI persisted probably in the northern hemisphere. Taxonomic groups: MIC = *Chiromachetes* + *Chiromachus ochropus* + Indian *Iomachus* + *Monodopisthacanthus* + *Palaeocheloctonus*; OPH = *Hormiops* + *Hormurus* + *I. politus* + *Liocheles sensu lato* + *Opisthacanthus* (*Opisthacanthus*); ZAF = *Cheloctonus* + *Hadogenes* + *Opisthacanthus* (*Nepabellus*). Adapted after Golonka (2000).

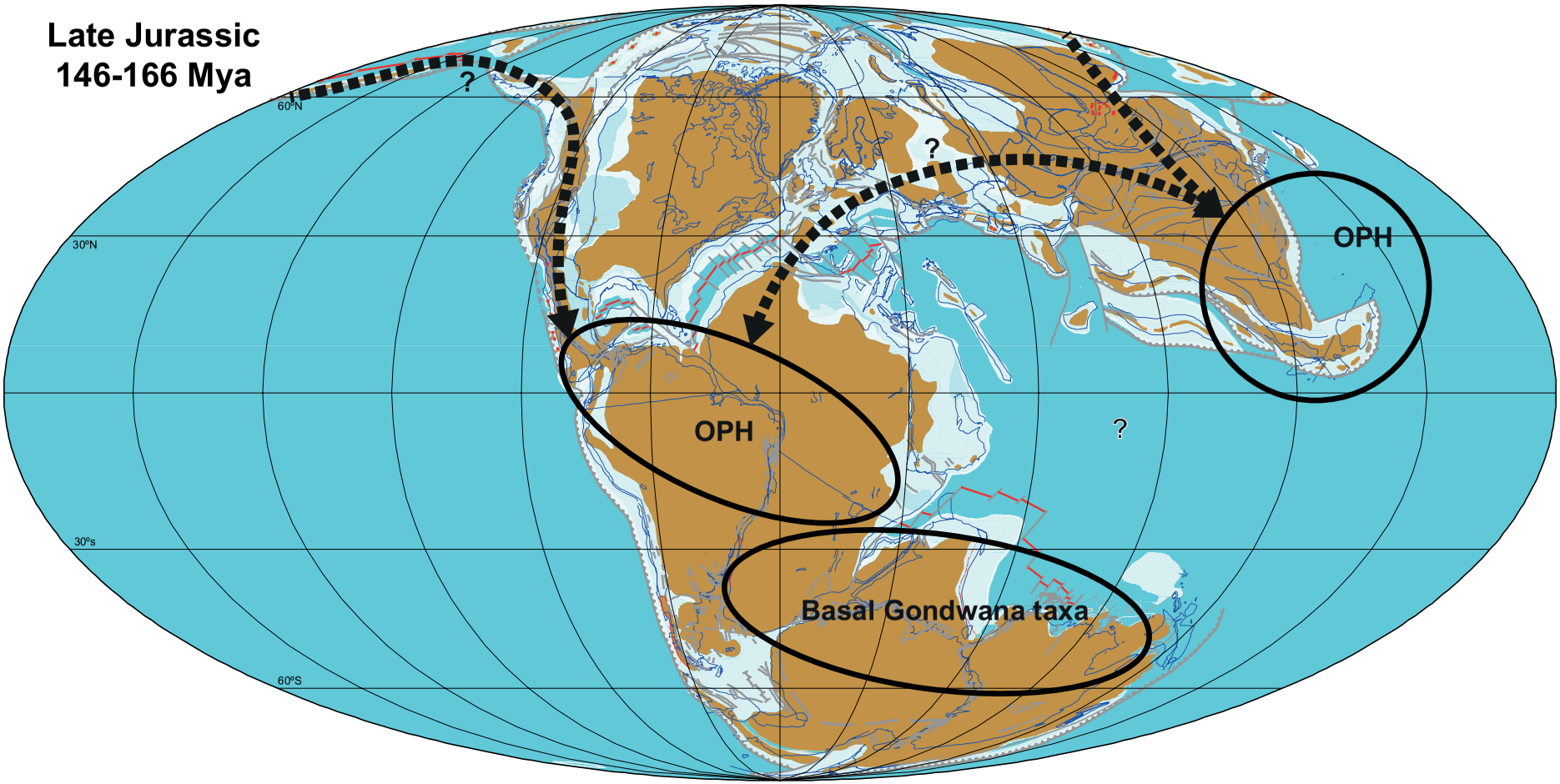
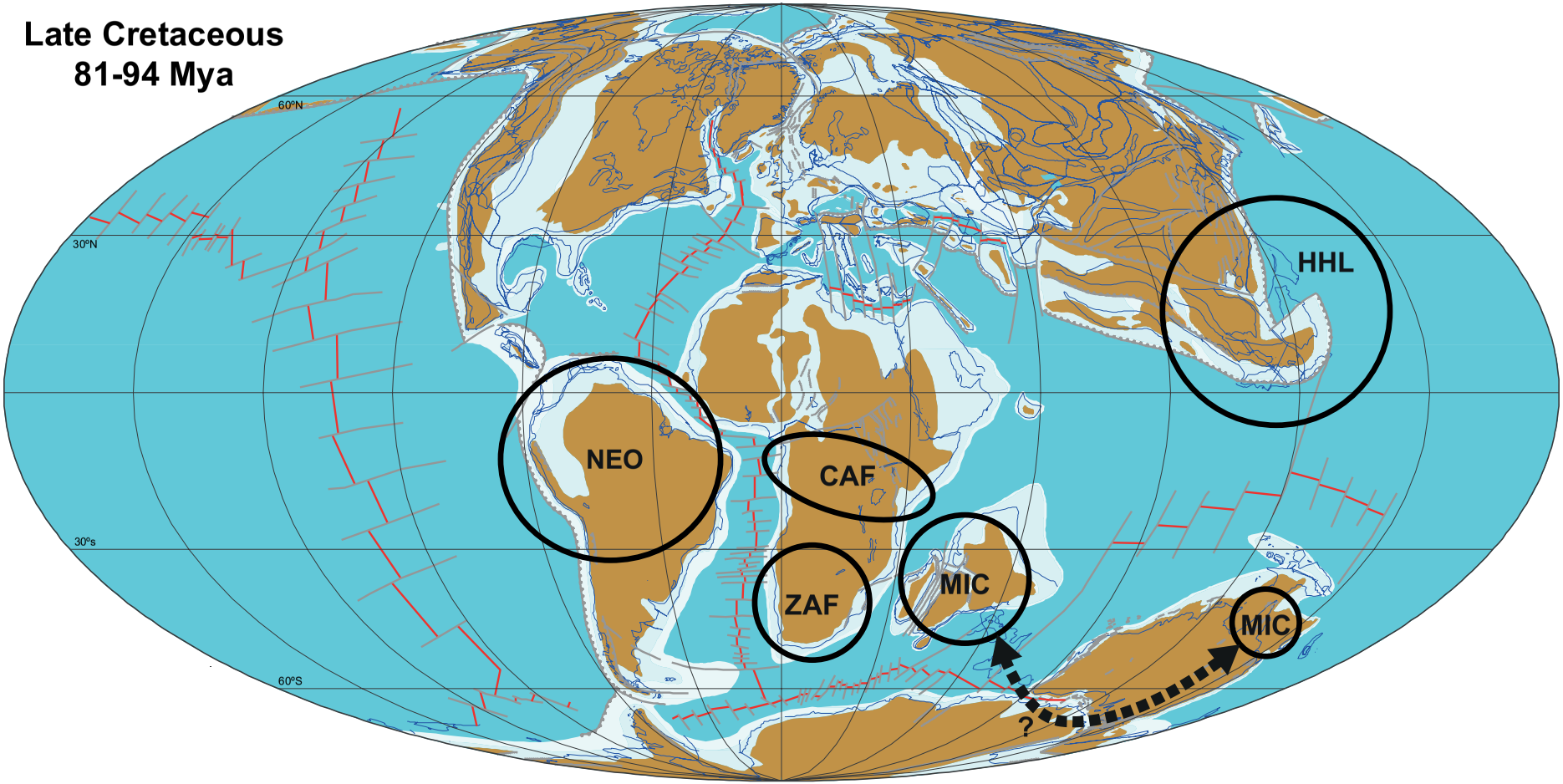

Late Jurassic
146-166 Mya
60°N
30°N
30°s
60°S
?
?
?
OPH
OPH
Basal Gondwana taxa

Fig. 68. Paleogeographic reconstruction of the Earth for the Late Cretaceous (81–94 Mya). Late Cretaceous Thermal Maxima and the associated sea level rise isolated HHL from OPI (= CAF + NEO + CAF). The rifting of Africa from South America resulted in the divergence of CAF and NEO. Connections between Australian and Indian-Malagasy-Seychellian taxa of MIC apparently persisted, possibly through the Kerguelen Plateau. Taxonomic groups: CAF = *I. politus* + *O.* (*O.*) *lecomtei*; HHL = *Hormiops* + *Hormurus* + *Liocheles sensu lato*; MIC = *Chiromachetes* + *Chiromachus ochropus* + Indian *Iomachus* + *Monodopisthacanthus* + *Palaeocheloctonus*; NEO = Neotropical *Opisthacanthus* (*Opisthacanthus*) spp.; ZAF = *Opisthacanthus* (*Nepabellus*). Adapted after Golonka (2000).


Late Cretaceous
81-94 Mya
60°N
30°N
30°s
60°S
NEO
CAF
ZAF
MIC
MIC
HHL
?

cotra, the Arabian Peninsula and the Middle East, also favours the Laurasian Origin hypothesis.

Origin of the genus Hormurus. The present phylogeny supports an Asian origin for the Australo-Papuan liochelids. The genus *Hormiops* was retrieved as basal to the (*Liocheles* + *Hormurus*) group (see chapter II), discounting the Gondwanaland origin hypothesis for at least this part of the family. The two *Hormiops* species known are endemic to the Con Dao Islands off the southern coast of Vietnam and to Pulau Tioman off the northeastern coast of the Malay Peninsula respectively whereas basal *Liocheles* species are found on mainland southeast Asia and Sumatra. Cladogenesis between *Hormiops* and (*Hormurus* + *Liocheles*) is estimated at 68 Mya (56–82 Mya). The *Hormiops* ancestral lineage may have become stranded on "paleo-mountains" of the central Sunda Shelf during marine transgressions of the Late Cretaceous-Paleocene and then diverged from the *Hormurus-Liocheles* stock. The continental core of Sundaland is composed of numerous Gondwana fragments assembled from the Permian to the Cretaceous (Metcalfe, 1990, 1996, 1998, 1999, 2001, 2002, 2006). Because collisions of these many continental terranes probably induced massive compression forces on the existing shelf, Sundaland in the Late Cretaceous is interpreted as an emergent landmass with an elevated topography (Hall, 2009), in contrast with the current geological setting of shallow marine waterways and low relief. Thus at the end of the Mesozoic, highlands of the Sunda shelf probably functioned as biotic refugia during sea levels rises. Nowadays, small emergent granitic islands such as the Con Dao and Tioman islands are the vestiges of these ancient mountain systems where the relict liochelid genus *Hormiops* survives.

Liochelids could only have reached Australasia by extending their range through dispersal from Eurasia across Lydekker's line. *Hormurus* is thus regarded as a recent radiation derived from Asian ancestors that colonized the proto-Indonesian Archipelago in the mid Tertiary (figs 69, 71, 72) when the Australian, Eurasian and Pacific plates started to collide. This hypothesis is corroborated by the weak phylogenetic resolution within the genus (see chapter II) possibly resulting from an elevated speciation rate early in the history of the radiation. A similar scenario involving colonization of the nascent Australo-Papuan Archipelago by Asian ancestors followed by a rapid diversification has been invoked to explain the extant distribution patterns

Fig. 69. Palaeogeographic reconstruction of the Earth for the Late Cretaceous–EarlyTertiary (58–81 Mya). Separation of the India-Seychelles block from Madagascar putatively induced the divergence of INC and MOP. Connections between Australian and Malagasy taxa of the MOP lineage apparently persited, possibly through the Kerguelen Plateau. Taxonomic groups: CAF = *I. politus* + *O.* (*O.*) *lecomtei*; HHL = *Hormiops* + *Hormurus* + *Liocheles sensu lato*; INC = *Chiromachetes* + *Chiromachus ochropus* + Indian *Iomachus*; MOP = *Monodopisthacanthus* + *Palaeocheloctonus;* NEO = Neotropical *Opisthacanthus* (*Opisthacanthus*) spp.; ZAF = *Opisthacanthus* (*Nepabellus*). Adapted after Golonka (2000).

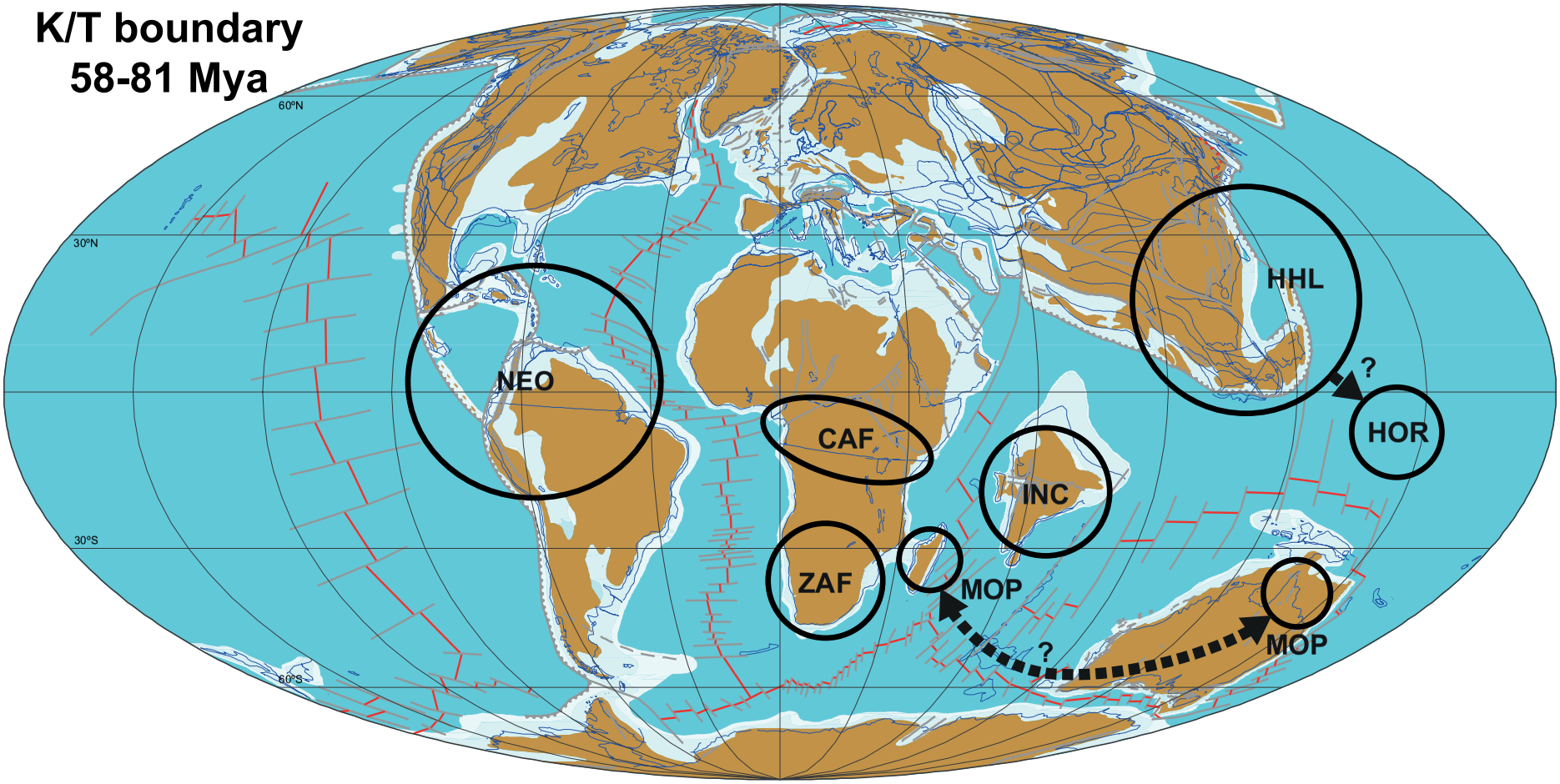

K/T boundary
58-81 Mya
60°N
30°N
30°S
60°S
NEO
CAF
ZAF
INC
MOP
MOP
HHL
HOR
?
?

Fig. 70. Paleoclimatic reconstruction of the Earth for the Late Cretaceous–EarlyTertiary (58–81 Mya) showing the different biomes. Dispersals of tropical plants according to the palynological record are indicated (Morley, 2000). Adapted after Golonka (2000), Scotese (2002) and Willis & McElwain (2002).

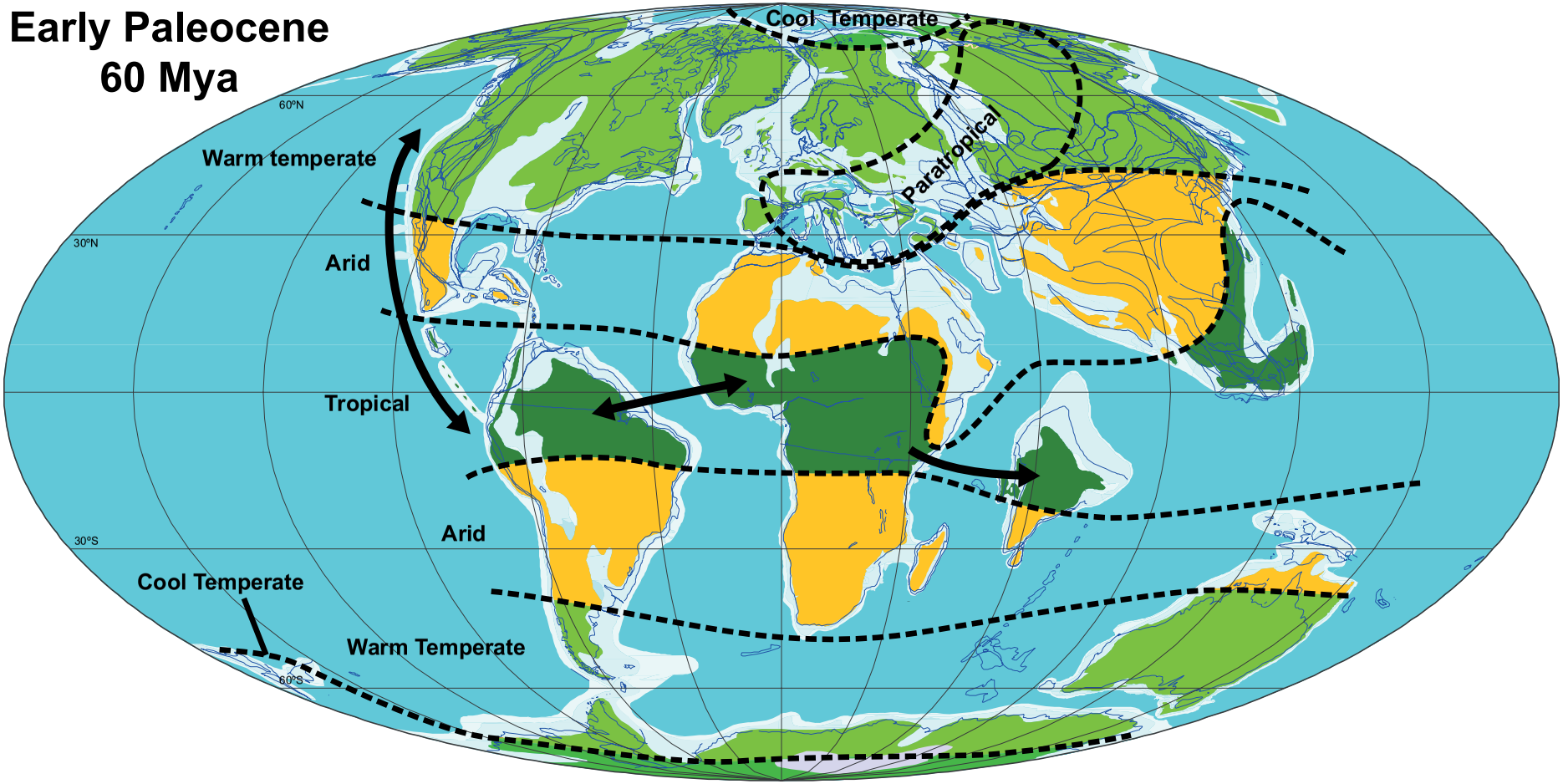
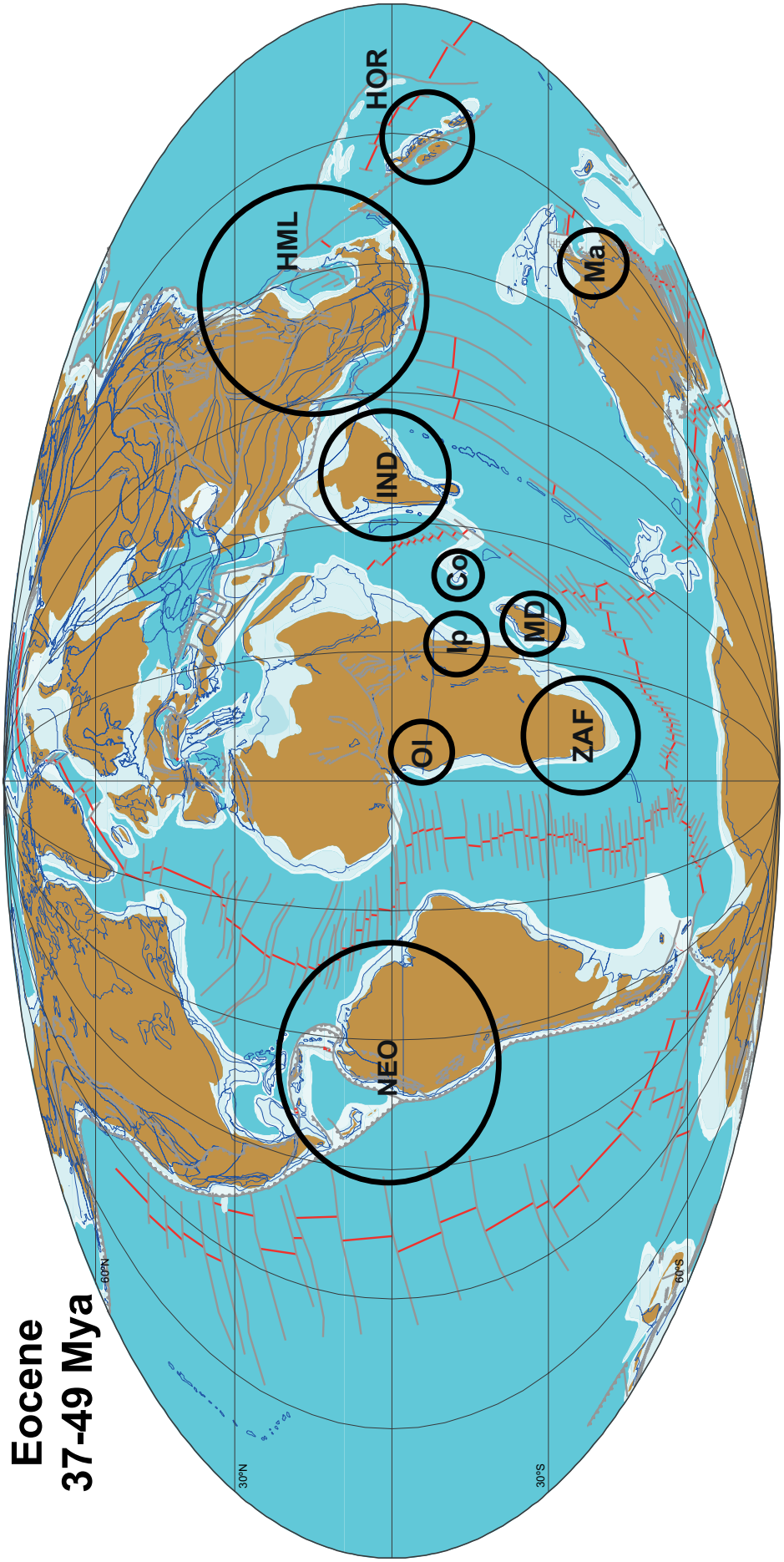

Early Paleocene
60 Mya
Cool Temperate
Paratropical
Warm temperate
Arid
Tropical
Arid
Cool Temperate
Warm Temperate
60°N
30°N
30°S
60°S

Fig. 71. Paleogeographic reconstruction of the Earth for Eocene (37–49 Mya). Separation of India and the Seychelles putatively induced the divergence of *Chiromachus ochropus* (C. L. Koch, 1837) from IND. *Iomachus politus* Pocock, 1896 and *Opisthcanthus lecomtei* (Lucas, 1858) were isolated by the fragmentation of the moist forests of the Equatorial African Belt, whereas the HHL lineage colonized the nascent Australasian Archipelago, leading to the evolution of the genus *Hormurus* Thorell, 1876. *Opisthacanthus* (*Monodopisthacanthus*) *apios* n. sp. finally parted from its Malagasy relatives with the subsidence of the last Indian Ocean Gondwana connections. Taxonomic groups: Co = *Chiromachus ochropus*; HML = *Hormiops* + *Liocheles sensu lato*; HOR = *Hormurus;* IND = *Chiromachetes* + Indian *Iomachus*; Ip = *I. politus;* Ma = *O.* (*M.*) *apios*; MD = Malagasy *Monodopisthacanthus* + *Palaeocheloctonus;* NEO = Neotropical *Opisthacanthus* (*Opisthacanthus*) spp.; Ol = *O.* (*O.*) *lecomtei*; ZAF = *Opisthacanthus* (*Nepabellus*). Adapted after Golonka (2000).


Eocene
37-49 Mya
HOR
HML
IND
Ma
Co
Ip
MD
Ol
ZAF
NEO
60°N
30°N
30°S
60°S

and high diversity of *Livistona* palms (Crisp *et al.*, 2009) and several squamates (Reptilia) in the region, i.e. agamid lizards (Hugall & Lee, 2004), elapid snakes (Keogh, 1998), pythonid snakes (Rawlings *et al.*, 2008), and varanoid lizards (Fuller *et al.*, 1998; Ast, 2001). The striking contrast between the Australo-Papuan *Hormurus* (62 species) and its Asian counterparts *Hormiops* (2 species) and *Liocheles* (6 species) in terms of species diversity provides additional support for the theory that island arcs were used as stepping-stones by the scorpions. The various subduction systems of the south west Pacific provides the perfect canvas for an explosive diversification of life forms. During the Tertiary, numerous chains of volcanic islands were initiated by intense tectonic activity along plate margins (appendix 3.5.1.2) leading to the formation of an extensive, intricate and constantly changing network of new territories and potential dispersal corridors. Colonization of these emergent islands from nearby landmasses resulted in the establishment of high rates of endemism while the complex and rapid geological evolution induced numerous vicariance and coalescence events that further contributed to increase the biological diversity of the region. As a result, many Australo-Papuan organisms such as palms, pythons and varanids (Ast, 2001; Rawlings *et al.*, 2008; Crisp *et al.*, 2009) are much more speciose than their Asian relatives, mirroring the trend observed in liochelid scorpions.

According to Crisp *et al.* (2009), the Australo-Papuan clade of *Livistona* R. Brown, 1810 palms diverged from its Asian sister group 5.9–16.8 Mya. Divergence between the Australian agamids and their close relatives in southeast Asia has been estimated between 14 and 41 Mya (Oligo-Miocene) (Hugall & Lee, 2004) and most Australasian python lineages have their origin in the Eocene to Miocene period (Rawlings *et al.*, 2008). These dates are consistent with the latest geological model (Hall, 1998, 2001, 2002; Hall *et al.*, 2009) that places the beginning of plate tectonics interactions and associated development of island arcs of the south west Pacific in the Early Eocene–Early Oligocene (55–35 Mya) (appendix 3.5.1.2). However, contrary to those of palms, agamids and pythons, divergence times for liochelid scorpions inferred from the present analysis contradict this chronology. The age of cladogenesis between *Hormurus* and *Liocheles* is estimated at 61 Mya (50–73 Mya) and the origin of diversification within *Hormurus* at 38 Mya (32–45 Mya) (fig. 61, tab. 22), implying that *Hormurus* must have been present in the Australo-Papuan region before the Eocene and thus before the recognized emergence of the

archipelago. This suggest that subduction systems of the proto-Pacific basin started to develop in response to the gradual northward drift of the Australasian plate at least since the Paleocene, slightly earlier than the temporal sequence currently acknowledged.

Colonisation of the Australo-Papuan Archipelago. Islands provide a climatically and ecologically stable environment that, due to the absence of competition with more evolved taxa, may allow the persistence of relict organisms that have disappeared elsewhere (Cronk, 1997). Because they probably represent the remnants of an old stock once widespread across the Australasian Region, basal *Hormurus* species, especially the PIA clade, provide significant evidence about potential dispersal corridors used by ancestral lineages to colonize the Australasian Archipelago from Sundaland. All these species occur on oceanic islands that were once part of active volcanic arcs (figs 72–73). The distribution pattern of the Pacific islands boas of the genus *Candoia* Gray, 1842 (Boidae, Serpentes) is very similar to that of the basal *Hormurus*: they are found from Sulawesi, through Maluku, New Guinea, Palau, the Bismarck Archipelago, Manus Island, Solomon Islands, Loyalty Islands (New Caledonia), to American Samoa, but are not present in Asia and Australia (McDowell, 1987; Cadle, 1987; Austin, 2000; see appendix 3.5.2, fig. 89B). Thus, origins of both *Candoia* and *Hormurus* may result from dispersal along the same biogeographical track of volcanic islands.

It is hypothesized here that by the Middle Eocene *Hormurus* ancestors were present on the majority of the emergent lands of the various tectonic arc systems of the south west Pacific (fig. 72). The opening of the Solomon Sea as a back-arc basin in the late Eocene about 40–35 Mya (appendix 3.5.1.2, fig. 84B) induced the isolation of the stem lineage of the PIA clade (fig. 73). This basal group was thus initially restricted to New Caledonia, the eastern tip of Papua New Guinea, and Rennell Island before descendant species subsequently colonized Solomon Islands and Samoa from the center of origin. In the consensus area cladogram for the Australasian/Pacific region (see appendix 3.5.2, fig. 90) proposed by Turner *et al.* (2001) and VanWelzen *et al.* (2003), New Caledonia and Samoa form a cluster, basal to all other Australo-Papuan landmasses suggesting that these islands were probably among the first to be invaded by Asian biotas. The plant genus *Cupaniopsis* Radlkofer, 1879 (see Adema, 1991) is the sole

Fig. 72. Paleogeographic reconstruction of the Australasian region for the Middle Eocene (40 Mya). Basal *Hormurus* Thorell, 1876 species, including those belonging to the PIA clade are mapped. The Sulawesi-Philippines-Halmahera and Izu-Bonin-Mariana arcs resulting from the subduction of the Asian, Australian and Pacific crusts beneath the Philippine Sea Plate, and the Outer Melanesian Arc (OMA) resulting from the southward subduction of the Pacific plate constituted potential dispersal corridors between Sundaland and the nascent Australasian Archipelago (dashed lines). Modified from Hall (1998, 2001, 2002).

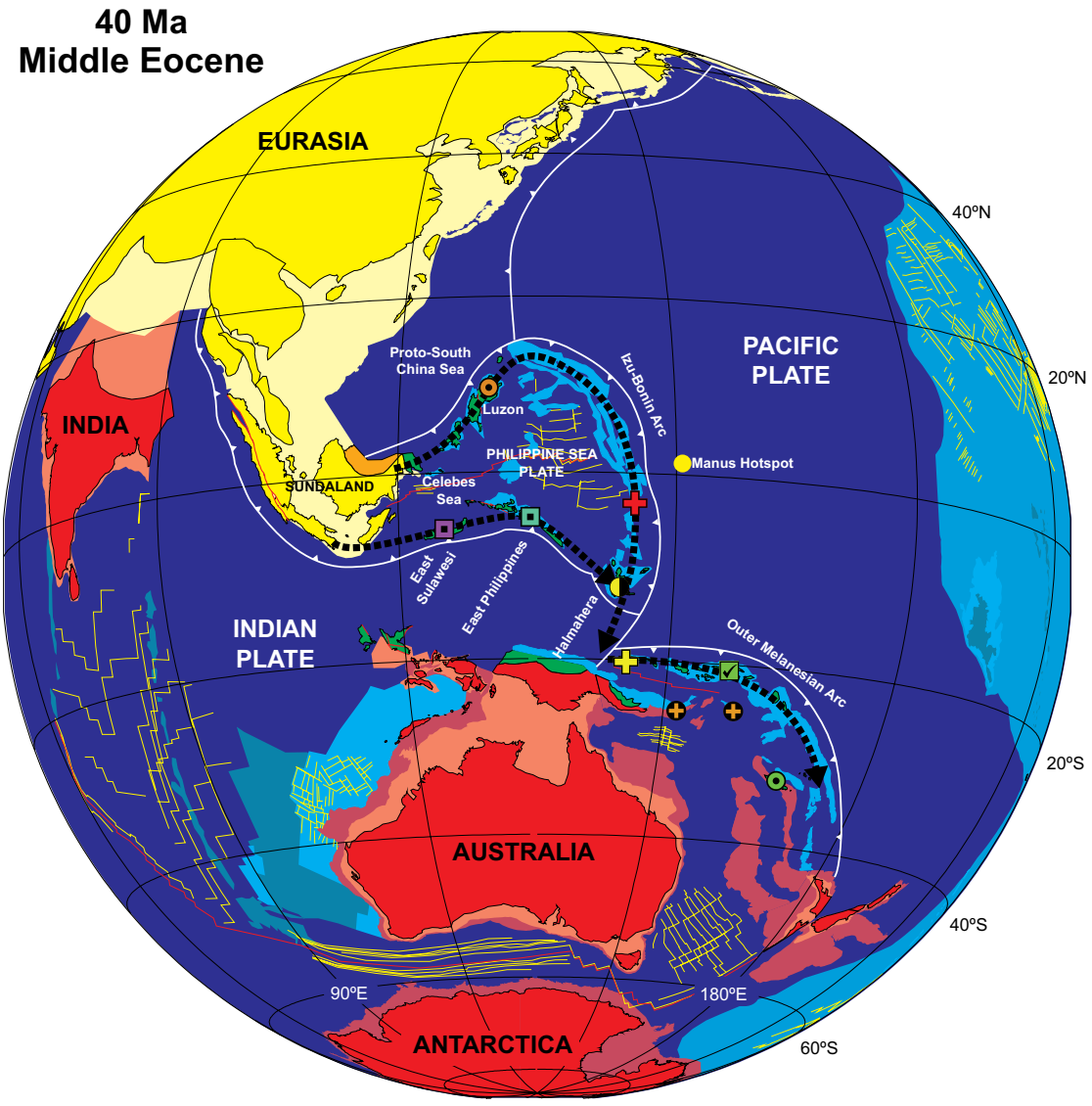
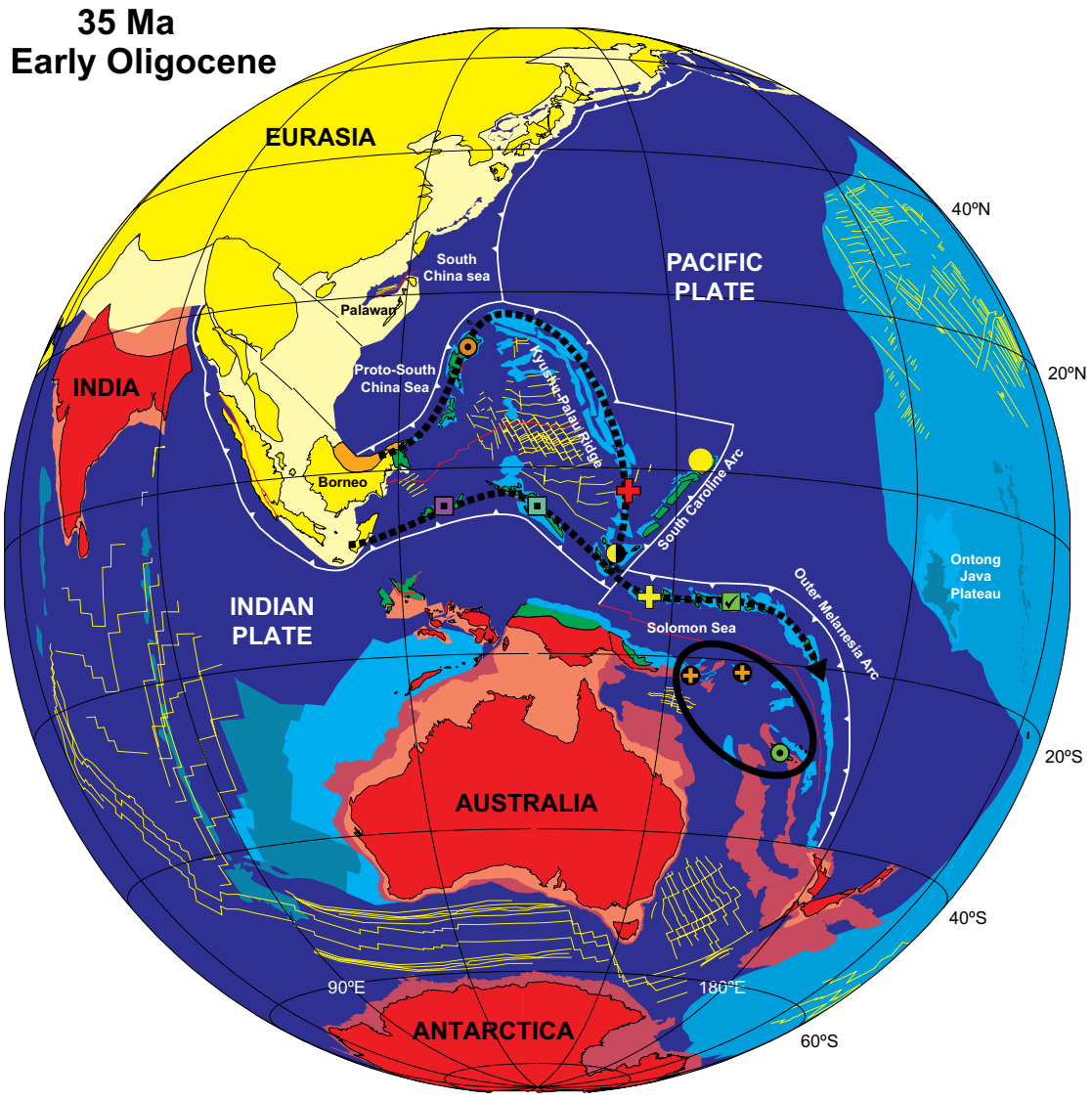

40 Ma
Middle Eocene
EURASIA
INDIA
SUNDALAND
Proto-South
China Sea
Luzon
Izu-Bonin Arc
PACIFIC
PLATE
PHILIPPINE SEA
PLATE
Manus Hotspot
Celebes
Sea
East
Sulawesi
East Philippines
Halmahera
INDIAN
PLATE
Outer Melanesian Arc
AUSTRALIA
ANTARCTICA
40°N
20°N
20°S
40°S
60°S
90°E
180°E

Fig. 73. Paleogeographic reconstruction of the Australasian region for the Early Oligocene (35 Mya). Basal *Hormurus* Thorell, 1876 species, including those belonging to the PIA clade are mapped. Multiple arc systems extending from the Sundaland margin into the west Pacific, i.e. the east Philippines-Halmahera arc, the Izu-Bonin-Mariana arc, the South Caroline arc, and the OMA, provided a large territory for *Hormurus* to diversify. The opening of the Solomon Sea induced the isolation and divergence of the PIA clade from the rest of the genus. Modified from Hall (1998, 2001, 2002).


35 Ma
Early Oligocene
EURASIA
PACIFIC
PLATE
South
China sea
Palawan
Proto-South
China Sea
Kyushu-Palau Ridge
INDIA
Borneo
South Caroline Arc
Outer Melanesia Arc
Ontong
Java
Plateau
INDIAN
PLATE
Solomon Sea
AUSTRALIA
ANTARCTICA
40°N
20°N
20°S
40°S
60°S
90°E
180°E

organism supporting the New Caledonia-Samoa grouping. However, cicadas of the genus *Baeturia* Stål, 1866 and several macrolepidoptera taxa, which were not included in these analyses, provide more evidence for a biogeographical track between Solomon islands, New Caledonia and Samoa (Robinson, 1975; Holloway, 1979, 1983; De Boer, 1982; Duffels, 1988). Because many of these cicada and lepidoptera groups are also recorded on the small island of Rotuma which is part of a chain of islets and sea-mounts, remnants of the Vitiaz Trench Lineament (appendix 3.5.1.2, fig. 85), eastward migration along this island arc has been invoked to explain their presence in Samoa (Robinson, 1975; Holloway, 1979, 1983; Duffels, 1988). Ancestors of the PIA clade most likely invaded the Solomon Islands from Rennell, then the Vitiaz arc from the Solomons to finally reach Samoa in the Late Miocene (fig. 76). The occurence of *Hormurus* in Fiji, Vanuatu, and Rotuma is currently unknown. Determining which of these islands are actually inhabited by *Hormurus* species will provide important evidence pertaining to the timing of colonization.

Between 25–30 Mya, collisions of the northern margins of the Australian craton with the southern edge of Sundaland, the East Philippines-Halmahera-South Caroline Arc, and the Ontong Java Plateau provoked a massive geological upheaval involving the rearrangement of major plate boundaries in the Australasian region (figs 74-75; Hall, 2001, 2002; Hill & Hall, 203). The Solomon Sea-South Fiji basins were significantly widened, the OMA (Outer Melanesian Arc) was displaced further away from the passive margins of the Australian plate and underwent a rupture between the islands of Halmahera and New Britain. Some *Hormurus* species were then probably stranded on the eastern part of the arc and diverged from the insular south-east Asian ancestral stock. Thus, by the end of the Oligocene, the genus had already diversified into at least three lineages. It had also probably colonized Australia and New Guinea. The invasion of the Australian craton by Melanesian *Hormurus* species was enabled by the collision of the East Philippines-Halmahera-South Caroline Arc with the north eastern margins of New Guinea (fig. 75). Liochelids subsequently reached Australia most likely via the Cape York Peninsula or/and the Top End of the Northern Territory. However, the poor phylogenetic resolution within *Hormurus* and the lack of DNA samples from any of these two regions (see chapter II for details) does not permit this hypothesis to be satisfactory tested.

Fig. 74. Paleogeographic reconstruction of the Australasian region for the Middle Oligocene (30 Mya). Basal *Hormurus* Thorell, 1876 species, including those belonging to the PIA clade are mapped. Collision of the Australian plate with the southern edge of Sundaland, the East Philippines-Halmahera-South Caroline Arc, and the Ontong Java Plateau led to a significant widening of the Solomon Sea-South Fiji Basin and to the disruption of the OMA. A distinct lineage was thus isolated and evolved independantly on the eastern part of the arc. Modified from Hall (1998, 2001, 2002).

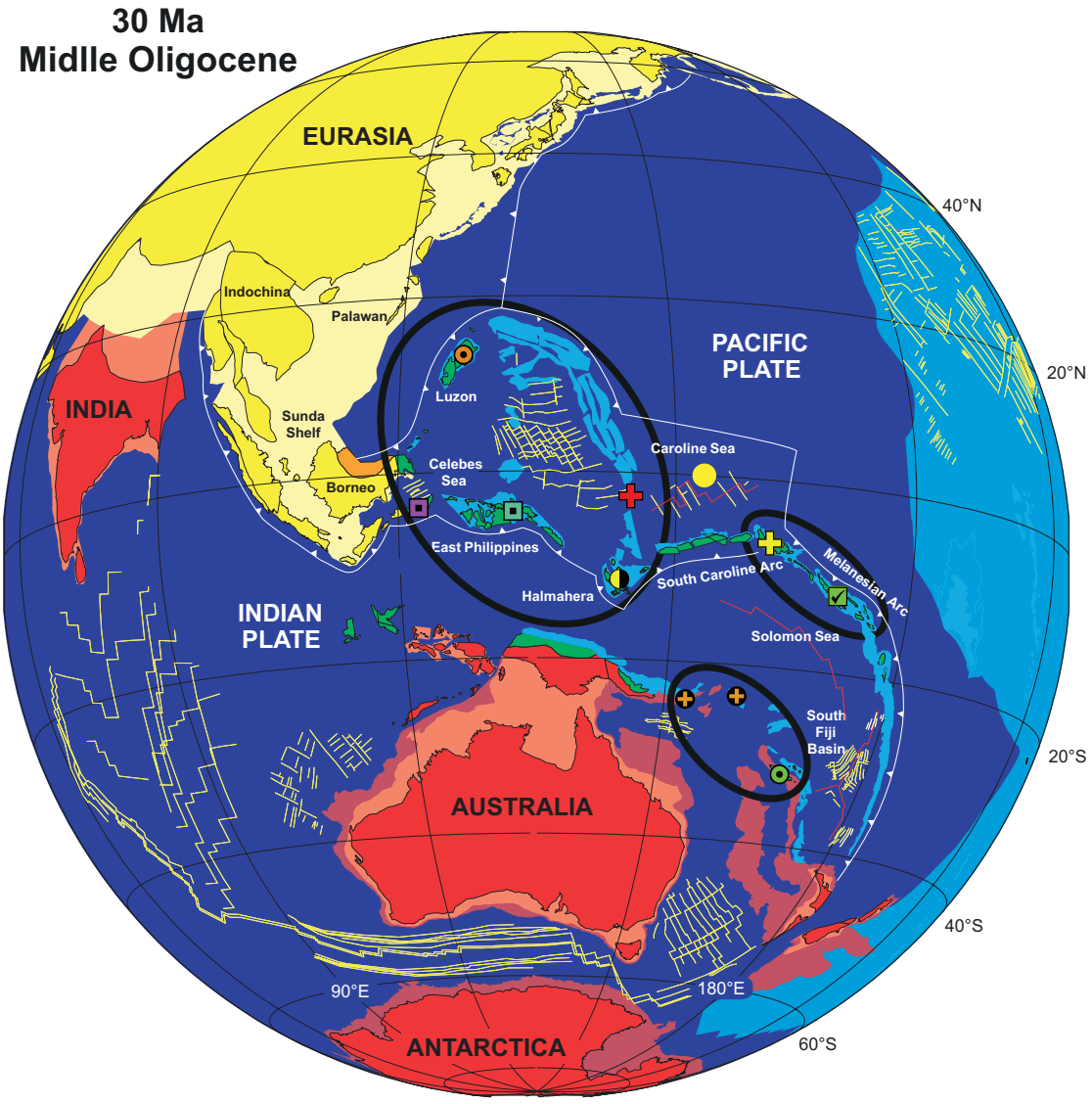

30 Ma
Midlle Oligocene
EURASIA
Indochina
Palawan
PACIFIC
PLATE
INDIA
Luzon
Sunda
Shelf
Caroline Sea
Celebes
Sea
Borneo
East Philippines
South Caroline Arc
Melanesian Arc
Halmahera
INDIAN
PLATE
Solomon Sea
South
Fiji
Basin
AUSTRALIA
ANTARCTICA
40°N
20°N
20°S
40°S
60°S
90°E
180°E

Fig. 75. Paleogeographic reconstructions of the Australasian region for the Late Oligocene (25 Ma). Collision of the east Philippines-Halmahera-South Caroline arc with the New Guinea north eastern margins allowed the southward expansion of the genus onto the Australian craton (dashed line). Modified from Hall (1998, 2001, 2002).

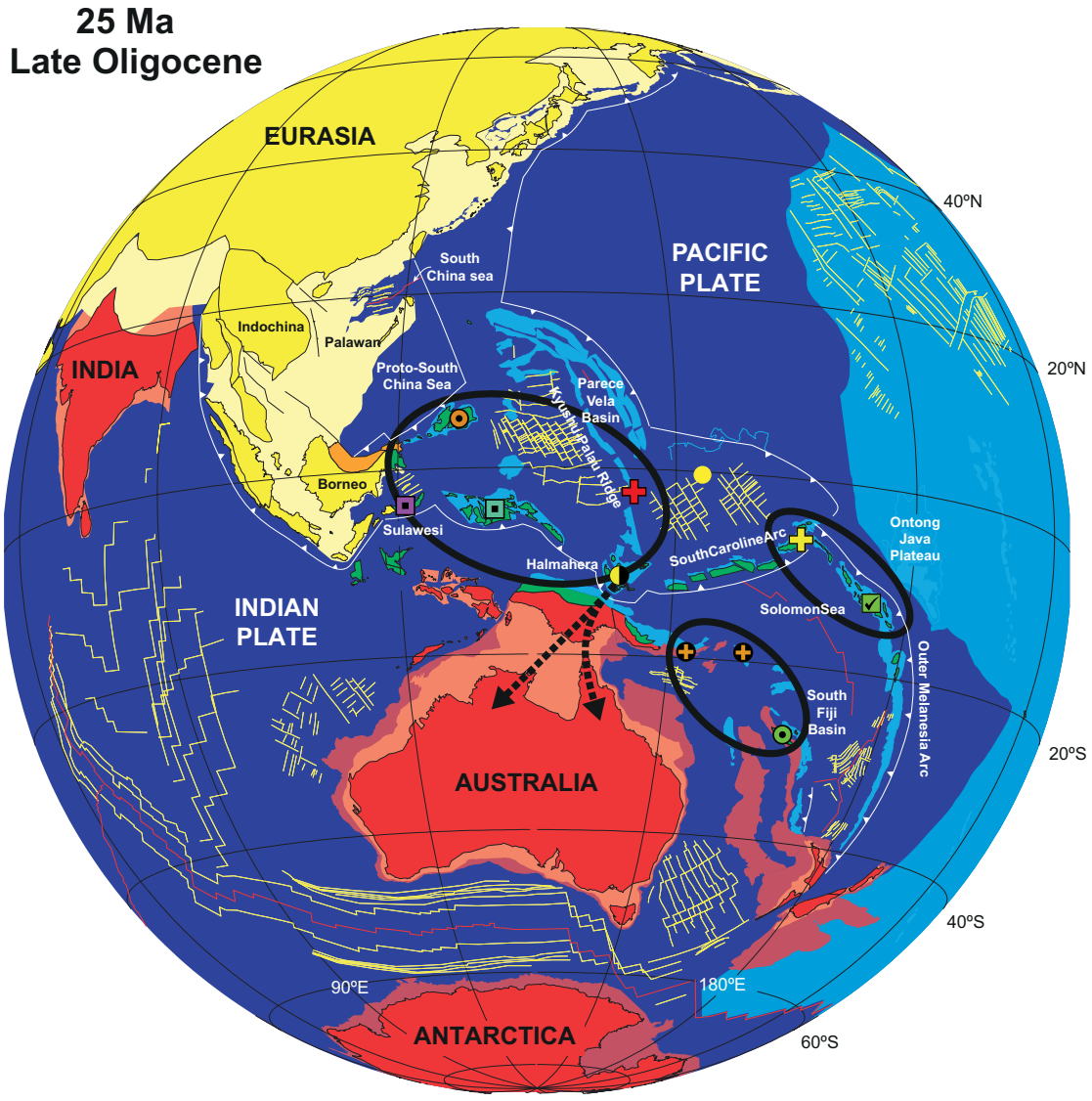
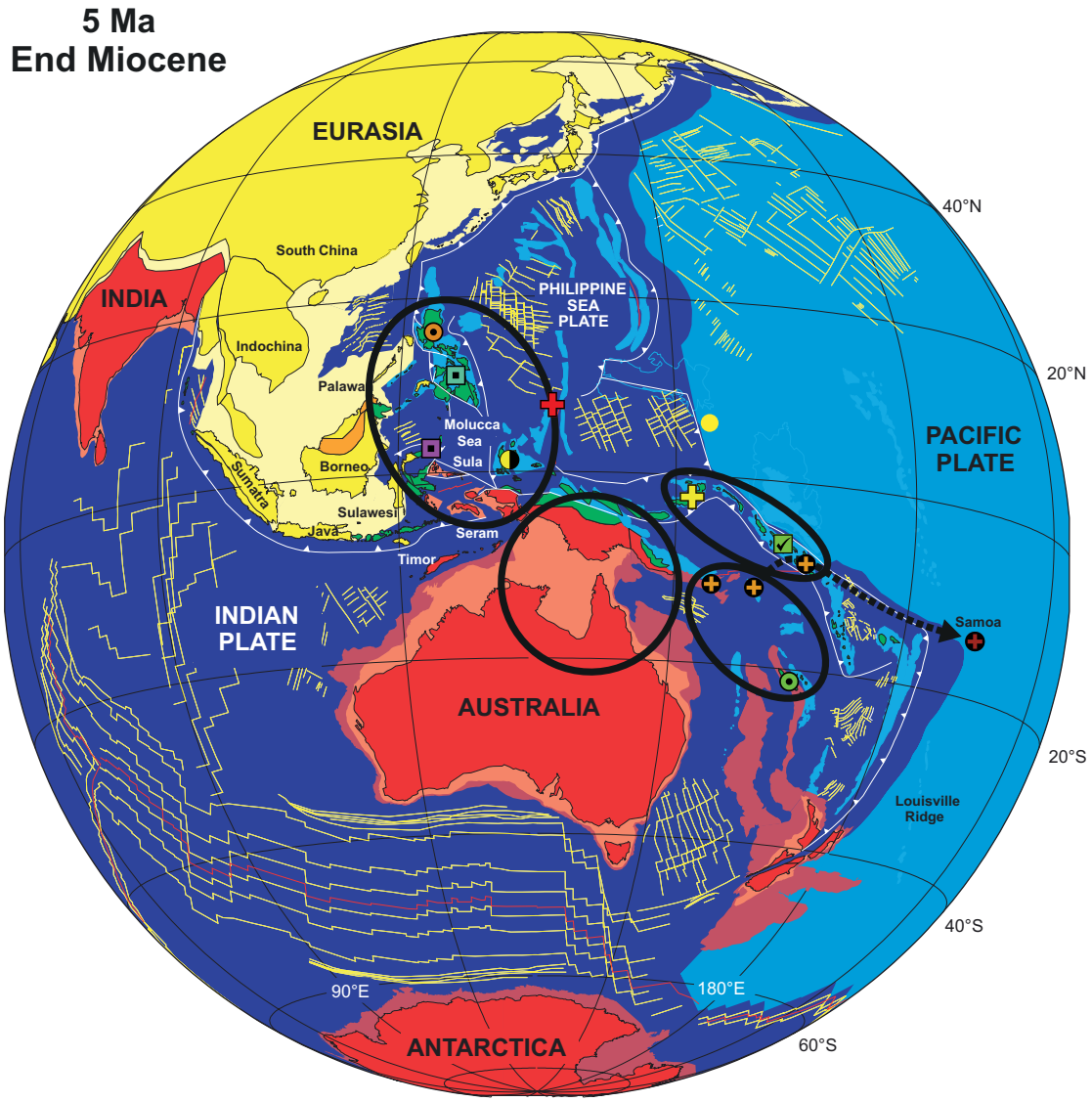

25 Ma
Late Oligocene
EURASIA
PACIFIC PLATE
INDIA
INDIAN PLATE
AUSTRALIA
ANTARCTICA
South China sea
Indochina
Palawan
Proto-South China Sea
Parece Vela Basin
Kyushu-Palau Ridge
Borneo
Sulawesi
Halmahera
SouthCarolineArc
Ontong Java Plateau
SolomonSea
South Fiji Basin
Outer Melanesia Arc
40°N
20°N
20°S
40°S
60°S
90°E
180°E

Fig. 76. Paleogeographic reconstructions of the Australasian region for the Late Miocene (5 Ma). Collision of the east Philippines-Halmahera-South Caroline arc with the New Guinea north eastern margins allowed the southward expansion of the genus onto the Australian craton (dashed line). Modified from Hall (1998, 2001, 2002).

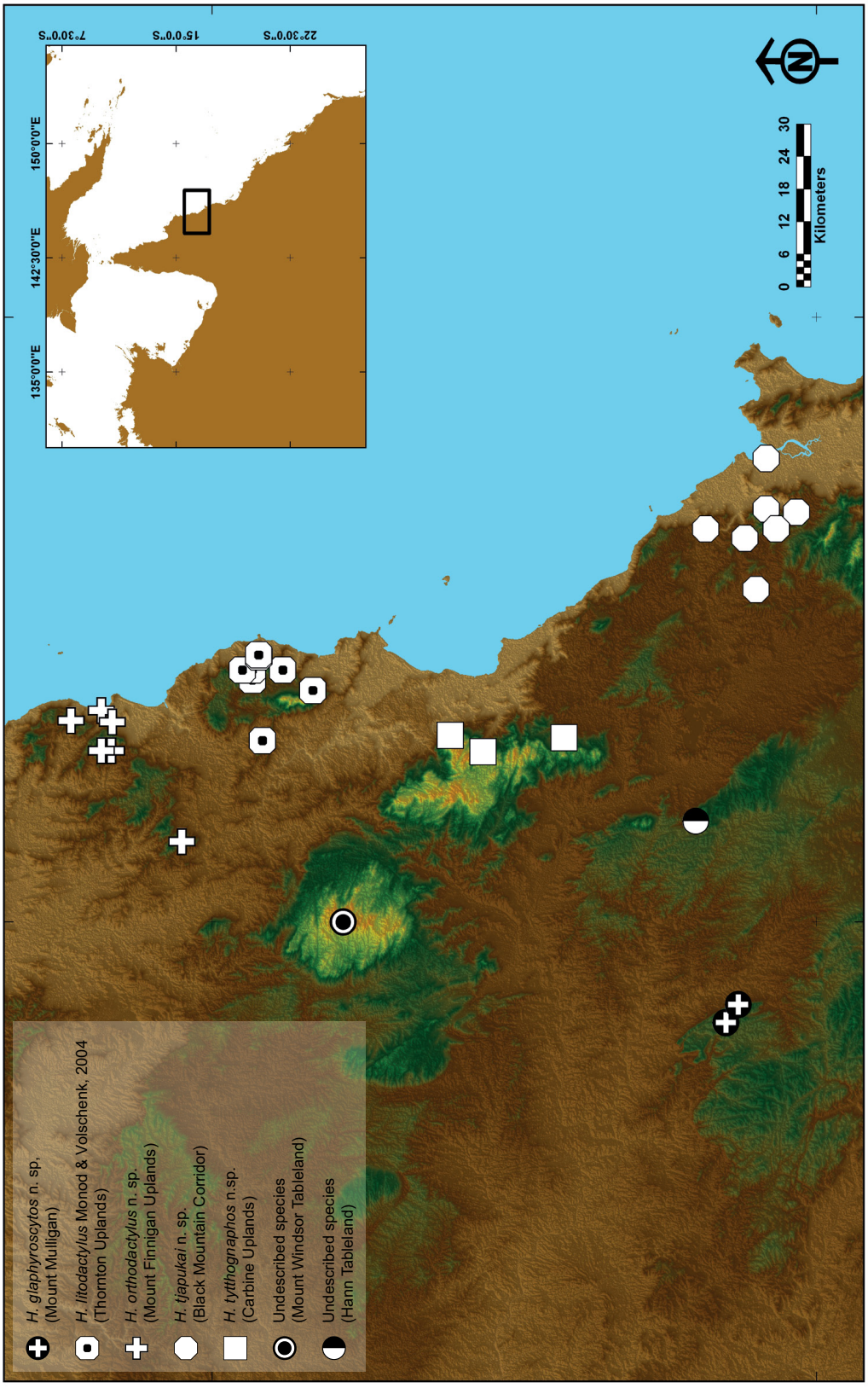

5 Ma
End Miocene
EURASIA
South China
INDIA
Indochina
PHILIPPINE
SEA
PLATE
Palawa
Molucca
Sea
Sula
Borneo
Sumatra
Sulawesi
Java
Seram
Timor
PACIFIC
PLATE
INDIAN
PLATE
AUSTRALIA
Samoa
Louisville
Ridge
ANTARCTICA
40°N
20°N
20°S
40°S
60°S
90°E
180°E

Evolution and diversity of the Australian Hormurus. Divergence of the Australian *Hormurus* from the Papuan stock is estimated ca. 22 Mya (fig. 61) and probably resulted from an increase of the sea levels and the ensuing flooding of the lowlands and the disruption of landbridges. Two marines transgressions with sea level rises of at least 5 m above the current state were reported during the Early Miocene (Miller *et al.*, 1999, 2005) and are potentially responsible for this cladogenesis event. The lack of topological structure in the cladograms and the high diversity of *Hormurus* in Australia may be attributed to an extremely rapid adaptive radiation on the continent mainly driven by the Neogene onset of aridification resulting in the fragmentation of previously continuous mesic habitats and disruption of paleodrainage basins. The occurrence of several *Hormurus* species in remnant patches of rainforests in the Northern Territory Top End (*H. extensus* Locket, 1997) and the Western Australia Kimberley (*H. chydaestigmata* n. sp. and *H. dodecatrichos* n. sp.) indicates that the genus was previously more widespread across the continent. These species are probably relicts of an old stock that manage to survive in forest refugia and along river systems. Whereas Melanesian *Hormurus* diversified by means of consecutive speciation and integration events along island arcs that are now parts of larger composite landmasses, distribution patterns of the Australian species seemingly result (1) from the fragmentation of a once widespread rainforest habitat due to the onset of aridification and decline of rainforests during the Middle Miocene (Bowler, 1982; Truswell, 1993; Kershaw *et al.*, 1994; McPhail *et al.*, 1994; White, 1998; Morley, 2000; Bowman *et al.*, 2009) and (2) from the subsequent, successive expansions and contractions of the remnant forest refugia. This is reflected in the difference in distribution pattern between these two groups of species. Distribution patterns in New Guinea are difficult to understand because most of the terranes or eco-regions contributed to a mixed biota with several points of origin (see Polhemus, 1996). New Guinean species may have relatively large distributional ranges which overlap extensively with those of other species. On the other hand, spatial diversification in Australia was probably much more “linear” than in New Guinea, without the resulting disjunct distributions and overlapping ranges observed in New Guinea. Up to three different *Hormurus* species may be found at a single locality in New Guinea, whereas localities in Australia usually support only a single species

with close relatives occurring in adjacent areas. For instance, in the Queensland Wet Tropics, the various highland rainforest refugia recognized as centers of endemism (fig. 77; Winter *et al.*, 1984; McDonald, 1992; Williams *et al.*, 1996; Williams, 1997; Williams & Pearson, 1997; Moritz *et al.*, 2001; Yeates *et al.*, 2002) each harbour a distinct *Hormurus* species. *Hormurus glaphyroscytos* n. sp. is restricted to Mount Mulligan, *H. litodactylus* Monod & Volschenk, 2004 to the Thornton Uplands, *H. orthodactylus* n. sp. to the Mount Finnigan Uplands, *H. tjapukai* n. sp. to the Black Mountain Corridor, *H. tytthognaphos* n. sp. to the Carbine Uplands and both the Mount Windsor Tableland and the Hann Tableland are home to endemic undescribed species.

Directions for future research. Liochelid DNA samples from the Cape York, Torres Strait Islands and Northern Territory, which represent biogeographical “transitions” between the Australian and Papuan regions and are thus extremely important to understand the biogeography of the genus, are currently lacking. Additionally, species from East Indonesia and New Guinea, another pivotal biogeographic region linking Asia to Melanesia, are also poorly sampled, hampering a precise assessment of the geographic and temporal sequence of colonisation of the different parts of the Australasian Archipelago. Filling these major gaps in the dataset will most likely significantly improve the reconstruction of the phylogeny of *Hormurus* and help clarify the biogeography of these scorpions at a finer scale.

Fig. 77. Distribution map of *Hormurus* Thorell, 1876 in the Wet Tropics (Queensland, Australia). Legend: = *H. glaphyroscytos* n. sp. (Mount Mulligan), = *H. litodactylus* Monod & Volschenk, 2004 (Thornton Uplands), = *H. orthodactylus* n. sp. (Mount Finnigan Uplands), = *H. tjapukai* n. sp. (Black Mountain Corridor), = *H. tytthognaphos* n. sp. (Carbine Uplands), = undescribed species (Mount Windsor Tableland), = undescribed species (Hann Tableland).


H. glaphyroscytos n. sp.
(Mount Mulligan)
H. litodactylus Monod & Volschenk, 2004
(Thornton Uplands)
H. orthodactylus n. sp.
(Mount Finnigan Uplands)
H. tjapukai n. sp.
(Black Mountain Corridor)
H. tythognaphos n.sp.
(Carbine Uplands)
Undescribed species
(Mount Windsor Tableland)
Undescribed species
(Hann Tableland)
135°0'0"E
142°30'0"E
150°0'0"E
7°30'0"S
15°0'0"S
22°30'0"S
0 6 12 18 24 30
Kilometers

3.5 APPENDICES

3.5.1 GEOLOGICAL HISTORY AND BIOGEOGRAPHY OF THE INDO-PACIFIC REGION

Given the complex tectonic history of the Indo-Pacific Region, and especially that of the Pacific basin and Australasian Region, biogeographical areas in Southeast Asia and the West Pacific cannot be considered as being derived from a single ancestral area, but rather have multiple origins. Therefore, current distribution patterns of flora and fauna in this region cannot be explained by vicariance alone and dispersal followed by speciation must have played an important role in the biogeographic processes. The identification of potential dispersal corridors is required to formulate plausible biogeographical hypotheses. Thus, a detailed overview of the paleogeography of the Indo-Pacific Region and its implications for the biogeography of various biotas is presented here.

3.5.1.1 THE INDIAN OCEAN

The Indian subcontinent. India as a continental fragment of Gondwana was involved in the following sequence of tectonic events: (1) East Gondwana, comprising Antarctica-Madagascar-India-Australia rifted from east Africa in the Mid-Jurassic about 155–170 Mya (Plummer & Belle, 1995; Gnos *et al.*, 1997; Jokat *et al.*, 2003, 2005); (2) According to the published models (Müller *et al.*, 2000; Reeves & deWit, 2000; Chand *et al.*, 2001), separation of India from east Antarctica is estimated at 130–110 Mya but preliminary results of an ongoing research project indicate that this geotectonic event is probably much younger (Jokat & König, 2007); (3) Following the break-up of the India-Seychelles block from Madagascar between 96 and 83 Mya, India initiated its northward drift (Plummer, 1995; Storey *et al.*, 1995; Pande *et al.*, 2001; Reeves & deWit, 2000); (4) The Seychelles separated from India ca. 65 Mya, at the Cretaceous/Tertiary (K/T) boundary (Plummer & Belle, 1995; Gnos *et al.*, 1997). The separation was associated with intense volcanism on the west coast of India known as the Deccan Traps (Courtillot *et al.*, 1988; Duncan & Pyle, 1988; Cox, 1988); (5) The initial collision between the Indian and Eurasian plates probably took place at approximately the same time, between 66 and 55 Mya (Beck *et al.*, 1995; Jaeger *et al.*, 1989). Willems *et al.* (1996) dated the final closure of the remnant Tethys sea during the middle Eocene (ca. 42 Mya).

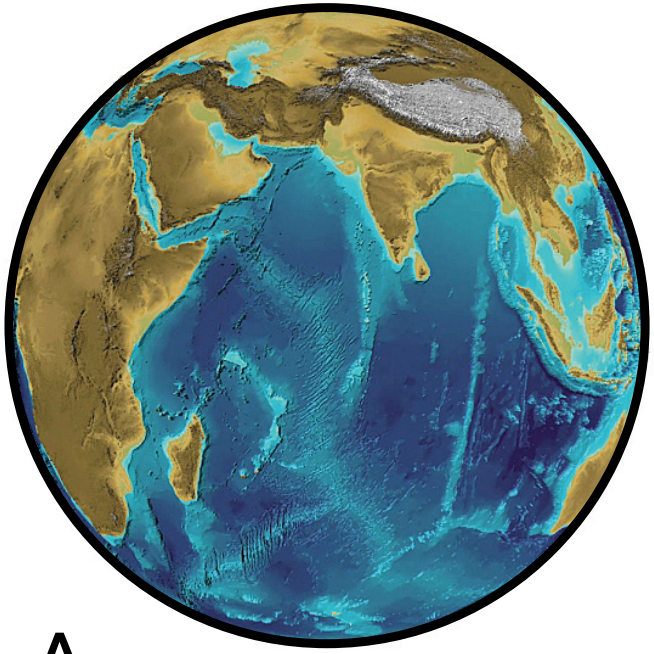
Survival of ancient Gondwanan lineages on the Indian sub-continent, despite dramatic climatic changes and Late Cretaceous volcanism followed by dispersal of these lineages into Asia when India finally collided with the Eurasiatic plate, account for the presence of many organisms in tropical Asia (Bossuyt & Milinkovitch, 2001; Conti *et al.*, 2002; Gower *et al.*, 2002; Wilkinson *et al.*, 2002; Karanth, 2006; Klaus *et al.*, 2010). Mostly because of incongruences between the timing of geological events inferred from geological studies and those inferred from various biogeographical studies based on fossils and molecular clocks, the age of the India-Asia collision and the northern extent of Greater India is still debated (Hall, 2002; Ali & Aitchinson, 2005, 2008). Presence of Laurasian taxa in the Indian Maastrichian implies a terrestrial connection between India and Laurasia as early as the end of the Cretaceous (Sahni *et al.*, 1982; Jaeger *et al.*, 1989; Prasad & Rage, 1991, 1995; Rage, 1995, 1996; Rage & Jaeger, 1995). Besides, distribution ranges and phylogenies of various amphibians (Bossuyt & Milinkovitch, 2001; Bossuyt *et al.*, 2006; VanBocxlaer *et al.*, 2006) also suggest late Cretaceous connections between India and Eurasia. Intolerance of amphibians towards salt water lends some credibility to the assumption that vicariance events rather than transoceanic dispersal are responsible for their geographical occurrence. Several theories have been proposed to explain these early biotic exchanges between India and Southeast Asia: (1) an intra-Tethyan island arc (Kohistan-Dras or Dazhuqu island arc) resulting from a subduction system induced in the Tethys sea by the northward drift of the Indian plate (Sahni *et al.*, 1987; Aitchison *et al.*, 2000, 2004; Ali & Aitchison, 2008); (2) a proto-Himalayan landmass developing between the two continents (Acharyya & Lahiri, 1991); (3) a more western position of the Southeast Asia and China blocks before they were pushed eastward by the India-Eurasia collision (Rage, 1988); (4) a rearrangement of South Asiatic blocks (Jaeger *et al.*, 1989). Among these hypotheses, the first appears to be the most plausible. Ali & Aitchison (2008) recently proposed a revised geological scenario for the Indian Ocean and argued that direct connections and migrations between Laurasia and India were certainly not possible before 57 Mya given the wide marine gap between the two continents.

According to most of the global paleogeographic reconstructions, India was isolated from other adjacent Gondwanan landmasses during its northward drift (Besse & Courtillot,

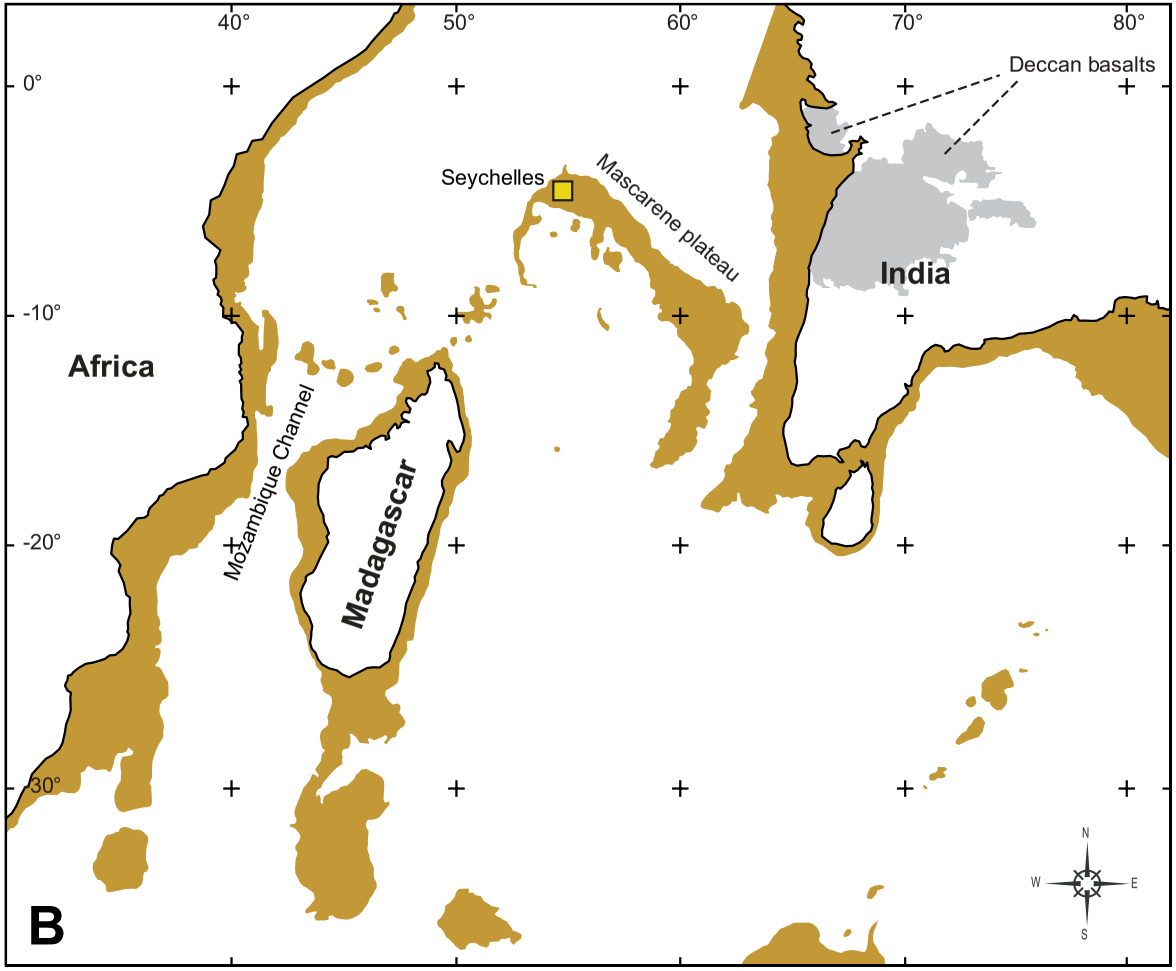
1988; Scotese, 2001; Hedges, 2003), and its biota is considered to have evolved independently for at least 25 million years before the collision with Asia. However, data from various fossils, contemporary faunas (Sahni, 1984; Krause *et al.*, 1997, 1999; Sampson *et al.*, 1998; Buckley *et al.*, 2000; Vences *et al.*, 2001; Carrano *et al.*, 2002; VanBocxlaer *et al.*, 2006; Bossuyt *et al.*, 2006; Masters *et al.*, 2006) and angiosperms (Krutzsch, 1987; Morley, 2000, 2003; Mehrotra, 2003; Moyle, 2004) indicate that terrestrial exchanges occurred between India and Africa and Madagascar during the Late Cretaceous up until the Early Paleogene, long after Gondwana fragmentation. It is likely that minor physiographic features (principally ocean islands) provided temporary causeways and/or stepping stones along which land animals could have migrated to/from the Indian sub-continent. Several recent geological models may account for late Cretaceous biotic interchanges between India and other Gondwanan landmasses especially Africa: (1) a landbridge between India and Madagascar via the Mascarene Plateau (Patriat & Ségoufin, 1988; Besse & Courtillot, 1988; Rage, 1996; 2003) may have allowed biotic exchanges between India and Madagascar at least until the Late Cretaceous and possibly until the Eocene-Oligocene (fig. 78B). Notable drops in sea level at the K/T boundary (Maastrichian) (Hallam, 1992; Adatte *et al.*, 2002) probably exposed submerged oceanic ridges allowing dispersal along these transient island arcs. (2) Owen (1983), Briggs (1989; 2003) and Parson & Evans (2005) acknowledged a different longitudinal position of the Indian sub-continent, close enough to the African east coast to allow at least a filtered interchange of taxa between Africa and India during the late Cretaceous. (3) Chatterjee & Scotese (1999) suggested that India and Africa were joined by a continuous landbridge named Greater Somalia in the late Cretaceous and Paleogene. Gheerbrant & Rage (2006) considered exchanges between India and Africa during the Late Cretaceous and Paleogene as plausible but argued that it cannot be confirmed on the basis of animal fossil evidence.

Madagascar. As mentioned in the preceding section, biotic exchanges between Madagascar, the Seychelles islands and India probably persisted well after the fragmentation of Gondwana. Portions of the Mascarene and Chagos-Laccadive Plateaus may have been temporarily emergent several times during the last 65 Myr and formed a dispersal corridor between

Fig. 78. Geographical configurations of the Indian Ocean. A, present day bathymetric map (from GEBCO, http://www.gebco.net/). B, paleogeographic reconstruction at the K/T boundary (65 Mya) (modified from Patriat & Ségoufin, 1988). The Seychelles Plateau that possible acted as a dispersal corridor between India and Madagascar during Cenozoic sea level low-stands is clearly visible in both illustrations.



A


40°
50°
60°
70°
80°
0°
-10°
-20°
-30°
Deccan basalts
Seychelles
Mascarene plateau
India
Africa
Mozambique Channel
Madagascar
N
W
E
S

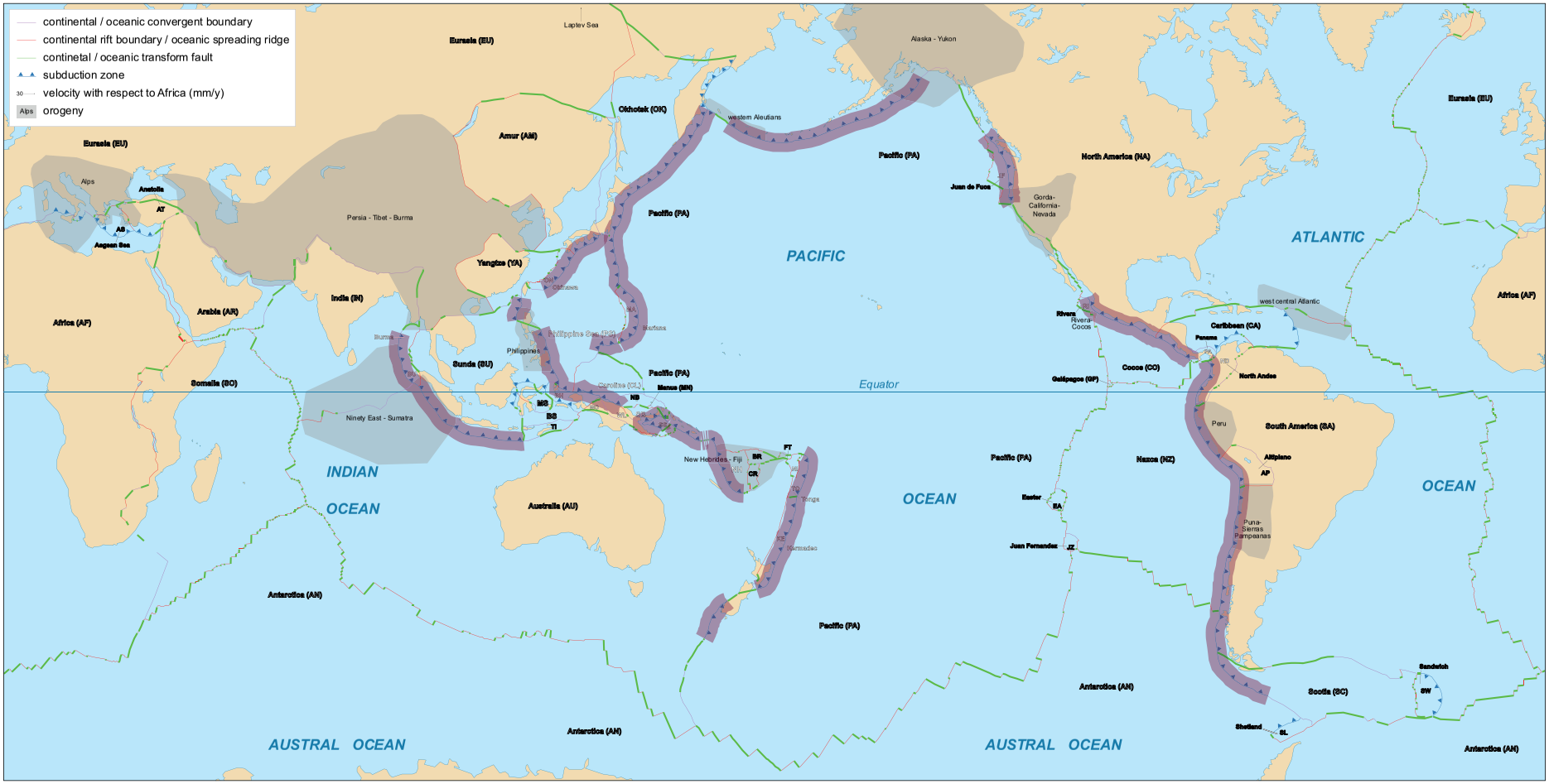
B

Madagascar and India, known as the “Lemurian stepping stones” (Schatz, 1996). Moreover, post-Gondwanan transoceanic dispersal between Madagascar and Africa has been documented in numerous mammal and reptile groups (Yoder *et al.*, 1996, 2003; Raxworthy *et al.*, 2002; Poux *et al.*, 2005; Noonan & Chippindale, 2006). MacCall (1997) proposed that large areas of the Mozambique Channel (fig. 78) were dry land from 45 Mya (Middle Eocene) to 26 Mya, thus providing a possible dispersal corridor between Madagascar and the African east coast. Although interesting, this concept is not fully supported by geological evidence (Rabinowitz & Woods, 2006). Despite the Comoros islands (formed in late Miocene) and topographic highs along the Davies Ridge (uplifted 43–50 Mya) possibly having been above sea level episodically during the Cenozoic, they would have constituted only isolated islands surrounded by deep water, and not a continuous land bridge as suggested by McCall (1977). However, animals could conceivably have island-hopped by rafting on logs or vegetation mats between Africa and Madagascar and vice versa. The distance necessary for the animals to raft across the Mozambique Channel is relatively short, Madagascar being only ca. 400 km away from its nearest point in Africa, and sweepstakes dispersal from Madagascar to Africa is favoured by wind and current directions (Masters *et al.*, 2006).

3.5.1.2 AUSTRALASIA AND THE PACIFIC

Mainland East and Southeast Asia is a mosaic of various continental slivers that assembled progressively over the last 250 million years (Metcalfe, 1998, 1999, 2001, 2002, 2006). Three waves of separation and northward drifting of fragments (microplates) from the northern margin of eastern Gondwana occurred in the Devonian, early to mid-Permian, and late Triassic to late Jurassic, respectively. Amalgamation and accretion of these Gondwanan terranes with Laurasia occurred progressively between the late Devonian and the Cretaceous. Since the Mesozoic, motions of the Pacific plate have induced intense seismic and volcanic activity at its margins, resulting in a nearly continuous series of oceanic trenches and active continental margins commonly known as the Pacific Ring of Fire (fig. 79). Subduction zones of the north-western section of this ring caused the emergence in the Late Cretaceous (84-100 Mya) of the Okhotsk-Chutkotka arc (fig. 80A; Nokleberg *et al.*, 1994, 2000) that may have acted

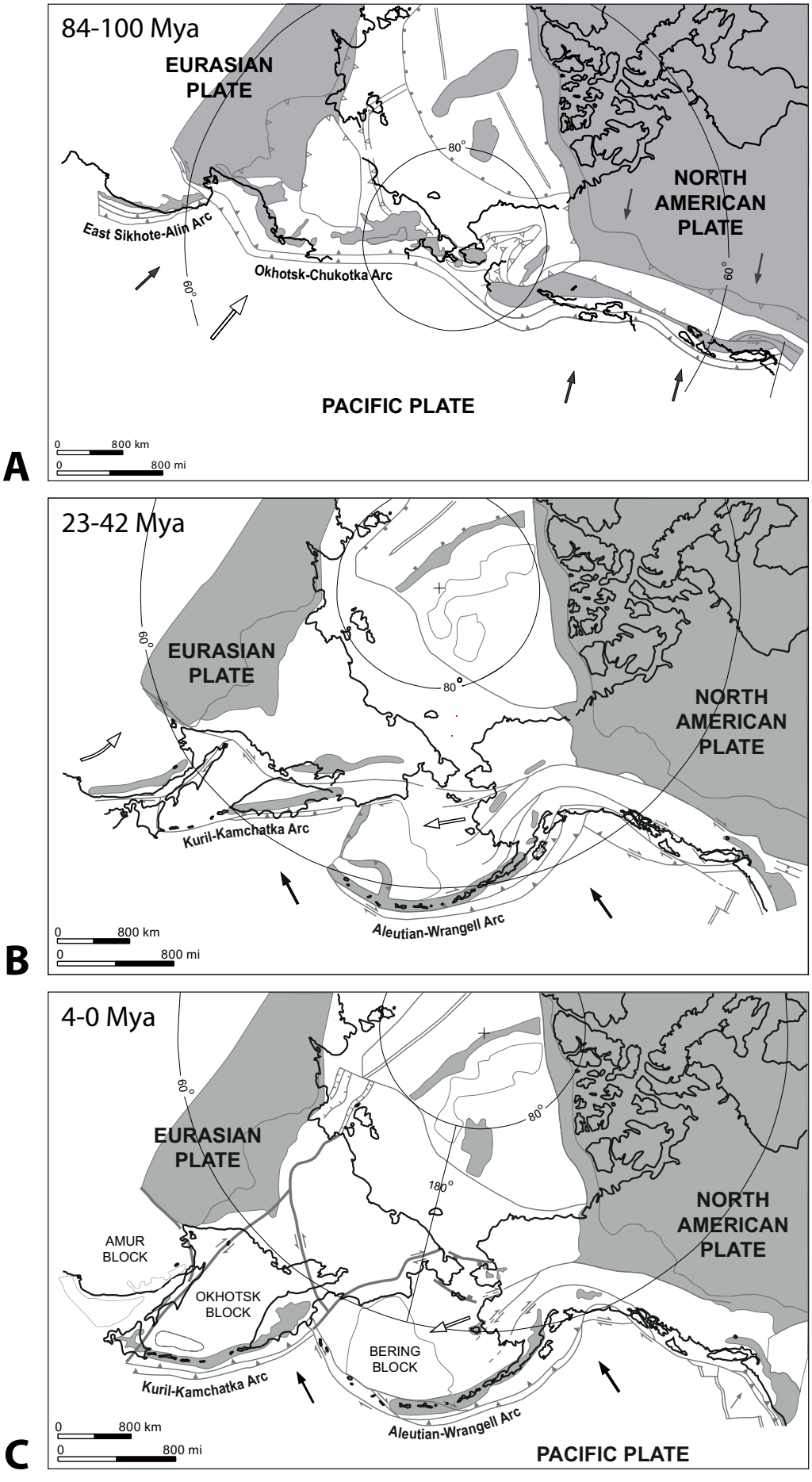
Fig. 79. Pacific Ring of Fire. Present day map showing the active subduction zones and associated island arcs surrounding the Pacific plate. Adapted from a file created by Eric Gaba and downloaded from http://commons.wikimedia.org/.


continental / oceanic convergent boundary
continental rift boundary / oceanic spreading ridge
continetal / oceanic transform fault
subduction zone
30 velocity with respect to Africa (mm/y)
Alps orogeny
Laptev Sea
Eurasia (EU)
Alaska - Yukon
Okhotsk (OK)
western Aleutians
Amur (AM)
Pacific (PA)
North America (NA)
Juan de Fuca
Gorda-
California-
Nevada
Eurasia (EU)
Alps
Anatolia
AT
AS
Aegean Sea
Persia - Tibet - Burma
Pacific (PA)
PACIFIC
ATLANTIC
Yangtze (YA)
India (IN)
Africa (AF)
Arabia (AR)
Africa (AF)
Rivera
Rivera-
Cocos -
west central Atlantic
Caribbean (CA)
Panama
Philippines
Sunda (SU)
Cocos (CO)
Galápagos (GP)
North Andes
Somalia (SC)
Pacific (PA)
Manus (MN)
Equator
NB
BS2
BS
TI
Ninety East - Sumatra
Peru
South America (SA)
INDIAN
OCEAN
New Hebrides - Fiji
FT
BR
CR
Pacific (PA)
Nazca (NZ)
Altiplano
AP
OCEAN
OCEAN
Australia (AU)
Tonga
Easter
EA
Juan Fernandez
JZ
Puna-
Sierras
Pampeanas
Antarctica (AN)
Pacific (PA)
Antarctica (AN)
Sandwich
SW
Scotia (SC)
Shetland
SL
AUSTRAL OCEAN
Antarctica (AN)
AUSTRAL OCEAN
Antarctica (AN)

as a migration pathway between Japan and Alaska. The Kuril-Kamchatka arc and the Aleutian arc originated at 65–50 Mya (figs 80B/D; Kimura & Tanaki, 1985; Scholl *et al.*, 1992; Nokleberg *et al.*, 2000) and at 46–55 Mya (figs 80B/D; Scholl *et al.*, 1986, 1987; Nokleberg *et al.*, 2000; Duncan & Keller, 2004; Jicha *et al.*, 2006) respectively, forming additional potential dispersal corridors. The northeastern Gondwanan fragment (composed of Australia and New Guinea) started to rift from East Antarctica between 100 and 135 Mya (Müller *et al.* 2000). Sea floor spreading between the two crustal fragments was probably initiated in the Late Cretaceous–Early Paleocene but remained limited until the Late Eocene (Müller *et al.* 2000). About 44–40 Mya the northward drift of the Australian craton accelerated significantly until the impact with the Southeast Asian volcanic islands of the Sunda Arc in the Late Oligocene–Early Miocene (25–20 Mya) (Hall, 2002). The collisions involved northern New Guinea, Sulawesi and the outer Banda Arc (Timor, Kai, Seram), and resulted in the uplift of new emerged land areas such as the Lesser Sunda Islands (inner Banda Arc) by volcanic activity. However, tectonic interactions between the Australian, Eurasian and Pacific plates started beforehand, in the Early Eocene–Early Oligocene (55–35 Mya), initiating the formation of a complex system of oceanic island arcs. These chains of volcanic islands represent potential dispersal corridors that may have permitted biotic exchanges between Sundaland and the Australo-Papuan archipelago before the collision between the Australian and Sundal continental crusts (figs 72-73).

Japan, Kuril-Kamchatka and Aleutian island arcs. In the Late Cenozoic–Early Mesozoic, the northward drift of the Pacific plate and its subduction beneath the Eurasian and North American continental plates was accompanied by major arc magmatism and subduction accretion (Nokleberg *et al.*, 2000; Stepashko, 2006). In the Early Cretaceous, the Japanese islands were already emergent landmasses that progressively increased in width during the Cenozoic with the accretion of various oceanic material and sequences of intense volcanic activity (Taira, 2001). Besides, the various subduction systems in the northern portion of the Pacific Basin induced the emergence of several volcanic island arcs along the eastern margin of the Russian Northeast and western Alaska (fig. 80). The Okhotsk-Chutkotka volcanic belt was active from the Cretaceous to the Early Tertiary (Nokleberg *et al.*, 1994, 2000) until the Okhotsk block

Fig. 80. Phanerozoic tectonic model for the Circum-North Pacific. A, Cenomanian through Santonian (100–84 Mya). B, Middle Eocene through Early Miocene (42–23 Mya). C, Pliocene through present (4–0 Mya). Adapted from Nokleberg *et al.* (2000).


84-100 Mya
EURASIAN PLATE
NORTH AMERICAN PLATE
PACIFIC PLATE
East Sikhote-Alin Arc
Okhotsk-Chukotka Arc
80°
60°
60°
0 800 km
0 800 mi
A
23-42 Mya
EURASIAN PLATE
NORTH AMERICAN PLATE
Kuril-Kamchatka Arc
Aleutian-Wrangell Arc
60°
80°
0 800 km
0 800 mi
B
4-0 Mya
EURASIAN PLATE
NORTH AMERICAN PLATE
PACIFIC PLATE
AMUR BLOCK
OKHOTSK BLOCK
BERING BLOCK
Kuril-Kamchatka Arc
Aleutian-Wrangell Arc
60°
80°
180°
0 800 km
0 800 mi
C

(a fragment of the Kula/Pacific plate) collided with the Siberian continent, displacing the subduction zone along the terrane's southern margins, hence initiating the formation of the Kuril-Kamchatka igneous arc and its associated archipelagos (Kimura & Tanaki, 1985; Scholl *et al.*, 1992; Nokleberg *et al.*, 2000). Accretion of the Okhotsk terrane to the Eurasian plate also triggered the uplift of the Kamchatka Peninsula, of the northern tip of the Sakhaline island and of the eastern tip of Hokkaido island (Nokleberg *et al.*, 2000; Barnes, 2003). Around 47–55 Mya, the northward motion of the Pacific Plate shifted to its present west-northwest direction, triggering the formation of another island arc, the Aleutian arc (Scholl *et al.*, 1986, 1987; Nokleberg *et al.*, 2000; Duncan & Keller, 2004; Jicha *et al.*, 2006). Therefore, by the Late Cretaeous (100–85 Mya), the island arc systems of the northern Pacific Basin provided a potential dispersal track between the northern Japanese islands and Alaska (figs 80A, B). Furthermore, a land connection between Asia and North America, commonly known as Beringia, had also been established across the Bering Strait, providing a major intercontinental migration pathway (Lomolino *et al.*, 2006). These northern connections persisted through most of the Cenozoic and permitted regular biotic exchanges between Eurasia and Laurentia (fig. 81), hence the continuity of the Late Cretaceous to Eocene floras and faunas of northeastern Asia and western North America (Graham, 1972; Wolfe, 1975; Matthews, 1979; Hamilton, 1983; Hsü, 1983; Tiffney, 1985; Briggs, 1987; Moran, 1989; Beard & Dawson, 1999; Manchester, 1999; Sereno, 1999; Tiffney & Manchester, 2001; Bowen *et al.*, 2002; Archibald *et al.*, 2005; Martin *et al.*, 2005; Archibald & Makarkin, 2006; Krassilov *et al.*, 2009; Manchester *et al.*, 2009). Global greenhouse conditions prevailed from the Cretaceous to the Early Cenozoic. All continents had warm and equable climates with high humidity and rainfall, and deciduous forests extended all the way to the poles, allowing temperature-sensitive taxa to reach high-latitude regions. Two major thermal maxima were recorded in the Mid-Cretaceous (ca. 120–80 Mya) (Clark & Jenkins, 1999; Bralower *et al.*, 2002; Huber *et al.*, 2002) and in the Early Paleogene (ca. 60–45 Mya) (Jenkyns, 1980; Kennett & Scott, 1991; Zachos *et al.*, 1993, 1994, 2008; Katz *et al.*, 1999; Norris & Röhl, 1999; Peters & Sloan, 2000; Bralower *et al.*, 2002; Francis & Poole, 2002; Poole *et al.*, 2005; Rose, 2006; Francis *et al.*, 2008). Although sea levels were generally high during this time interval, significant drops occurred at ca. 71 Mya and at 67–66 Mya (Haq *et al.*, 1987; Keller, 2001; Miller *et al.*,

Fig. 81. Paleogeographic reconstruction of the Pacific Ocean for the Mid Cretaceous (ca. 96 Mya). The dashed line indicates a potential dispersal corridor, commonly referred as Beringia, between Eurasia and Laurentia. Modified from Li & Powell (2001).

Eurasia
Neo-Tethys
Australia
Antarctica
Africa
Eurasia
NAmerica
Palaeo Pacific
Ocean

1999; Abramovich *et al.*, 2002), exposing submerged areas. In the Mid–Late Eocene (45 Mya), a long-term progressive decrease of global temperature associated with major sea level drops (Haq *et al.*, 1987; Miller *et al.*, 2005) and drier climates (Raven & Axelrod, 1974; Morley, 2000) induced the contraction and extinction of tropical habitats in the northern hemisphere, severing important dispersal corridors.

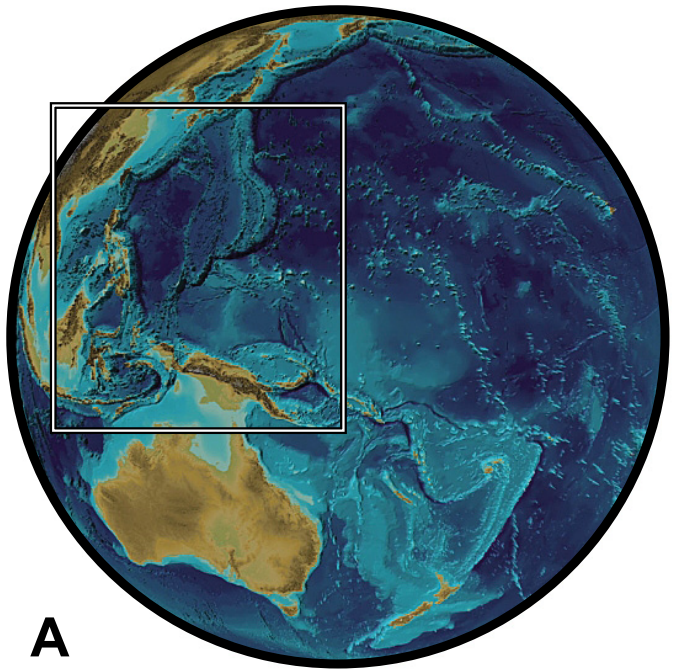
Sulawesi, Philippines, Halmahera and Solomon Islands. Australia separated from Antarctica in the Early-Mid Cretaceous but only started to drift away toward the Asian continent in the Late Cretaceous-Early Paleocene (fig. 7; Müller *et al.* 2000). The northern margin of the Australian plate was subducted toward the northeast, beneath the Asian plate inducing the formation of volcanic island arcs along these margins (Hamilton, 1988; Polhemus, 1996). In the Early Eocene (55 Mya), there were probably several microplates and their associated island arc systems between the Australian and Asian-Pacific plates, but as the oceanic crust was subducted to the north of Australia, micro-plates were progressively eliminated and their forearcs were obducted as ophiolites (Sepik, Papuan and New Caledonia ophiolites) onto the northern Australian passive margin at different times in the Eocene–Early Miocene (Hall, 2002; Schellart *et al.*, 2006; Hall *et al.*, 2009). In the Middle Eocene (45 Mya), northern New Guinea became a passive margin, and northward subduction of the ocean crust was established beneath the nascent Philippine Sea Plate along the East Sulawesi-East Philippines-Halmahera Arc, which was an extension of the Sunda-Java Trench system (Hall, 1998, 2002). Luzon (northern Philippines) was part of a second arc system that extended along the northern and eastern borders of the Philippine Sea plate (figs 72, 73; see Palau section). Meanwhile, the Pacific Plate was subducted at its southern margin beneath the Australian Plate, inducing the formation of the Outer Melanesian Arc (OMA) system. The OMA extended from New Guinea along the eastern rim of the Australian continental Plate (Hamilton, 1979; Lee & Lawver, 1995; Daly & al., 1991; Hall, 2001, 2002; Schellart *et al.*, 2006; see figs 72, 73). The Solomon Archipelago was part of the OMA and probably started to emerge in the Late Eocene–Early Miocene (Petterson *et al.*, 1999; Schellart *et al.*, 2006; Neall & Trewick, 2008). By the late Eocene the Sulawesi-Philippines-Halmahera and Outer Melanesian Arcs were probably forming a continuous island

arc system connecting Southeast Asia to the Pacific through the Australo-Papuan region.

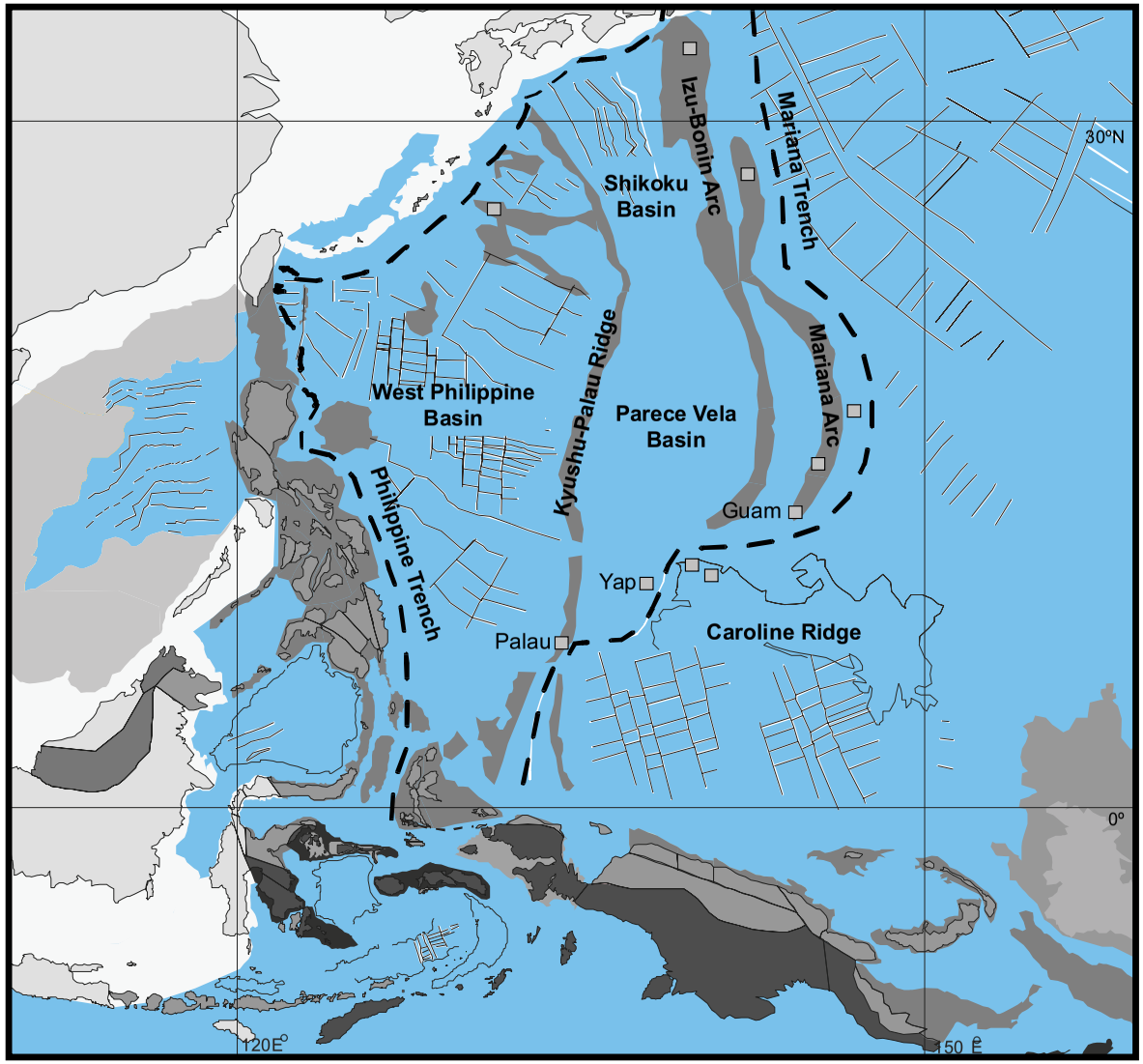
Palau. While the Australian plate was drifting northward toward Eurasia, the Pacific Plate was moving westward inducing the development of active subduction systems and associated volcaniism in the convergence zones. The formation of a complex arc system, known as Izu-Bonin-Mariana (IBM), was initiated in the Early–Middle Eocene (50–40 Mya) by the subduction of the Pacific plate beneath the eastern rim of the Philippine Sea plate (Honza, 1991; Hall, 2002; Kobayashi, 2004; Neal & Trewick, 2008). By the Late Eocene–Early Oligocene, the proto-northern Philippines and the IBM constituted an island arc stretching from north Borneo along the northern margins of the Philippine Sea Plate. The islands of Palau form the southern tip of the Kyushu-Palau Ridge, a submerged chain of sea-mounts, remnants of active volcanic arcs resulting from the IBM subduction system (fig. 82). The proto-Kyushu-Palau Ridge was active from 40–30 Mya, before the opening of the Shikoku-Parece Vela back-arc basins and the eastward retreat of the IBM Trench between 30–15 Mya (fig. 83). Volcanism on the Kyushu-Palau Ridge ceased at 28 Mya, soon after the Shikoku-Parece Vela Basins started to open, whereas volcanism in Palau remained active until about 20 Mya. The northern part of the Kyushsu-Palau Ridge quickly eroded and is now submerged (Kobayashi, 2004). The islands of Palau are primarily composed of volcanic rocks and a limestone cap, dated at 37.7–20.1 Mya (Meijer er al., 1983; Haston *et al.*, 1988; Haston & Fuller, 1991) and 40 Mya, respectively, which is synchronous with events of volcanism at the southern Kyushu-Palau Ridge (Kobayashi, 2004).

New Caledonia. New Caledonia is a fragment of submerged continental crust that rifted from Gondwana in the late Cretaceous, about 65 Mya (fig. 84A; Yan & Kroenke, 1993; Rawling & Lister, 1999; Kroenke, 1984, 1996; Lafoy *et al.*, 2005; Schellart *et al.*, 2006): the eastern continental margin of the Australian plate was fragmented by sea floor spreading into the Tasman Sea (85–52 Mya), into the Coral Sea (62–52 Mya), into the New Caledonia Basin (62–56 Mya), and into the D'Entrecasteaux basin (34–28 Mya), gradually widening the gap between Australia and New Caledonia. Eastward subduction of the Loyalty back-arc Basin was initiated

Fig. 82. A, bathymetric map of the West Pacific, the area shown in B is indicated. B, annotated map of the major bathymetric and geographical features of the Izu-Bonin-Mariana arc system (modified from MacPherson & Hall, 2001).



A


Izu-Bonin Arc
Mariana Trench
30°N
Shikoku Basin
Kyushu-Palau Ridge
Mariana Arc
West Philippine Basin
Parece Vela Basin
Philippine Trench
Guam
Yap
Palau
Caroline Ridge
0°
120E°
150 E

B

Fig. 83. Paleogeographic reconstructions of the Izu-Bonin-Mariana arc system. A, 40–30 Mya. B, 15–10 Mya. C, at present. Thick arrows denote motions of the Pacific plate. Active volcanic islands are denoted by triangle and extinct or non-volcanic islands are shown by circles. From Kobayashi (2004).

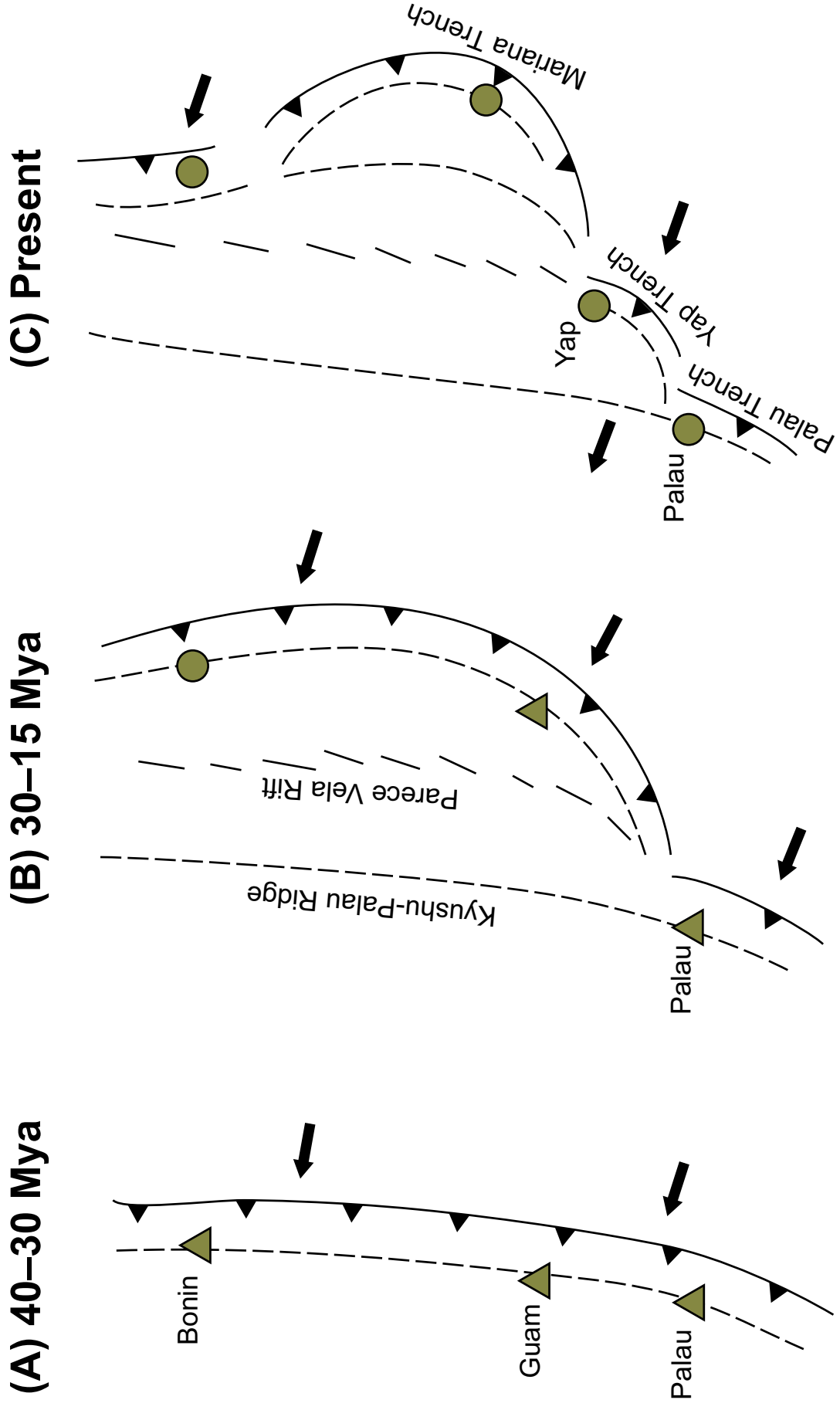
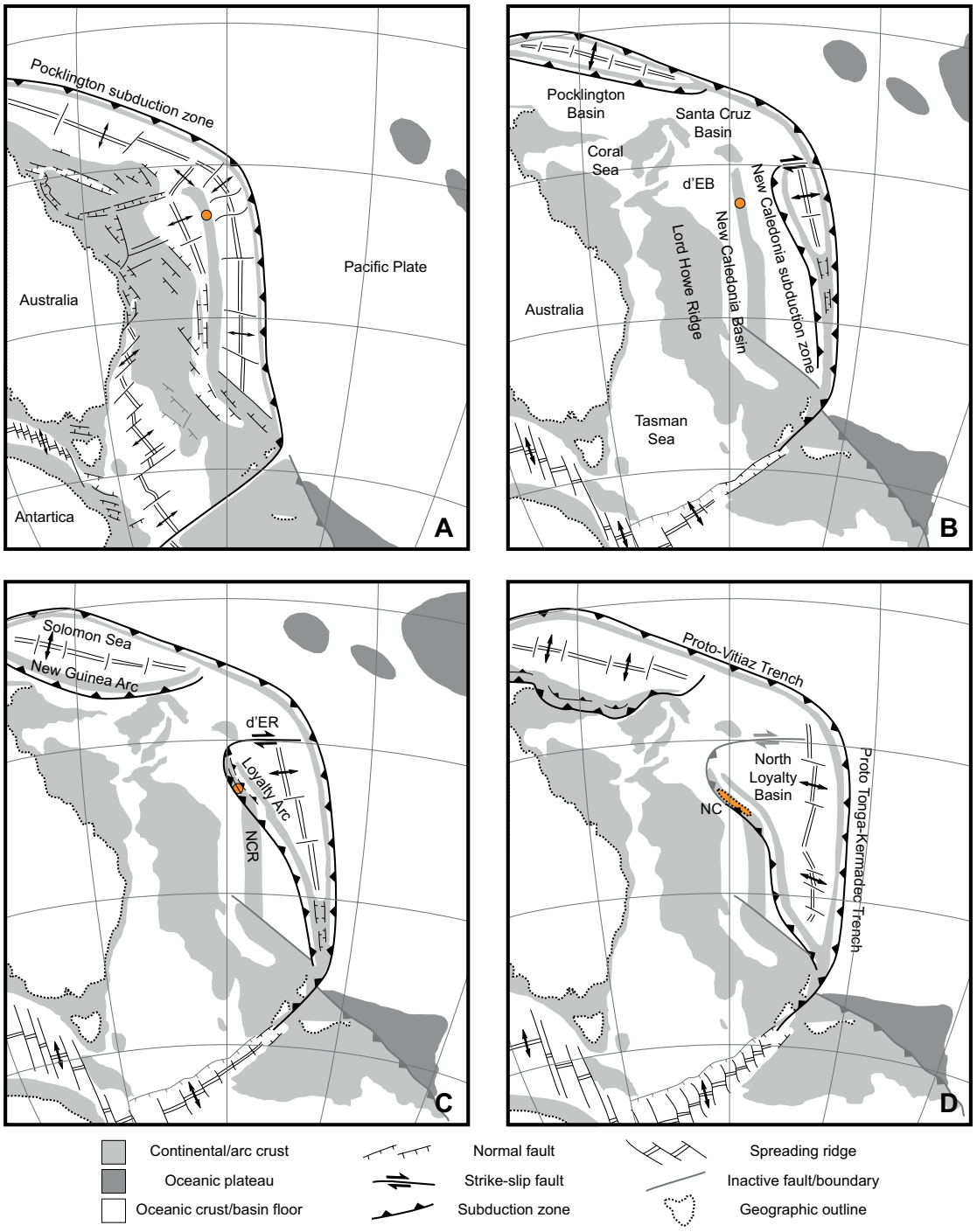

(A) 40–30 Mya
Bonin
Guam
Palau
(B) 30–15 Mya
Parece Vela Rift
Kyushu-Palau Ridge
Palau
(C) Present
Mariana Trench
Yap
Yap Trench
Palau Trench
Palau

Fig. 84. Paleogeographic reconstructions of the Southwest Pacific region for the Late Cretaceous and Cenozoic periods. A, 65 Mya (Early Paleocene). B. 40 Mya (Eocene). C, 35 Mya (Late Eocene). D, 30 Mya (Oligocene). The continental crust fragment that later formed the basement of New Caledonia is indicated in each map by an orange circle. Legend: d'EB = d'Entrecasteaux Basin; d'ER = d'Entrecasteaux Ridge; NC = New Caledonia; NCR = New Caledonia Ridge. Modified from Schellart *et al.* (2006).

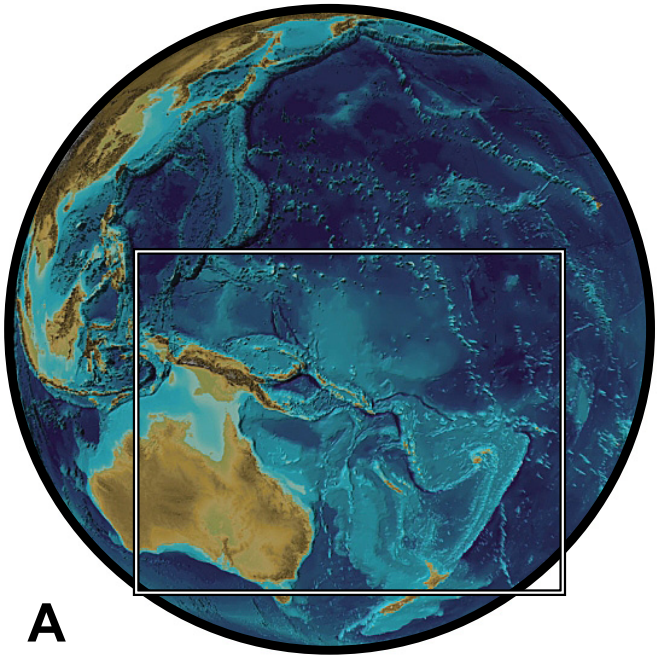

Pocklington subduction zone
Pacific Plate
Australia
Antartica
A
Pocklington Basin
Santa Cruz Basin
Coral Sea
d'EB
New Caledonia subduction zone
New Caledonia Basin
Lord Howe Ridge
Australia
Tasman Sea
B
Solomon Sea
New Guinea Arc
d'ER
Loyalty Arc
NCR
C
Proto-Vitiaz Trench
North Loyalty Basin
NC
Proto Tonga-Kermadec Trench
D
Continental/arc crust
Oceanic plateau
Oceanic crust/basin floor
Normal fault
Strike-slip fault
Subduction zone
Spreading ridge
Inactive fault/boundary
Geographic outline

ca. 50 Mya along the newly formed New Caledonia subduction zone (fig. 84B; Schellart *et al.*, 2006). New Caledonia was not an emergent island until its continental basement collided with one of the intra-oceanic island arcs mentioned above, i.e. the forearc of the Loyalty Ridge, in the Late Eocene. Collisional orogenesis and obduction of a large ophiolite nappe resulting from this convergence occured between 38 and 33 Mya (fig. 84C; Aitchison *et al.*, 1995; Cluzel *et al.*, 2001; Schellart *et al.*, 2006; Neall & Trewick, 2008). A recent study on post-obduction fluvial aggradation (Chardon & Chevillotte, 2006) confirmed that New Caledonia was an emergent landmass since the Oligocene (35–30 Mya). The New Caledonia and Loyalty Ridges were also extended to the north by the d'Entrecasteaux Ridge, an ancient transform fault active in the Eocene, and therefore probably connected with the proto Vitiaz Trench which is part of the OMA system (fig. 84C, D; Schellart *et al.*, 2006).

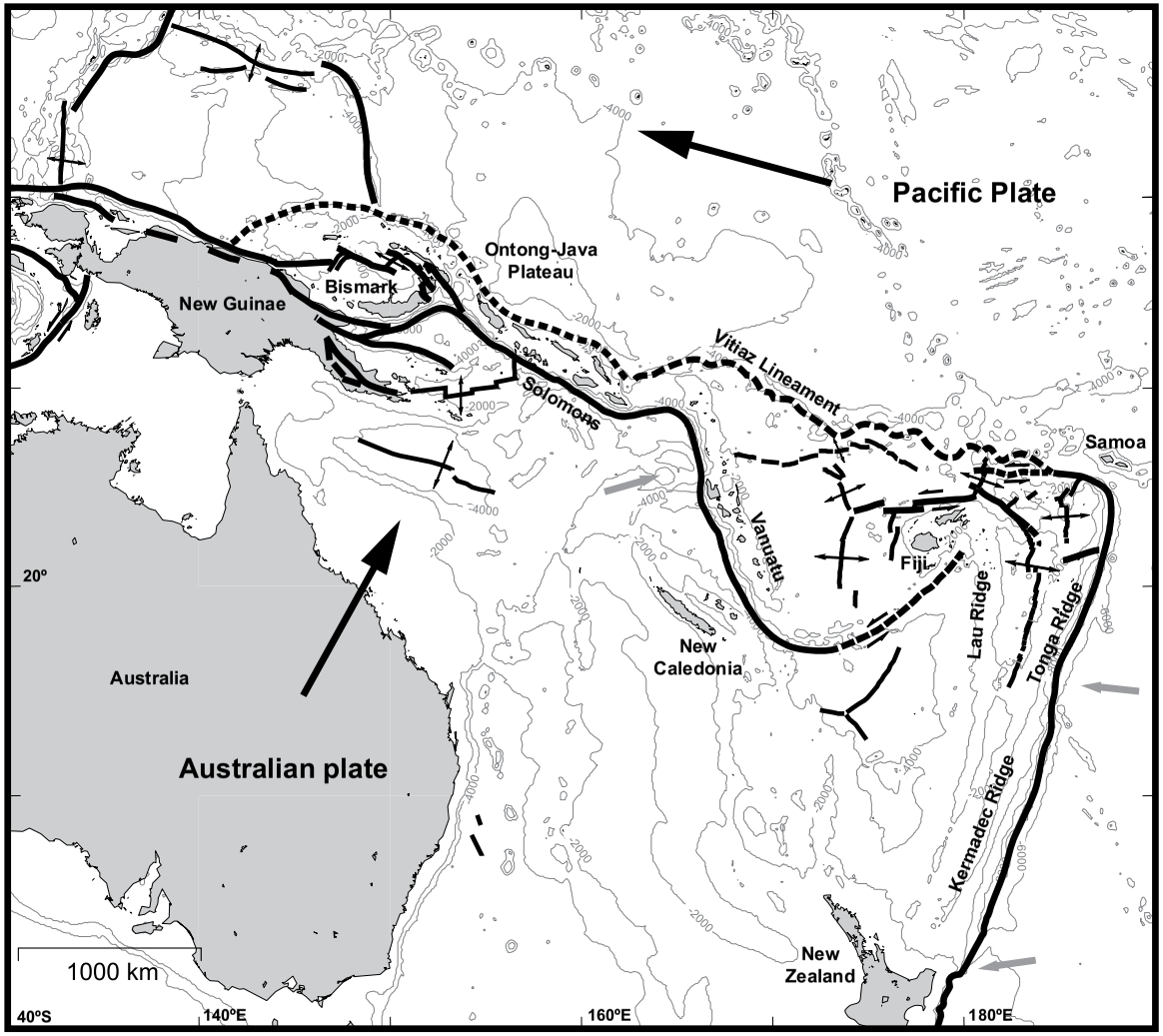
Samoa. The Samoa archipelago is composed of volcanic islands that started to emerge around 13.5 Mya (Johnson *et al.*, 1986; Ewart, 1988; Hart *et al.*, 2004). These islands have never been in contact with any continental landmasses and lie in the middle of the SW Pacific Ocean. However, during Late Eocene–Oligocene times the Bismarck Archipelago, Vanuatu, Fiji and Tonga-Kermadec were joined into a once continuous island arc that extended from the Santa Cruz group (north of Vanuatu) to Samoa along the southern margin of the Vitiaz Trench (fig. 85; Ewart, 1988; Hall, 2002; Ruellan & Lagabrielle, 2005). The Vitiaz Lineanement separates the Cretaceous Pacific lithosphere from the upper Cenozoic back-arc basins lithosphere (Brocher & Holmes, 1985; Pelletier & Auzende, 1996); it is regarded as the former convergent plate boundary between the Pacific and Australia plate, which was active from the Eocene to the late Miocene (Falvey, 1975, 1978; Schellart *et al.*, 2006). Subduction along the Vitiaz Trench stopped during the late Miocene when it collided with the Ontong Java and north Melanesian Plateaus which were carried by the Pacific plate. The Samoan islands started to developed at approximately the same period. Thus plants and animals may have colonized Samoa before the islands of the Vitiaz Arc were submerged by erosion.

New Guinea. The geology of New Guinea is considered among the most complex in

Fig. 85. A, bathymetric map of the West Pacific, the frame indicates the area shown in B. B, annotated map of the major bathymetric and geographical features of the West Pacific Region (modified from Ruellan & Lagabrielle, 2005).



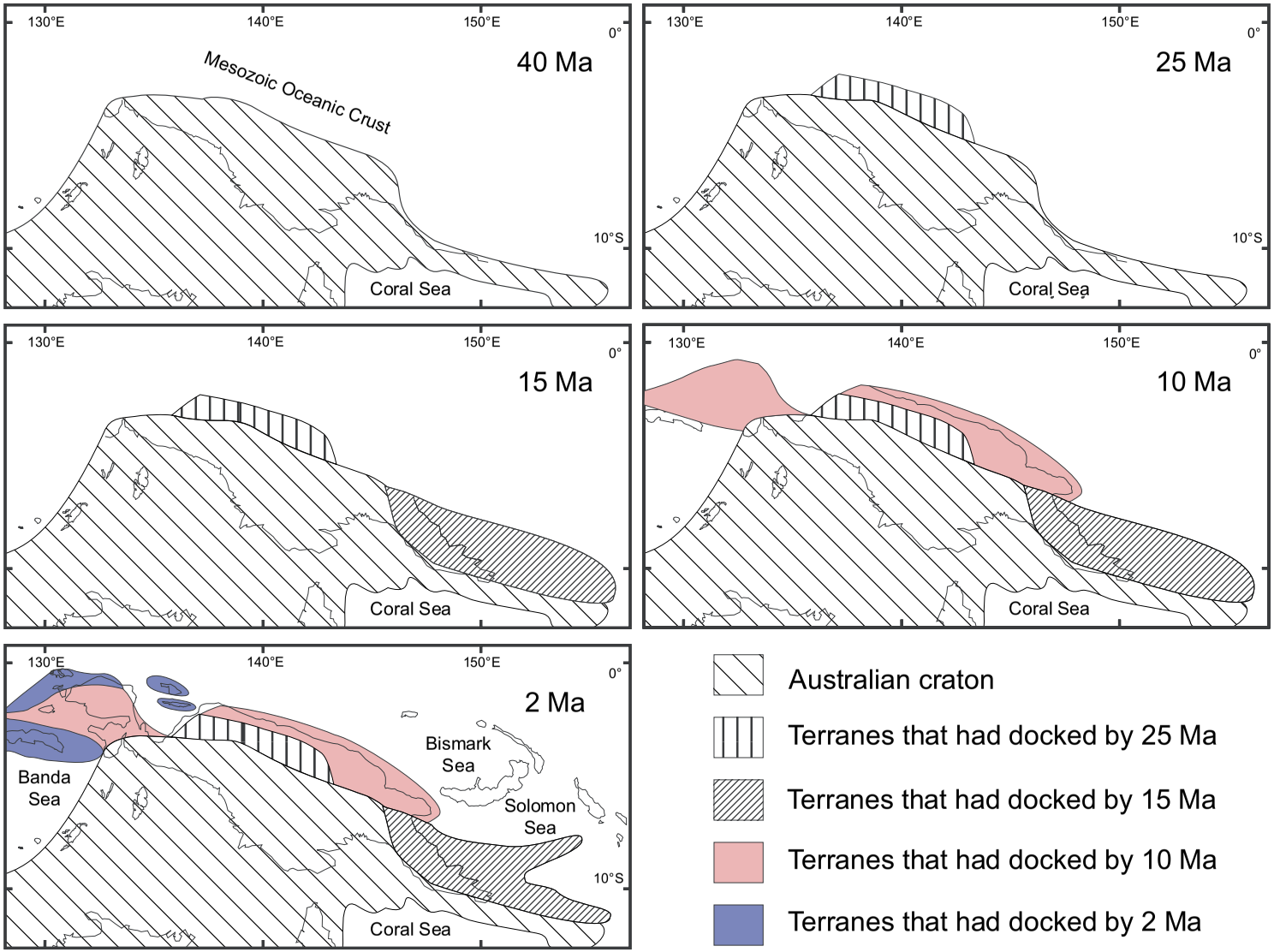
A


Pacific Plate
Ontong-Java Plateau
Bismark
New Guinae
Vitiaz Lineament
Solomons
Samoa
Vanuatu
Fiji
Lau Ridge
Tonga Ridge
New Caledonia
Australia
Australian plate
Kermadec Ridge
New Zealand
20°
1000 km
40°S
140°E
160°E
180°E

B

the world. Its present shape results from interactions of five tectonic plates, numerous microcontinents, and several island arc systems. Pigram and Davies (1987) demonstrated that New Guinea is composed of a southern part (the Australian craton) and a northeastern part, the latter composed of at least 32 tectonostratigraphic terranes, which are remnants of Pacific island arcs that accreted to the Australian craton from the Eocene to the Pliocene (50–5 Mya; see fig. 86). Most of the terranes identified by Pigram & Davies (1987) have oceanic origin (ophiolites), but terranes from western New Guinea are predominantly of continental origin (microcontinents rifted from Australia). All New Guinean terranes are covered with rainforest, but each is faunistically and floristically distinct, with considerable local endemism. Disjunctions in the distributions of many New Guinean taxa do not correlate with ecological factors but with the major geological boundaries in New Guinea (Heads, 1999; 2001a; 2001b). Recent analyses (Michaux, 1994; Flannery, 1995; DeBoer & Duffels, 1995, 1996a, 1996b; Polhemus & Polhemus, 1998; Heads, 2002) suggest that some distributions of animals and plants in New Guinea are incompatible with early dispersal models of New Guinea biogeography (Axelrod & Raven, 1982). Geological dynamics of island arcs and the biological responses they triggered are now considered the major causes for contemporary patterns of animal and plant distribution in New Guinea and the Pacific (Polhemus, 1996). Biotic dispersal associated with island arcs can be passive (tectonic rafting), active (island hopping) or both: (1) taxa may disperse to an arc and subsequently undergo sequential speciation along adjacent islands of this arc (pseudo-vicariance), creating a pattern in which related taxa occupy adjacent sectors of the arc; (2) migration of the arc or dislocation of several of its sectors may occur subsequently leading to the isolation of taxa far from their original source areas; (3) taxa which have dispersed along an arc and subsequently speciated can also be integrated into a potentially unrelated biota by the collision of the arc with another arc or a continental margin. This process of speciation/integration can be repeated multiple times, resulting in landmasses with high species diversity and mixed biota such as northern New Guinea. Such biotic fusions shape plant and animal assemblages that are disharmonious, exhibit composite multicentric origins and have their centers of diversity located around the sites of accreted arc terranes (ophiolites).

Fig. 86. The accretion of New Guinea as reconstructed by Pigram and Davies (1987).

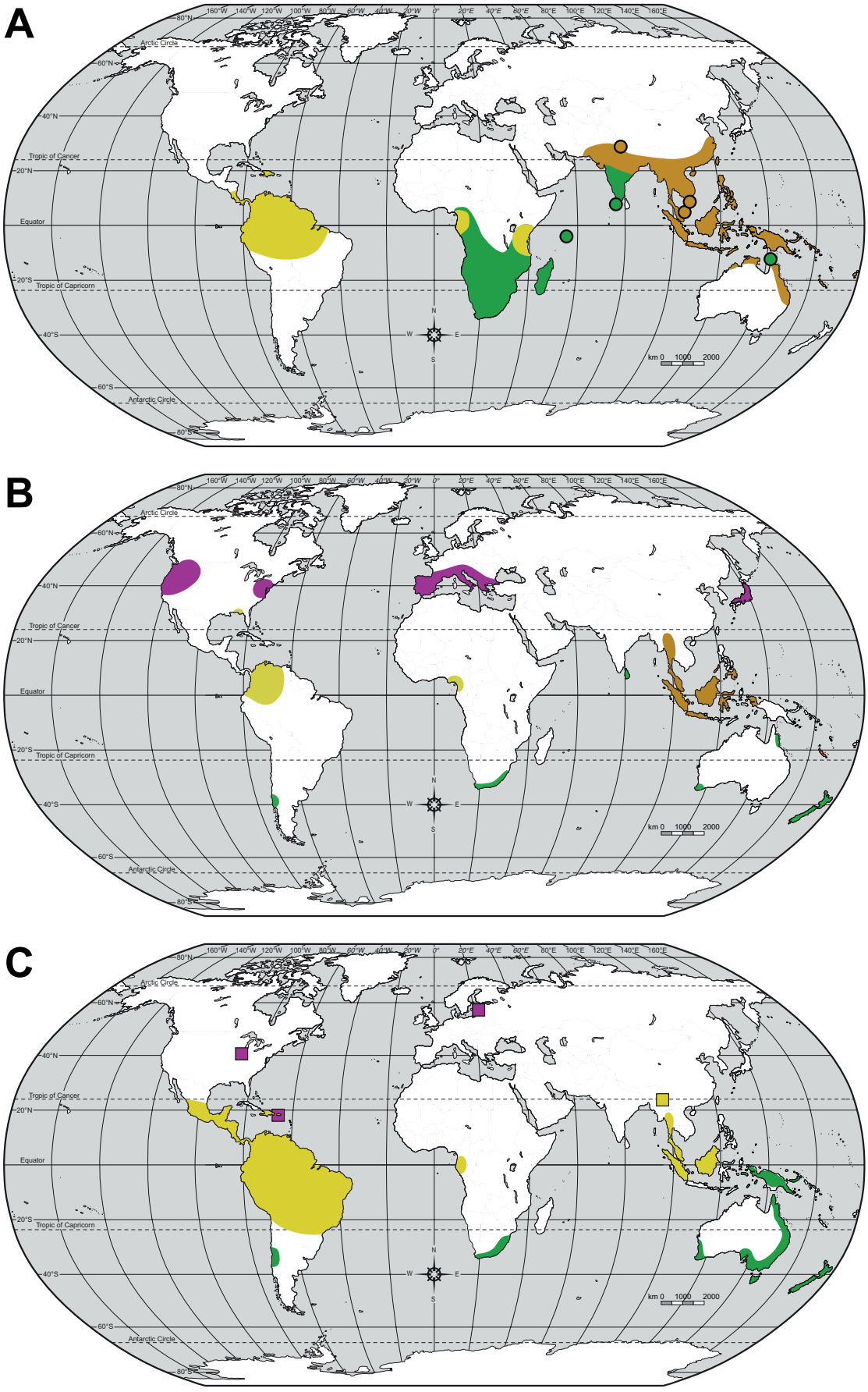

130°E
140°E
150°E
0°
10°S
40 Ma
Mesozoic Oceanic Crust
Coral Sea
25 Ma
Coral Sea
15 Ma
Coral Sea
10 Ma
Coral Sea
2 Ma
Banda Sea
Bismark Sea
Solomon Sea
Coral Sea
Australian craton
Terranes that had docked by 25 Ma
Terranes that had docked by 15 Ma
Terranes that had docked by 10 Ma
Terranes that had docked by 2 Ma

3.5.2 AREA CLADOGRAMS AND BIOGEOGRAPHICAL PATTERNS

A distribution pattern common to several taxonomic groups provides evidence for potential biogeographical tracks. However, organisms with different ecological characteristics and dispersal mechanisms are likely to display distinct distribution patterns. For instance, area cladograms of animals are more congruent with the Gondwanan break-up than those of plants, possibly because the latter are more likely to disperse by trans-oceanic rafting or anemochory (SanMartin & Ronquist, 2004). Therefore only arthropod groups with an ancient origin, restricted to mesic habitat, and with low vagility were considered relevant to identify biogeographical patterns congruent with that of the highly endemic species of Liochelidae in the Indo-Pacific region. Except for the basal mesothelids and mygalomorphs, most spiders are regarded as poor subjects for biogeographical studies due to their high vagility (Raven, 1980), and are thus unsuitable for comparison with the scorpions of the present study. On the other hand, the arachnid orders Amblypygi, Palpigradi, Schizomida and Thelyphonida represent good candidates for a biogeographic synthesis. However, the lack of recent phylogenies based on morphology and molecules for these groups prevents their use as model organisms for assessing potential biogeographic patterns. Opiliones (harvestmen), the putative sister group of scorpions (Schultz, 2007b), remain the only arachnid order for which extensive phylogenetic and biogeographical studies are available.

Onychophora. Velvet worms (Phylum Onychophora Grube, 1853), the putative sister group of Euarthropoda (Edgecombe, 2010), are divided into two extant families (Monge-Najera, 1995) that exhibit similar distributional ranges as the liochelid groups (fig. 87C). The Peripatopsidae Bouvier, 1907 have a classic circum-austral (Gondwanan) distribution with species in Australia, Chile, New Guinea, New Zealand, South Africa and Tasmania, whereas the Peripatidae Evans, 1902 are restricted to the Caribbean Islands, the Neotropics, Northern India, Southeast Asia (Malaysia and various Indonesian islands) and West Africa. The earliest known fossil of a terrestrial onychophoran, † *Helenodora inopinata* Thompson & Jones, 1980, was discovered in the Mazon Creek fossil deposits, Illinois (Upper Carboniferous). Although it is not morphologically very different from current taxa, its taxonomic and phylogenetic position

Fig. 87. Distribution maps. A. Indo-Pacific Liochelidae Fet & Bechly, 2001: basal Gondwana group (green), Afrotropical/Neotropical OPI clade (yellow), and Australasian HHL clade (brown). B, Suborder Cyphophthalmi Simon, 1879 (Opiliones, Arachnida): Pettalidae Shear, 1980 (green), Sironidae Simon, 1879 (violet), Troglosironidae Shear, 1993 (orange), Neogoveidae Shear, 1980 (yellow), and Stylocellidae Hansen & Sørensen, 1904 (brown); Modified from Boyer *et al.* (2007). C, Phylum Onychophora Grube, 1853: Peripatopsidae Bouvier, 1907 (green), Onychophoran fossils including † *Helenodora inopinata* Engel & Grimaldi, 2001, † *Succinipatopsis balticus* Poinar, 2000 and † *Tertiapatus dominicanus* Poinar, 2000 (violet squares), and Peripatidae Evans, 1902 including † *Cretoperipatus burmiticus* Engel & Grimaldi, 2000 (yellow); Assembled with information from Dr. Georg Mayer's website (http://www.onychophora.com/).


A
B
C
Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
Antarctic Circle
km 0 1000 2000

remain unclear (Thompson & Jones, 1980). However, several Onychophora fossils discovered in Cretaceous and Cenozoic amber show close affinities with the living onychophorans (order Euonychophora), indicating that the group was previously more widely distributed, with representatives in the northern hemisphere. † *Succinipatopsis balticus* Poinar, 2000 (Baltic amber, Eocene) and † *Tertiapatus dominicanus* Poinar, 2000 (Dominican amber, Miocene) are currently placed in distinct extinct families, i.e. † Succinipatopsidae and † Tertiapatidae, respectively (Poinar 1996, 2000). However, the discovery in Myanmar amber (Cretaceous) of an older species († *Cretoperipatus burmiticus* Engel & Grimaldi, 2002) belonging to the modern family Peripatidae suggests that the two previous taxa probably belong to modern families as well, pending a thorough morphological reexamination (Grimaldi *et al.*, 2002). Thus, the two families most likely diverged after being isolated on either parts of Pangea (Monge-Najera, 1995), i.e. Peripatopsidae in Gondwana and Peripatidae in Laurasia. Subsequent climatic changes with the contraction of northern tropical habitats probably forced the Peripatidae to migrate to lower latitudes (Morley, 2000). The two families are currently isolated by arid belts in America and Africa and by sea in Asia and Oceania.

Cyphophthalmi. Cyphophthalmid harvestmen constitute so far the sole arachnid group with a worldwide distribution, for which phylogeny and biogeography have been extensively studied based on morphological and molecular data. It is considered here as the most complete, detailed and reliable source of information to infer biogeographical patterns. Studies of other groups lack a solid phylogeny or focus only on a restricted geographical area, either because of the limited distributional range of the organisms studied or because of the limited scope of the survey. Therefore, distribution patterns and biogeography of Cyphophthalmi were thoroughly compared with results from the present work on liochelid scorpions and from other publications cited herein.

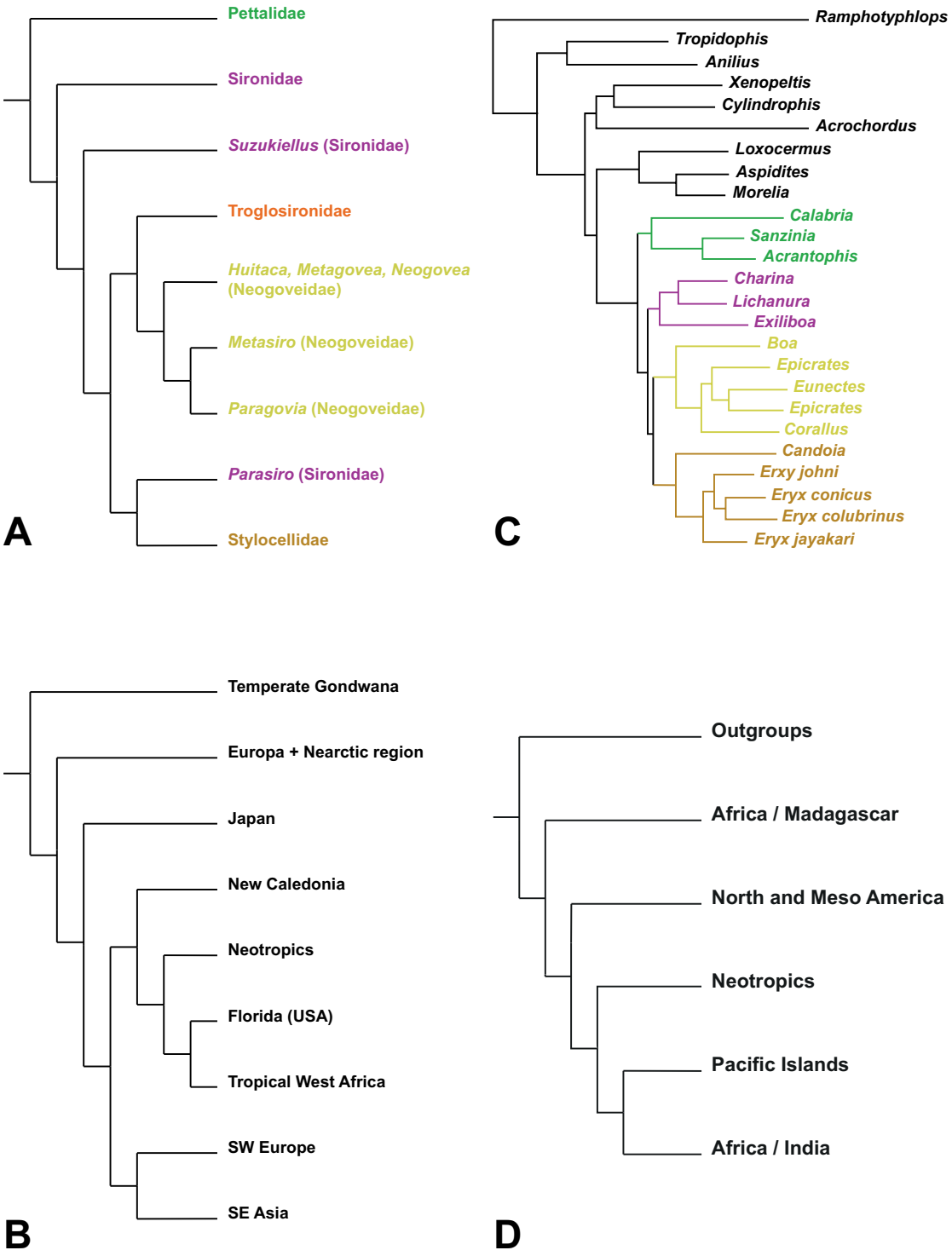
The comprehensive phylogenetic and biogeographical analysis of the complete suborder by Boyer *et al.* (2007) retrieved four major clades occupying distinct biogeographic areas (fig. 87B): (1) the Pettalidae Shear, 1980, a temperate (circum-Antarctic) southern Gondwana clade with species in Australia, New Zealand, South Africa, South America and Sri Lanka, (2)

the Sironidae Simon, 1879, a Laurasian clade with species in the Palearctic and Nearctic regions, (3) the Neogoveidae Shear, 1980, a 'tropical northern Gondwana' clade with Afrotropical and Neotropical species, and (4) the Stylocellidae Hansen & Sørensen, 1904, a Southeast Asian clade. Boyer *et al.* (2007) proposed 2 alternative phylogenetic hypotheses, i.e. one based on parsimony analysis of combined morphological and molecular data (fig. 88A) and one based on maximum likelihood analysis of ribosomal DNA data only. The two analyses recovered the four clades but also significantly different inter-clade relationships: the Pettalidae were retrieved as basal to all other cyphophthalmi in the first tree, whereas Stylocellidae were basal to all other taxa in the second. The first cladogram (fig. 88A) appears to be the best phylogenetic estimate for the following reasons: (1) it was retrieved under seven of the eleven combinations of parameters of the sensitivity analysis, while the other topology was only retrieved under one of these parameters sets; (2) a more recent study by Clouse & Giribet (2010) unambiguously yielded a similar topology. The first phylogenetic pattern is also congruent with the postulated biogeography of Onychophora: it supports a potential diversification of Cyphophthalmi induced by isolation of two ancestral lineages on Gondwana and Laurasia, with subsequent territorial expansion of Laurasian forms into southern landmasses. However, whereas onychophorans completely disappeared from the higher latitudes of the northern hemisphere with only fossils remaining, Laurasian lineages of Cyphophthalmi (Sironidae) still survive in Palearctic and Neartic regions.

Some conclusions of Boyer *et al.* (2007) are commented on below and alternative hypotheses are suggested to reconcile Cyphophthalmi biogeography with other datasets:

(I) The Stylocellidae were only recorded west of Lyddeker's line until the recent discovery of several species in West Papua and in the eastern Philippines (Clouse & Giribet, 2007; Clouse & Giribet, 2010; Clouse *et al.*, 2011). These findings suggest that the dataset for the Cyphophthalmi is incomplete, probably due to sampling artefacts. Very few zoological surveys specifically targeting the cryptic soil and leaf-litter fauna were recently conducted in New Guinea and its adjacent islands (Clouse & Giribet, 2010), and the Melanesian region remains for the most part unexplored. Cyphophthalmids are probably more widely distributed in East Indonesia (Maluku, West Papua) than implied by their distribution as presently known. Furthermore, it is

Fig. 88. Phylogenetic relationships of cyphophthalmid opilions obtained from analysis of morphology and molecules by Boyer *et al.* (2007). A, cladogram (simplified from Boyer *et al.*, 2007). B, area cladogram. Colours correspond to those assigned to each family in the distribution map (fig. 76). Phylogenetic relationships of boid snakes obtained from Bayesian analysis of mitochondrial and nuclear data by Noonan & Chippindale (2006A). C, detailed cladogram (adapted from Noonan & Chippindale, 2006A). D, area cladogram. Colours correspond to those assigned to each clade in the distribution map (fig. 79).


Pettalidae
Sironidae
Suzukiellus (Sironidae)
Troglosironidae
Huitaca, Metagovea, Neogovea (Neogoveidae)
Metasiro (Neogoveidae)
Paragovia (Neogoveidae)
Parasiro (Sironidae)
Stylocellidae
A
Ramphotyphlops
Tropidophis
Anilius
Xenopeltis
Cylindrophis
Acrochordus
Loxocermus
Aspidites
Morelia
Calabria
Sanzinia
Acrantophis
Charina
Lichanura
Exiliboa
Boa
Epicrates
Eunectes
Epicrates
Corallus
Candoia
Erxy johni
Eryx conicus
Eryx colubrinus
Eryx jayakari
C
Temperate Gondwana
Europa + Nearctic region
Japan
New Caledonia
Neotropics
Florida (USA)
Tropical West Africa
SW Europe
SE Asia
B
Outgroups
Africa / Madagascar
North and Meso America
Neotropics
Pacific Islands
Africa / India
D

plausible that they occur further east in Papua New Guinea, Bismarck Archipelago, and the Solomon Islands, like liochelid scorpions and various Australasian faunas with Southeast Asian origins (Hugall & Lee, 2004; Keogh, 1998; Rawlings *et al.*, 2008; Fuller *et al.*, 1998; Ast, 2001).

(II) Boyer *et al.* (2007) invoked a pan-Gondwana distribution followed by subsequent massive extinction events to explain the surprising close relationship of the Troglosironidae Shear, 1993, a clade endemic to New Caledonia, with the Neotropical/Afrotropical Neogoveidae. They conceded that their hypothesis was disputable because it was not corroborated by patterns observed in other taxa. The split between Neogoveidae and Troglosironidae putatively occurred 124–221 Mya (Triassic), and diversification within Troglosironidae is evaluated at only 28–45 Mya (Eocene) (Boyer *et al.*, 2007; Sharma & Giribet, 2009), a date congruent with the proposed emergence of New Caledonia in the Eocene (Aitchison *et al.*, 1995; Cluzel *et al.*, 2001; Schellart *et al.*, 2006; Chardon & Chevillotte, 2006). Sharma *et al.* (2009) argued that the significant difference between the ancient origin of the New Caledonian family and its more recent diversification may be due to extinction. However, they did not formally endorse Boyer *et al.*'s (2007) theory of an ancient Gondwana origin, citing incongruence with geological evidence of a total submersion of New Caledonia until the Eocene, and acknowledged that dispersal via transient volcanic islands may be an equally plausible alternative to explain the presence of Cyphophthalmi taxa in New Caledonia: "One possibility is that extensive volcanism created ephemeral islands that harboured metapopulations of Troglosironidae until the reemergence and subsequent recolonization of the mainland in the Eocene (Heads, 2005) — a hypothesis that paradoxically requires some oceanic dispersal ability in the ancestors of extant Troglosironidae". Neither Boyer *et al.* (2007) nor Sharma & Giribet (2009) consider the potential occurrence of long-branch attraction in their phylogenetic analyses. However, given the probability of incomplete data (see above), this cannot be completely ruled out (Graybeal, 1998; Bergsten, 2005). Troglosironidae may indeed be sister to Southeast Asian Stylocellidae rather than to the Neogoveidae. Their occurence in New Caledonia could in this case be explained by geo-dispersal from Asia over the various island arcs that developped in the Australasian region during the last 40 Mya.

(III) The position of the Japanese genus *Suzukiellus* Juberthie, 1970 remains ambigu-

ous. In Boyer *et al.* (2007) it is placed either in Sironidae or as sister to (Neogoveidae + Trogloseronidae). However, phylogenies produced from morphological datasets alone (Giribet & Boyer, 2004; DeBivort & Giribet, 2004) diagnosed a close affinity with the temperate Gondwana Pettalidae rather than with the Laurasian Sironidae. Results from Boyer *et al.* (2007) suggest that Cyphophthalmi may have reached the Neotropics via a dispersal route between northeastern Eurasia and North America (Beringia or islands of the Pacific Ring of Fire). However, further studies on the phylogenetic placement of *Suzukiellus* are required before solid conclusions can be drawn.

Boyer *et al.* (2007) suggested that the origin of Cyphophthalmi (174–312 Mya) and Pettalidae (178–215 Mya) predated the fragmentation of Gondwana whereas the Neogoveidae and Stylocellidae probably diverged subsequently at 124–221 Mya and 83–148 Mya, respectively (tab. 24). Boyer *et al.* (2007) constrained their molecular clock with the timing of geological events. However, this methodology is questionable because of the possibility of assigning a geological event to the wrong node and because of potential circular reasoning. On the other hand, Giribet *et al.* (2010) and Clouse & Giribet (2010) used fossils as calibration points. Both studies retrieved ages significantly older than those obtained by Boyer *et al.* (2007) (see tab. 23) and contradict the biogeographical hypothesis proposed here. However, Clouse & Giribet (2010) purposely excluded two cyphophthalmid fossils (Dunlop & Giribet, 2003; Poinar, 2008) from the calibration set because they were deemed uninformative given their recent age compared to that of the crown group. They were also omitted in Giribet *et al.* (2010). Although the minimum age of Cyphophthalmi can unambiguously be estimated at 400 Mya (Dunlop *et al.*, 2004), the diversification of modern groups might be much more recent and these two fossils dated at 40 and 100 Mya are the only evidence available of the past occurrence of cyphophthalmids on Earth. Despite being relatively young, they could be used to constrain the minimum age of extant families. Although fossils may not be the oldest occurrence of a given taxon, they nonetheless provide evidence for the presence of the group at a certain point in time and therefore should be used as calibration points. The current age estimate of Cyphophthalmi phylogeny is thus questionable because some evidence was excluded from the analysis.

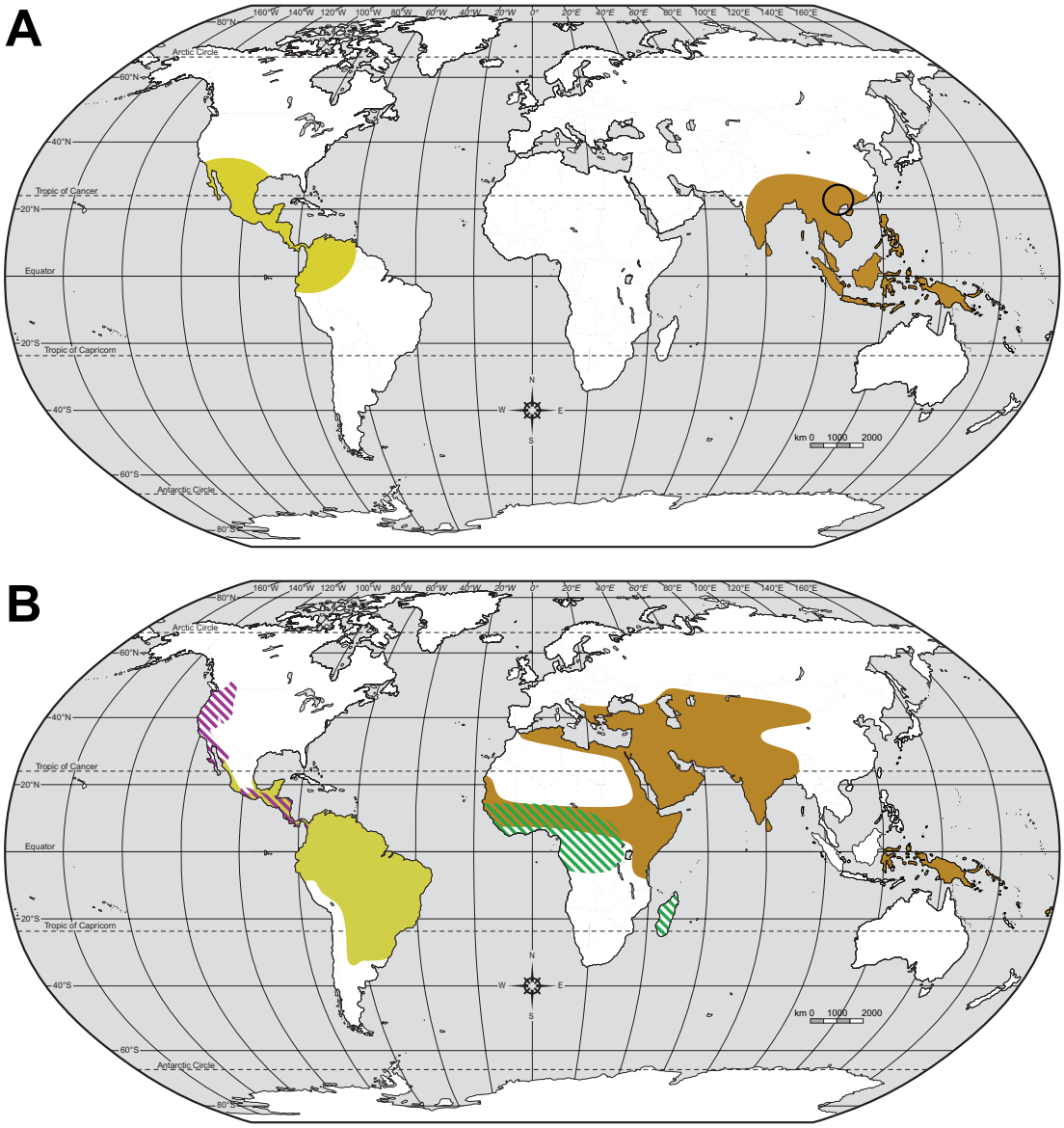
Table 24. Age estimates of selected cyphopthalmid families according to recent publications.

	Boyer *et al.*, 2007	Giribet *et al.*, 2009	Clouse & Giribet, 2010
Cyphophthalmi Simon, 1879	174–312 Mya	326–362 Mya	-
Petallidae Shear, 1980	178–215 Mya	202–240 Mya	-
Sironidae Simon, 1879	-	267–336 Mya	280–344 Mya
Neogoveidae Shear, 1980	124–221 Mya	202–244 Mya	-
Stylocellidae Hansen & Sørensen, 1904	83–148 Mya	228–270 Mya	246–301 Mya

Platystictidae. Forest damselflies of the family Platystictidae Laidlaw, 1924 (Odonata) are divided into three sub-families, i.e. the Palaemnematinae Tillyard & Fraser, 1938 in Meso- and northern South America, the Platystictinae Tillyard & Fraser, 1938 in Southeast Asia and Australasia, and the Sinostictinae Wilson, 1997 in Southeastern Asia (VanTol *et al.*, 2009; see fig. 89A). Ancestors of the Platystictidae most likely originated in East Gondwana and Sinostictinae appear to be sister to the other two clades (Palaemnematinae + Platystictinae) (Bybee *et al.*, 2008). Contrary to the previous animal groups reviewed, Platystictidae are confined to the Neotropics and Southeast Asia and are absent from Africa. This distribution pattern is referred to as 'tropical amphi-transpacific' and is observed in many tropical plants (Van Steenis, 1962). The absence of taxa on the African continent is attributed to extinction of northern temperate paratropical biotas in Europa before they were able to reach Tertiary refugias in Africa, whereas relicts of these lineages survive in Meso/South America and Southeast Asia (Morley, 2000).

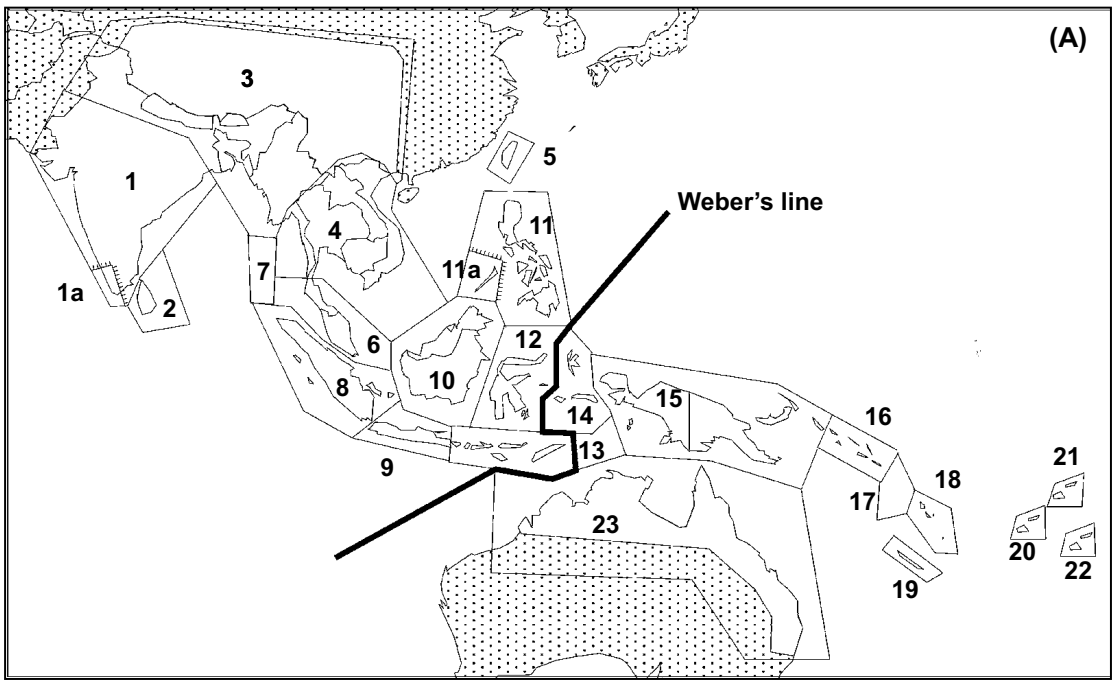
Boidae. The evolutionary history and the distribution patterns of boid snakes (figs 88C, D, 88B) are consistent with the timing of the final sequence of Gondwana fragmentation in the Late Cretaceous (Noonan & Chippindale, 2006A). The affinities between the Neotropical taxa (*Boa* Linnaeus, 1758, *Corallus* Daudin, 1803, *Epicrates* Wagler, 1830, *Eunectes* Wagler, 1830) and the Afro-Indian genus *Eryx* Daudin, 1803, and the date estimate of their divergence support the hypothesis of a land connection between the India-Madagascar block and South America via Antarctica in the Campanian (70–83 Mya) (Noonan & Chippindale, 2006A, 2000B; see paragraph 3.5.2). Alternatively, the persistence of biotic exchanges between Africa and South America until the Paleocene can also explain this relationship. In addition, comparison between boid distribution and biogeographic patterns observed in other organisms allows the formulation of a theory regarding the enigmatic distribution of the genus *Candoia* Gray, 1842 on Pacific Islands (Austin, 2000; Noonan & Chippindale, 2006A; Noonan & Sites Jr., 2010): (1) species of the Afro-Indian lineage may have been previously widespread across Southeast Asia, (2) colonized the Australasian Archipelago from Sundaland like many other organisms before, (3) and were driven to extinction, possibly because of competition with other snake lineages occurring in the area.

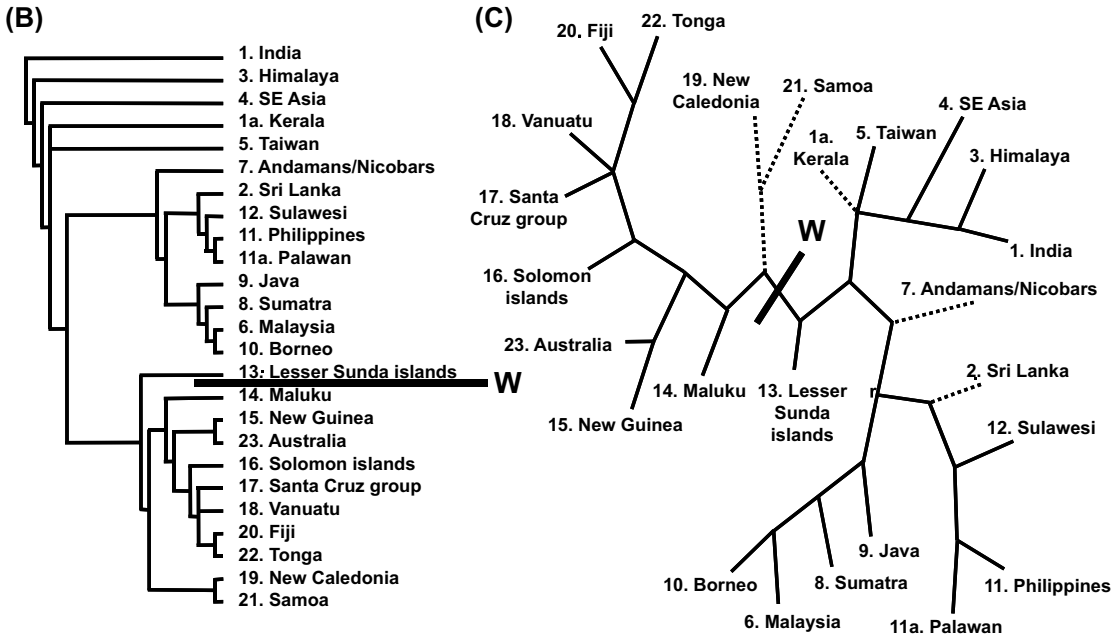
Fig. 89. A, Distribution maps. A Platystictidae Laidlaw, 1924 (Odonata, Insecta): Sinostictinae Wilson, 1997 (black circle), Palaemnematinae Tillyard & Fraser, 1938 (yellow), Platystictinae Tillyard & Fraser, 1938 (brown). B, Boidae Gray, 1825 (Squamata, Reptilia), sensu Noonan & Chippindale (2006): North/Central America clade (*Charina* Gray, 1849, *Exiliboa* Bogert, 1968, *Lichanura* Cope, 1861, *Ungaliophis* Müller, 1880) in violet hatchings; Africa/Madagascar clade (*Acrantophis* Jan, 1863 *Calabria* Gray, 1828, *Sanzinia* Gray, 1849) in green hatchings; Neotropical clade (*Boa* Linnaeus, 1758, *Corallus* Daudin, 1803, *Epicrates* Wagler, 1830, *Eunectes* Wagler, 1830) in yellow; Afro-Indian *Eryx* Daudin, 1803 and Pacific Island *Candoia* Gray, 1842 in brown.


A
B
Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
Antarctic Circle
km 0 1000 2000

Generalized area cladogram of Australasia. Turner *et al.* (2001) and VanWelzen *et al.* (2003) assembled a large matrix of phylogenetic and distributional data for 29 very diverse animal and plant groups from Southeast Asia and the West Pacific that they submitted to historical biogeographic analyis (Brooks Parsimony analysis; Wiley, 1988a,b; Brooks, 1990; Brooks *et al.*, 2001). The majority rule consensus tree derived from this analysis (fig. 90) suggests that the Melanesian Archipelago, Australia and some of the western Pacific Islands were mainly colonized by taxa native to Sundaland.

Fig. 90. Historical biogeographical analysis of the Southeast Asian and West Pacific area by VanWelzen *et al.* (2003). A, areas discriminated. B, majority-rule consensus area cladogram (rooted in India). C, same area cladogram shown as unrooted network. Legend: 1 = India (1a Kerala); 2 = Sri Lanka; 3 = Himalayas; 4 = Southeast Asia mainland; 5 = Taiwan; 6 = Malay Peninsula; 7 = Andamans/Nicobars; 8 = Sumatra; 9 = Java; 10 = Borneo; 11 = Philippines (11a = Palawan); 12 = Sulawesi; 13 = Lesser Sunda Islands; 14 = Maluku; 15 = New Guinea; 16 = Solomon Islands; 17 = Santa Cruz Group; 18 = Vanuatu; 19 = New Caledonia; 20 = Fiji; 21 = Samoa; 22 = Tonga; 23 = Australia; W = Weber's line. Weber's line demarcates regions in the Malay Archipelago with a mainly Southeast Asian mainland influence from the region dominated by the Australian/New Guinean realm.


(A)
Weber's line
1
1a
2
3
4
5
6
7
8
9
10
11
11a
12
13
14
15
16
17
18
19
20
21
22
23


(B)
1. India
3. Himalaya
4. SE Asia
1a. Kerala
5. Taiwan
7. Andamans/Nicobars
2. Sri Lanka
12. Sulawesi
11. Philippines
11a. Palawan
9. Java
8. Sumatra
6. Malaysia
10. Borneo
13. Lesser Sunda islands
W
14. Maluku
15. New Guinea
23. Australia
16. Solomon islands
17. Santa Cruz group
18. Vanuatu
20. Fiji
22. Tonga
19. New Caledonia
21. Samoa
(C)
20. Fiji
22. Tonga
19. New Caledonia
21. Samoa
4. SE Asia
18. Vanuatu
1a. Kerala
5. Taiwan
3. Himalaya
17. Santa Cruz group
W
1. India
16. Solomon islands
7. Andamans/Nicobars
23. Australia
2. Sri Lanka
14. Maluku
13. Lesser Sunda islands
12. Sulawesi
15. New Guinea
9. Java
10. Borneo
8. Sumatra
11. Philippines
6. Malaysia
11a. Palawan

CHAPTER IV
-
TAXONOMIC REVISION

4.1 METHODS

Examination and imaging (see chapter 1, paragraph 1.1 for details). Specimens were examined with two stereomicroscopes: a NIKON SMZ1500 and a ZEISS Stemi SV8. Ultrasonic treatment (sonication) was used to "clean" the specimens of external debris (Nowak *et al.*, 2008). High resolution images were taken with a Microptics ML 1000 digital imaging system (Microptics, USA). CombineZM (Hadley, 2005) was used to produce the final images. Drawings were produced using a stereomiscroscope (NIKON SMZ1500 or ZEISS Stemi SV8) mounted with a camera lucida. The sketches were subsequently inked with Koh-I-Noor Rapidograph pens and scanned for further processing and editing. Photographs and illustrations were edited in Photoshop CS5 (Adobe Systems, San Jose, CA, USA) (background removal, contrast and colour adjustment) and plates were prepared with Illustrator CS5 (Adobe Systems, San Jose, CA, USA).

Terminology follows Stahnke (1970), Stockwell (1989), Sissom (1990) and Hjelle (1990) for pedipalp segmentation (fig. 12), Prendini *et al.* (in prep) for pedipalp carinae, Vachon (1974) for trichobothrial patterns, Couzjin (1976) for leg segmentation (fig. 12), Prendini (2000) for metasomal carinae, and Lamoral (1979) and Monod & Volschenk (2004) for hemispermatophores.

Taxonomic revision was conducted following the phylogenetic species concept (Cracraft, 1983, 1989; Nixon & Wheeler, 1990; Wheeler, 1990). Most of the type material, including types of nominal species currently considered to be junior synonyms, was examined. The non-type material was divided into morphospecies that were assigned to described taxa or treated as new to science. Scientific names referring to the morphology or distributional range were attributed to each new taxa. The literature was thoroughly investigated. As most of the material studied by previous authors was reexamined in the course of the present work, it was possible to trace the identity of each specimen in most cases. Thus, the material mentioned in previous publications was used to select the 31 valid species that are included in the present section (10 described species, 10 described species currently considered as junior synonyms, and 11 undescribed species that were misidentified by former workers). The dichotomous identification keys for the genera *Hormiops*, *Hormurus* and *Liocheles* and the descriptions of the species

selected were generated with Delta Editor (Dallwitz *et al.*, 2000).

Mapping. Distribution maps were produced using ArcGIS version 9.3 (Environmental Systems Research Institute, Redlands, CA, USA), by superimposing point locality records on SRTM 90 m digital elevation data (Jarvis *et al.*, 2008) and SRTM 1 km (30 arc-second) global bathymetry datasets (Becker *et al.*, 2009). Geographical coordinates for records without GPS data were traced by reference to gazetteers, the GEOnet Names Server (http://earth-info.nga.mil/gns/html/index.html), or detailed route maps of various earlier expeditions.

4.2 TAXONOMIC EMENDATIONS

One subfamily is elevated to family level (Hormurinae). Two genera formerly placed into synonymy are reinstated (*Hormiops*, *Hormurus*), and one is synonymized (*Tibetiomachus*). Ten species formerly placed into synonymy are reinstated (eight *Hormurus* spp., two *Liocheles* spp.), 51 are new (one *Hormiops*, 48 *Hormurus*, one *Liocheles*, one *Opisthacanthus* (*Monodopisthacanthus*)), six are transferred from *Liocheles* to *Hormurus* and three are synonymized (*C. tirupati*, *H. underwoodi*, *T. himalayensis*). Two subspecies are elevated to species rank (*I. laeviceps malabarensis*, *L. australasiae longimanus*) and one is synonymized (*L. australasiae brevidigitatus*).

Family **HORMURIDAE**, **new combination**
Notes
The classification of Prendini (2000) and Prendini & Wheeler (2005) is followed in the present study: Hemiscorpiidae is considered a valid family, sister to Liochelidae. However, as pointed out by Soleglad *et al.* (2005), the name “Hormurinii” (Laurie, 1896) has priority over “Liochelidae” (Fet & Bechly, 2001). Thus the family Liochelidae is renamed Hormuridae.

Genus ***IOMACHUS*** Pocock, 1893
Iomachus malabarensis Pocock, 1900, **new rank**
Iomachus nitidus Pocock, 1900 = *Chiromachetes tirupati* Lourenço, 1997, **new synonymy**
Notes
Examination of the holotype of *C. tirupati* Lourenço, 1997 indicates that it is a junior synonym of *Iomachus nitidus* Pocock, 1900. The female holotype of *C. fergusoni* remains therefore the sole *Chiromachetes* specimen known.

Genus ***HORMIOPS*** Fage, 1933
Hormiops davydovi Fage, 1933
Hormiops infulcra, **new species**

Genus ***HORMURUS*** Thorell, 1876
Hormurus actaeolophos, **new species**
Hormurus aethes, **new species**
Hormurus agastachys, **new species**

Hormurus ankamuti, **new species**
Hormurus anekasankylis, **new species**
Hormurus ankistros, **new species**
Hormurus asychnachaena, **new species**
Hormurus asynaptodactylus, **new species**
Hormurus bandjin, **new species**
Hormurus boholiensis Kraepelin, 1914
Hormurus caudicula (C. L. Koch, 1867), **new combination**
Hormurus chthamalochoros, **new species**
Hormurus chydaeostigmata, **new species**
Hormurus davydovi (Birula, 1903), **new combination**
Hormurus dechangei (Becker, 1880), **new combination**
Hormurus dodecatrichos, **new species**
Hormurus eukteanospatha, **new species**
Hormurus extensus (Locket, 1997), **new combination**
Hormurus goliath, **new species**
Hormurus glaphyroscytos, **new species**
Hormurus halmaherae, **new species**
Hormurus hylaios, **new species**
Hormurus hypselankylis, **new species**
Hormurus insculptus Thorell, 1888
Hormurus ischnoryctes, **new species**
Hormurus karschii Keyserling, 1885
Hormurus khangalu, **new species**
Hormurus kilkerranicus, **new species**
Hormurus kukunyungkal, **new species**
Hormurus kuukayau, **new species**
Hormurus laevitropis, **new species**
Hormurus leptochela, **new species**
Hormurus litodactylus (Monod & Volschenk, 2004), **new combination**
Hormurus macrochela, **new species**
Hormurus mesochtonus, **new species**
Hormurus microkypheus, **new species**
Hormurus milneanus, **new species**
Hormurus muralagi, **new species**
Hormurus neocaledonicus (Simon, 1877), **new combination**
Hormurus nesiotes, **new species**
Hormurus nyawagi, **new species**
Hormurus ochthonastes, **new species**
Hormurus ochyroscapter, **new species**
Hormurus oreios, **new species**
Hormurus oreospyridus, **new species**
Hormurus orthodactylus, **new species**
Hormurus papuanus Kraepelin, 1914
Hormurus penta (Francke & Lourenço, 1991), **new combination**
Hormurus polisorum (Volschenk, Locket & Harvey, 2001), **new combination**
Hormurus samoa, **new species**
Hormurus scopaeus, **new species**
Hormurus solomonensis, **new species**
Hormurus tagulae, **new species**
Hormurus tetrakaideca, **new species**
Hormurus tjapukai, **new species**
Hormurus tytthognaphos, **new species**
Hormurus umpila, **new species**
Hormurus waigiensis (Gervais, 1943), **new combination**
Hormurus wallaman, **new species**
Hormurus weberi Pocock, 1894
Hormurus xerogaios, **new species**

Hormurus yelae, **new species**

NOMINA DUBIA
Hormurus cumingii (Gervais, 1844), **new combination**

Genus ***LIOCHELES*** Sundevall, 1883
Liocheles Sundevall, 1883 = *Tibetiomachus* Lourenço & Qi, 2006, **new synonymy**
Liocheles australasiae (Fabricius, 1775) = *Liocheles australasiae brevidigitatus* Werner, 1936, **new synonymy**
Liocheles complanatus (C. L. Koch, 1837), **new combination**
Liocheles longimanus (Werner, 1939), **new combination**
Liocheles malaya, **new species**
Liocheles nigripes (Pocock, 1897), **new combination** = *Tibietiomachus himalayensis* Lourenço & Qi, 2006, **new synonymy**
Liocheles suspectus (Thorell, 1888), **new combination**

Genus ***OPISTHACANTHUS*** Peters, 1861
Subgenus ***OPISTHACANTHUS*** Peters, 1861
Opisthacanthus (*Opisthacanthus*) *elatus* (Gervais, 1844) = *Hormurus underwoodi* Marx, 1888, **new synonymy**
Notes
Marx (1888) mentioned a new species for the genus *Hormurus*, i.e. *Hormurus underwoodi* Marx, 1888 but did not provide any description, type locality or museum repository in his publication. Besides, the two illustrations were insufficient for specific diagnosis. The specimen that was identified by Marx as a new species and named *H. underwoodi*, was rediscovered in the collection of the Smithsonian Museum in Washington. It is a badly preserved female from Santa Barbara, California (USNM 00751) belonging to the species *Opisthacanthus elatus*. Thus, *H. underwoodi* is a junior synonym of *O. elatus*.

Subgenus ***MONODOPISTHACANTHUS*** Lourenço, 2001
Opisthacanthus (*Monodopisthacanthus*) *apios*, **new species**

4.3 IDENTIFICATION KEYS

4.3.1 KEY TO GENERA

1. Chela manus, retrolateral surface, *Esb* trichobothrium basal, level with *Eb* group.....1
   Chela manus, retrolateral surface, *Esb* trichobothrium more distal to *Eb* group, midway between *Eb* group and *Esb* or close to *Est*, sometimes slightly ..... ***Hormurus***

2(1). Chela, movable finger, dentition, inner accessory denticles (IAD) present; chela, (♂), movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed); chela (♂), fixed finger, supra-basal notch distinct and deep, supra-basal lobe projecting downward, present and distinct; prosomal carapace, three pair of lateral ocelli .....***Liocheles***
   Chela, movable finger, dentition, inner accessory denticles (IAD) absent; Chela (♂), movable finger, supra-basal lobe absent, margin straight or nearly so, at most a low hump; chela (♂), fixed finger, supra-basal notch absent, supra-basal lobe absent or at most weakly developped; prosomal carapace, two pairs of lateral ocelli ....***Hormiops***

4.3.2 KEY TO SPECIES OF THE GENUS *Hormiops*

1. Prosomal carapace (♂), anteromedian area entirely smooth or nearly so; prosomal carapace (♀), mediolateral area smooth or nearly so; pectines, fulcrae absent; metasoma, segment II, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinclty larger than preceding granules) ....***Hormiops infulcra***
   Prosomal carapace (♂), anteromedian area, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); prosomal carapace (♀), mediolateral area at least sparsely granular; pectines, fulcrae present; metasoma, segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granul es).....***Hormiops davydovi***

4.3.3 KEY TO SPECIES OF THE GENUS *Hormurus*

1. Metasoma, segment II, ventrosubmedian carinae, medial spiniform granules absent.....2
   Metasoma, segment II, ventrosubmedian carinae, 1–2 pairs of small/vestigial medial spiniform granules.....26
   Metasoma, segment II, ventrosubmedian carinae, 1–3 pairs of well developed medial spiniform granules.....54

2(1). Patella, trichobothriotaxy, retrolateral surface, *em*–*esb* series, relative position 2 groups [esb_{1-2}][em_{1-2}].....3
   Patella, trichobothriotaxy, retrolateral surface, *em*–*esb* series, relative position esb_1 closer to em_{1-2} or far away from esb_2, 2 groups [esb_2][esb_1/em_{1-2}] OR groups [esb_{1-2}] [em_{1-2}] together.....14

3(2). Femur, dorsal retrol*at*eral (*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina 4
   Femur, dorsal retrol*at*eral (*drl*) carina equally developed than *dps* carina 10

4(3). Chela manus, ventral retrolateral (*vrl*) carina costate; femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; femur, prolateral median (*plm*) carina vestigial with 2 large spines (one proximal and one midway); patella, ventral intercarinal surface smooth or nearly so 5

Chela manus, ventral retrolateral (*vrl*) carina granular or crenelate; femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; femur, prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; patella, ventral intercarinal surface entirely granular, at least a reticulated network of granules 7

5(4). Chela (♂), movable finger, supra-basal lobe wider than high (low); fixed finger, supra-basal lobe conical/well developed; chela manus, retrolateral surface, position of *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; chela manus, dorsal retrol*at*eral (*drl*) carina as a smooth ridge or slightly costate 6
Chela (♂), movable finger, supra-basal lobe conical, as high as wide or higher than wide; supra-basal lobe low/reduced; chela manus, retrolateral surface, position of *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; chela manus, dorsal retrol*at*eral (*drl*) carina costate or granular ....***Hormurus chydaeostigmata***

6(5). Patella, prolateral process, shape forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; prosomal carapace (♂), anteromedian area, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); prosoma with minute spiniform granules; patella, prolateral process low.....***Hormurus scopaeus***

Patella, prolateral process, shape forming a single large spine; prosomal carapace (♂), anteromedian area entirely granular, at least sparsely; prosoma with larger spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules; patella, prolateral process strongly developped, high .....***Hormurus agastachys***

7(4). Chela, fixed finger, trichobothriotaxy, *esb*, *eb*, *est* and *et* trichobothrium ca. equidistant from each other (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*..... 8
Chela, fixed finger, trichobothriotaxy, *esb* trichobothria closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*.....9

8(7). Chela manus, ventral prolateral (*vpl*) carina absent or obsolete; pecten (♂) length, moderate, distal edge reaching to, but not beyond, distal edge of coxa of leg IV; metasoma, segment I, ventrosubmedian carinae, sub-posterior spiniform granules weak to absent; chela (♂), fixed finger, supra-basal lobe projecting downward, present and distinct.....***Hormurus leptochela***
Chela manus, ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules; pecten (♂) length, short, distal edge not reaching to distal edge of coxa of leg IV; metasoma, segment I, ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules; chela (♂), fixed finger, supra-basal lobe absent or at most weakly developped .....***Hormurus litodactylus***

9(7). Chela (♂), fixed finger, supra-basal lobe absent or at most weakly developped; prosomal carapace, anteromedian area, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); pecten (♂) length, moderate, distal edge reaching to, but not beyond, distal edge of coxa of leg IV; chela (♂), movable finger, supra-basal lobe absent, margin straight or nearly so, at most a low hump.....***Hormurus orthodactylus***
Chela (♂), fixed finger, supra-basal lobe projecting downward, present and distinct; prosomal carapace, anteromedian area entirely smooth or nearly so; pecten (♂) length, short, distal edge not reaching to distal edge of coxa of leg IV; chela (♂), movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed) ....***Hormurus tytthognaphos***

10(3). Tergites IV–VI (♀), posttergites, mesial and lateral surface smooth (or nearly so) 11
Tergites IV–VI (♀), posttergites mesially smooth, laterally granular 13
Tergites IV–VI (♀), posttergites, mesial and lateral surfaces granular ....***Hormurus polisorum***

11(10). Femur, length, short (equal to or shorter than carapace); prosomal carapace (♂), anteromedian area entirely granular, at least sparsely; prosomal carapace (♀), anteromedian area entirely granular, at least sparsely; chela (♂), fingers, supra-basal lobe and corresponding notch with a distinct posterior gap.....12
Femur, length, long (longer than carapace, up to 2 times longer); prosomal carapace (♂), anteromedian area, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); prosomal carapace (♀), anteromedian area, microsculptures, granulation, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); chela (♂), fingers, supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap .....***Hormurus anekasankylis***

12(11). Chela (♂), fixed finger, supra-basal lobe low/reduced; chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium (if on proximal of manus) midpalm or slightly less than midpalm; chela manus, retrolateral surface, *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; Chelicerae, colouration, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace).....***Hormurus aethes***
Chela (♂), fixed finger, supra-basal lobe conical/well developed; chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium (if on proximal of manus) on proximal 1/3 of manus; chela manus, retrolateral surface, *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Chelicerae, colouration, dorsal surface dark (manus as dark as or darker than carapace) ....***Hormurus papuanus***

13(10). Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium (if on proximal of manus) midpalm or slightly less than midpalm; patella, dorsal retrol*at*eral (*drl*) carina absent or obsolete; prosomal carapace, anteromedian area, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); prosoma with minute spiniform granules .....***Hormurus yelae***
Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium (if on proximal of manus) on proximal 1/3 of manus; patella, dorsal retrol*at*eral (*drl*) carina distinct, at least a low ridge or a row of granules; prosomal carapace, anteromedian area entirely granular, at least sparsely; prosoma with large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules .....***Hormurus karschii***

14(2). Coxae III, antero-distal tip, shape without swelling or bulge.....15
Coxae III, antero-distal tip, shape with a distinct swelling/bulge oriented posteriorly, at least weak, usually more pronouced in males.....22
Coxae III, antero-distal tip, shape hook-like shaped.....***Hormurus ankistros***

15(14). Femur, retrolateral ventral intercarinal surface smooth or nearly so.....16
Femur, retrolateral ventral intercarinal surface at least sparsely granular.....19

16(15). Patella, prolateral process forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; femur, dorsal retrol*at*eral (*drl*) carina equally developed than dorsal prosubmedian (*dps*) carina; pecten (♂) length, long, distal edge reaching beyond distal edge of coxa of leg IV; metasoma, segment I, ventrosubmedian carinae, sub-posterior spiniform granules weak to absent 17
Patella, prolateral process forming a single large spine; femur, dorsal retrol*at*eral (*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina; pecten (♂) length, moderate, distal edge reaching to, but not beyond, distal edge of coxa of leg

IV; metasoma, segment I, ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules 18

17(16). Chela (♂), movable finger, supra-basal lobe wider than high (low); chela, fixed finger, trichobothriotaxy, *esb* trichobothrium closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; chelicerae, colouration, dorsal surface dark (manus as dark as or darker than carapace); prosomal carapace, median ocelli separated by at least half a diameter of a median occellus or more..... .....***Hormurus solomonensis***
Chela (♂), movable finger, supra-basal lobe conical, as high as wide or higher than wide; chela, fixed finger, trichobothriotaxy, *esb*, *eb*, *est* and *et* trichobothria ca. equidistant from each other (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; chelicerae, colouration, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace); prosomal carapace, median ocelli close together (less than an ocellus diameter) ....***Hormurus oreospyridus***

18(16). Chela (♂), fingers, supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; chela manus, retrolateral surface, *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; chela, fixed finger, trichobothriotaxy, *esb*, *eb*, *est* and *et* trichobothria ca. equidistant from each other (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; chela manus, dorsal retrol*at*eral (*drl*) carina costate or granular .....***Hormurus tagulae***
Chela (♂), fingers, supra-basal lobe and corresponding notch with a distinct upper/anterior gap; chela manus, retrolateral surface, *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; chela, fixed finger, trichobothriotaxy, *esb* trichobothrium closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; chela manus, dorsal retrol*at*eral (*drl*) carina as a smooth ridge or slightly costate .....***Hormurus xerogaios***

19(15). Chela manus, ventral prolateral (*vpl*) carina absent or obsolete; metasoma, segment I, ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules; chela, fixed finger, trichobothriotaxy, *esb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers; Telson dark (as dark as metasoma) 20
Chela manus, ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules; metasoma, segment I, ventrosubmedian carinae, sub-posterior spiniform granules weak to absent; chela, fixed finger, trichobothriotaxy, *esb* trichobothrium in proximal region of fixed finger; Telson pale (as pale as or paler than metasoma) 21

20(19). Chela manus, ventral retrolateral (*vrl*) carina costate; patella, prolateral process forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; femur, dorsal retrol*at*eral (*drl*) carina equally developed than dorsal prosubmedian (*dps*) carina; prosomal carapace, anteromedian area entirely granular, at least sparsely .....***Hormurus nesiotes***
Chela manus, ventral retrolateral (*vrl*) carina granular or crenelate; patella, prolateral process, shape forming a single large spine; femur, dorsal retrol*at*eral (*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina; prosomal carapace, anteromedian area, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV) .....***Hormurus halmaherae***

21(19). Chela (♂), movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed); chela (♂), fingers, supra-basal lobe and corresponding notch with a distinct posterior gap; chela (♂), fixed finger, supra-basal lobe conical/well developed; chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium (if on proximal of manus) on proximal 1/3 of manus ....***Hormurus euktaenospatha***

Chela (♂), movable finger, supra-basal lobe weakly developed, low hump; chela (♂), fingers, supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; chela (♂), fixed finger, supra-basal lobe low/reduced; chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium (if on proximal of manus) midpalm or slightly less than midpalm.....***Hormurus asychnachaena***

22(14). Femur, length, short (equal to or shorter than carapace); patella, dorsal retrol*at*eral (*drl*) carina absent or obsolete 23
Femur, length, long (longer than carapace, up to 2 times longer); patella, dorsal retrol*at*eral (*drl*) carina distinct, at least a low ridge or a row of granules 24

23(22). Telson, colouration pale (as pale as or paler than metasoma); femur, dorsal retrol*at*eral (*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina; femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; femur, prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity .....***Hormurus davydovi***
Telson, colouration dark (as dark as metasoma); femur, dorsal retrol*at*eral (*drl*) carina equally developed than *dps* carina; femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; femur, prolateral median (*plm*) carina vestigial with 2 large spines (one proximal and one midway) .....***Hormurus microkypheus***

24(22). Femur, dorsal retrol*at*eral (*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina; chela (♂), fixed finger, supra-basal lobe low/reduced; femur, ventral retrosubmedian (*vrs*) carina partial, expressed only proximally; leg IV, femora, ventromedian carinae present .....***Hormurus asynaptodactylus***
Femur, dorsal retrol*at*eral (*drl*) carina equally developed than dorsal prosubmedian (*dps*) carina; chela (♂), fixed finger, supra-basal lobe conical/well developed; femur, ventral retrosubmedian (*vrs*) carina absent or obsolete; leg IV, femora, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules) 25

25(24). Chela (♂), movable finger, supra-basal lobe wider than high (low); femur, retrolateral ventral intercarinal surface smooth or nearly so; prosomal carapace, superciliary carinae with at least few granules; stigma (spiracle), long (at least 1/3 of sternite wid th).....***Hormurus goliath***
Chela (♂), movable finger, supra-basal lobe conical, as high as wide or higher than wide; femur, retrolateral ventral intercarinal surface at least sparsely granular; prosomal carapace, superciliary carinae without granules; stigma (spiracle) short (less than 1/3 of sternite width).....***Hormurus waigiensis***

26(1). Prosomal carapace (♂), anteromedian area entirely smooth or nearly so.....27
Prosomal carapace (♂), anteromedian area, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV).....30
Prosomal carapace (♂), anteromedian area entirely granular, at least sparse ly.....48

27(26). Chela manus, ventral retrolateral (*vrl*) carina costate; femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; femur, prolateral median (*plm*) carina vestigial with 2 large spines (one proximal and one midway); patella, ventral intercarinal surface smooth or nearly so 28
Chela manus, ventral retrolateral (*vrl*) carina granular or crenelate; femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; Femur, prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; patella, ventral intercarinal surface with at least a reticulated network of granules 29

28(27). Chela (♂), fingers, supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; femur, retrolateral ventral intercarinal surface at least sparsely granular; chela (♂), movable finger, supra-basal lobe not overlapping with fixed finger; chela manus, trichobothriotaxy, retrolateral surface, accessory trichobothria absent (11 trichobothria, orthobothriotaxic).....***Hormurus khangalu***
Chela (♂), fingers, supra-basal lobe and corresponding notch with a distinct posterior gap; femur, retrolateral ventral intercarinal surface, microsculptures, granulation smooth or nearly so; chela (♂), movable finger, supra-basal lobe overlapping with retrolateral surface of fixed finger (in front of notch); chela manus, trichobothriotaxy, retrolateral surface, accessory trichobothria present, one (12 trichobothria, neobothr iotaxic).....***Hormurus dodecatrichos***

29(27). Femur, retrolateral ventral intercarinal surface smooth or nearly so; prosomal carapace, anteromedian area, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); tergite VII (♀), posttergite granular at least posteriorly; chela manus, dorsal retrol*at*eral (*drl*) carina costate or granular .....
.....***Hormurus wallaman***
Femur, retrolateral ventral intercarinal surface at least sparsely granular; prosomal carapace, anteromedian area entirely smooth or nearly so; tergite VII (♀), posttergite entirely smooth or nearly so; chela manus, dorsal retrol*at*eral (*drl*) carina as a smooth ridge or slightly costate .....***Hormurus glaphyroscytos***

30(26). Chela manus, ventral prolateral (*vpl*) carina absent or obsolete 31
Chela manus, ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules 40

31(30). Femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; femur, prolateral median (*plm*) carina vestigial with 2 large spines (one proximal and one midway) 32
Femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; femur, prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity 36

32(31). Femur, dorsal retrol*at*eral (*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina 33
Femur, dorsal retrol*at*eral (*drl*) carina equally developed than dorsal prosubmedian (*dps*) carina 35

33(32). Chela (♂), fingers, supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; chela (♂), movable finger, supra-basal lobe not overlapping with fixed finger; chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium on proximal 1/3 of manus; metasoma, segment I, ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules.....34
Chela (♂), fingers, supra-basal lobe and corresponding notch with a distinct posterior gap; chela (♂), movable finger, supra-basal lobe overlapping with retrolateral surface of fixed finger (in front of notch); chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium midpalm or slightly less than midpalm; metasoma, segment I, ventrosubmedian carinae, sub-posterior spiniform granules weak to abse nt.....***Hormurus extensus***

34(33). Chela (♂), movable finger, supra-basal lobe wider than high (low); chela manus, retrolateral surface, *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; Patella, trichobothriotaxy, retrolateral surface, esb_1 trichobothrium closer to em_{1-2} or far away from esb_2, 2 groups [esb_2][esb_1/em_{1-2}] OR groups [esb_{1-2}] [em_{1-2}] together; chela manus, dorsal retrol*at*eral (*drl*) carina as a smooth ridge or slightly costate .....***Hormurus ochyroscapter***
Chela (♂), movable finger, supra-basal lobe conical, as high as wide or higher than wide; chela manus, retrolateral surface, *Esb* trichobothrium more distal than Eb

group, close to *Est*, sometimes slightly more distal than *Est*; Patella, trichobothriotaxy, retrolateral surface, *em*–*esb* series, 2 groups [esb_{1-2}][em_{1-2}]; chela manus, dorsal retrol*at*eral (*drl*) carina costate or granular .....***Hormurus tetrakaideca***

35(32). Chela manus, retrolateral surface, position of *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; Chela manus, dorsal retrol*at*eral (*drl*) carina as a smooth ridge or slightly costate; chela manus, ventral retrolateral (*vrl*) carina costate; chela, fixed finger, dorsal surface, depression around *dst*/*dsb*/*db* trichobothrium 3 distinct depressions (one around each trichobothrium) ....***Hormurus laevitropis***
Chela manus, retrolateral surface, *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Chela manus, dorsal retrol*at*eral (*drl*) carina costate or granular; chela manus, ventral retrolateral (*vrl*) carina granular or crenelate; chela, fixed finger, dorsal surface, a single large smooth depression grouping *dst*/*dsb*/*db* trichobothria .....***Hormurus kukunyungkal***

36(31). Femur, dorsal retrol*at*eral (*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina 37
Femur, dorsal retrol*at*eral (*drl*) carina equally developed than dorsal prosubmedian (*dps*) carina 39

37(36). Chela, fixed finger, dorsal surface, a single large smooth depression grouping *dst*/*dsb*/*db* trichobothria; femur, retrolateral ventral intercarinal surface at least sparsely granular; chela, fixed finger, trichobothriotaxy, *est* trichobothria *esb* closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; prosomal carapace, median ocelli close together (less than an ocellus diameter) ....***Hormurus insculptus***
Chela, fixed finger, dorsal surface, 3 distinct depressions around *dst*/*dsb*/*db* trichobothria (one around each trichobothrium); femur, retrolateral ventral intercarinal surface smooth or nearly so; chela, fixed finger, trichobothriotaxy, *est* trichobothria *esb*, *eb*, *est*, *et* ca. equidistant from each other (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; prosomal carapace, median ocelli separated by at least half a diameter of a median ocellus or more.....38

38(37). Chela, ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; patella, ventral intercarinal surface smooth or nearly so; prosomal carapace, anteromedian area entirely smooth or nearly so; tergite VII (♀), posttergite entirely smooth or nearly so.....***Hormurus ischnoryctes***
Chela, ventral intercarinal surface, granulation distributed across entire surface; Patella, ventral intercarinal surface entirely granular, at least a reticulated network of granules; prosomal carapace, anteromedian area, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); tergite VII (♀), posttergite granular at least posteriorly ....***Hormurus wallaman***

39(36). Chela manus, retrolateral surface, *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; tergite VII (♀), posttergite entirely smooth or nearly so; chela (♂), movable finger, supra-basal lobe wider than high (low); chela, ventral intercarinal surface, granulation distributed across entire surface ....***Hormurus caudicula***
Chela manus, retrolateral surface, *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; tergite VII (♀), posttergite granular at least posteriorly; chela (♂), movable finger, supra-basal lobe conical, as high as wide or higher than wide; chela, ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially ....***Hormurus nyawaygi***

40(30). Patella, trichobothriotaxy, retrolateral surface, *em*–*esb* series, 2 groups [esb_{1-2}][em_{1-2}] ..

.....41
Patella, trichobothriotaxy, retrolateral surface, *em*–*esb* series, esb_1 closer to em_{1-2} or far away from esb_2, 2 groups [esb_2][esb_1/em_{1-2}] OR groups [esb_{1-2}][em_{1-2}] together ... .45

41(40). Hemispermatophore, transversal ridge at approximately the same level with base of lamellar hook.....42
Hemispermatophore, transversal ridge below base of lamellar hook..... .....***Hormurus umpila***
Hemispermatophore, transversal ridge well below base of lamellar hook..... .....***Hormurus hypselankylis***

42(41). Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium midpalm or slightly less than midpalm; chela manus, retrolateral surface, *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*.....43
Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium on proximal 1/3 of manus; chela manus, retrolateral surface, *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*.....44

43(42). Chela (♂), movable finger, supra-basal lobe wider than high (low); femur, dorsal retrol*at*eral (*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina; femur, retrolateral ventral intercarinal surface smooth or nearly so; Tergite VII (♀), posttergite entirely smooth or nearly so .....***Hormurus actaeolophos***
Chela (♂), movable finger, supra-basal lobe conical, as high as wide or higher than wide; femur, dorsal retrol*at*eral (*drl*) carina equally developed than dorsal prosubmedian (*dps*) carina; femur, retrolateral ventral intercarinal surface at least sparsely granular; Tergite VII (♀), posttergite granular at least posteriorly ....***Hormurus bandjin***

44(42). Chela, fixed finger, trichobothriotaxy, *esb*, *eb*, *est* and *et* trichobothria ca. equidistant from each other (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; chela, fixed finger, dorsal surface, a single large smooth depression grouping the *dst*/*dsb*/*db* trichobothria; chelicerae, colouration, dorsal surface dark (manus as dark as or darker than carapace); pectines, marginal lamellae, number two..... .....***Hormurus hylaios***
Chela, fixed finger, trichobothriotaxy, *esb* trichobothrium closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; chela, fixed finger, dorsal surface, 3 distinct depressions around *dst*/*dsb*/*db* trichobothria (one around each trichobothrium); chelicerae, colouration, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace); pectines, marginal lamellae, number three.....***Hormurus macrochela***

45(40). Chela (♂), fingers, supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap.....46
Chela (♂), fingers, supra-basal lobe and corresponding notch with a distinct posterior gap.....***Hormurus muralagi***
Chela (♂), fingers, supra-basal lobe and corresponding notch with a distinct upper/anterior gap.....***Hormurus ankamuti***

46(45). Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium midpalm or slightly less than midpalm; femur, dorsal retrol*at*eral (*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina; pecten (♂) length, short, distal edge not reaching to distal edge of coxa of leg IV; leg IV, femora, ventromedian carinae present ....***Hormurus ochthonastes***
Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichbothrium on proximal 1/3 of manus; femur, dorsal retrol*at*eral (*drl*) carina equally developed than dorsal prosubmedian (*dps*) carina; pecten (♂) length, moderate, distal edge reaching to, but not beyond, distal edge of coxa of leg IV; leg IV, femora, ventromedian carinae

absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules) 47

47(46). Chela manus, retrolateral surface, *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; chela, fixed finger, trichobothriotaxy, *esb*, *eb*, *est* and *et* trichobothria ca. equidistant from each other (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; tergite VII (♀), posttergite entirely smooth or nearly so; prosomal carapace (♀), posterolateral areas smooth or nearly so..... .....***Hormurus tjapukai***
Chela manus, retrolateral surface, *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; chela, fixed finger, trichobothriotaxy, *esb* trichobothria closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; tergite VII (♀), posttergite granular at least posteriorly; prosomal carapace (♀), posterolateral areas at least sparsely granular .. ..***Hormurus kuukayau***

48(26). Femur, retrolateral ventral intercarinal surface smooth or nearly so.....49
Femur, retrolateral ventral intercarinal surface at least sparsely granular.....51

49(48). Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium midpalm or slightly less than midpalm; patella, prolateral process forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; prosomal carapace, anteromedian area entirely granular, at least sparsely; tergite VII (♀), posttergite entirely smooth or nearly so.....***Hormurus kilkerranicus***
Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothirum on proximal 1/3 of manus; patella, prolateral process forming a single large spine; prosomal carapace, anteromedian area, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); tergite VII (♀), posttergite granular at least posteriorly.....50

50(49). Chela, fixed finger, trichobothriotaxy, *esb*, *eb*, *est* and *et* trichobothria ca. equidistant from each other (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; chela manus, ventral prolateral (*vpl*) carina absent or obsolete; femur, dorsal retrol*at*eral (*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina; chela, fixed finger, dorsal surface, 3 distinct depressions araound *dst*/*dsb*/*db* trichobothria (one around each trichobothrium) .....***Hormurus wallaman***
Chela, fixed finger, trichobothriotaxy, *esb* trichobothrium closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; chela manus, ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules; femur, dorsal retrol*at*eral (*drl*) carina equally developed than *dps* carina; chela, fixed finger, dorsal surface, a single large smooth depression grouping *dst*/*dsb*/*db* trichobothria .....***Hormurus mesochtonus***

51(48). Patella, trichobothriotaxy, retrolateral surface, *em*–*esb* series, 2 groups [esb_{1-2}][em_{1-2}]; Prosoma, microsculptures, granules, size minute spiniform granules.....52
Patella, trichobothriotaxy, retrolateral surface, *em*–*esb* series, esb_1 closer to em_{1-2} or far away from esb_2, 2 groups [esb_2][esb_1/em_{1-2}] OR groups [esb_{1-2}][em_{1-2}] together; Prosoma, microsculptures, large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules.....53

52(51). Chela manus, retrolateral surface, *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; Femur, dorsal retrol*at*eral (*drl*) carina equally developed than dorsal prosubmedian (*dps*) carina; femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; femur, prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity .....***Hormurus chthamalochoros***
Chela manus, retrolateral surface, *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; femur, dorsal retrol*at*eral

(*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina; femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; Femur, prolateral median (*plm*) carina vestigial with 2 large spines (one proximal and one midway) .....***Hormurus oreios***

53(51). Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium midpalm or slightly less than midpalm; patella, dorsal retrol*at*eral (*drl*) carina absent or obsolete; Femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; femur, prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity .....***Hormurus milneanus***
Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothirum on proximal 1/3 of manus; patella, dorsal retrol*at*eral (*drl*) carina distinct, at least a low ridge or a row of granules; femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; Femur, prolateral median (*plm*) carina vestigial with 2 large spines (one proximal and one midway) ....***Hormurus waigiensis***

54(1). Femur, dorsal retrol*at*eral (*drl*) carina less strongly developed than dorsal prosubmedian (*dps*) carina 55
Femur, dorsal retrol*at*eral (*drl*) carina equally developed than dorsal prosubmedian (*dps*) carina 56
Femur, dorsal retrol*at*eral (*drl*) carina more strongly developed than dorsal prosubmedian (*dps*) carina .....***Hormurus samoa***

55(54). Patella, trichobothriotaxy, retrolateral surface, *em–esb* series, 2 groups [esb_{1-2}][em_{1-2}]; chela manus, ventral retrolateral (*vrl*) carina costate; femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; femur, prolateral median (*plm*) carina vestigial with 2 large spines (one proximal and one midway) .....***Hormurus penta***
Patella, trichobothriotaxy, retrolateral surface, *em–esb* series, esb_1 closer to em_{1-2} or far away from esb_2, 2 groups [esb_2][esb_1/em_{1-2}] OR groups [esb_{1-2}][em_{1-2}] together; chela manus, ventral retrolateral (*vrl*) carina granular or crenelate; femur, [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; femur, prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity .....***Hormurus weberi***

56(54). Femur, length, short (equal to or shorter than carapace).....57
Femur, length, long (longer than carapace, up to 2 times longer).....58

57(56). Patella, trichobothriotaxy, retrolateral surface, *em–esb* series, 2 groups [esb_{1-2}][em_{1-2}]; femur, retrolateral ventral intercarinal surface at least sparsely granular; prosomal carapace, anteromedian area entirely granular, at least sparsely; tergites IV–VI (♀), posttergites, mesial and lateral surfaces granular ....***Hormurus neocaledonicus***
Patella, trichobothriotaxy, retrolateral surface, *em–esb* series, esb_1 closer to em_{1-2} or far away from esb_2, 2 groups [esb_2][esb_1/em_{1-2}] OR groups [esb_{1-2}][em_{1-2}] together; femur, retrolateral ventral intercarinal surface smooth or nearly so; prosomal carapace, anteromedian area, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); tergites IV–VI (♀), posttergites, mesial and lateral surface smooth (or nearly so) ....***Hormurus boholiensis***

58(56). Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium midpalm or slightly less than midpalm; chela manus, ventral prolateral (*vpl*) carina absent or obsolete; patella, prolateral process forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; patella, dorsal retrol*at*eral (*drl*) carina absent or obsolete .....***Hormurus dechangei***
Chela manus, trichobothriotaxy, dorsal surface, *Dt* trichobothrium on proximal 1/3 of

manus; chela manus, ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules; patella, prolateral process forming a single large spine; patella, dorsal retrol*at*eral (*drl*) carina distinct, at least a low ridge or a row of granules .....***Hormurus waigiensis***

4.3.4 KEY TO SPECIES OF THE GENUS *Liocheles*

1. Chela manus, trichobothriotaxy, ventral surface, V_3–V_4 close together, proximal part of manus.....2
   Chela manus, trichobothriotaxy, ventral surface, V_3–V_4 apart from each other.....3

2(1). Chela (♂), fingers, supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap.....***Liocheles longimanus***
   Chela (♂), fingers, supra-basal lobe and corresponding notch with a distinct posterior gap.....***Liocheles suspectus***
   Chela (♂), fingers, supra-basal lobe and corresponding notch with a distinct upper/anterior gap.....***Liocheles nigripes***

3(1). Chelicerae, colouration, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace); patella, prolateral process forming a single large spine; chela, dorsal intercarinal surface with distinct spiniform granules; patella, dorsal intercarinal surface smooth or nearly so, prolateral edge and proximal end may be weakly granular.....4
   Chelicerae, colouration, dorsal surface dark (manus as dark as or darker than carapace); patella, prolateral process forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; chela, dorsal intercarinal surface, vestigial granulation, at most low granules; patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules ....***Liocheles australasiae***

4(3). Chela manus, ventral retrolateral (*vrl*) carina costate; chela, dorsal intercarinal surface, microsculptures present, across entire surface; patella, retrolateral ventral intercarinal surface at least sparsely granular; prosomal carapace, lateral ocelli equidistant, close together, almost touching each other.....***Liocheles complanatus***
   Chela manus, ventral retrolateral (*vrl*) carina granular or crenelate; chela, dorsal intercarinal surface, microsculptures limited to prolateral and retrolateral edges, absent from the median part; patella, retrolateral ventral intercarinal surface smooth or nearly so; prosomal carapace, lateral ocelli, third ocellus apart from first and second ocelli .....***Liocheles malaya***

4.4 DESCRIPTIONS AND DIAGNOSES

Abbreviations used:

AMNH, American Museum of Natural History, New York, USA.
AMS, Australian Museum, Sydney, Australia.
BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii, USA.
CAS, California Academy of Sciences, San Francisco, USA.
CNHM, Cabinet d'Histoire Naturelle de Metz, Metz, France.
HL, Henrik Krehenwinkel personal collection.
IOS, incorrect original spelling.
ISS, incorrect subsequent spelling.
juv., juvenile.
LM, Lionel Monod personal collection, to be deposited in the collection of the MHNG.
LP, Lorenzo Prendini DNA sample collection, AMNH.
MIS, misidentification.
MCSNG, Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy.
MHNG, Muséum d'histoire naturelle, Geneva, Switzerland.
MNHN, Muséum National d'Histoires Naturelles, Paris, France.
MRHN, Musée Royal d'Histoire Naturelle de Belgique, Brusselles, Belgium.
NHML, Natural History Museum, London, United Kingdom.
NHMW, Naturhistorisches Museum Wien, Vienna, Austria.
NMB, Naturhistorisches Musem, Basel, Switzerland.
NP, national park.
NTM, NorthernTerritory Museum of Arts and Sciences, Darwin, Northern Territory, Australia.
NNHM, National Natuurhistorisch Museum, Leiden, The Netherlands.
sub., subadult.
PHY, Phyllodrom e. V., Museum und Institut für Regenwaldökologie, Leipzig, Germany.
RMBR, Raffles Museum of Biodiversity Research, Singapore.
QM, Queensland Museum, Brisbane, Australia (Queensland).
UE, unjustified emendation.
USNM, United State National Musem of Natural History (Smithsonian Institution), Washington, DC, USA.
WAM, Western Australian Museum, Perth, Australia.
ZMAK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.
ZMB, Zoologisches Museum, Humboldt Universität, Berlin, Germany.
ZMH, Zoologisches Staatsinstitut, Zoologisches Museum Hamburg, Hamburg, Germany.

FAMILY **HORMURIDAE** Laurie, 1896

Hormurini Laurie, 1896b: 128 (subfamily).
Type genus *Hormurus* Thorell, 1876 (elevated to subfamily rank by Soleglad *et al.*, 2005: 32, 35).

SYNONYMS

Opisthacanthinae Kraepelin, 1905: 343.
Type genus *Opisthacanthus* Peters, 1861 (see Notes).
Liochelidae Fet & Bechly, 2001: 280, 281 (synonymized with Hormurinae by Soleglad *et al.*, 2005: 32, 35).
Type genus *Liocheles* Sundevall, 1833.
Hadogeninae Lourenço, 1999: 930 (synonymized by Prendini, 2001a: 170, 171).
Type genus *Hadogenes* Kraepelin, 1894.

NON AVAILABLE NAME

Ischnuridae Simon, 1879: 92 (part).
Type genus *Ischnurus* C. L. Koch, 1837 (= *Liocheles* Sundevall, 1833); see Fet & Bechly (2000, 2001) and ICZN (2003).

REFERENCES

Ischnurini (subfamily): Pocock, 1893: 316–318; Kraepelin, 1894: 108–110; Laurie, 1896b: 128; Lönnberg, 1897: 187.
Hormurini: Laurie, 1896b: 128.
Ischnurinae: Kraepelin, 1899: 142; Kraepelin, 1901: 271; Kraepelin, 1905: 345; Birula, 1917a: 162; Birula, 1917b: 58; Pavlovsky, 1924: 79; Pavlovsky, 1925: 192; Werner, 1934: 278; Kästner, 1941: 234; Millot & Vachon, 1949: 428; Bücherl, 1964: 59; L. E. Koch, 1977: 159; Lourenço, 1989: 163; Stockwell, 1989: 211, 212; Nenilin & Fet, 1992: 5.
Ischnuridae: Becker, 1880: 135; Pocock, 1900: 76 (part); Kraepelin, 1913: 162; Fage, 1933: 27; Lourenço, 1989 (part); Tikader & Bastawade, 1983: 475, 477; Francke, 1985: 17 (part); Lourenço, 1985: 28–34, 47–49, tab. 1, pl. 12; Sissom, 1990: 121 (part); Locket, 1995: 192; Kovařík, 1997: 184; Kovařík, 1998: 132; Fet & Bechly, 2000; Prendini, 2000: 33–34; Volschenk *et al*., 2001: 162, 163.
Hormurinae: Kraepelin, 1905: 343; Birula, 1917a: 162; Birula, 1917b: 58; Pavlovsky, 1925: 192, Soleglad *et al.*, 2005: 31–35, tab. 6.
Ischnuraria ('tribe'): Birula, 1917a: 161, 162 (part); Birula, 1917b: 58, 59 (part).
Hadogenidae: Lourenço, 2000: 26.
Liochelinae: Soleglad & Fet, 2003: 113;.
Liochelidae: Monod & Volschenk, 2004: 676, 677; Kamenz *et al.*, 2005: 108, tab. 1; Prendini & Wheeler, 2005: 481, tab. 5, 10; Kamenz & Prendini, 2008: 30, 33, 43; Volschenk & Prendini, 2008: 239, 242, 249, tab. 1.

GENUS ***HORMIOPS*** Fage, 1933

Hormiops Fage, 1933: 30
Type species *Hormiops davydovi* Fage, 1933

REFERENCES

Hormiops: Kästner, 1941: 234; Francke, 1985: 9, 17; Nenilin & Fet, 1992: 19, 20; Kovařík, 1998: 132; Lourenço & Monod, 1999: 338–343.
Liocheles: Fet, 2000: 395; Lourenço, 1989: 170; Prendini, 2000: 72.

DISTRIBUTION

Malaysia, Vietnam.

DIAGNOSIS

PEDIPALP. Chela fingers, dentition, inner accessory denticles (IAD) absent. TRICHOBOTHRIOTAXY. Chela manus, *Esb* trichobothrium basal, in same axis as *Eb* group. Fixed finger, *db* trichobothrium on dorsal surface. CARINAE. Patella, dorsal retrolateral (*drl*) carina distinct, at least a low ridge or a row of granules; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete. Femur, prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway). MACROSCULPTURE. Chela fingers smooth or nearly so. Chela fixed finger, dorsal surface, *db*, *dsb* and *dst* trichobothria not in distinct depressions, surrounding areas smooth.
PROSOMAL CARAPACE. Anterior furcated suture/sulci obsolete or absent. Median occular tubercle not elevated; superciliary carinae absent; two pairs of lateral ocelli.
MESOSOMA. Tergites I–VI, lateral transversal sulcus absent or vestigial (extremely shallow). Tergites III–VII, posttergites without reticulated network of ridges and dimples (even surface).
Pectinal teeth, short, not curved, sensory papillae covering distal portion only.
METASOMA markedly flattened laterally (wider than long). Segment I, ventral surface without posterior spiniform granules. Segment V, ventral surface without smooth shiny depression on posterior half between ventrolateral carinae; ventrolateral carinae, posterior half with strong conical tooth. Telson shorter than metasomal segment V.
HEMISPERMATOPHORE. Lamella without longitudinal 'spine' (*ls*) on external surface; lamellar tip at approximately same level with base of lamellar hook, sometimes slightly below. Distal lobe well developed, forming a distinct hump. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; posterior edge of basal lobe forming 90° angle with lamella.

Hormiops davydovi Fage, 1933

Hormiops davydovi Fage, 1933: 32–33, fig. 1, 2, pl. I, figs a–c

References

Hormiops davydovi: Fage, 1936: 181; Kästner, 1941: 234, fig. 215; Takashima, 1945: 94, 95; Fage, 1946: 71; Vachon, 1974, fig. 80; Kovařík, 1998: 132; Lourenço & Monod, 1999: 343, 344, figs 1–4.
Liocheles australasiae: Fet, 2000: 395.
Liocheles davydovi: Prendini, 2000: 72; Monod & Volschenk, 2004: 686.

Material examined

Syntypes: VIETNAM, Poulo-Condore [=Con Son Island], S off the coast of VIETNAM, in forest, under stones, II.1930/IV.1931, Dawidoff leg. 1932, 1 ♂, 1 ♀, 1 juv. (MNHN-RS 0562). **Additional Material**: VIETNAM, Poulo-Condor Island (=Con Son Island), M. Germain, 1 ♀, 11 imm. (MNHN-RS 0499).

Distribution (fig. 91)
Vietnam.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) absent; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe absent, margin straight or nearly so, at most a low hump; supra-basal notch absent; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe absent or at most weakly developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium basal, in same axis as *Eb* group; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb*–*et* axis; *esb* trichobothrium below *est*–*et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina costate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina distinct, at least a low ridge or a row of granules, costate or granular; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), as smooth ridge or faintly costate. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian

(*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) c*arina*e; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers, smooth or nearly so. Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria smooth (trichobothria not in distinct depressions). Chela manus, dorsal intercarinal surface, macrosculpture limited to prolateral and retrolateral edges, absent from the median part, granulation vestigial, at most low granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation absent; prolateral ventral intercarinal surface smooth or nearly so. Patella, dorsal intercarinal surface smooth or nearly so, prolateral edge and proximal end may be weakly granular; ventral intercarinal surface smooth or nearly so; retrolateral dorsal intercarinal surface smooth or nearly so; retrolateral ventral intercarinal surface smooth or nearly so; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface, granulation absent or limited to the proximal and retrolateral edges, densely granular; dorsal and prolateral intercarinal surfaces with small to medium–sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci vestigial or absent. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, not elevated; superciliary carinae absent. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; two pairs, first ocellus equal in size to second or second and third ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, extremely dense, giving tegument sand-like appearance; anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces smooth or nearly so; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, posttergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergites entirely granular, at least sparsely; I–VII, posttergites with minute spiniform granules, extremely densely distributed; III–VII, posttergites, reticulated network of ridges and dimples absent, even surface; I–VI, lateral transversal sulcus absent or vestigial (extremely shallow).

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; two marginal lamellae; fulcra present; seven pectinal teeth, short, not curved, sensory papillae covering distal portion only. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; markedly flattened laterally (wider than long). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae absent or obsolete; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, sub-posterior spiniform granules weak to absent, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral

carinae, posterior spiniform granules well developed; ventrosubmedian carinae, 2–3 pairs of well developed posterior spiniform granules, one pair of well developed sub-posterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, partial, expressed only in posterior half, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, diverging on distal part, anterior half with at least few small spiniform granules, posterior half with strong conical tooth; anal arch with few large conical teeth. Telson, total length shorter than metasomal segment V; vesicle smooth, without granules; unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae present. Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules absent; terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/5; 4/5; 4/5; 5/5.

HEMISPERMATOPHORE. Distal lamina straight or nearly so, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge at base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with base of lamellar hook, sometimes slightly below, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 90º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

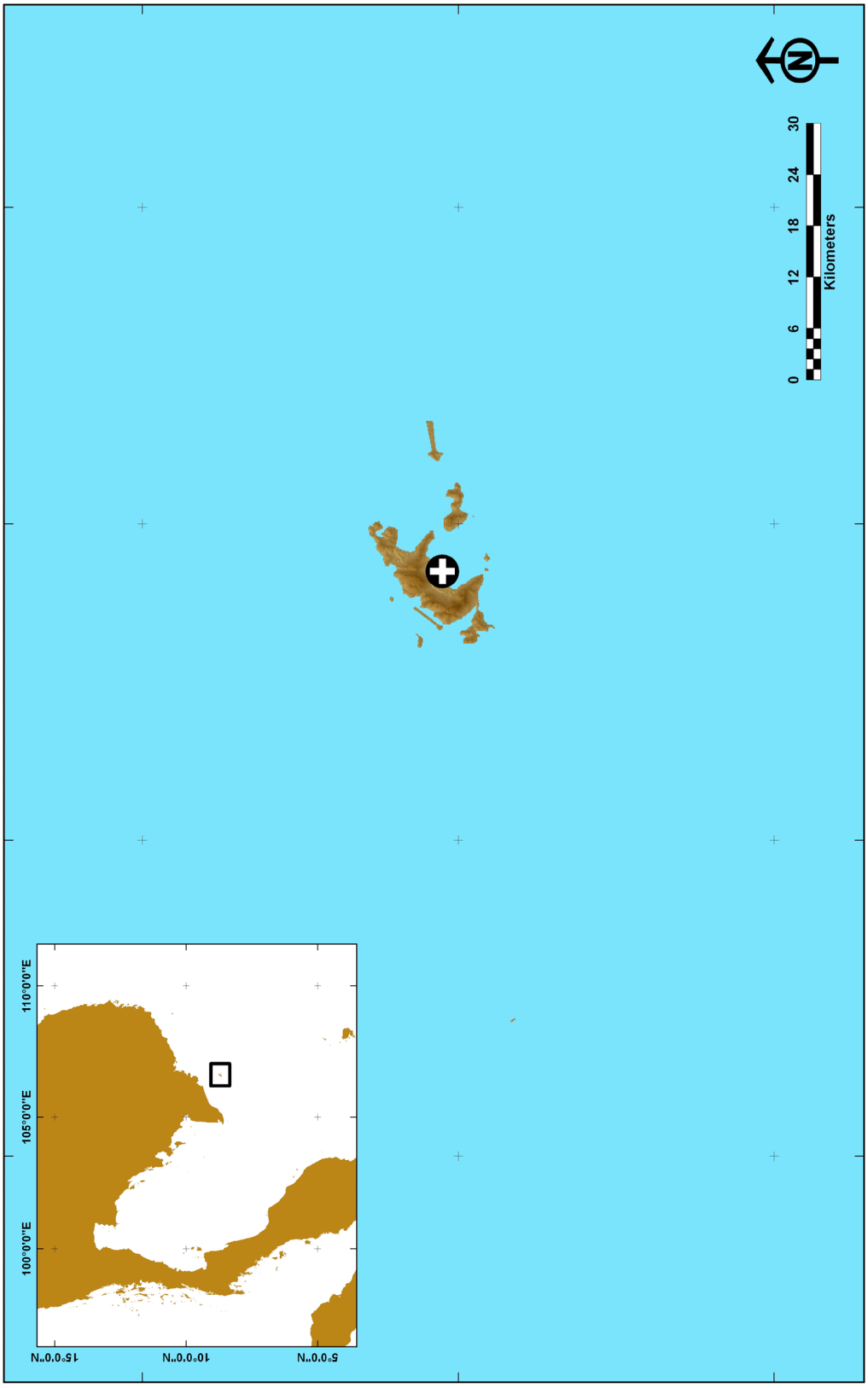
CARAPACE. Anteromedian surface entirely smooth or nearly so; posteromedian surface smooth or nearly so; anterolateral surfaces smooth or nearly so; mediolateral surface at least sparsely granular; posterolateral surfaces smooth or nearly so.

MESOSOMA. Tergites I–III, posttergites, mesial and lateral areas smooth; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergites entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples absent or vestigial, even surface.

VENTRAL MORPHOLOGY. Genital operculum oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. Pectines, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; six pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 91. Distribution map of *Hormiops davydovi* Fage, 1933.


N
0
6
12
18
24
30
Kilometers
100°0'0"E
105°0'0"E
110°0'0"E
5°0'0"N
10°0'0"N
15°0'0"N

Hormiops infulcra n. sp.

References

Hormiops davydovi: Kovařík, 2000: 57–58, figs 1–7 (MIS)

Material examined

Holotype: MALAYSIA, PAHANG, Pulau Tioman, foothills of Gunung Kajang, 02º47.139'Nx104º07.548'E, 59 m, 1–2.X.2001, rainforest, in rock crevices along a stream, L. Monod, 1 ♂. **Paratypes**: same data as holotype, 10 ♂♂, 13 ♀♀ (LM; LP 2185). **Additional material**: Pulau Tulai, 23.VIII.2003, P. K. L. Ng *et al.*, 1 ♀, 4 imm. (RMBR ZRC.ARA.456), 1 imm. (RMBR ZRC.ARA.457).

Distribution (fig. 92)

Malaysia, Pahang.

Etymology

The name *infulcra* is a construct from the Latin words in [not, without] and fulcrum. It is an invariable noun in apposition and refers to the absence of fulcrae in the pectines.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) absent; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe absent, margin straight or nearly so, at most a low hump; supra-basal notch absent; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe absent or at most weakly developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium basal, in same axis as *Eb* group; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb*–*et* axis; *esb* trichobothrium below *est*–*et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina costate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina distinct, at least a low ridge or a row of granules, costate or granular; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), as smooth ridge or faintly costate. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian

(*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) c*arina*e; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers smooth or nearly so. Chela fixed finger, Dorsal surface, area around *db*/*dsb*/*dst* trichobothria smooth (trichobothria not in distinct depressions). Chela, dorsal intercarinal surface, macrosculpture limited to prolateral and retrolateral edges, absent from the median part, granulation vestigial, at most low granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation absent; prolateral ventral intercarinal surface smooth or nearly so. Patella, dorsal intercarinal surface smooth or nearly so, prolateral edge and proximal end may be weakly granular; ventral intercarinal surface smooth or nearly so; retrolateral dorsal intercarinal surface smooth or nearly so; retrolateral ventral intercarinal surface smooth or nearly so; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface, granulation absent or limited to the proximal and retrolateral edges, densely granular; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci vestigial or absent. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, not elevated; superciliary carinae absent. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; two pairs, first ocellus equal in size to second or second and third ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, extremely dense, giving tegument sand-like appearance; anteromedian surface entirely smooth or nearly so; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces smooth or nearly so; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, posttergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, posttergites with minute spiniform granules, extremely densely distributed; III–VII, posttergites, reticulated network of ridges and dimples absent, even surface; I–VI, lateral transversal sulcus absent or vestigial (extremely shallow).

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; two marginal lamellae; fulcrae absent; six pectinal teeth, short, not curved, sensory papillae covering distal portion only. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; markedly flattened laterally (wider than long). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae absent or obsolete; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, sub-posterior spiniform granules weak to absent, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules well developed; ventrosubmedian carinae, 2–3 pairs of

well developed posterior spiniform granules, one pair of well developed sub-posterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae, ridges with at least few reduced spiniform granules distally; ventrolateral carinae with minute/small spiniform granules. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, partial, expressed only in posterior half, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, diverging on distal part, anterior half with at least few small spiniform granules, posterior half with strong conical tooth; anal arch with few large conical teeth. Telson, total length shorter than metasomal segment V; vesicle smooth, without granules; unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae present. Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules absent; terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/5; 4/5; 4/5; 4/5.

HEMISPERMATOPHORE. Distal lamina straight or nearly so, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge at base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with base of lamellar hook, sometimes slightly below, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 90º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface entirely smooth or nearly so; posteromedian surface smooth or nearly so; anterolateral surfaces smooth or nearly so; mediolateral surface smooth or nearly so; posterolateral surfaces smooth or nearly so.

MESOSOMA. Tergites I–III, posttergites, mesial and lateral areas smooth; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples absent or vestigial, even surface.

VENTRAL MORPHOLOGY. Genital operculum oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. Pectines, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; 5–6 pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 92. Distribution map of *Hormiops infulcra* n. sp.

N
0
3
6
9
12
15
Kilometers
95°0'0"E
100°0'0"E
105°0'0"E
0°0'0"
5°0'0"N
10°0'0"N

GENUS ***HORMURUS*** Thorell, 1876, **new combination**

Hormurus Thorell, 1876a: 14.

Type species by original designation *Ischnurus caudicula* C. L. Koch, 1867 [= *Hormurus caudicula* (C. L. Koch, 1867)]

REFERENCES

Hormurus: Thorell, 1876b: 249 (part); Karsch, 1879a: 21; Keyserling, 1885: 21 (part); Thorell, 1888: 338, 419 (part); Pocock, 1893: 320; Kraepelin, 1894: 131–133 (part); Lönnberg, 1897b: 199; Kraepelin, 1899: 153 (part); Pocock, 1902: 364; Kraepelin, 1916: 42; Birula, 1917a: 162; Birula, 1917b: 58; Kopstein, 1921: 135 (part); Giltay, 1931: 13 (part); Werner, 1934: 280 (part); Kästner, 1941: 234 (part); Mello-Leitão, 1942: 125 (part); Roewer, 1943: 235 (part); Vachon, 1953: 8 (part); Chapin, 1957: 66, 67 (part); Pérez Minocci, 1974: 37; Tikader & Bastawade, 1983: 499, 500 (part).

Liocheles: Karsch, 1880: 408 (part); Takashima, 1945, 1948, 1949; L. E. Koch, 1977: 159, 160 (part); Lourenço, 1983: 404 (part); Francke, 1985: 9 (part); Lourenço, 1985: 35, 47 (part); Lourenço, 1989: 171 (part); Stockwell, 1989: 87, 111, 116, 117, 119, 140, 169, 207, 212, 223, 236, 238 (part); Sissom, 1990: 126 (part); Nenilin & Fet, 1992: 19, 20 (part); Kovařík, 1995: 201 (part); Kovařík, 1998c: 133 (part); Fet & Bechly, 2000: 26, 27 (part); Kovařík, 2000: 60 (part); Monod, 2000: 58–62 (part); Volschenk *et al.*, 2001: 163 (part); Soleglad *et al.*, 2003: 19, 57, 58, 67, 112, 113, 142, 146, tabs 3, 4, 9 (part); Monod & Volschenk, 2004: 677 (part); Soleglad *et al.*, 2005: 32, 34, tab. 6 (part); Prendini & Wheeler, 2005: tabs 5, 10 (part); Kamenz & Prendini, 2008: 11, 30, 34, 35, 43 (part); Volschenk & Prendini, 2008: tab. 1.

DIAGNOSIS

PEDIPALP. Chela fingers, dentition, inner accessory denticles (IAD) present. TRICHOBOTHRIOTAXY. Chela manus, *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est* or close to *Est*, sometimes slightly more distal than *Est*. Fixed finger, *db* trichobothrium on dorsal surface. CARINAE. Patella, dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae present at least as smooth ridge. Femur, prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, *db*, *dsb* and *dst* trichobothria in distinct smooth depressions, surrounding areas granular (at least in the most proximal part).
PROSOMAL CARAPACE. Anterior furcated suture/sulci present and distinct. Median ocular tubercle raised at least slightly; superciliary carinae present. Three pairs of lateral ocelli.
MESOSOMA. Tergites I–VI with lateral transversal sulcus; III–VII, posttergites with a distinct reticulated network of ridges and dimples (uneven surface).
PECTINAL TEETH long, straight, sensory papillae entirely covering.
METASOMA not markedly flattened laterally (as thick as large or slightly thicker, more rounded). Segment I, ventral surface without posterior spiniform granules. Segment V, ventral surface without smooth shiny depression on posterior half between ventrolateral carinae. Telson equal to or slightly longer than metasomal segment V.
HEMISPERMATOPHORE. Lamella without longitudinal 'spine' (*ls*) on external surface absent; lamellar tip at approximately same level with base of lamellar hook, or below. Distal lobe well developed, forming a distinct hump. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; posterior edge of basal lobe forming a 135–150° angle with lamella.

Hormurus bandjin, n. sp.

References

Liocheles waigiensis (nec L. E. Koch, 1977; MIS): Monteith, 1978: 57; Monod & Volschenk, 2004: fig. 5a.

Liocheles caudicula: Monod, 2000: 36, 77–85 (part), fig. 26, map 9 (part).

Material examined

Holotype: AUSTRALIA, N QUEENSLAND, Hinchinbrook Island. Gayundah Creek, 10 m, 7–15. XI.1984, 7–14.XI.1984, V. Davies & J. Gallon (Expedition to Gayundah III; Dennis, Gonzo & Doug; 13.XI.1984), 1 ♂ (QM-S 17297). **Paratypes**: same data as holotype, 2 ♀♀, 2 ♂♂ sub., 1 ♀ sub., 1 juv. (QM-S 17297), 1 ♂, 1 ♀ (QM-S 42710); G. Monteith, D. Cook & G. Thompson, 1 ♂ (QM-S 23260), 1 ♀ (QM-S 23257); 1 juv. (QM-S 17198), 1 juv. (QM-S 17199). Upper Gayundah Ck, 850 m, 9–11.XI.1984, G. Monteith & D. Cook, 1 ♀ (QM-S 23258). Thorsborne trail, Zoe Falls to Mulligan Falls, 3.XII.2004, R. Wyss & L. Monod, (1) Zoe Falls (69): 21 m, 18°24'30.2''Sx146°19'20.9''E, vine thicket, in rock crevices (boulders), dry, near the falls. (2) Sweetwater Creek (70): 171 m, 18°25'33.3''Sx146°19'42.9''E, patch of rainforest around creeks, under rocks and in rock crevices. (3) Mulligan Falls (71): 42 m, 18°26'32.0''Sx146°19'28.3''S, around campsite, lowland rainforest, lots of small boulders, in crevices, 3 ♂♂, 7 ♀♀ (LM; LP 5558); Little Ramsay Bay, vine forest along a creek (not many boulders), 1.XII.2004, 17 m, 18°20'50.1''Sx146°17'53.5''E, under stones and in rock crevices. R. Wyss & L. Monod, 1 ♂, 8 ♀♀, 3 juv./sub. (LM; LP 5556); Banksia Creek to North Zoe Bay, rainforest with many big boulders), 2.XII.2004, under stones and in narrow rock crevices, 36 m, 18°22'09.7''Sx 146°18'53.1''E, 36 m / 18°22'37.1''Sx146°18'37.8''E, 34 m, R. Wyss & L. Monod, 3 ♂♂, 3 ♀♀ (LM; LP 5557).

Distribution (fig. 94)

Australia, Queensland.

Etymology

The name *bandjin* is an invariable noun in apposition and refers to the Aboriginal tribe Bandjin (Tindale, 1974) from Hinchinbrook Island and Lucinda Point. The species is considered endemic to Hinchinbrook Island.

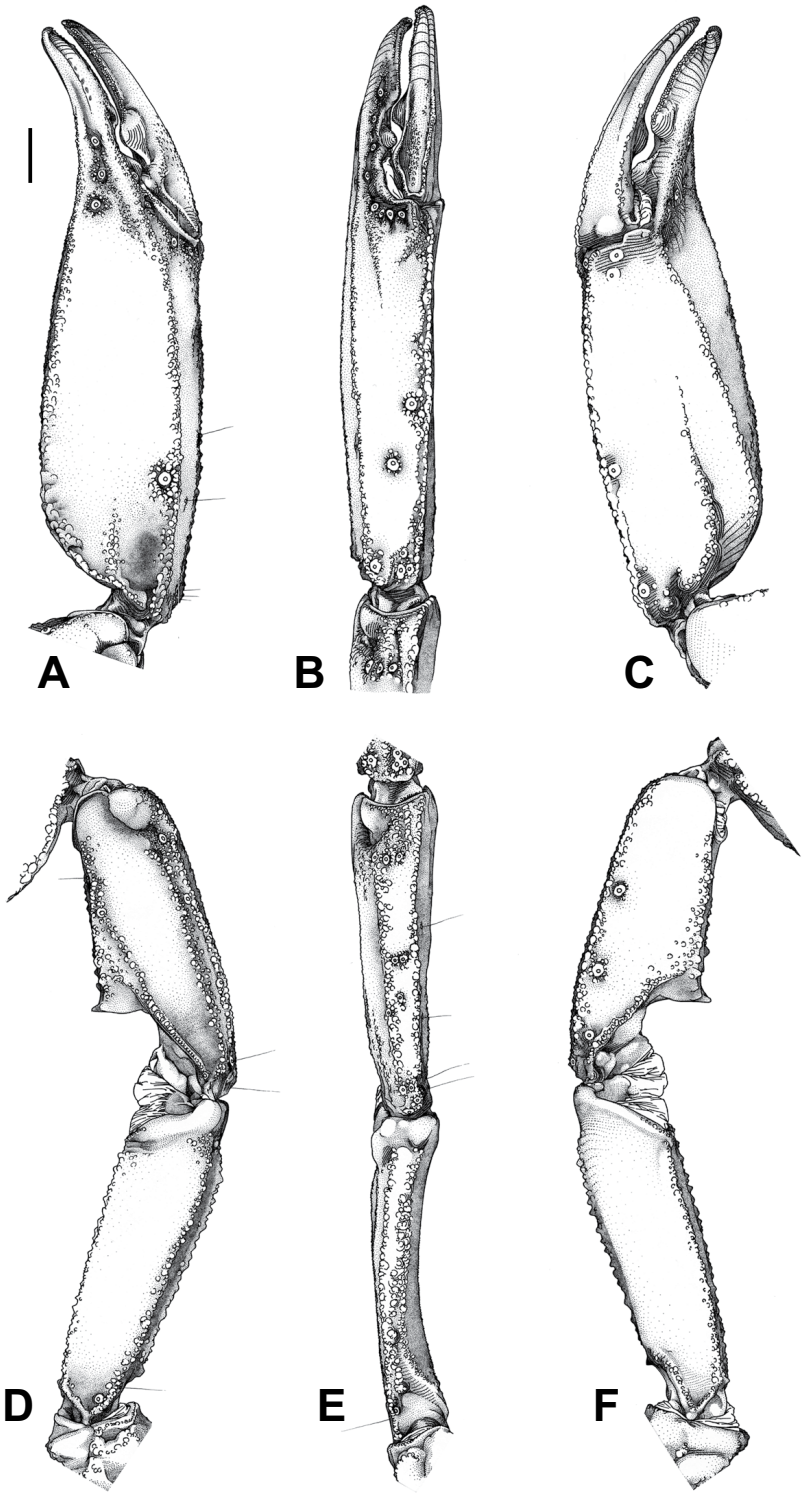
DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, conical (as high as wide or higher than wide), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY (fig. 93). Chela manus, no accessory trichobothria; *Dt* trichobothrium, midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est–esb* similar to distance *esb–eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb–et* axis; *esb* trichobothrium in line with *est–et* axis, in proximal region

Fig. 93. *Hormurus bandjin* n. sp., male, pedipalp with trichobothrial pattern.A, chela, dorsal aspect. B, idem, external aspect. C, idem, ventral aspect. D, femur and patella, dorsal aspect. E, idem, external aspect. F, idem, ventral aspect. Scale line, 2 mm.


A
B
C
D
E
F

of fixed finger; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules, granular (at least sparsely), equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, posttergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, posttergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, posttergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; two marginal lamellae; fulcrae present; seven pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀, not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, 1–2 pairs of small/vestigial medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae, ridges with at least a few small/medium spiniform granules, subposterior spiniform granules absent; ventrolateral carinae with at least few minute/small spiniform granules. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae, ridges with at least few reduced spiniform granules distally; ventrolateral carinae with minute/small spiniform granules. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, with distinct spiniform granules, at least distally; ventrolateral carinae present and distinct, anterior half with at least few small spiniform granules, posterior half with at least small spiniform granules, with medium spiniform granules more strongly developed than preceding granules (anterior half); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

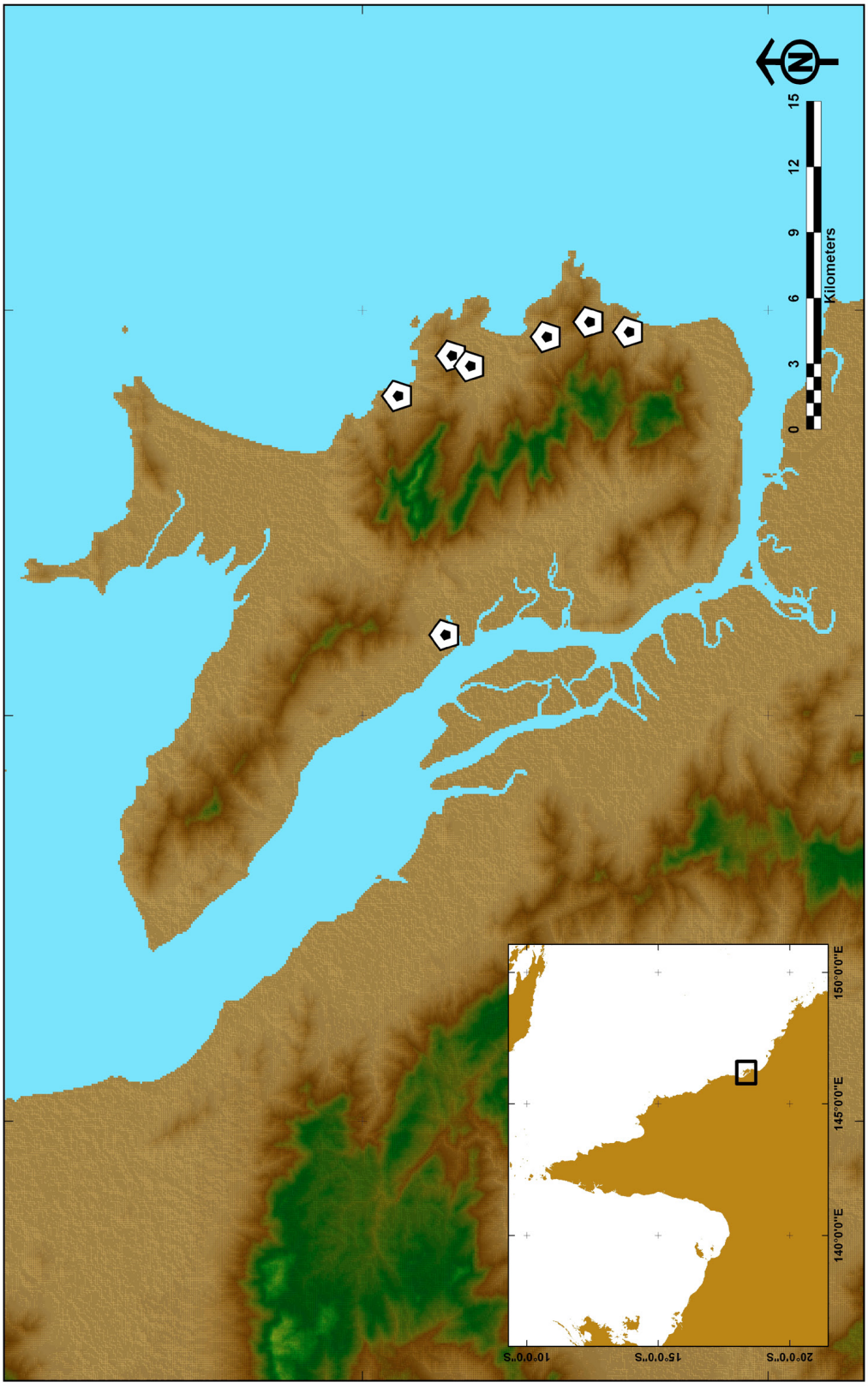
LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 5/5; 5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal ‘spine’ (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with base of lamellar hook, sometimes slightly below, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface present, small to medium,

pointing downward; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.
PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.
CARAPACE. Anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.
MESOSOMA. Tergites I–III, posttergites, mesially smooth, laterally granular; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite, granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; six pectinal teeth.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 94. Distribution map of *Hormurus bandjin* n. sp.


N
0
3
6
9
12
15
Kilometers
10°0'0"S
15°0'0"S
20°0'0"S
140°0'0"E
145°0'0"E
150°0'0"E

Hormurus boholiensis Kraepelin, 1914

Hormurus boholiensis Kraepelin, 1914: 333

References

Scorpio (*Ischnurus*) *cumingii*: Gervais, 1843: 131, *nomen nudum* (no description published); Gervais, 1844b: 69, 70.
Hormurus australasiae: Thorell, 1888: 331.
Hormurus caudicula boholiensis: Giltay, 1931: 12, 13, 18, 19.
Liocheles australasiae: L. E. Koch, 1977: 161.
Liocheles caudicula boholiensis: Takashima, 1945: 96.
Hormurus boholiensis: Kraepelin, 1914: 333; Weidner, 1959: 101.
Liocheles boholiensis: Monod, 2000: 72–76, pl. 22–24, map 8.

Material examined

Lectotype: PHILIPPINES, BOHOL, X.1863, 1 ♀, 1 ♀ juv. (ZMH). **Paralectotype**: Same data as lectotype, 1 ♀ juv. (ZMH). **Additional material**: PHILIPPINES, LUZON, Manilla, Mr. Cuming, 1 ♀ (NHML). Mount Makiling, Baker, 1 ♀ (AMNH). Subig Bay, II.1907, S. C. Thompson, 1 imm. (CAS).

Distribution (fig. 98)

Philippines, Luzon.

Notes

This species, formerly synonymized with *L. australasiae*, belongs to the genus *Hormurus*.

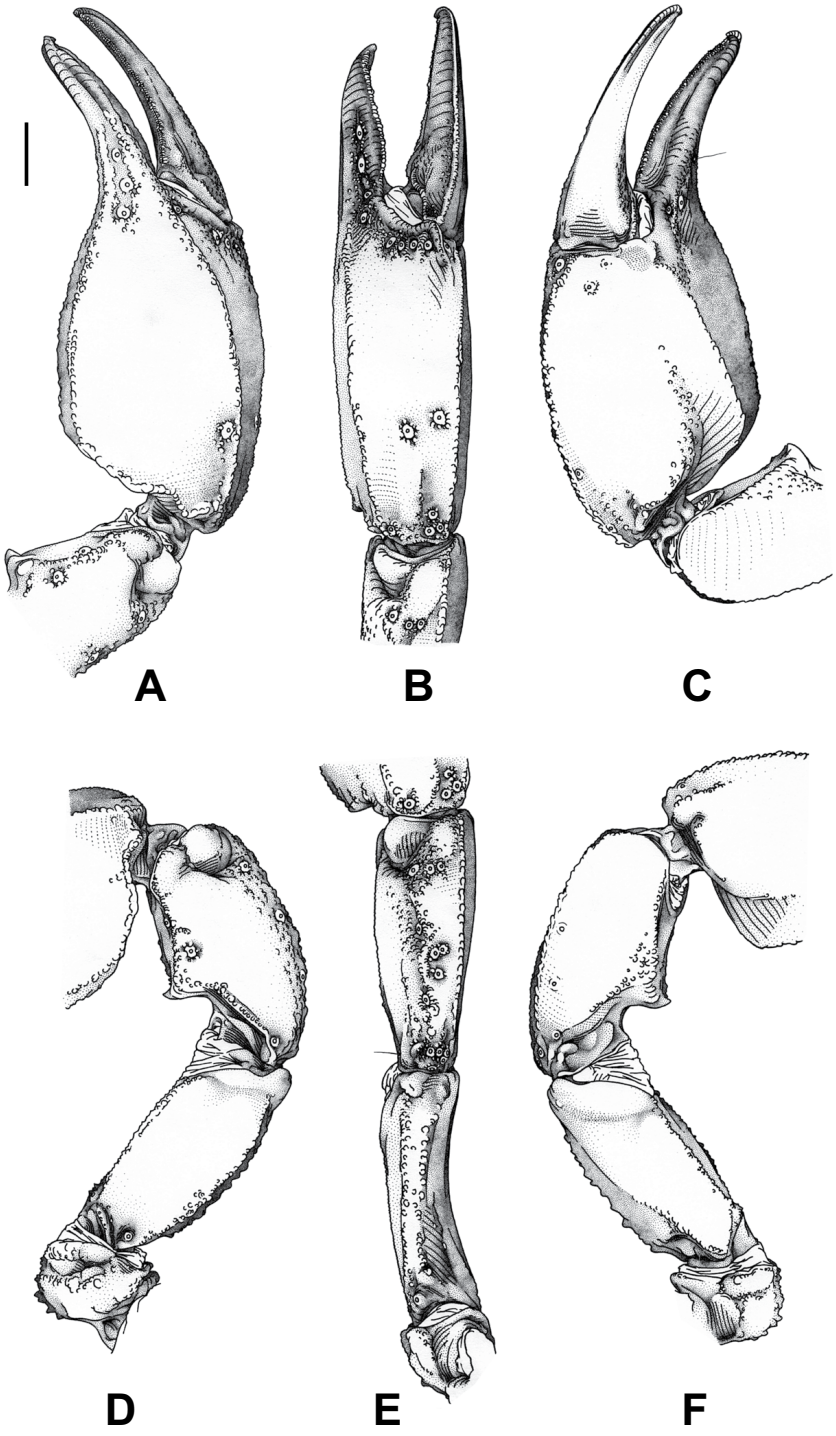
DESCRIPTION. ADULT FEMALE

COLORATION. Tergites, uniform.

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent; basal lobe absent. TRICHOBOTHRIOTAXY (fig. 95). Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in a single group or in 2 groups [esb_1] [esb_2/em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) +

Fig. 95. *Hormurus boholiensis* Kraepelin, 1914, female holotype, pedipalp with trichobothrial pattern.A, chela, dorsal aspect. B, idem, external aspect. C, idem, ventral aspect. D, femur and patella, dorsal aspect. E, idem, external aspect. F, idem, ventral aspect. Scale line, 2 mm.


A
B
C
D
E
F

retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface smooth or nearly so; ventral intercarinal surface, granulation absent or vestigial and limited to the retrolateral edge; prolateral intercarinal surface at least sparsely granular.

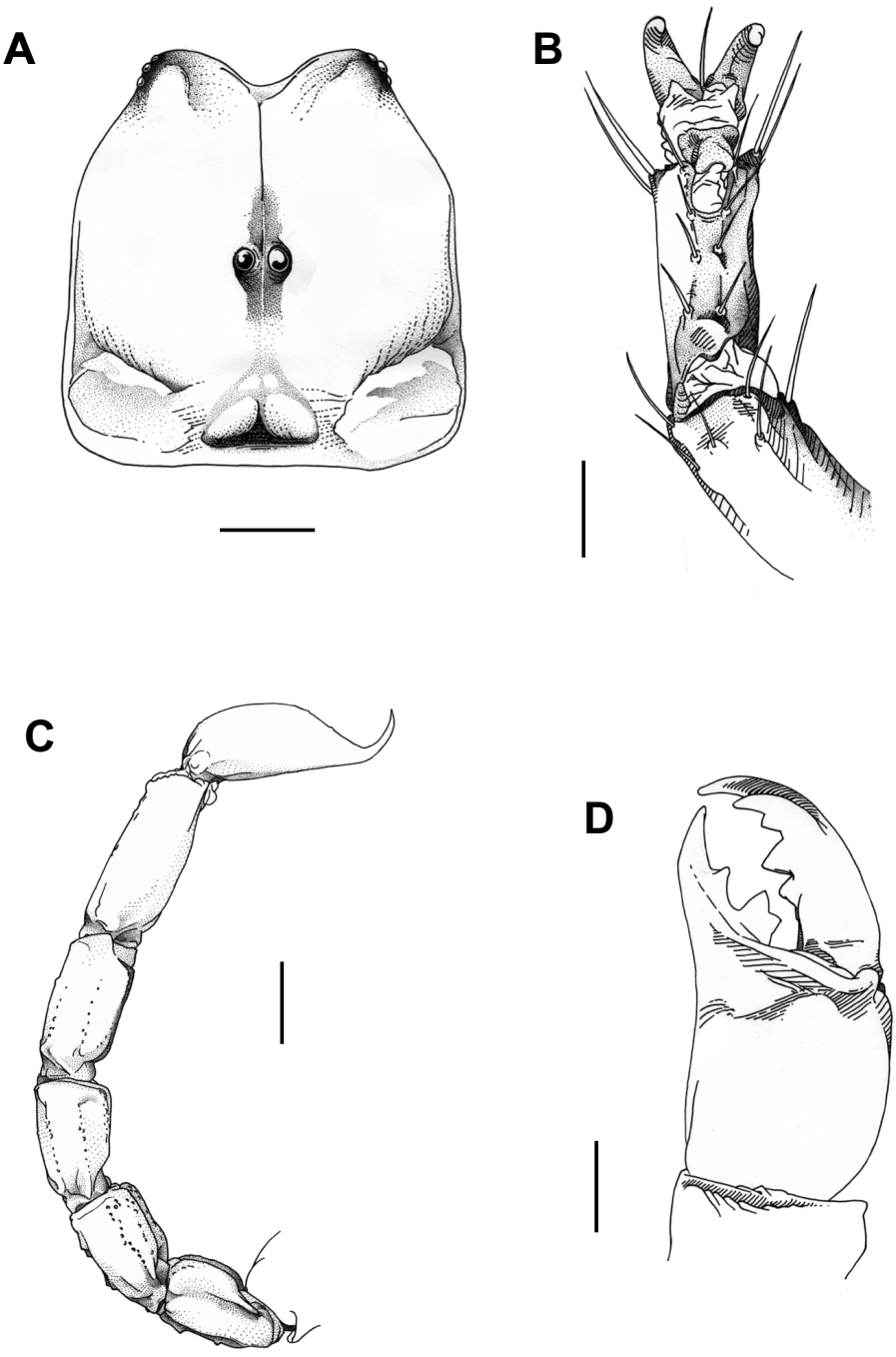
PROSOMAL CARAPACE (fig. 96A). Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–III, posttergites, mesial and lateral areas smooth; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM (fig. 97), shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. GENITAL OPERCULUM (fig. 97) oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES (fig. 97), length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; three marginal lamellae; fulcrae present; six pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA (fig. 96C). Segments I–V not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina

Fig. 96. *Hormurus boholiensis* Kraepelin, 1914, female holotype. A, carapace, dorsal aspect. B, left tarsus IV, ventral aspect. C, metasoma, lateral aspect. D, left chelicera, dorsal aspect. Scale lines, 2 mm (A, C), 1 mm (D), 0.5 mm (B).


A
B
C
D

present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, 1–3 pairs of well developed medial granules. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, one pair of well developed sub-posterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi (fig. 96B), two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 3/4; 3/4; 3–4/4; 4/4.

Fig. 97. *Hormurus boholiensis* Kraepelin, 1914, female holotype. Pectines and genital operculum, ventral aspect. Scale line, 1 mm (D).

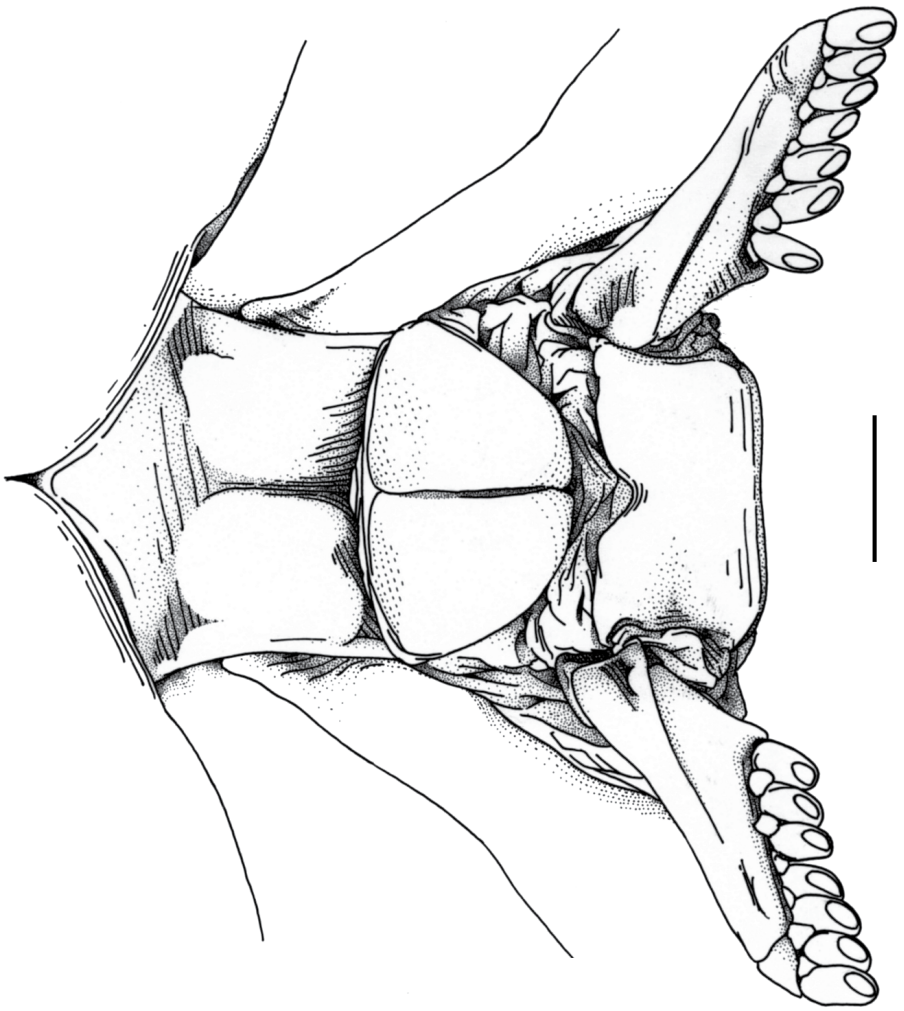
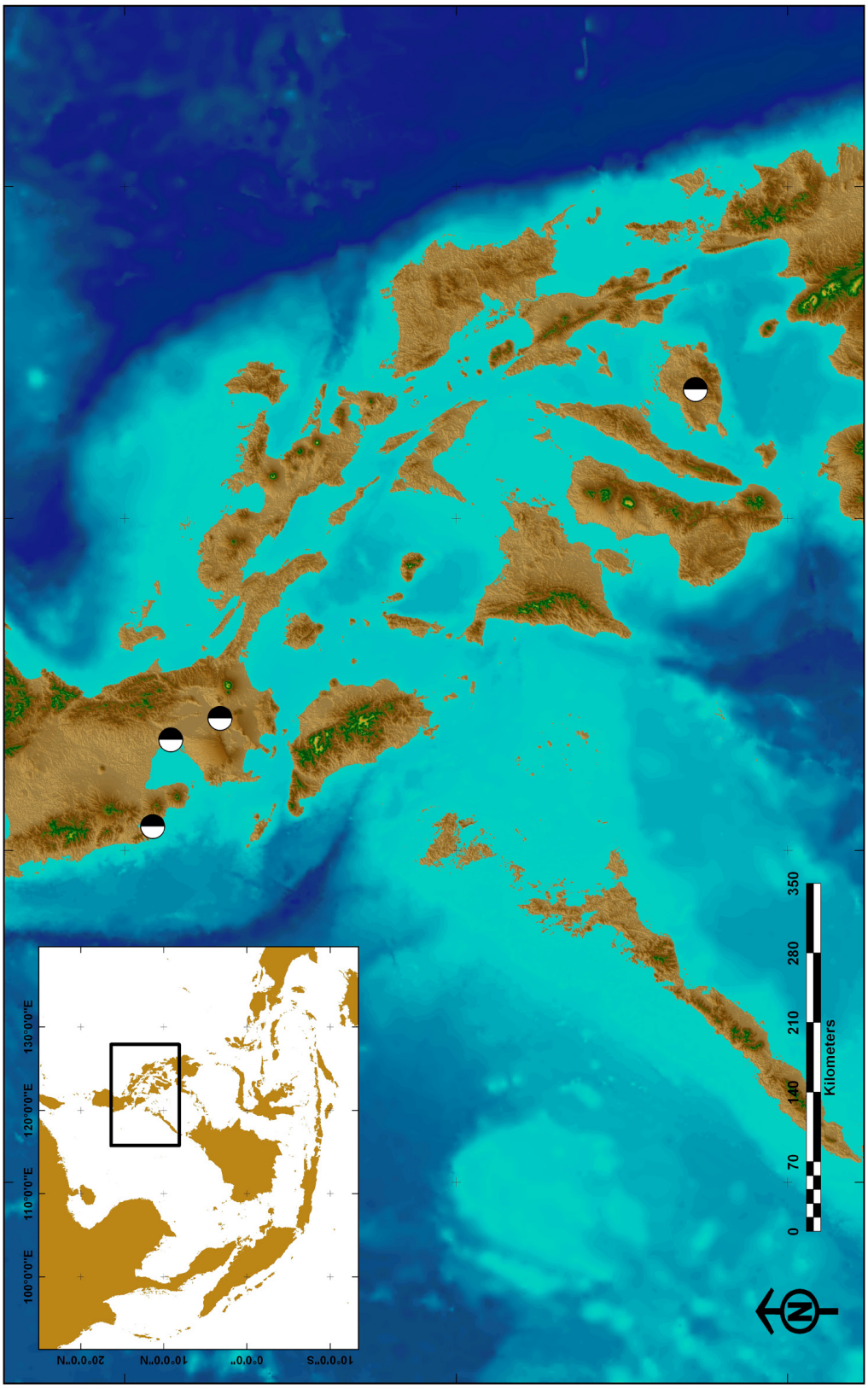


Fig. 98. Distribution map of *Hormurus boholiensis* Kraepelin, 1914.


0
70
140
210
280
350
Kilometers
N
100°0'0"E
110°0'0"E
120°0'0"E
130°0'0"E
20°0'0"N
10°0'0"N
0°0'0"
10°0'0"S

Hormurus caudicula (C. L. Koch, 1867), **new combination**

Ischnurus caudicula C. L. Koch, 1867: 237–239.

References

Scorpio (Ischnurus) caudicula: Gervais, 1844a: 237, pl. XII, figs 45, 46; Gervais, 1844b: 69.

Hormurus caudicula: Thorell, 1876a: 14; Thorell, 1876b: 249, 250; Karsch, 1879a: 21; Keyserling, 1885: 27–31, pl. III, fig. 2 (part); Kraepelin, 1894: 135–137, pl. II, fig. 66; Kraepelin, 1899: 155 (part); Kraepelin, 1901: 272 (part); Werner, 1902: 603; Kraepelin, 1914: 333 (part); Kraepelin, 1916: 43; Kopstein, 1921: 137, 138 (part); Fage, 1933: 27; Fage, 1936: 180 (part); Fage, 1946: 71; Weidner, 1959: 101; Vachon, 1974: fig. 98.

Hormurus caudicula caudicula: Giltay, 1931: 13, 18, 19 (part).

Liocheles caudicula: Lourenço, 1985: pl. 7, fig. 2; Lourenço, 1989: pl. 4, fig. 2; Monod, 2000: 77–85, pl. 25, map 9 (part).

Liocheles caudicula caudicula: Takashima, 1945: 96.

Ischnurus caudicula: Weidner, 1959: 101.

Liocheles waigiensis: L. E. Koch, 1977: 166–172, figs 18, 47, 82, 83, maps 9a, b (part); L. E. Koch, 1981: 877 (part); Locket, 1995: 197, fig. 14c, tab. 1; Kovařík, 1998: 134 (part); Volschenk, Locket & Harvey, 2001: 162 (part); Monod & Volschenk, 2004: 675, 686 (part); Kamenz & Prendini, 2008: 11, 43, pl. 133.

Material examined

Holotype: AUSTRALIA, SE QUEENSLAND, Brisbane, 1 ♀ (ZMH 244). **Paratypes** ? (Koch collections, labelled in register as types): AUSTRALIA, SE QUEENSLAND, Brisbane, 14.VI.1949, E. Browning, 2 ♂♂, 1 ♀, 1 juv. (NHML 1913.9.1.2395-7). **Additional material**: AUSTRALIA, NEW SOUTH WALES, Castelnau (272.79), 1 ♂ (MNHN, RS 0496). QUEENSLAND. 1 ♀ (WAM 98/1850). Acacia Ridge, Brisbane, 10.XII.1961, Grass tree stump, R. G. Winks, 1 ♀ (QM-S 17073). Amama Walking track, Amamoor State Forest, 26°21'25.7''Sx 152°38'01.9''E, 103 m, 24.VIII.2006, rainforest, near creek, scree of medium to large boulders, in rock crevices, L. Monod, 3 ♂♂, 1 ♀, 6 imm. (QM; LP 6361). Bahr's Scrub, 29.I.1981–23.V.1981, G. Monteith (107 A/2), 1 ♀ (QM-S 17187). Bauple State Forest, 10.VIII.1972, P. Ogilivie, 1 ♀, 1 juv. (QM-S 17147). Binjour Plateau, Redvale Road, 25°33'Sx151°28'E, 340 m, 23.IX–21.XII.1997, open forest, pitfall trap (5098), G. Monteith & D. Cook, 2 ♂♂ (QM-S 46058). The Bluff (Keysland), 26°15'Sx151°43'E, 530 m, 24.X–24.XI.1995, vine scrub, pitfall trap, G. Monteith, 1 ♂ (QM-S 41629); 26°14'Sx151°42'E, 500 m, 24.XI.1995–3.III.1996, open forest, Intercept trap, G. Monteith, 1 ♂ (QM-S 24694). Brisbane District, 23.VII.1916, E. Shaw, 1 ♀ (QM-S 17039). Near Brisbane, E. Shaw, 2 ♀♀ (QM-S 17085). Upper Brookfield, CNVF with Araucaria, general collecting, 28.XI.1980, V. Davies & R. Raven, 1 ♀ (QM-S 17112). Buhot Creek, Burbank, 27°35.5'S 153°10.3'E, V.2003–VI.2003, riparian forest, 1 ♂, 1 ♀ (LP 2339). Bundaberg, C. L. Carter (W53), 1 ♀ (QM-S 17089). Cameron Scrub, knoll top, 27º30'Sx152º44'E, 90 m, 11.XI.1998–13.I.1999, vine scrub, pitfall (7557), G. Monteith, D. Cook & G. Thompson, 8 ♂♂, 1 ♀ (QM-S 73960); snig track, 27°31'Sx152°44'E, 120 m, 15.IX–11.XI.1998, vine scrub, pitfall (7384), G. Monteith, D. Cook, G. Thompson, 1 ♂ (QM-S 73941); knoll top, 27°31'Sx152°44'E, 90 m, 15.IX–11.XI.1998, vine scrub, pitfall (7380), G. Monteith, D. Cook, G. Thompson, 2 ♂♂, 1 juv. (QM-S 73942). Capalaba, in rotting log, 23.VII.1973, R. S. Green, 1 ♀ (QM-S 17098); 25.X.1973, Moroney, 2 ♀♀ (QM-S 17145). Carnarvon National Park, Mount Moffatt section, 24°54'49"S 148°02'01"E, 13.XII.2002, pitfall trap,upper slope of steep-sided ridge, brown heavy clay, C. Eddie, R. Perry & D. Harboe, 1 ♀ (LP 2340). Collaroy Private Holding, 9.X.1974, open eucalyptus forest, W.New, 1 ♀ (QM-S 17159). Connondale National Park, 26°41'50.0"Sx152°33'12.4"E, 17.III.1999, blacklighting amongst boulders, E. S. Volschenk & P. A. Aitken, 1 ♀ (LP 1502). Dayboro, Ocean View, 1945, P. G. Gallier (W 1623), 1 ♀, 26 pullus (QM-S 17074). Eumundi, 1 ♀ (WAM-66-334). Goodna, 24.III.1913, H. Hacker, 1 ♀, 18 pullus (QM-S 17075). Frazer Island, 28.I.1977, I.G.Filmer, 1 ♀ (QM-S 17136). Gayndah, B.Spencer, 1 ♀ (NHML 1893.7.7.1). Goodnight Scrub, near Morganville, 2.XII.1973, under logs, V. E. Davies, 1 ♀, 1 juv. (QM-S 17148). Gympie, 16.VII.1994, J. Marilyn, 1 ♂ (QM-S 25824). Heads, 15 mls S of Boonah, 27.XII.1971, A. M. & M. J. Douglas, 2 ♂♂, 1 ♂ (freshly molted, badly preserved), 4 juv. (WAM 72/290 to 72/296). Helidon, 17m from road, 15.XII.1972, under logs, V. E. Davies & R. McK. (?), 1 ♂ (QM-S 17055). Holland Park, Brisbane, 25.V.1937, H. Richardson, 1 ♀ (QM-

S 17043). Hurdle Gully, 10.8 km WSW Monto, 24°54'Sx151°01'E, 320 m, 23.IX–20.XII.1997, vine scrub, intercept (5087), G. Monteith & D. Cook, 1 ♂ (QM-S 46038). Ipswich, T. Lowe, 1 juv. (QM-S 17051). Jimna State Forest, Pig Pocket, 4.VII.1978, open grassy forest near creek, in hollow log, K. R. McDonald, 1 ♂, 1 ♀, 3 juv. (QM-S 17104). "Kolane", 38 km NE of Wandoan, 150°18'Ex25°49'S, 12.IX.1975, A. Elliot, 1 ♀ (QM-S 17052). The Knobby, 27°30'S 152°35'E, 240 m, 15.IX–11.XI.1998, vine scrub, pitfall (7297), G. Monteith, D. Cook, G. Thompson, 3 ♂♂ (QM-S 73931); 11.XI.1998–13.I.1999, pitfall (7567), G. Monteith, D. Cook, G. Thompson, 2 ♂♂ (QM-S 73932). Kroombit Tops Eastern Escarpment, 16.XII.1983, 1 ♂ (QM-S 17186). Moggill road, the Gap, Brisbane, 20.VIII.1975, under log, A. Huxley, 1 ♂ (QM-S 17158). Mt Gavial, 3 km SSW, 23°37'x150°28'E, 320 m, 17.XII.1998–14.III.1999, vine forest, pitfall (87491), D. J. Cook, 1 ♂, 1 juv. (QM-S 73937). Mt Gavial, 1 km S, 23°36'x150°29'E, 400 m, 17.XII.1998–14.III.1999, open forest, pitfall (7486), D. J. Cook, 2 ♂♂ (QM-S 73933). Mt. Glorious, 22 km NW Brisbane, 535 m, 15.II.1983, in fallen log, A. Hiller, 1 ♀ (QM-S 17067); 29.II.1947, P. W. Slupley, 1 ♀ (QM-S 17041). Mt Hopeful, 2 km SSE, 23°45'Sx150°32'E, 440 m, 27.IX–15.XII.1999, vine scrub, pitfall (9012), D. & I. Cook, 1 ♂ (QM-S 73936). Mount Jim Crow NP, 23°12'56.2''Sx150°37'46.7''E, 117 m, 14.VIII.2006, vine thicket, under rocks and in rock crevices, L. Monod, 1 ♂, 3 ♂♂, 5 imm. (QM; LP 6360). Mt. Juburra, Beaudesert, 2.V.1960, under rock in creek bed, J. H.Calaby, 1 ♀ (WAM 98/1836). Mt Walsh, 1 km N, 25°34'S 152°03'E, 320 m, 19.XII.1999–28.VI.2000, vine scrub, pitfall trap (9454), D. J.Cook, 1 ♂, 2 ♀♀, 3 juv. (QM-S 59088). Near Murumba Creek, Jimna State Forest, 8.VI.1978, Open Ironbark forest, K. R. MacDonald, 1 ♂ (QM-S 17095). Nambour, 7.II.1962, under dry bark on fern post, SC.IQ. (?), W. A. Smith, 1 ♀, 18 pullus (QM-S 17032); A. Scharff, 1 ♂ (NHML). Nangur State Forest, 25°05'Sx152°01'E, 13.I.2001, rainforest, under rocks, M. S. Harvey, 1 juv. (WAM T62941). Nipping Gully, Site 2, 25°40'Sx151°26'E, 200 m, 9.XI–18.XII.1998, rainforest, pitfall (7398), G. Monteith & C. Gough, 1 ♂ (QM-S 73954); Site 3, 25°41'Sx151°25'E, 150 m, 9.X–18.XII.1998, open forest, pitfall (7500), G. Monteith & C. Gough, 1 ♂ (QM-S 73949). Olsen's Caverns, X–XI.1991, retrieved from pool, J. Augustine, 1 ♂, 1 juv. (QM-S 59593). Palmgrove NP, NW Taroom, 24°56'08''Sx149°21'09''E, 8.VIII.2001, *Acacia harpophylla* open forest, under rotten log, S. Vigar, 1 ♂ (QM-S 58434). Perry's Knob, 27°36'Sx152°36'E, 200 m, 15.X–11.XI.998, vine scrub, pitfall (7295), G. Monteith, D. Cook, G. Thompson, 1 ♂ (QM-S 73939). Reedy Creek, 30 km NW Kingaroy, 9.V.1981, M. Timmons, 2 ♀♀ (QM-S 17068). Rockhampton, M. Chozet (489.70), 1 ♂, 1 ♀, 1 juv. (MNHN, RS 0493). Rundle Range SEUT (?), 26.III.1975, R.K (?), L.M. (?), V. E. Davies, 1 ♀, 2 juv. (QM-S 17204). St John's Wood, Brisbane, 13.I.1962, R. Freeman, 1 ♀ (QM-S 17072). Samford, 20.XII.1991, 1 ♂ (QM-S 20498). 26 mi SW Sarina, 220m, 19.XI.1962, E. S. Ross & D. Q. Cavagnaro, 1 ♂, 2 ♀♀, 1 juv. (CAS). Stafford, Brisbane, turf bought from Toogoolawah, 14.VIII.1979, Mrs Hodge, 1 ♀ (QM-S 17070). "Stockhaven", 3 km SE, 25°48'Sx151°59'E, 450 m, 10.X–19.XII.1998, rainforest, pitfall (7515), G. Monteith & C. Gough, 2 ♂♂ (QM-S 73945). Tanah Merah, second storey verandah, 16.I.1990, A. Bowley, 1 ♀ (QM-S 23092). Taringa, Brisbane, 5.IV.1939, E. Needham, 1 ♂ (QM-S 17033). Wandoan, 28.X.1979, A. Rozefelds, 2 ♀♀ (QM-S17128); 25°39'34''Sx150°19'33''E, 7.XII.2000, P. Sparshott (jar #1, QM10 Receipt 702886), 1 ♂ (QM-S 55005). Wetheron, 3.5 km SW, 25°34'Sx151°41'E, 150 m, 10.X–19.XII.1998, vine scrub, pitfall (7509), G. Monteith & C. Gough, 3 ♂♂ (QM-S 73950); 19.XII.1998–27.I.1999, pitfall (7587), G. Monteith & C. Gough, 1 ♂ (QM-S 73935). Wetheron, 3 km SW, 25°34'Sx151°42'E, 150 m, 19.XII.1998–27.I.1999, vine scrub, pitfall (7586), G. Monteith & C. Gough, 3 ♂♂ (QM-S 73952); 10.X–19.XII.1998, pitfall (7507), G. Monteith & C. Gough, 3 ♂♂, 1 juv. (QM-S 73953). East Woodmillar, 25°41'Sx151°36'E, 350m, 25.I.1999, vine scrub & brigalow, G. Monteith, C. Gough & G. Thompson (7430), 1 ♂ (QM-S 73955). Bank of Yabba Creek, Jimna State Forest, Peach Tree Recreation Area, Eugenia track, 26°38'15.0''Sx152°27'18.3''E, 462 m, 24.VIII.2006, vine scrub (very dry), in rock crevices (scree of medium size boulders), L. Monod, 2 ♂♂, 1 ♀, 2 imm. (QM; LP 6362). SOUTH AUSTRALIA. Adelaide, amongst Queensland bananas, A.Bottcher, 1 ♀ (WAM 98/1851).

Distribution (fig. 99)
Australia, Queensland.

DESCRIPTION. ADULT MALE
COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or

paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.
MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, posttergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, posttergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, posttergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.
VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; seven pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.
METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, 1–2 pairs of small/vestigial medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae, ridges with at least a few small/medium spiniform granules, subposterior spiniform granules absent; ventrolateral carinae with at least few minute/small spiniform granules. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae, ridges with at least few reduced spiniform granules distally; ventrolateral carinae with minute/small spiniform granules. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, with distinct spiniform granules, at least distally; ventrolateral carinae present and distinct, anterior half with at least few small spiniform granules, posterior half with at least small spiniform granules, with medium spiniform granules more strongly developed than preceding granules (anterior half); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.
LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral

margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus.Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 5/4–5; 5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

BOOK LUNGS. Lamellar surface with simple trabeculae, with arcuate bow-like structures. Posterior spiracle edge with chisel-like structures.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

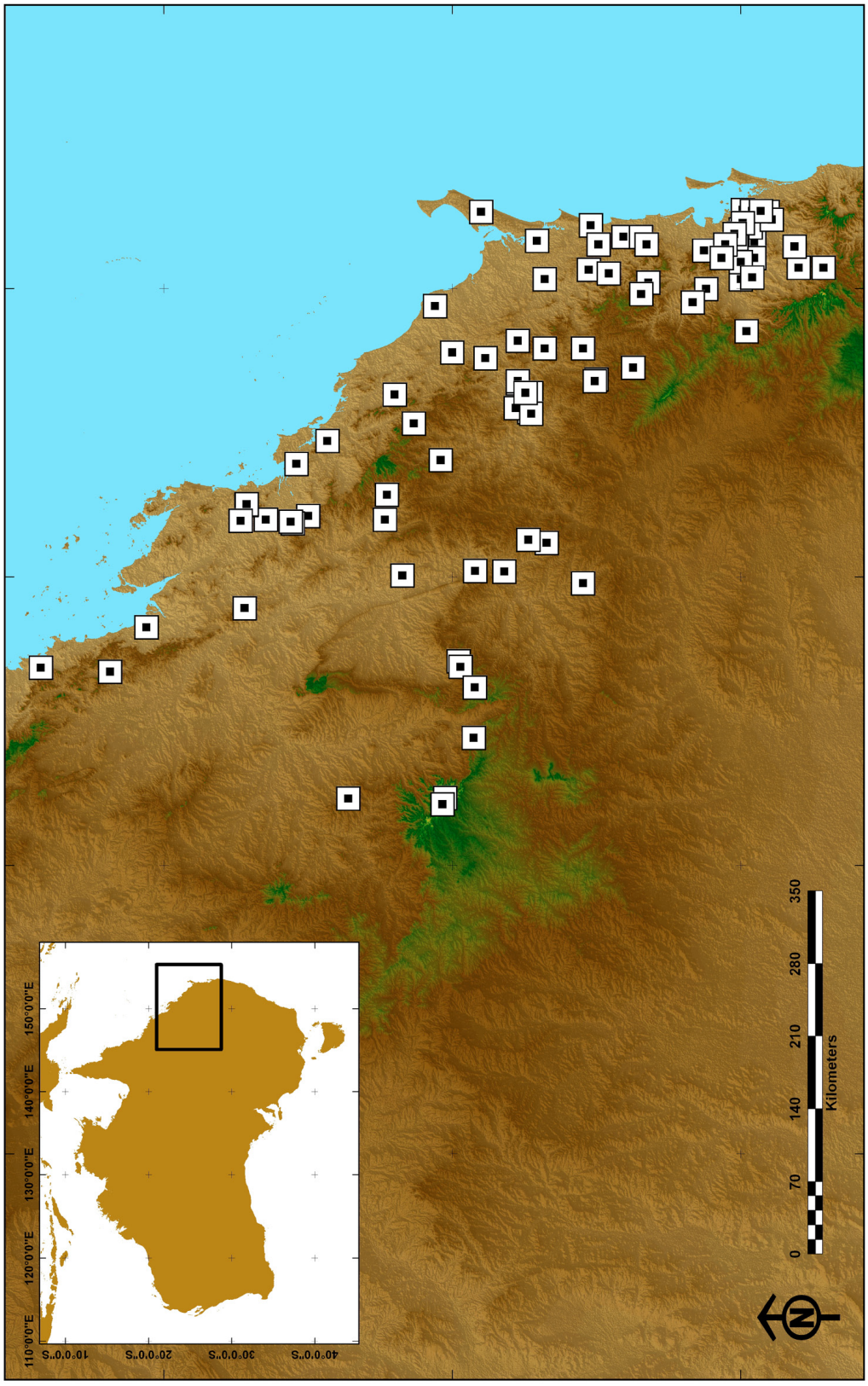
CARAPACE. Anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–III, posttergites, mesial and lateral areas smooth; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples distinct, uneven surface.

VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; six pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 99. Distribution map of *Hormurus caudicula* (C. L. Koch, 1867).


110°0'0"E
120°0'0"E
130°0'0"E
140°0'0"E
150°0'0"E
10°0'0"S
20°0'0"S
30°0'0"S
40°0'0"S
0
70
140
210
280
350
Kilometers
N

Hormurus davydovi (Birula, 1903), **new combination**

Opisthacanthus davydovi Birula, 1903: XXXIV, XXXV.

References

*H*ormurus *caudicula* (nec C. L. Koch, 1867; MIS): Thorell, 1888: 426, 427 (part).
Hormurus papuanus (nec Kraepelin, 1914; MIS): Hirst, 1914: 325; Kopstein, 1921: 138 (part).
Opisthacanthus davydovi: Kopstein, 1921: 141; Kopstein, 1923: 186; Giltay, 1931: 18; Takashima, 1945: 94; Lourenço, 1979: 33.
Hormurus caudicula papuanus (nec Kraepelin, 1914; MIS): Giltay, 1931: 10, 11, 13, 18, 19, fig. 4.
Liocheles weberi: Lourenço, 1983: 411, figs 18–21.
Liocheles waigiensis (nec Gervais, 1843; MIS): Kovařík, 2002: 15 (part).

Type material (non examined)

Holotype: INDONESIA, Maluku, Aru Islands, Vammor Island, Dobo, 1 ♂ (ZISP 935).

Material examined

INDONESIA. Maluku, Aru Islands, V. Rosenberg, 1 ♀, 1 juv. (NNHM 42). S Manoembaai, 20.III.1929, I.G.9223, S.A.R. le Prince Léopold, 1 ♂, 1 ♀, 2 imm. (MRHN). Papua, Mimika River Expedition, Wollaston, 1 ♂, 1 femelle, 3 sub., 4 juv. (NHML 1911.12.28.1-5). Alkmaar, 3.VIII.1907, Nieuw Guinea Expeditie 1907, 2 ♀♀ (NNHM 174). Digoel River, Nieuw Guinea Expeditie 1904, Dr J. W. R. Koch, 1 ♀, 1 juv. (NNHM 176). Geitenkamp, 20.VII.1907, Nieuw Guinea Expeditie 1907, 1 ♀, 1 juv. (NNHM 177). Kab. Merauke, Kec. Kouh, near Kampung Manggel or Kampung Yaniruma, approx. 5°20'Sx139°50'E, VI.1993, P. M. Taylor, 1 ♀ (USNM 00751). Sabang, 4.VII.1907, Nieuw Guinea Expeditie 1907, 1 ♂, 2 ♀♀, 1 juv. (NNHM 178). Van Weels kamp, V.1907, Nieuw Guinea Expeditie 1907, 1 ♀ (NNHM 179). West Papua, Etna Baai, Nieuw Guinea Expeditie 1904, Dr J. W. R. Koch, 3 ♂♂, 1 ♀ (NNHM 175).

Distribution (fig. 100)

Indonesia, Maluku.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est–esb* greater than distance *esb–eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb–et* axis; *esb* trichobothrium in line with *est–et* axis, in proximal region of fixed finger; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em–esb* series with four trichobothria in a single group or in two groups [esb_2][esb_1/em_{1-2}]; *eb* series with five trichobothria in two groups

[eb_1] and [$eb_{2–5}$] or [eb_1/$eb_{4–5}$] and [$eb_{2–3}$]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules, granular (at least sparsely), equally or less strongly developed than prolateral prolateral ventrosubmedian (*plvs*); prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface smooth or nearly so; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, large, ca. 1/5 of the carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, close together (less than a diameter), at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules, evenly and sparsely distributed; anteromedian surface entirely granular at least sparsely; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, posttergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, posttergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, posttergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip with a distinct swelling/bulge oriented posteriorly, at least weak, usually more pronouced in ♂. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or

equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; seven pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

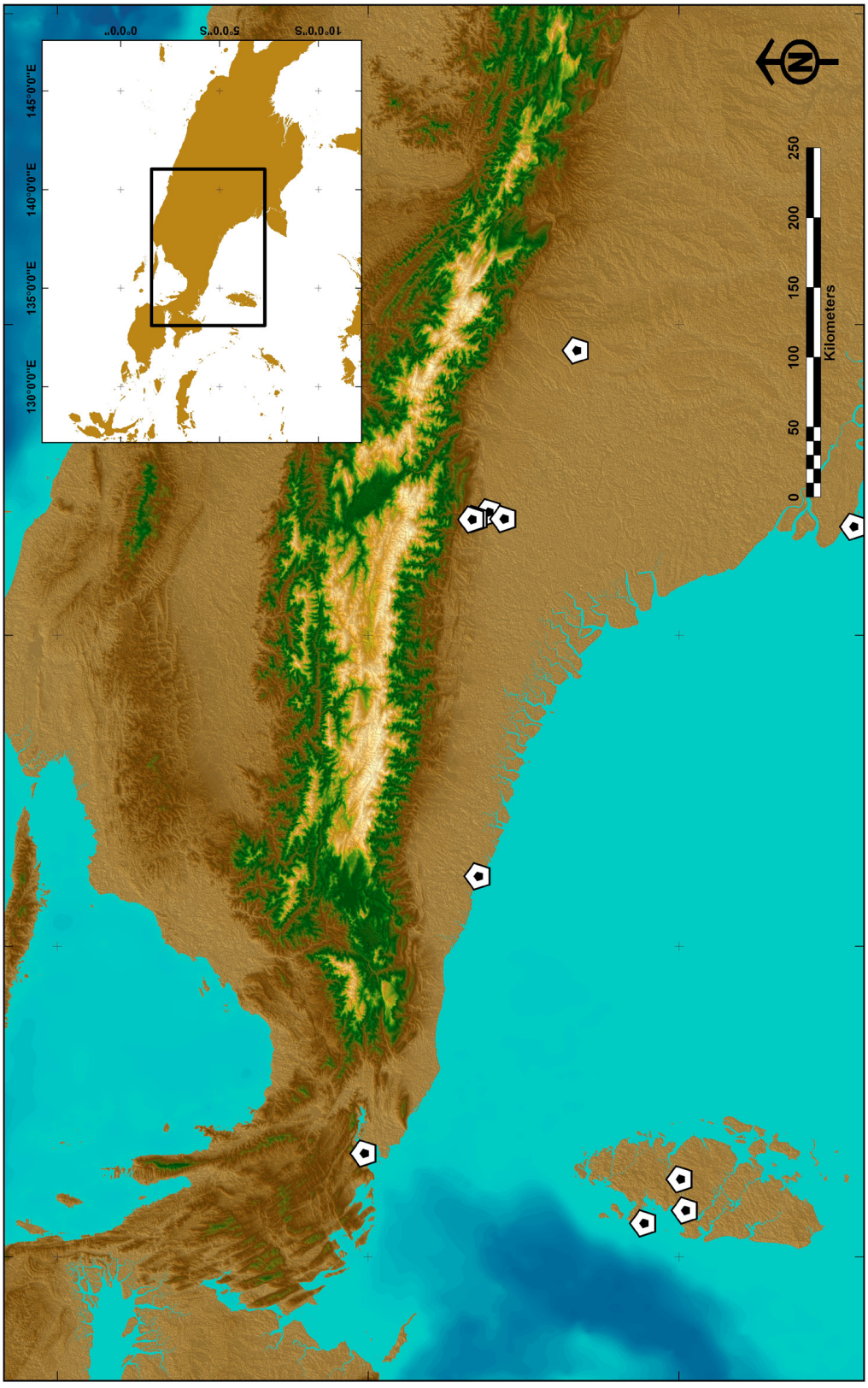
METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, sub-posterior spiniform granules weak to absent, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, sub-posterior spiniform granules absent, medial spiniform granules absent. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus.Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/5; 4–5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, sub-distal, not more than mid-lamella; basal extrusion absent; transverse ridge present and distinct, merging with anterior edge below base of lamellar hook, below base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal ‘spine’ (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed (‘spoon’ shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.
PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.
CARAPACE. Anteromedian surface entirely granular, at least sparsely; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.
MESOSOMA. Tergites I–III, posttergites, mesially smooth, laterally granular; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, longer than wide, approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; 6–7 pectinal teeth.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 100. Distribution map of *Hormurus davydovi* (Birula, 1903).


0
50
100
150
200
250
Kilometers
130°0'0"E
135°0'0"E
140°0'0"E
145°0'0"E

Hormurus dechangei (Becker, 1880)

Ischnurus dechangei Becker, 1880: 143, 144, pl. III, fig. 3

References

Hormurus caudicula: Kraepelin, 1894: 135; Kraepelin, 1899: 155 (part).

Type material (non examined)

Syntypes: PHILIPPINES, Manilla, sex unknown (in MRHN according to Fet (2000) but the specimens could not be found when requested on loan and is probably lost).

Material examined

PHILIPPINES, LUZON, Zambales Mountains, 4 ♀♀, 1 juv. (LM, LP 7789).

Distribution (fig. 101)

Phillipines, Luzon.

Notes

Hormurus dechangei was described from Manilla (Luzon, Philippines) and *H. boholiensis* also occurs in the vicinty (see above). Several specimens recently collected in the Zambales Mountains, a mountain range located on the western side of Luzon Island, were examined in the course of the present work and appeared to be clearly distinct from *Hormurus boholiensis. Hormurus boholiensis* has smooth carapace and tergites whereas the prosomal and tergal cuticle of the Zambales specimens were markedly granular. Thus, the latter are tentatively attributed to *H. dechangei* based on Becker's original description that mentioned a granular carapace and tergites ("Cephalothorax granulé .....; des granulations au bord des Segments abdominaux") and the proximity of the type locality to the Zambales Mountains.

DESCRIPTION. ADULT FEMALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, dark (as dark as tergites). Telson, dark (as dark as metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est–esb* similar to distance *esb–eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb–et* axis; *esb* trichobothrium below *est–et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em–esb* series with four trichobothria in a single group or in two groups [esb_2][esb_1/em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*)

carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in three distinct smooth depressions (one around each trichobothrium). Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence. Tergites I–VII, posttergites with minute spiniform granules, uniformly and sparsely distributed; I–III, posttergites, mesially smooth, laterally granular; IV–VI, posttergites, mesially smooth, laterally granular; VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; three marginal lamellae; fulcrae present; six pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete;

dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, 1–3 pairs of well developed medial granules. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, one pair of well developed sub-posterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

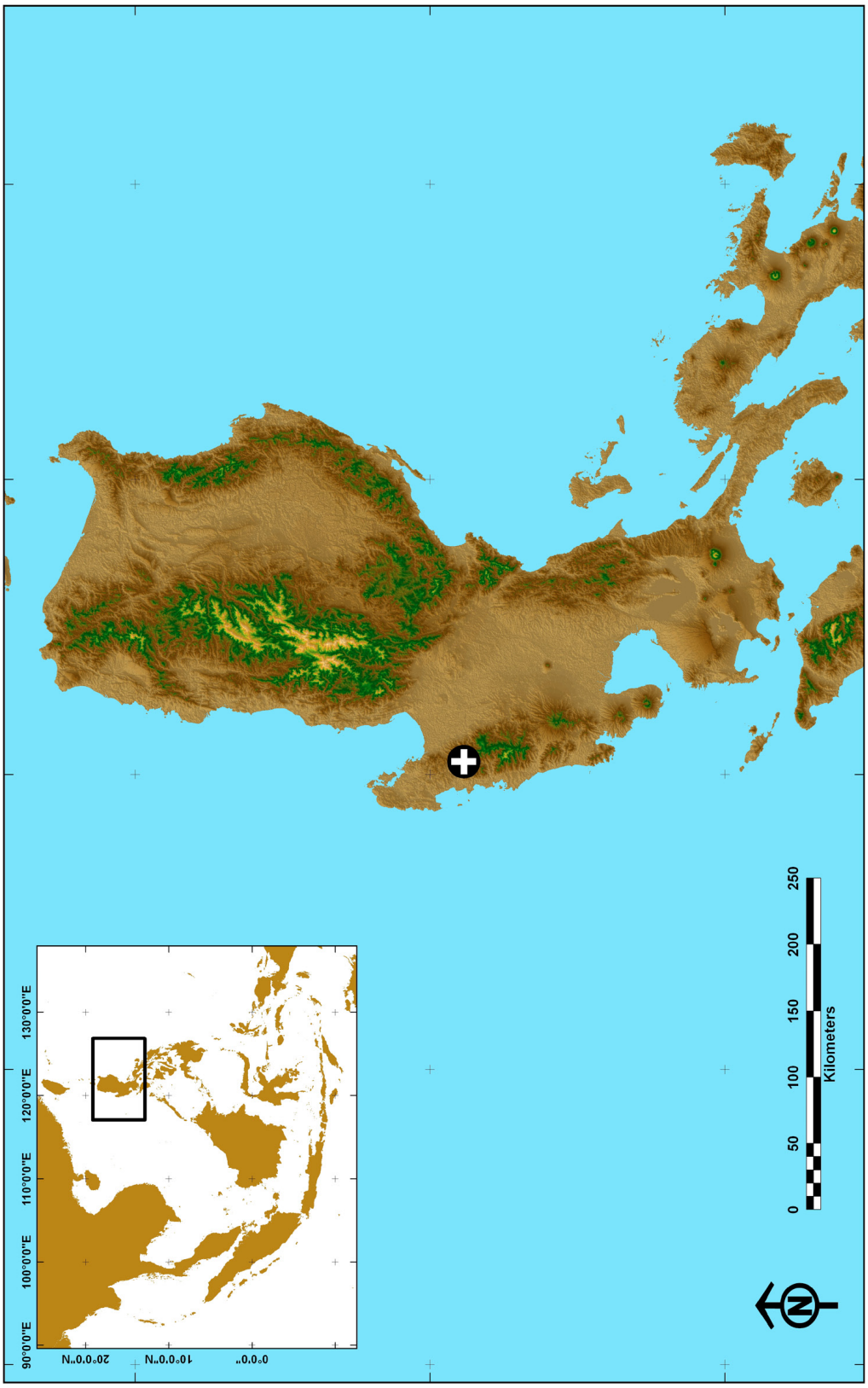
LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 3/4; 4/4; 4/4; 4/4.

JUVENILE MALE.

VENTRAL MORPHOLOGY. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; eight pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 101. Distribution map of *Hormurus dechangei* (Becker, 1880).


0
50
100
150
200
250
Kilometers
90°0'0"E
100°0'0"E
110°0'0"E
120°0'0"E
130°0'0"E
20°0'0"N
10°0'0"N
0°0'0"

Hormurus dodecatrichos, n. sp.

References

Liocheles waigiensis: L. E. Koch, 1977: 169 (part).

Material examined

Holotype: AUSTRALIA, WESTERN AUSTRALIA, KIMBERLEY, Mitchell River NP, trail to Surveyors Pool, 14°38'26.9''Sx125°46'21.9''E, 238 m, granitic boulders beside creek, under rocks and in crevices near the water, 7.VIII.2009, L.Monod, 1 ♂ (WAM). **Paratypes**: same data as holotype, 3 ♀♀, 1 imm. (WAM, MHNG). **Additional material**: AUSTRALIA, WESTERN AUSTRALIA, KIMBERLEY, Crystal Creek, W-side Mitchell Plateau, 14°29'Sx125°48'E, 2.XI.1976, B.R.Wilson & C.Bryce, 1 imm. (WAM 98/1858). N side mouth of Hunter River Estuary, Prince Frederick Harbour, 15º02'Sx125º21'E, STN 2, 25.VII.1977, basalt scree, vine thicket forest, B.R.Wilson, 1 ♂ (WAM 98/1859). 'Jameson Arch', Mount Jameson, 59 km NW of Elizabeth Homestead, 16º03'50''Sx125º41'25''E (WGS84), 28.I.2004, under arch, sandstone boulders, P.G.Kendrick (K14#3), 2 imm. (WAM T54103); 16º03'47''Sx125º41'29''E (WGS84), 28.I.2004, vine thicket, base of slope, sandstone, P.G.Kendrick (K14#1), 1 ♀ (WAM T54104). Kimberley Coastal Camp, opposite Walsh Point, Mitchell Plateau, 14º34'Sx125º55'E, 23–25.IX.1995, on ground at night, A.F.Longbottom (S.1833a), 1 ♀ (WAM 98/1863). Mitchell Plateau, cliff at SE base of Warrender Hill [STN 2], 14º31'54''Sx125º49'29''E, under rock (basalt), vine thicket, 1.XI.1976, B.R.Wilson & C.Bryce, 1 ♀ (WAM 98/1957). Mitchell River NP, top of Enid Falls that drops from a plateau of King Leopold Sandstones into a deep gorge through which Rufous Creek flows southward to join the Roe River, campsite [STN E5 (4)], 15º07'Sx125º33'E, 15.VIII.1974, B.R.Wilson, 1 ♂, 2 ♀♀, 5 imm. (WAM 74/1545-1552); top of Enid Fall (by chopper), 15°07'21.7''Sx125°32'57.7''E, 157 m, vine thicket beside creek, under rocks and in crevices, 6.VIII.2009, L. Monod, 1 ♂, 1 ♀, 2 imm. (WAM, MHNG). Prince Regent Reserve, campsite [STN W6 (1)], 15º34'Sx125º33'E, in a NW/SE 300 m wide valley of King Leopold Sandstones through which Youwanjela Creek runs south-eastwards to meet a major tributary of the upper Prince Regent River, 20.VIII.1974, sandstone, under stone, B.R.Wilson, 1 imm. (WAM 74/1544).

Distribution (fig. 102)

Australia, Western Australia.

Etymology

The name *dodecatrichos* is a construct from the Greek words *dodeka* [twelve] and *thrix* [hair]. It is an invariable noun in apposition and refers to the neobotriotaxic pattern of the retrolateral surface of the pedipal chela manus: the species possess an accessory trichobothrium for a total of twelve instead of the usual eleven trichobothria observed in other species of the genus.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, wider than high (low), overlapping with retrolateral surface of fixed finger (in front of notch); supra-basal notch distinct and deep; supra-basal lobe and corresponding notch with a distinct posterior gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal

than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so; one accessory trichobothria between [*Esb*-*Est*] and Eb_{1-3}. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, as smooth ridge or slightly costate; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina costate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), as smooth ridge or faintly costate. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) carinae; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in three distinct smooth depressions (one around each trichobothrium). Chela, dorsal intercarinal surface entirely and densely granular, very minute spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface smooth or nearly so; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface smooth or nearly so; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface entirely smooth or nearly so; median surface smooth or nearly so; posteromedian surface at least sparsely granular; anterolateral surfaces smooth or nearly so; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence;

pretergites, posterior margin smooth. Tergites I–VI, posttergites, median area smooth, lateral areas at least sparsely granular posteriorly; VII, posttergite, anteromedian area smooth; lateral and posteromedian areas granular; I–VII, posttergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, posttergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; two marginal lamellae; fulcrae present; 8–9 pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, 1–2 pairs of small/vestigial medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with at least few minute/small spiniform granules. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with minute/small spiniform granules. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, with distinct spiniform granules, at least distally; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

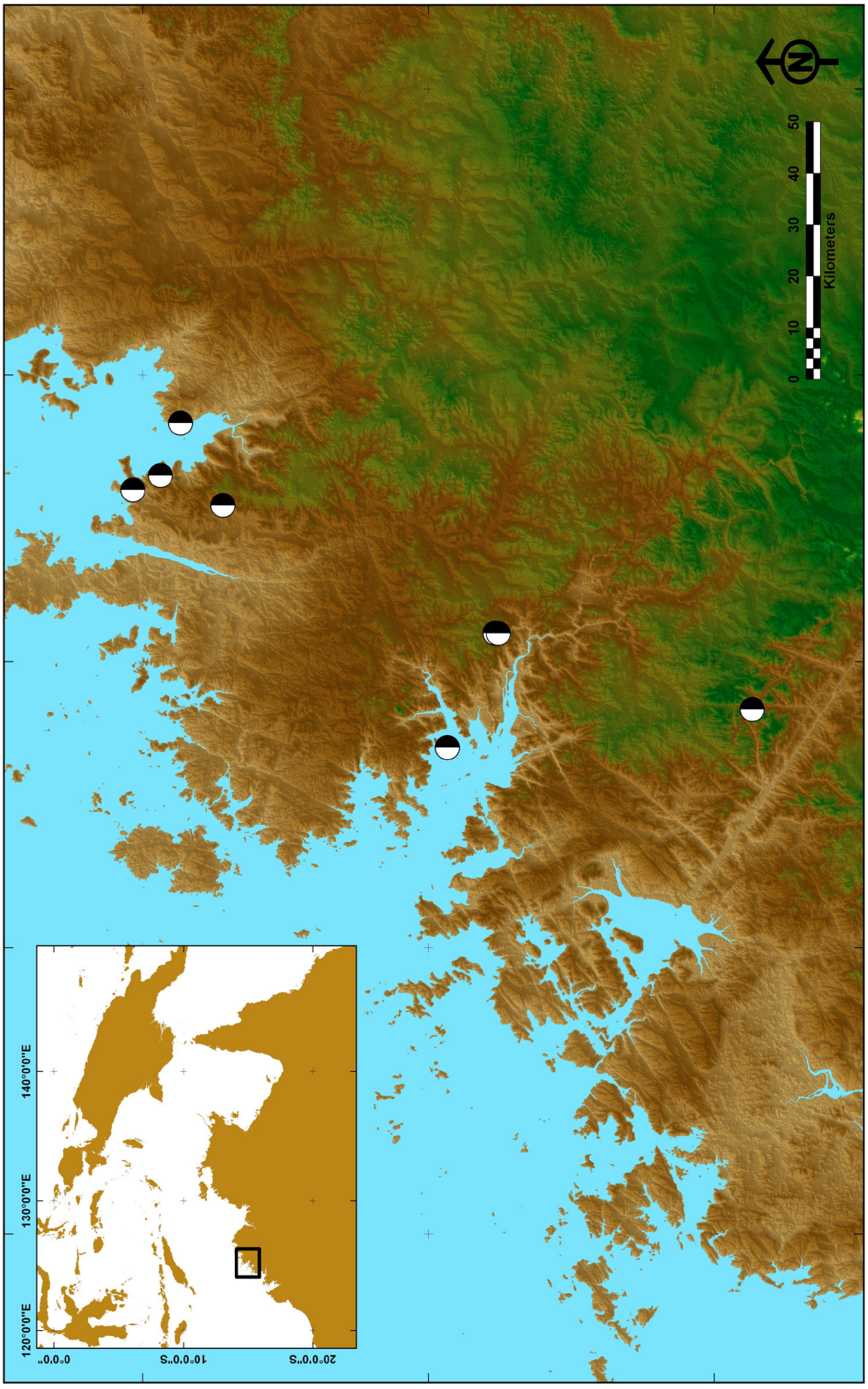
LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 5/5; 5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal ‘spine’ (*ls*) on external

surface absent to weak; accessory hook (*Iah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.
PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.
CARAPACE. Anteromedian surface entirely smooth or nearly so; posteromedian surface smooth or nearly so; anterolateral surfaces smooth or nearly so; mediolateral surface at least sparsely granular; posterolateral surfaces smooth or nearly so.
MESOSOMA. Tergites I–III, posttergites, mesial and lateral areas smooth; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples distinct, uneven surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; seven pectinal teeth.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 102. Distribution map of *Hormurus dodechatrichos* n. sp.


N
0
10
20
30
40
50
Kilometers
120°0'0"E
130°0'0"E
140°0'0"E
0°0'0"
10°0'0"S
20°0'0"S

Hormurus extensus (Locket, 1997), **new combination**

Liocheles extensa (IOS) Locket, 1997: 331 (see Notes).

Synonyms

Liocheles longimanus Locket, 1995: 191–198, figs 1–14; a homonym of *Liocheles australasiae longimanus* (Werner, 1939)

References

Liocheles longimanus: Kovařík, 1998: 134.
Liocheles extensus: Volschenk, Locket & Harvey, 2001: 162.
Liocheles waigiensis (L.E.Koch, 1977; MIS): Volschenk, Locket & Harvey, 2001: 162 (part); Monod & Volschenk, 2004: 675, 686 (part).
Liocheles extensa: Monod, 2000: 86–90, pl. 31, map 10.

Material examined

Holotype: AUSTRALIA, NORTHERN TERRITORY, Oenpelli area, 12º23.5'Sx133º03.5'E, 21–22.VII.1992, A. Wells & J. Webber, 1 ♂ (NTM A000196). **Paratype**: AUSTRALIA, NORTHERN TERRITORY, Kakadu National Park, 13º15.80'Sx139º39.0'E, 20.II.1994, under decaying bark in monsoon vine forest, G. Wallis, 1 ♂ (NTM A000197). **Additional material**: AUSTRALIA, NORTHERN TERRITORY, Gorge NE of Mount Gilruth, 13.02S 133.05E, 10–13.VII.1979, rainforest, G. B. Monteith & D. J. Cook, 1 ♀, 1 imm. (QM-S 23252). Kakadu National Park, Gubara Pools, 12°49'36.8''Sx132°52'49.8''E, 35 m, monsoon forest inside gorge (sandstone), in rock crevices, 20.VIII.2009, L. Monod, 1 ♀ (WAM); Jim Jim Falls, 13º17'Sx132º50'E, 31.V.1992, under rocks, M. S. Harvey & J. M. Waldock, 4 imm. (WAM 98/1852-5); Jim Jim Fall walking track, (1) 13°16'24.3''Sx132°49'56.3''E, 64 m, (2) 13°16'22.2''Sx132°49'55.3''E, 129 m, monsoon forest, in rock crevices, 21–22.VIII.2009, L. Monod, 2 ♂♂, 5 ♀♀, 2 imm. (WAM, MHNG); Koolpin Creek, 13°29'45.6''Sx132°34'29.2''E, 107 m, vine thicket by the side of the creek, in rock crevices, 24.VIII.2009, L. Monod, 3 ♀♀ (WAM, MHNG); Maguk walking trail, 13°19'01.2''Sx132°26'23.4''E, 98 m, monsoon forest by the side of the pools, in rock crevices, 23.VIII.2009, L. Monod, 3 ♂♂, 5 ♀♀, 2 imm. (WAM, MHNG); Radon Gorge, (1) 12°45'02.7''Sx132°54'17.8''E, 86 m, (2) 12°45'10.1''Sx132°54'18.7''E, 65 m, monsoon forest at foothills of sandstone outcrop beside creek, in rock crevices, 20/26.VIII.2009, L. Monod, 3 imm. (WAM).

Distribution (fig. 103)

Australia, Northern Territory.

Notes

Liocheles extensa was introduced as a replacement name for *Liocheles longimanus* Locket, 1995. Fet (2000) indicated that it was incorrectly formed and changed it to a correct masculine form, i.e. 'extensus'.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, conical (as high as wide or higher than wide), overlapping with retrolateral surface of fixed finger (in front of notch); supra-basal notch distinct and deep; supra-basal lobe and corresponding notch with a distinct posterior gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal

lobe absent or at most weakly developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) ca*rin*ae; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in three distinct smooth depressions (one around each trichobothrium). Chela, dorsal intercarinal surface entirely and densely granular, very minute spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, extremely dense, giving tegument sand-like appearance; anteromedian surface, frontal lobes (area I)

smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, posttergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, posttergites with minute spiniform granules; uniformly and sparsely distributed, or extremely densely distributed; III–VII, posttergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; two marginal lamellae; fulcrae present; 7–8 pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, sub-posterior spiniform granules weak to absent, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules obsolete; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, 1–2 pairs of small/vestigial medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventrosubmedian carinae, ridges with at least a few small/medium spiniform granules, subposterior spiniform granules absent; ventrolateral carinae with at least few minute/small spiniform granules. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae, ridges with at least few reduced spiniform granules distally; ventrolateral carinae with minute/small spiniform granules. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half with at least small spiniform granules, with medium spiniform granules more strongly developed than preceding granules (anterior half); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

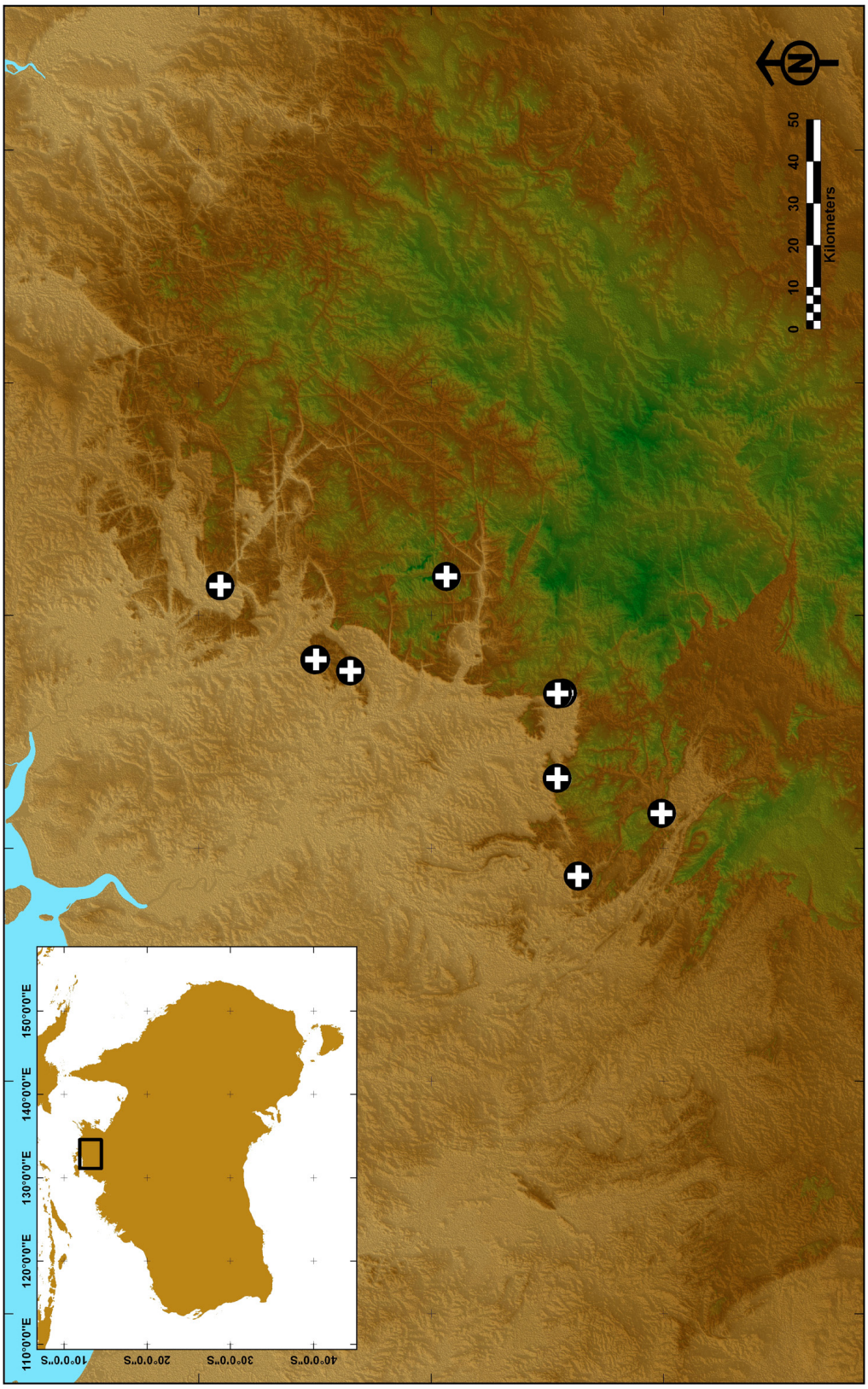
LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/ 4; 5/5; 5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal

lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.
PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.
CARAPACE. Anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.
MESOSOMA. Tergites I–III, posttergites, mesial and lateral areas smooth; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; 6–7 pectinal teeth.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 103. Distribution map of *Hormurus extensus* (Locket, 1997).


N
0
10
20
30
40
50
Kilometers
110°0'0"E
120°0'0"E
130°0'0"E
140°0'0"E
150°0'0"E
10°0'0"S
20°0'0"S
30°0'0"S
40°0'0"S

Hormurus goliath n. sp.

References

Hormurus caudicula karschi (UE) (MIS): Kraepelin, 1899: 155 (part); Kraepelin, 1901: 272 (part); Giltay, 1931: 13, 18, 19 (part).

Hormurus karschii (nec Keyserling, 1885; MIS): Rainbow, 1889: 118; Belfield, 1956: 45.

Liocheles karschii (nec Keyserling, 1885; MIS): L. E. Koch, 1977: 172–175, figs 19, 48, 84, 85, map 10; L. E. Koch, 1977: 877; Monod, 2000: 91–96, pl. 35, map 9 (part); Volschenk, Locket & Harvey, 2001: 162 (part); Monod & Volschenk, 2004: 675, 686 (part).

Liocheles caudicula (nec C. L. Koch, 1867; MIS): Lourenço, 1985: pl. 10, fig. 4; Lourenço, 1989: pl. 6, fig. 4.

Material examined

Holotype: PAPUA NEW GUINEA, MOROBE PROVINCE, Watut, IX.1980, J. K., 1 ♂ (MHNG). **Paratypes**: same data as holotype, 2 ♂♂, 2 ♀♀, 1 ♂ sub. (MHNG); VIII.1980, J. K., 1 ♀, 2 imm. (MHNG); XI.1980, J. K., 1 imm. (MHNG). **Additional material**: MISLABELLED: Efulen, Cameroon, 1 ♂ (NHML 1905.6.13.1). PAPUA NEW GUINEA, early 1943, Capt. Tinkham, 1 ♀ (AMNH); 1 ♂, 4 imm. (NHML). CENTRAL PROVINCE, Madew (=Madiu), Saint Joseph River (=Angabunga River), Sir William Ingram (P), W. Stalker (c.), 1 ♀ (NHML 1908.10.14.1). GULF PROVINCE, Murua (near Kerema), 3 m, 17–18.XII.1964, J. L. Gressitt, 1 ♀ sub, 1 juv. (BPBM); XII.1965, W. Steffan, 1 ♀ (BPBM). MOROBE PROVINCE, Aseki, IX.1980, J. K., 1 ♂, 1 ♀, 1 imm. (MHNG).

Distribution (fig. 104)

Papua New Guinea, Central Province, Morobe Province.

Etymology

Goliath is the name of a Philistine giant and refers to the large size of the species.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, dark (as dark as tergites). Telson, dark (as dark as metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap, or with a distinct posterior gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to $Eb_{1–2}$; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in a single group or in two groups [esb_2][esb_1/$em_{1–2}$]; *eb* series with five trichobothria in two groups [eb_1] and [$eb_{2–5}$] or [eb_1/$eb_{4–5}$] and [$eb_{2–3}$]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal

retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules, granular (at least sparsely), equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina distinct, at least a low ridge or a row of granules, costate or granular; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) c*arin*ae; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface smooth or nearly so; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, with at least few granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules, evenly and sparsely distributed; anteromedian surface entirely granular at least sparsely; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, posttergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, posttergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, posttergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip with a distinct swelling/bulge oriented posteriorly, at least weak, usually more pronouced in ♂. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or

equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; 8–10 pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve), long (at least 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, medial spiniform granules absent. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

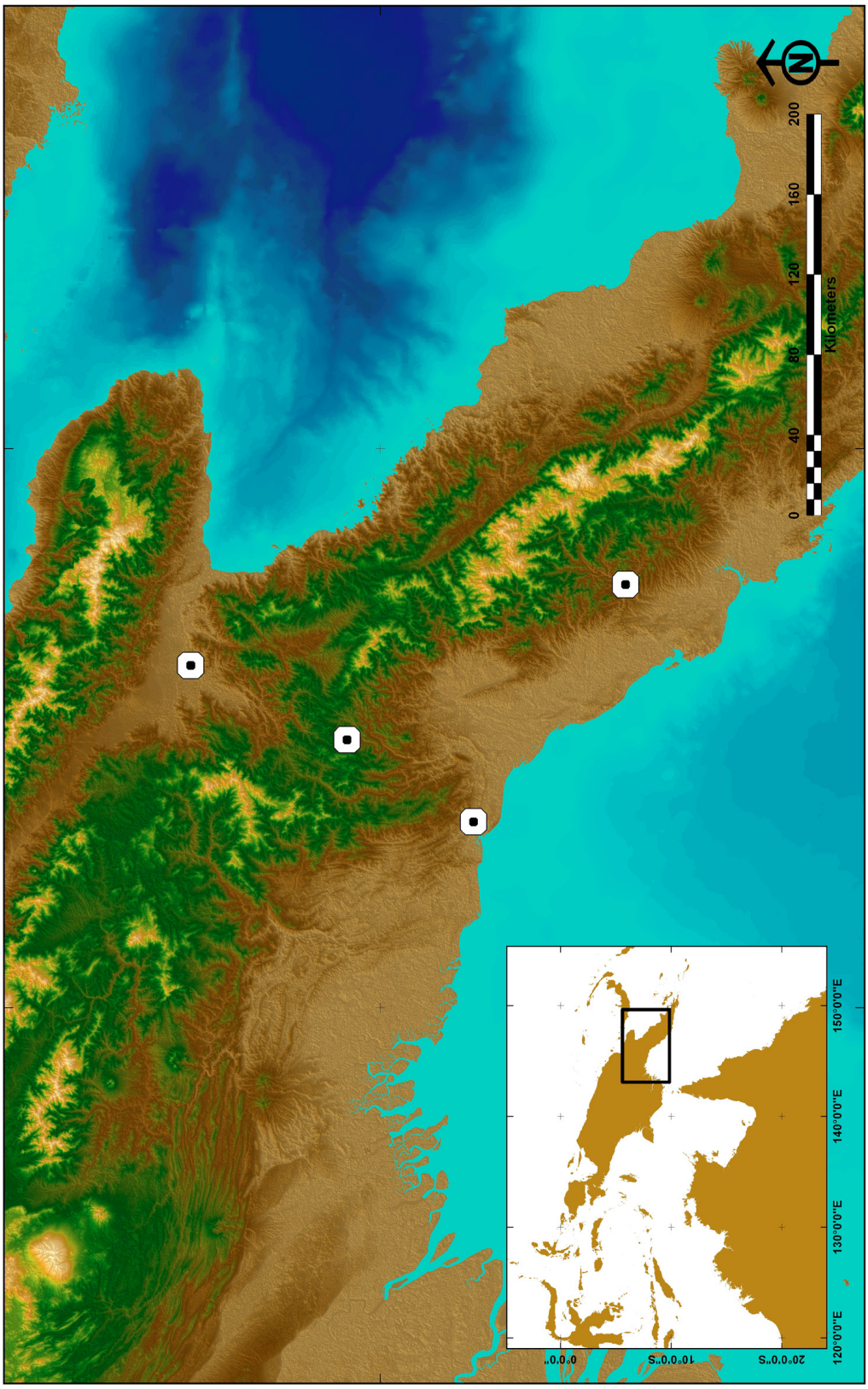
LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/4–5; 4–5/4–5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, sub-distal, not more than mid-lamella; basal extrusion absent; transverse ridge present and distinct, merging with anterior edge below base of lamellar hook, below base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal ‘spine’ (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface present, small to medium, pointing downward. Accessory carinae and accessory crest absent. Basal lobe well developed (‘spoon’ shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part,

forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.
PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.
CARAPACE. Anteromedian surface entirely granular, at least sparsely; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.
MESOSOMA. Tergites I–III, posttergites, mesially smooth, laterally granular; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, longer than wide, approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; eight pectinal teeth.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 104. Distribution map of *Hormurus goliath* n. sp.


N
0
40
80
120
160
200
Kilometers
120°0'0"E
130°0'0"E
140°0'0"E
150°0'0"E

Hormurus halmaherae n. sp.

References

Hormurus caudicula insculpta (ISS): Kraepelin, 1897: 1.
Hormurus caudicula caudicula: Roewer, 1943: 235 (MIS).
Liocheles waigiensis: Kovařík, 2002: 15 (part).

Material examined

Holotype: INDONESIA, MALUKU, HALMAHERA, Ternate, Gilolo, M. Raffray, 1 ♂ (MNHN-RS 0492). **Paratype**: same data as holotype, 1 ♀ (MNHN-RS 0492). **Additional material**: Dodinga, Halmahera, 1 ♀ (ZMB 3144); Bernstein, 1 ♀ (NNHM 41).

Distribution (fig. 105)

Indonesia, Maluku.

Etymology

The name *halmaherae* refers to the Indonesian island where the species was discovered.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, dark (as dark as metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, conical (as high as wide or higher than wide), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb*–*et* axis; *esb* trichobothrium below *est*–*et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in a single group or in two groups [esb_2][esb_1/em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on

proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, posttergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, posttergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, posttergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; seven pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian

carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, medial spiniform granules absent. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/4–5; 4–5/4–5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, sub-distal, not more than mid-lamella; basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent. Accessory carinae accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.

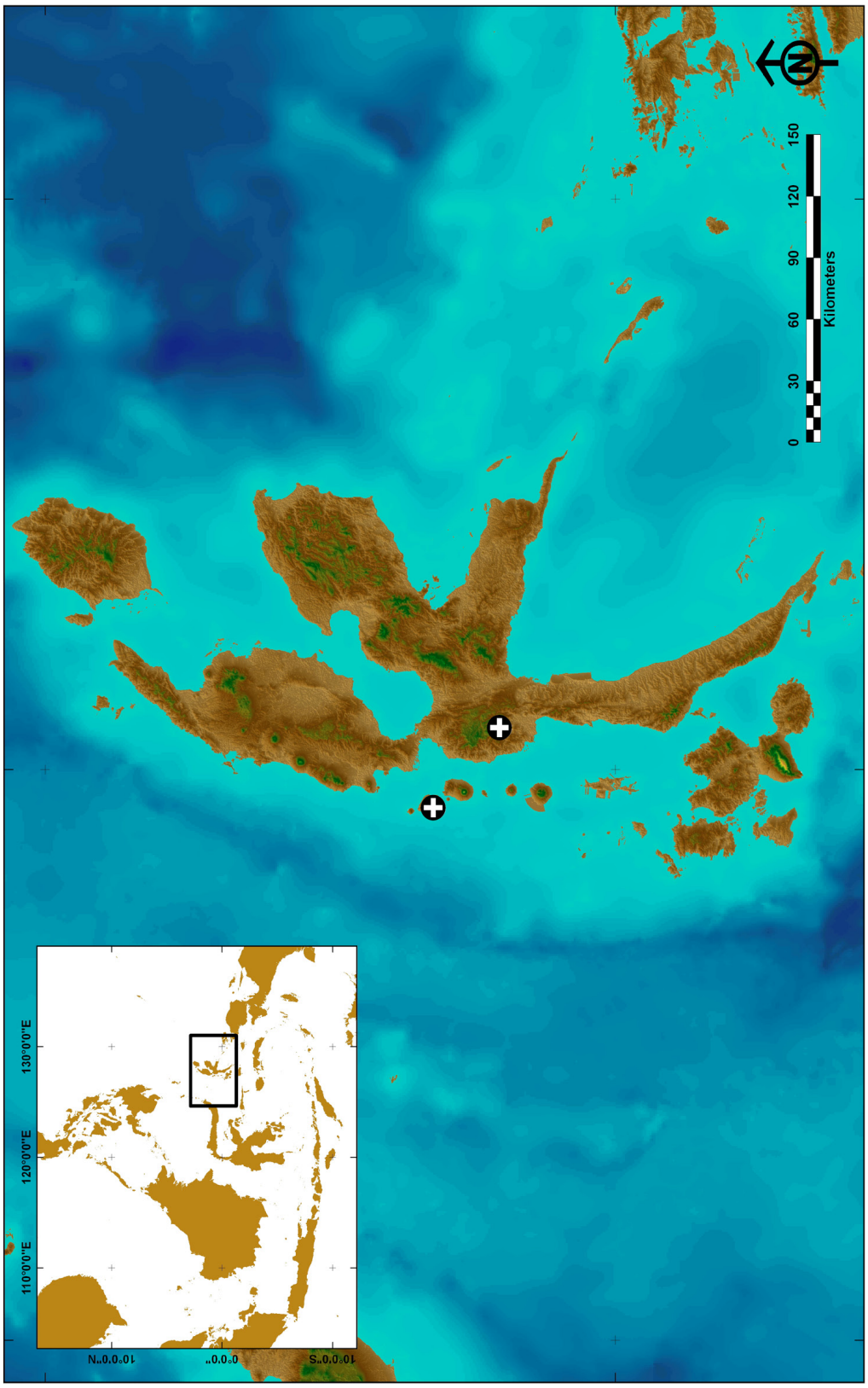
MESOSOMA. Tergites I–III, posttergites, mesial and lateral areas smooth; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.

VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or

wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; seven pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 105. Distribution map of *Hormurus halmaherae* n. sp.


N
0
30
60
90
120
150
Kilometers
110°0'0"E
120°0'0"E
130°0'0"E

Hormurus insculptus Thorell, 1888

Hormurus insculptus Thorell, 1888: 422–426.

Synonyms

Hormurus caudicula novaeguineae Giltay, 1931: 11, 12, 18, 19, fig. 5.

References

Hormurus caudicula (MIS): Kraepelin, 1901: 272 (part); Werner, 1916: 92; Kopstein, 1923: 185, 186, Vachon, 1974: fig. 98.
Hormurus caudicula insculptus: Thorell, 1893: 387; Kraepelin, 1894: 138.
Hormurus caudicula insculpta (ISS): Kraepelin, 1899: 155; Kraepelin, 1901: 272 (part).
Hormurus insculptus: Kopstein, 1921: 140, 141.
Liocheles caudicula insculptus: Takashima, 1945: 96.
Liocheles waigiensis: L. E. Koch, 1977: 166 (part).

Material examined

Lectotypes of *H. insculptus*: INDONESIA, WEST PAPUA, Andai, VIII.1872, L. M. D'Albertis, 1 ♀ (MCSNG). **Paralectotypes of *H. insculptus***: same data as lectotype, 1 juv. (MCSNG). **Holotype of *H. caudicula novaguinea***: INDONESIA, WEST PAPUA, Sakoemi, 11.III.1929, S.A.R. le Prince Léopold, 1 ♂ juv. (MRHN). **Additional material**: INDONESIA, WEST PAPUA: Amberbaki, A. Raffray, 2 ♀♀ (MNHN-RS 0489). Dorey (=Manokwari), Collection Simon 5480, A. Raffray, 4 ♂♂, 1 ♀ (MNHN-RS 0494); 1877, A. Raffray, 4 ♂♂, 2 ♀♀ (MNHN-RS 0495). Manokwari, 12.VI.1903, 1 juv. (NNHM 180); 1.VI.1929, K. P. S. Crane, Field Museum Pacific Expedition 1928–29, 1 ♂ (badly preserved) (AMNH).

Distribution (fig. 106)

Indonesia, West Papua.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four V trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to $Eb_{1–2}$; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [es$b_{1–2}$][$em_{1–2}$]; *eb* series with five trichobothria in two groups [eb_1] and [$eb_{2–5}$] or [eb_1/$eb_{4–5}$] and [$eb_{2–3}$]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*)

carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, close together (less than a diameter), at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, posttergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, posttergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, posttergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; 7–8 pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick

as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, 1–2 pairs of small/vestigial medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half with at least small spiniform granules, with medium spiniform granules more strongly developed than preceding granules (anterior half); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/5; 4–5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, sub-distal, not more than mid-lamella; basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal ‘spine’ (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed (‘spoon’ shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close

to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

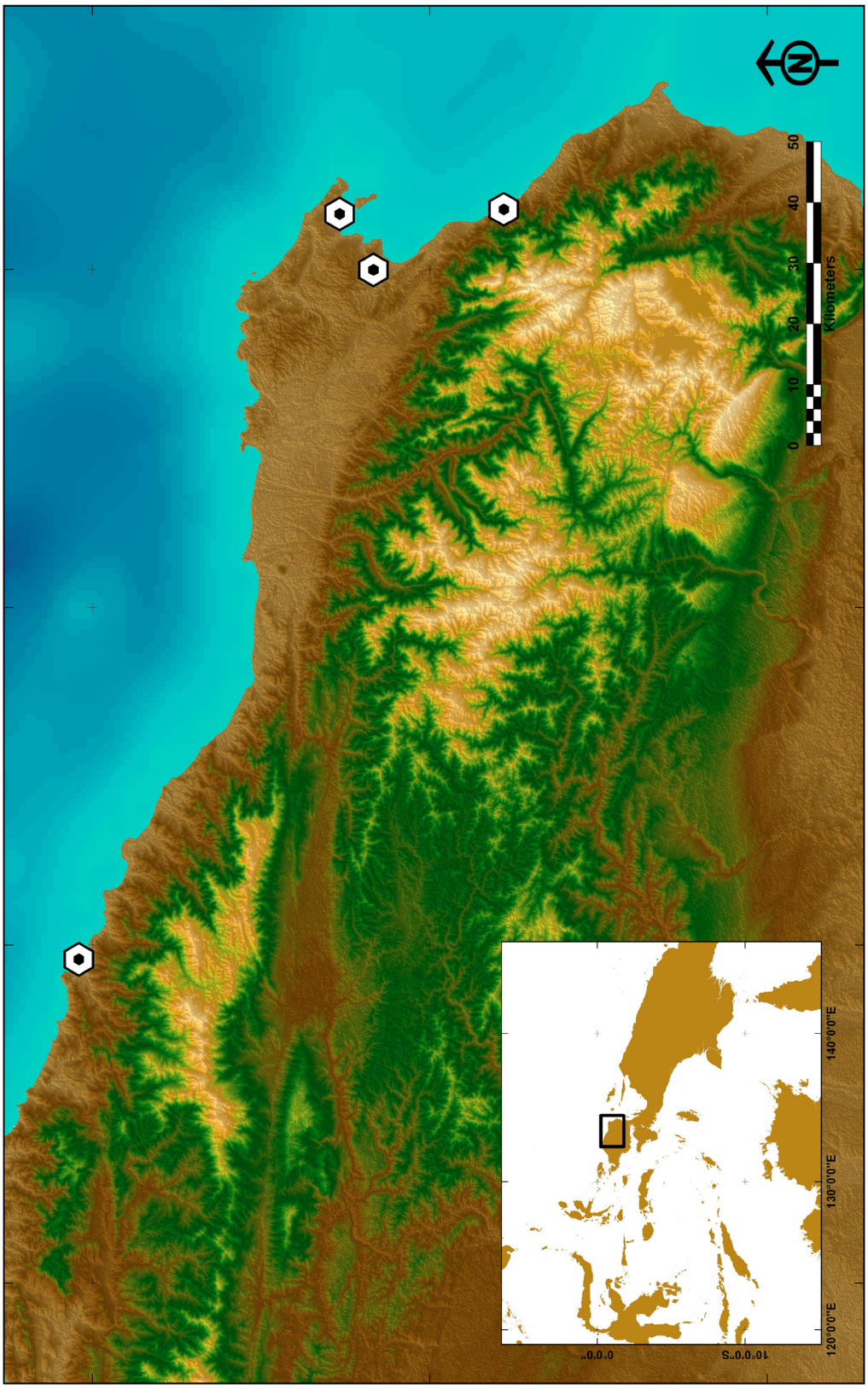
CARAPACE. Anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–III, posttergites, mesial and lateral areas smooth; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.

VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, longer than wide, approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; 7–8 pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 106. Distribution map of *Hormurus insculptus* Thorell, 1888.


N
0
10
20
30
40
50
Kilometers
140°0'0"E
130°0'0"E
120°0'0"E

Hormurus karschii Keyserling, 1885

Hormurus karschii Keyserling, 1885: 31–33, pl. III, fig. 3.

Synonyms

Hormurus karschi (UE) *keyensis* Kraepelin, 1914: 331 (synonymzed by L. E. Koch, 1977: 173).

References

Hormurus waigiensis (nec Gervais, 1843; MIS): Thorell, 1888: 338, 427, 428.
Hormurus caudicula karschii: Kraepelin, 1894: 137.
Hormurus karschi (UE): Kraepelin, 1914: 331; Kopstein, 1921: 138 (part); Kopstein, 1923: 186; Moritz & Fisher, 1980: 316.
Hormurus caudicula karschi (UE): Giltay, 1931: 13, 18, 19 (part).
Hormurus caudicula karschi (UE) *keyensis*: Giltay, 1931: 13, 18, 19.
Hormurus karschi (UE) *keyensis*: Kopstein, 1921: 139.
Liocheles caudicula karshii: Takashima, 1945: 96.
Liocheles caudicula keyensis: Takashima, 1945: 96.
Hormurus karschii keyensis: Weidner, 1959: 101.
Liocheles caudicula karshii: Takashima, 1945: 96.
Liocheles caudicula keyensis: Takashima, 1945: 96.
Liocheles karschii: Kovařík, 1998: 134; Monod, 2000: 41, 91 (part); Monod & Volschenk, 2004: 675, 686 (part).

Material examined

Syntypes of *H. karschii*: INDONESIA, WEST PAPUA, Segaar Bay, Gazelle, 1875, TYPES 2 ♂♂ (pinned specimens) (ZMB 3016). **Syntypes of *H. karschii keyensis***: INDONESIA, MALUKU, Kei Islands, 2.XI.1908, L. Marlon, 1 ♂, 1 ♀ (ZMH). **Additional material**: INDONESIA, MALUKU, Kei Islands, Pres. Captain Lingen (pv), 2 ♀♀ (NHML 1888-100). INDONESIA, WEST PAPUA, Sekroe, 1897, Maarx, S.Schädler, 1 imm. (NNHM 253); 1 ♂, 2 ♀♀, 2 imm. (NNHM 254).

Distribution (fig. 107)

Indonesia, Maluku, West Papua.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, dark (as dark as tergites). Telson, dark (as dark as metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, conical (as high as wide or higher than wide), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two

groups [eb_1] and [$eb_{2–5}$] or [eb_1/$eb_{4–5}$] and [$eb_{2–3}$]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules, granular (at least sparsely), equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina distinct, at least a low ridge or a row of granules, costate or granular; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface*,* area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules, evenly and sparsely distributed; anteromedian surface entirely granular at least sparsely; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, posttergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, posttergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, posttergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of

coxa of leg IV) short, distal edge not reaching to distal edge of coxa; three marginal lamellae; fulcrae present; 10–11 pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve), long (at least 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, medial spiniform granules absent. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

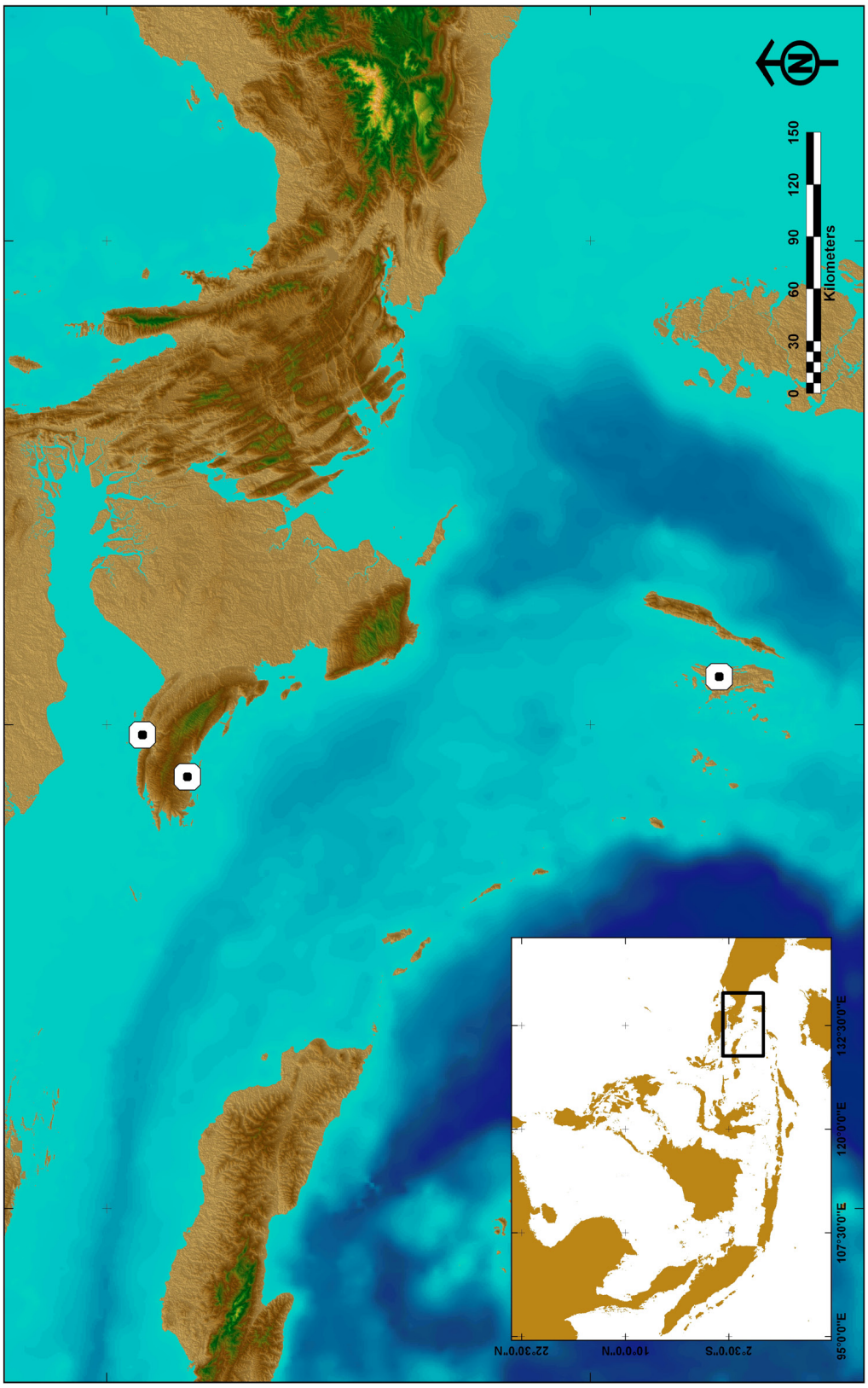
LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 5/5; 5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, sub-distal, not more than mid-lamella; basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, below base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal ‘spine’ (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface present, small to medium, pointing downward; accessory carinae and accessory crest absent. Basal lobe well developed (‘spoon’ shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle

with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.
PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.
CARAPACE. Anteromedian surface entirely granular, at least sparsely; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.
MESOSOMA. Tergites I–III, posttergites, mesially smooth, laterally granular; IV–VI, posttergites, mesially smooth, laterally granular; VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, longer than wide, approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; 9–10 pectinal teeth.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 107. Distribution map of *Hormurus karschii* Keyserling, 1885.


N
0
30
60
90
120
150
Kilometers
95°0'0"E
107°30'0"E
120°0'0"E
132°30'0"E
2°30'0"S
10°0'0"N
22°30'0"N

Hormurus litodactylus (Monod & Volschenk, 2004), **new combination**

Liocheles litodactylus Monod & Volschenk, 2004: 677–684, figs 2–4, 5a, 6–8.

Material examined

Holotype: AUSTRALIA, N QUEENSLAND, Mount Pieter Botte, 16º04'S 145º24'E, 950 m, 21.XI.1993, G. B. Monteith, H. A. Janetzki, L. Roberts & D. J. Cook, 1 ♂ (QM-S48320). **Paratypes**: same data as holotype, 3 ♀ (QM-S22452); Mount Pieter Botte, 16º04'S 145º24'E, 800–900 m, 9.XII.1993, G. B. Monteith, 2 ♀ (QM-S35476); Roaring Meg Valley, 16º04'S 145º25'E, 720 m, 22.XI.1993, G. B. Monteith, H. A. Janetzki, L. Roberts & D. J. Cook, 1 ♂, 2 sub. ♂, 1 ♀ (QM-S35475). **Additional material**: WITHOUT LOCALITY DATA: 2 ♀♀ sub., 1 juv. (QM-S 48314). AUSTRALIA, NE QUEENSLAND: Daintree National Park, Mount Sorrow ridge walk, (1) 16°04'38.2''Sx145°26'21.8''E, 700 m, (2) S 16°04'37.2''Ex145°26'31.3'', 638 m, (3) 16°04'37.0''Sx145°26'19.5''E, 699 m, 7.XII.2004, highland rainforest (very humid, misty, cool), under stones, in between roots of trees. L. Monod, 6 ♂♂, 5 ♀♀ (LM-LP 5559). 4.5–5.0 km W of Cape Tribulation (Top Camp), 760–780 m, 27.IX–7.X.1982, G. Monteith, D. Yeates & G. Thompson, 1 juv. (QM-S 17212); 1 juv. (QM-S 17173). Granite Outcrops, 0.5 km E Mount Pieter-Botte, 780 m, 5.X.1982, G. B. Monteith & D. Yeates, 1 ♀ sub. (QM-S 17171). Mc Dowall Range, 17 km N of Daintree, 600 m, 27.XI.1985, G. Monteith & D. Cook, 1 juv. (QM-S 17193). Mount Halcyon, 16°03'Sx145°45'E, 870 m, 22–24.XI.1993, G. B. Monteith, D. J. Cook, H. A. Janetzki & L. Roberts, 1 ♂ (QM-S 48321); 1 ♀, 2 ♂♂ sub., 1 juv. (QM-S 22453). Mount Hemmant, 16°07'S 145°25'E, 1050 m, 25–27.XI.1993, G. B. Monteith, D. J. Cook, H. A. Janetzki & L. Roberts, 1 ♂, 2 ♂♂ sub. (QM-S 35474). Thornton Peak, via Daintree, 200–900 m, 27.IX.1984, G. B. & S. R. Monteith, 1 ♀ (QM-S 17194).

Distribution (fig. 108)
Australia, Queensland.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe weakly developed, low hump, or absent, margin straight or nearly so, at most a low hump. Supra-basal notch: distinct but shallow, or absent; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe absent or at most weakly developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*)

carina present at least as a faint ridge or a distinct row of granules, granular (at least sparsely), equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, posttergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, posttergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, posttergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; two marginal lamellae; fulcrae present; 6–7 pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent

or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, medial spiniform granules absent. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae, ridges with at least a few small/medium spiniform granules, subposterior spiniform granules absent; ventrolateral carinae with at least few minute/small spiniform granules. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae, ridges with at least few reduced spiniform granules distally; ventrolateral carinae with minute/small spiniform granules. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, with distinct spiniform granules, at least distally; ventrolateral carinae present and distinct, anterior half with at least few small spiniform granules, posterior half with at least small spiniform granules, with small/vestigial spiniform granules not noticeably larger than preceding granules (anterior half); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 3/4; 3/4; 4/4; 4/4.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with base of lamellar hook, sometimes slightly below, above tip of distal lobe. Distal lobe well developed, forming a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); posteromedian surface at least

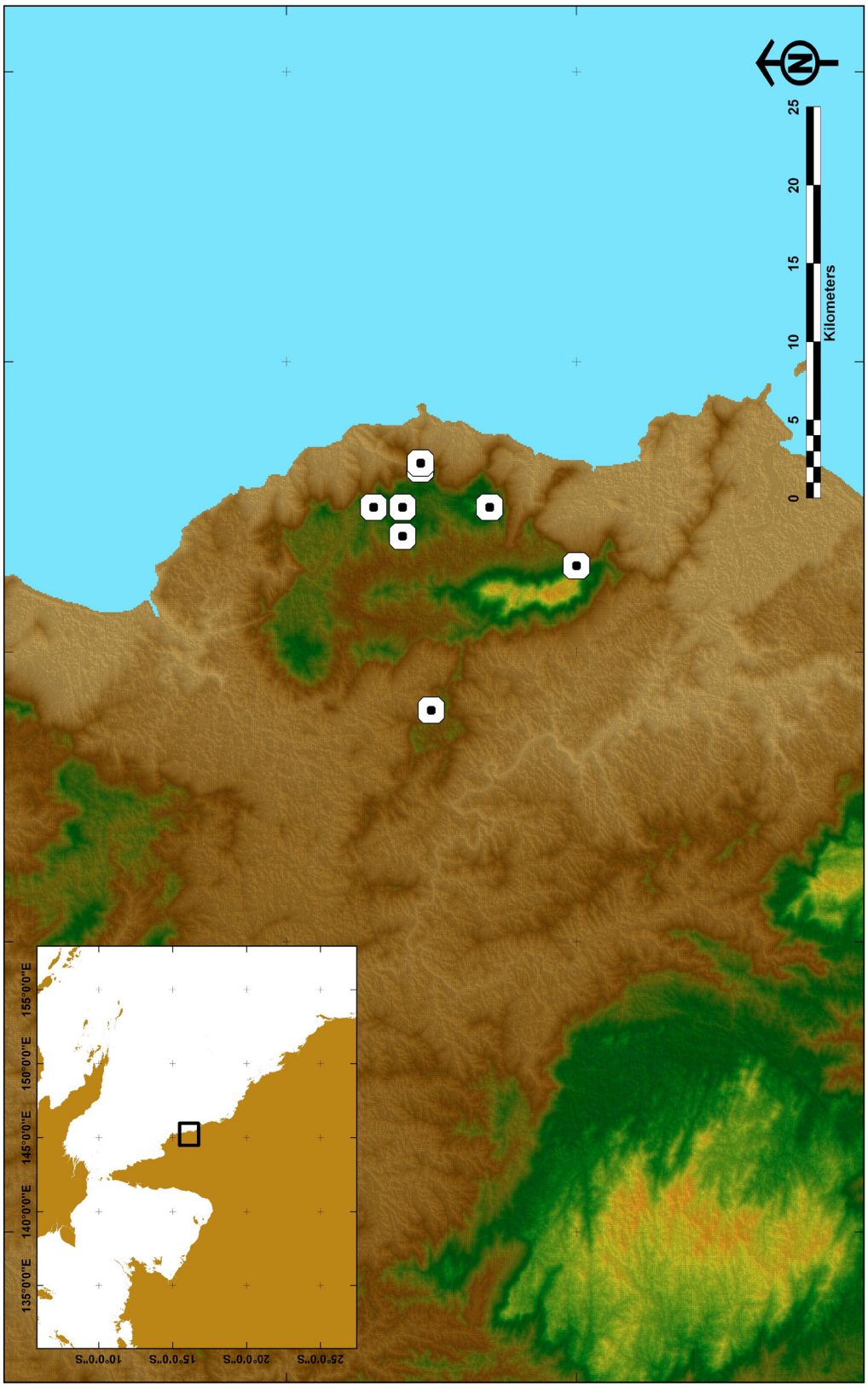
sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces smooth or nearly so.

MESOSOMA. Tergites I–III, posttergites, mesial and lateral areas smooth; IV–VI, posttergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples distinct, uneven surface.

VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; 5–6 pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. TELSON. Vesicle unmodified.

Fig. 108. Distribution map of *Hormurus litodactylus* (Monod & Volschenk, 2004).


N
0
5
10
15
20
25
Kilometers
135°0'0"E
140°0'0"E
145°0'0"E
150°0'0"E
155°0'0"E
10°0'0"S
15°0'0"S
20°0'0"S
25°0'0"S

Hormurus macrochela, n. sp.

References

Liocheles waigiensis (rec L. E. Koch, 1977; MIS): Volschenk, Locket & Harvey, 2001: 162 (part).

Material examined

Holotype: AUSTRALIA, NE QUEENSLAND, Palm Island, site 4, 18º44'Sx146º35'E, 100 m, rainforest. 22.II.2001, G. B. Monteith (8325), 1 ♂ (QM-S 59212). **Paratypes:** AUSTRALIA, NE QUEENSLAND, Palm Island, site 1, 18º45'Sx146º36'E, 450 m, rainforest, 20–21.II.2001, G. B. Monteith (8323), 1 ♂, 1 ♀ (QM-S 59206). **Additional material:** Magnetic Island, walking track Nelly bay to Arcadia, vine forest with lots of big granite boulders, along a dry creek, 28–29.XI.2004, 41 m, 19°08'33.7''Sx146°50'43.4''E, in rock crevices (very narrow or in between stones), R. Wyss & L. Monod, 5 ♂♂, 8 ♀♀, 2 imm. (LM; LP 5555).

Distribution (fig. 113)

Australia, Queensland.

Etymology

The name *macrochela* is a construct from the Greek words *makros* [long] and *chele* [claw]. It is an invariable noun in apposition and refers to the extreme elongation of the male pedipalps.

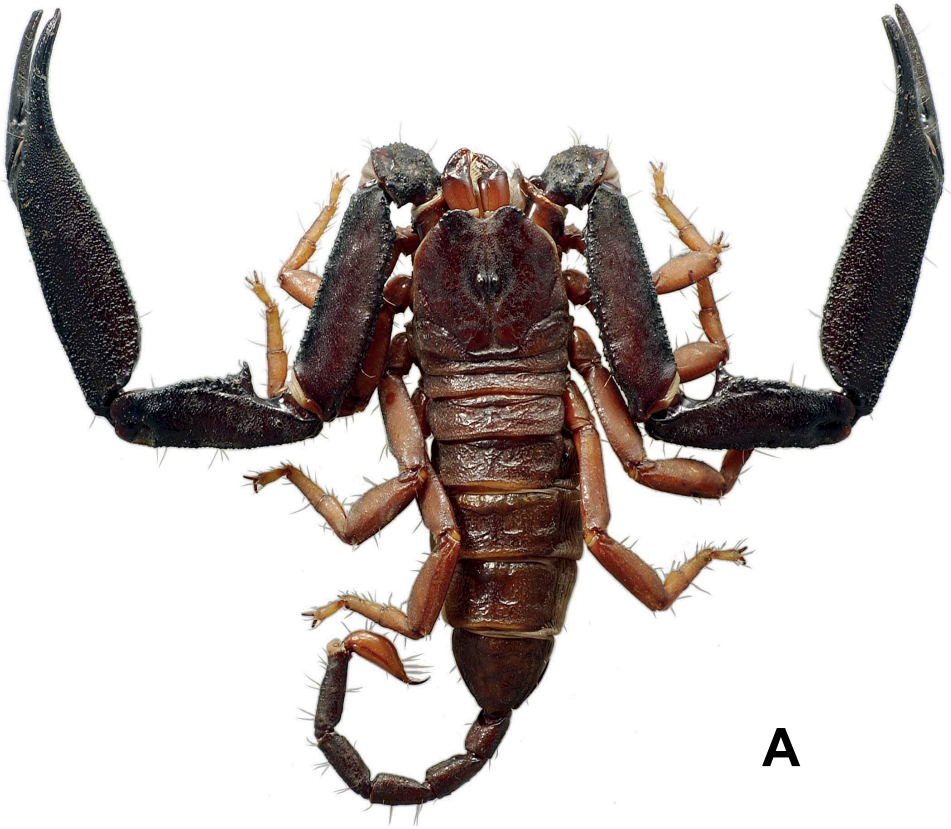
DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

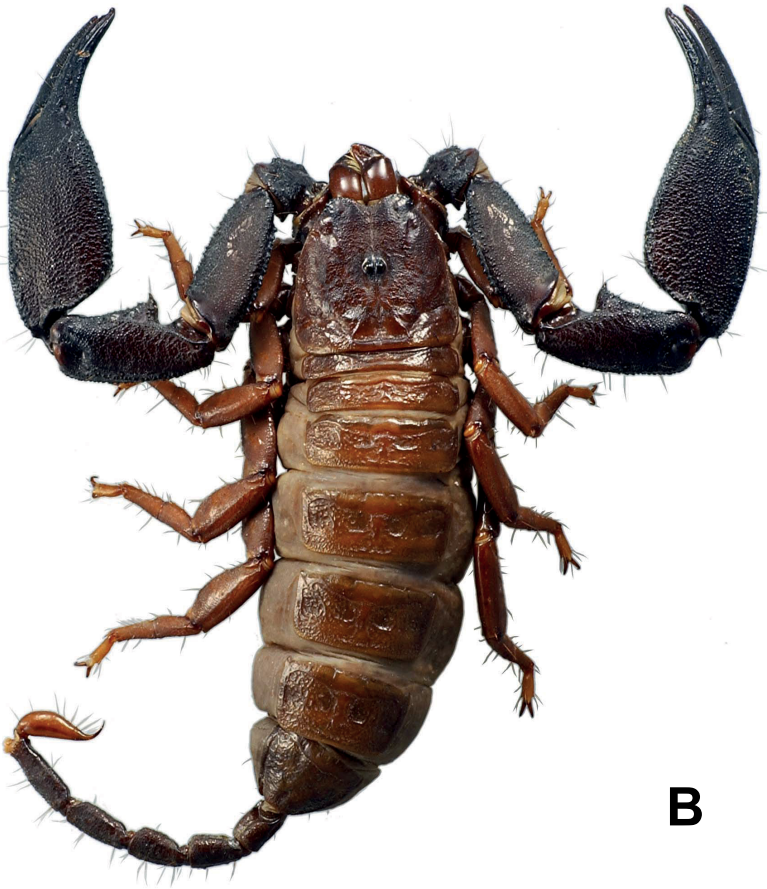
CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth; wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY (fig. 107). Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* tri*c*hobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est–esb* greater than distance *esb–eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb–et* axis; *esb* trichobothrium in line with *est–et* axis, in proximal region of fixed finger; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em–esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or 2 groups [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules, granular (at least sparsely or faintly), equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming a single large spine;

Fig. 109. *Hormurus macrochela* n. sp., habitus. A, male holotype, dorsal aspect. B, female paratype, dorsal aspect.

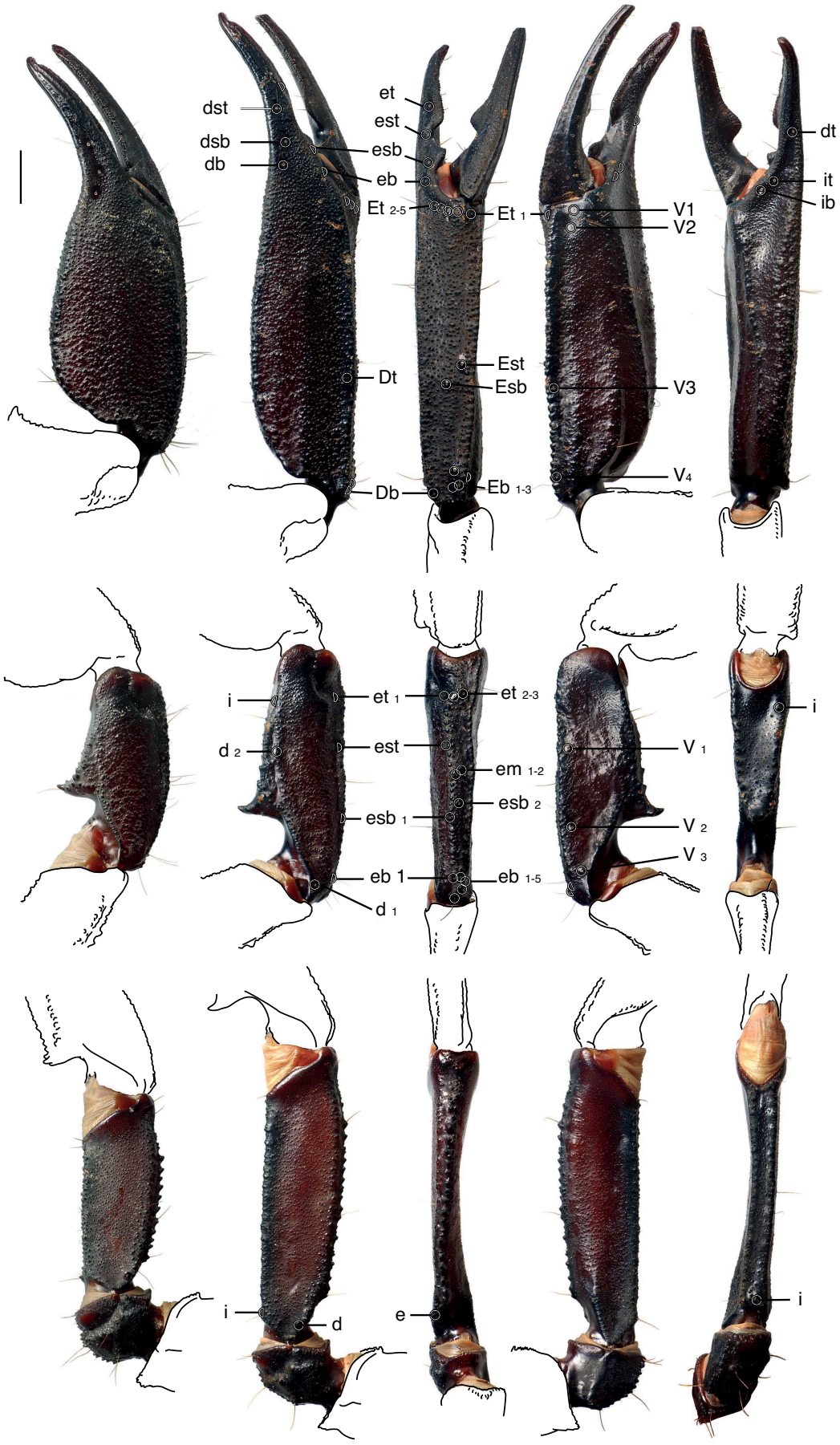


A



B

Fig. 110. *Hormurus macrochela* n. sp., male holotype, pedipalp with trichobothrial pattern. A, chela, dorsal aspect. B, idem, external aspect. C, idem, ventral aspect. D, femur and patella, dorsal aspect. E, idem, external aspect. F, idem, ventral aspect. Scale line, 3 mm.


dst
dsb
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Eb 1-3
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prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in three distinct smooth depressions (one around each trichobothrium). Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

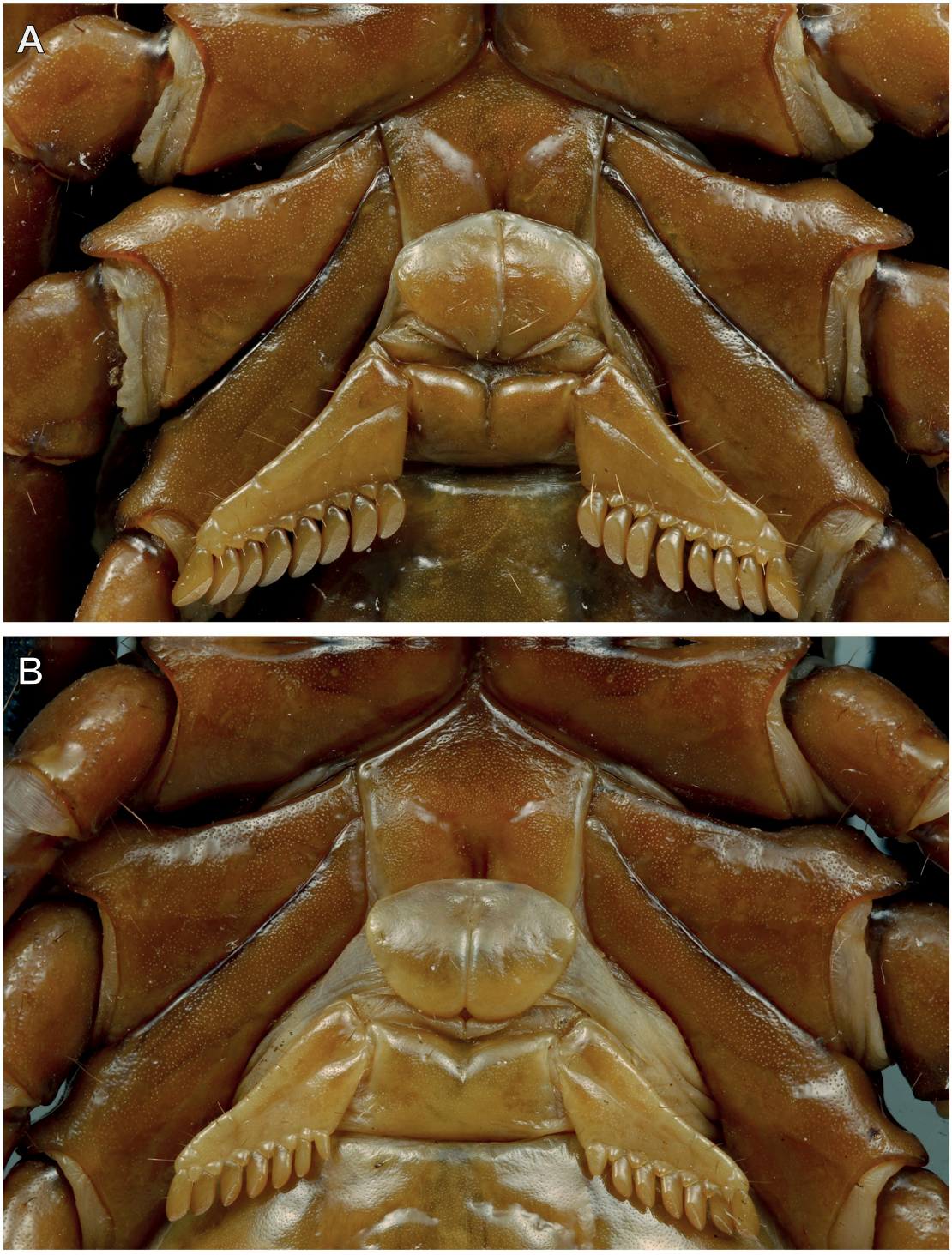
CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM (fig. 111A), shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES (fig. 111A), length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; eight pectinal teeth long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA (fig. 112). Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and

Fig. 111. *Hormurus macrochela* n. sp., pectines and genital opercula, ventral aspect. A, male holotype. B, female paratype.


A
B

distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, 1–2 pairs of small/vestigial medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae, ridges with at least a few small/medium spiniform granules, subposterior spiniform granules absent; ventrolateral carinae with at least few minute/small spiniform granules. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae, ridges with at least few reduced spiniform granules distally; ventrolateral carinae with minute/small spiniform granules. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, with distinct spiniform granules, at least distally; ventrolateral carinae present and distinct, anterior half with at least few small spiniform granules, posterior half with at least small spiniform granules, with medium spiniform granules more strongly developed than preceding granules (anterior half); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 5/5; 5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface present, large; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

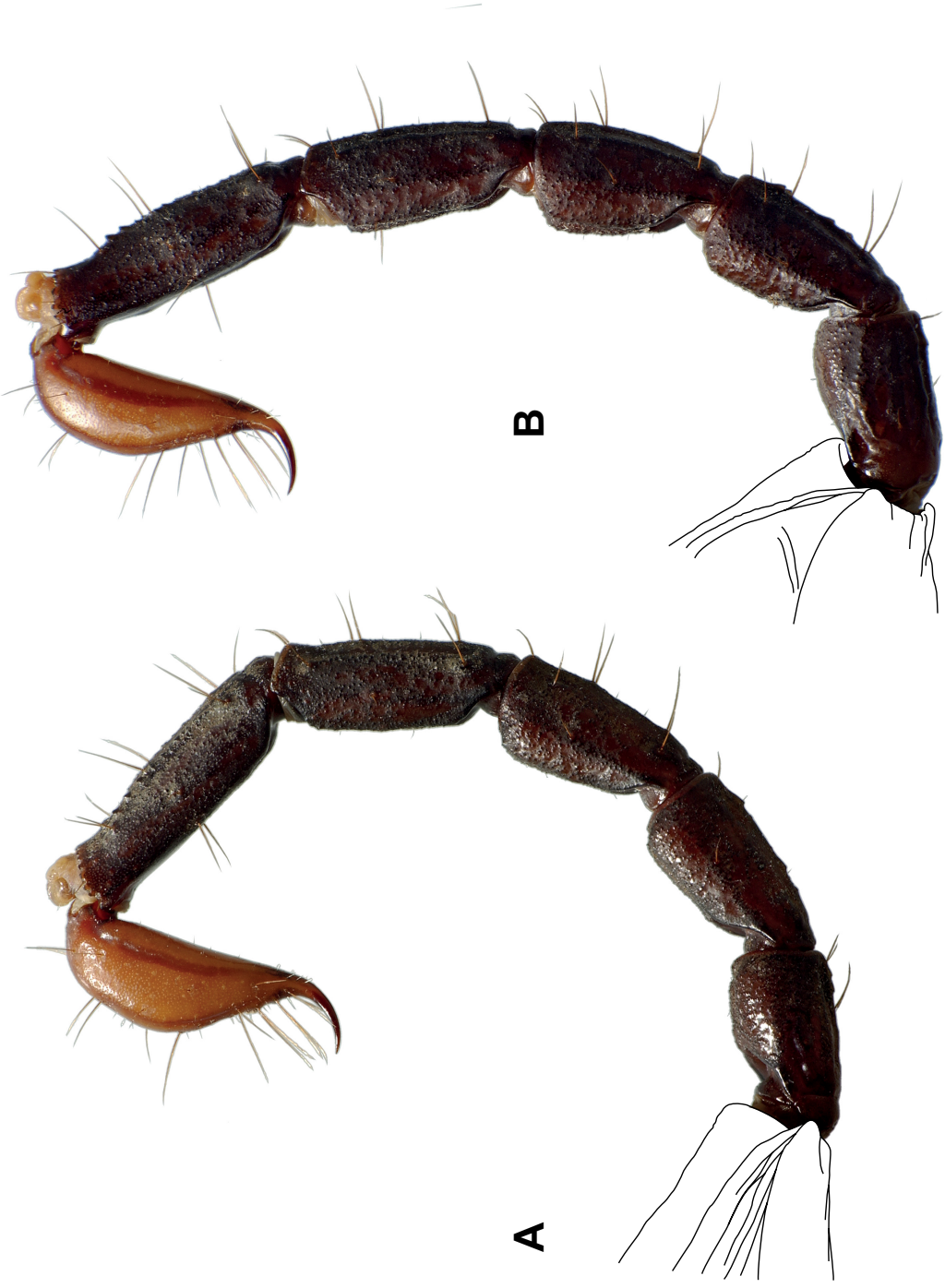
ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP (fig. 110). Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–III, post-tergites, mesially smooth, laterally granular; IV–VI, post-

Fig. 112. *Hormurus macrochela* n. sp., metasoma, lateral aspect. A, male holotype. B, female paratype.


B
A

tergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.

VENTRAL MORPHOLOGY (fig. 111B). GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa. Seven pectinal teeth.

METASOMA (fig. 112). Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 113. Distribution map of *Hormurus macrochela* n. sp.

N
0
6
12
18
24
30
Kilometers
130°0'0"E
140°0'0"E
150°0'0"E
160°0'0"E
0°0'0"
10°0'0"S
20°0'0"S

Hormurus microkypheus, n. sp.

References

Liocheles karschii: L. E. Koch, 1981: 877 (part) (MIS); Locket, 1995: 197, fig. 14a, tab. 1 (part); Volschenk, Locket & Harvey, 2001: 162 (part); Monod, 2000: 41, 91–95, map 11 (part).

Material examined

Holotype: AUSTRALIA, QUEENSLAND, TORRES STRAIT, Murray Island, Torres Strait, VII–VIII.1974, H. Heatwole & E. Cameron, 1 ♂, (WAM 98/1869-72). **Paratypes**: Same data as holotype, 1 ♀ (USNM 00949); 1 ♀, 1 ♂ sub., 1 ♂ juvenile (WAM 98/1869-72). Dauan Island, 30.VII.1975, forest, H. Heatwole, 1 juv. (WAM 98/1864). Gabba Island, 30.VII.1975, H. Heatwole, 1 juv. (WAM 98/1865). Mabwiag Island, Murray Island, 1 ♂ sub. (NHML); A. C. Haddon, 1 ♀ (NHML 1891.9.5.1). Waier Islet, 3.VIII.1974, H. Heatwole, 1 ♀, 1 ♀ sub. (WAM 98/1867-8).

Distribution (fig. 114)

Australia, Queensland

Etymology

The name *microkypheus* is a construct from the Greek words *mikros* [small, little] and *kyphos* [bend, hump]. It refers to the weakly developed, low supra-basal notch on the Denticulate edge of the movable finger of the male pedipalp chela.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, dark (as dark as tergites). Telson, dark (as dark as metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe weakly developed, low hump; gently rounded dorsally and lacking a sharp conical tooth; wider than high (low), not overlapping with fixed finger; supra-basal notch distinct but shallow; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, low/reduced; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to $Eb_{1–2}$; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in a single group or in two groups [esb_2][esb_1/$em_{1–2}$]; *eb* series with five trichobothria in two groups [eb_1] and [$eb_{2–5}$] or [eb_1/$eb_{4–5}$] and [$eb_{2–3}$]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules, granular (at least sparsely or faintly), equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian

(*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) ca*rina*e; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface smooth or nearly so; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, with at least few granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules, evenly and sparsely distributed; anteromedian surface entirely granular at least sparsely; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip with a distinct swelling/bulge oriented posteriorly, at least weak, usually more pronouced in ♂. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; ten pectinal teeth long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve), long (at least 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral

and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, medial spiniform granules absent. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/4; 4–5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, sub-distal, not more than mid-lamella; basal extrusion absent; transverse ridge present and distinct, merging with anterior edge below base of lamellar hook, below base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

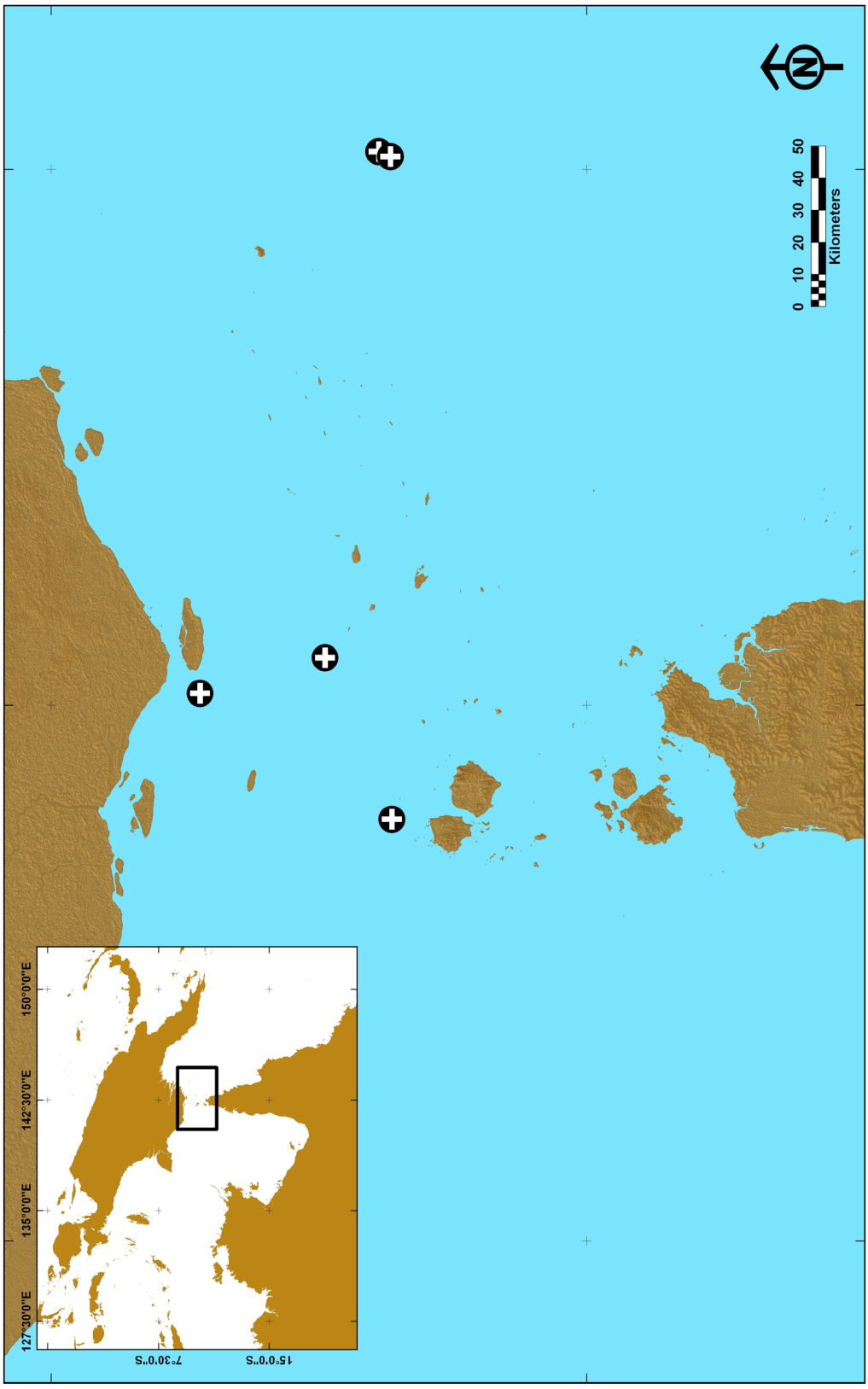
ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface entirely granular, at least sparsely; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–III, post-tergites, mesial and lateral areas smooth; IV–VI, post-tergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, longer than wide, approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; 9–10 pectinal teeth.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 114. Distribution map of *Hormurus microkipheus* n. sp.


N
0 10 20 30 40 50
Kilometers
127°30'0"E
135°0'0"E
142°30'0"E
150°0'0"E
7°30'0"S
15°0'0"S

Hormurus muralagi n. sp.

References

Hormurus caudicula var. insculpta: Kraepelin, 1901: 272 (part) (MIS).

Material examined

Holotype: AUSTRALIA, QUEENSLAND, TORRES STRAIT, Prince of Wales Island, 30.VI.1976, under rock on rocky hillside, savannah woodland, E. Cameron, 1 ♂ (NMNH 00306). **Paratypes:** Prince of Wales Island: 8.II.1975, savannah woodland under stones on rocky outcrops, E. Cameron, 1 juv. (WAM 98/1837); 13.II.1975, closed forest and adjacent edge of savannah, E. Cameron, 2 ♀♀ (WAM 98/1838-9); 16.II.1975, SE side of island, closed forest, E. Cameron, 1 ♂ sub. (WAM 98/1840). **Additional material:** Badu Island, 18.XII.1976, under rocks on hillside, vine thicket, H. Heatwole *et al.*, 1 ♀, (NMNH 00306); 18.XII.1976, rocky area with scrub vegetation, H. Heatwole *et al.*, 1 juv. (NMNH 00306); 19.XII.1976, hillside vine forest, H. Heatwole, 1 ♀, 1 juv. (NMNH 00306). Friday Island, Torres Strait, 5.VII.1976, E. Cameron, under rock, on rocky hillside, vine woodland, 1 juv. (NMNH 00306). Hammond Island, 4–8. VII.1974, H. Heatwole & E. Cameron, 2 ♀♀, 2 juv. (WAM 98/1828-31). Moa Island, 25.II.1975, closed forest, general collecting, E. Cameron, 1 juv. (WAM 98/1866). Thursday Island: H. W. Lix (1849-91), 1 ♂ (MNHN-RS 0487); O. Finsch, 1 ♂, 4 ♀♀, 3 sub., 3 juv. (ZMB 7543, 7412); 18.VII.1969, H. Heatwole, 1 ♂ sub. (WAM 98/1845); 29.VII.1975, H. Heatwole, 1 ♀ sub., 1 juv. (WAM 98/1848-9); 15.XII.1976, under rock on grassy slope, H. Heatwole *et al.*, 1 juv. (NMNH 00306); 3.VII.1979, H. Heatwole & E. Cameron, 1 ♂, 1 ♀ sub. (WAM 98/1846-7).

Distribution (fig. 115)

Australia, Queensland.

Etymology

The name *muralagi* refers to the Aboriginal tribe Muralag (Tindale, 1974) whose people inhabit the Prince of Wales Island and southwestern islands of Torres Strait where the species was discovered.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth; wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch with a distinct posterior gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est–esb* greater than distance *esb–eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb–et* axis; *esb* trichobothrium in line with *est–et* axis, in proximal region of fixed finger; two *i* trich*o*bothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em–esb* series with four trichobothria in a single group or in two groups [esb_2][esb_1/em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1]

and [eb_{2-5}] or [eb_{1}/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina costate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules, granular (at least sparsely or faintly), equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in three distinct smooth depressions (one around each trichobothrium). Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length

of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; 9–10 pectinal teeth long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

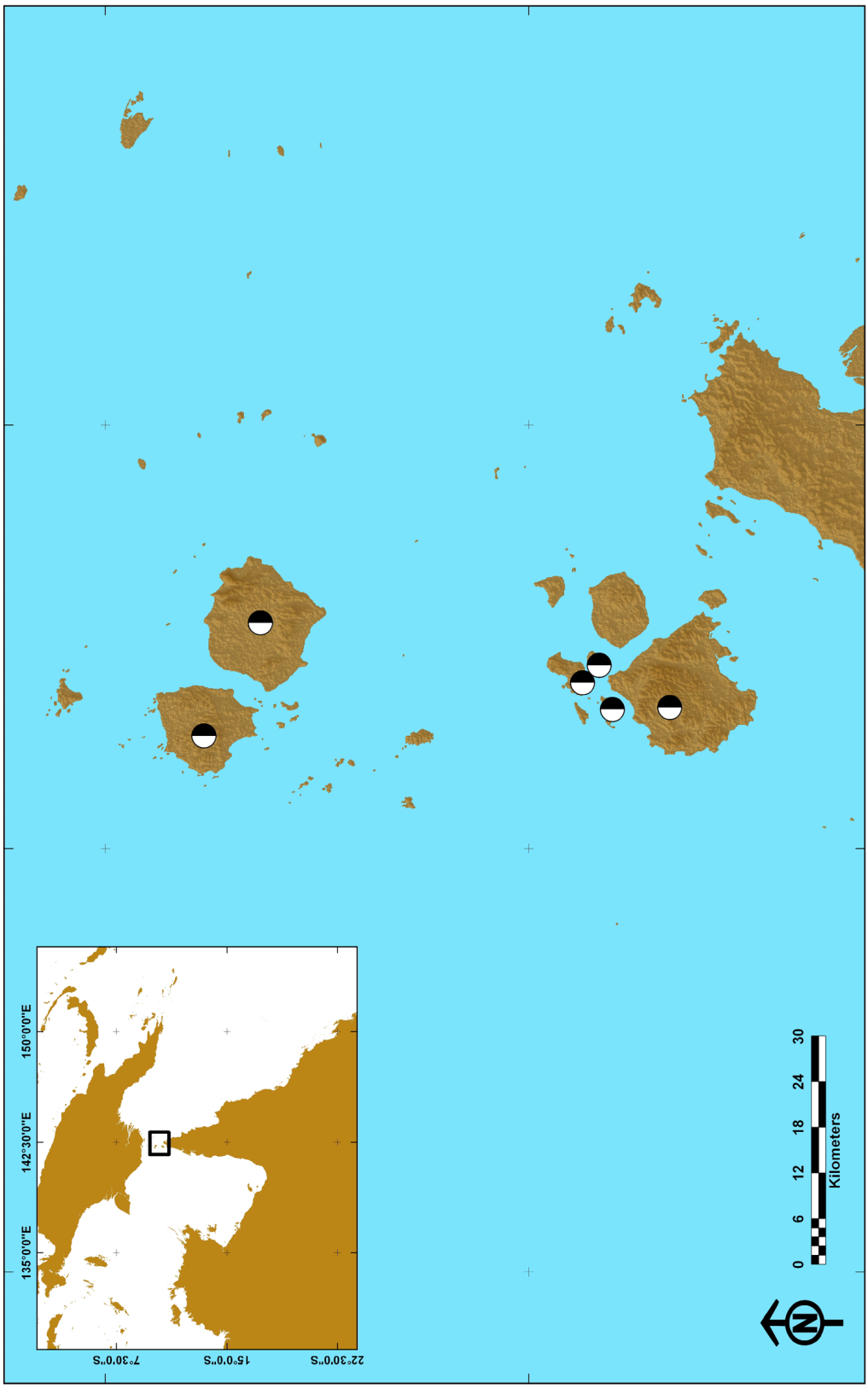
METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, 1–2 pairs of small/vestigial medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae, ridges with at least a few small/medium spiniform granules, subposterior spiniform granules absent; ventrolateral carinae with at least few minute/small spiniform granules. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae, ridges with at least few reduced spiniform granules distally; ventrolateral carinae with minute/small spiniform granules. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half with at least small spiniform granules, with medium spiniform granules more strongly developed than preceding granules (anterior half); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4–5/5; 5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface present, small to medium, pointing downward; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.
PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.
CARAPACE. Anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.
MESOSOMA. Tergites I–III, post-tergites, mesially smooth, laterally granular; IV–VI, post-tergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa. Six–eight pectinal teeth, number.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 115. Distribution map of *Hormurus muralagi* n. sp.


135°0'0"E
142°30'0"E
150°0'0"E
22°30'0"S
15°0'0"S
7°30'0"S
0
6
12
18
24
30
Kilometers
N

Hormurus neocaledonicus (Simon, 1877), **new combination**

Ischnurus neocaledonicus Simon, 1877b: 237, 238

Synonym

Hormurus sarasini Kraepelin, 1914: 332, 335, 336.

References

Liocheles neocaledonico: Simon, 1887: 113.
Hormurus caudicula: Kraepelin, 1894: 135; Kraepelin, 1901: 272 (part) (MIS).
Hormurus neocaledonicus: Kraepelin, 1914: 330, 332, 334, 335; Lampe, 1917: 201; Weidner, 1959: 101.
Hormurus caudicula neocaledonicus: Giltay, 1931: 13, 18, 19.
Hormurus caudicula sarasini: Giltay, 1931: 13, 18, 19.
Liocheles caudicula neocaledonicus: Takashima, 1945: 96.
Liocheles caudicula sarasini: Takashima, 1945: 96.
Hormurus sarasini: Weidner, 1959: 101; Forcart, 1961: 49.
Liocheles waigiensis: L. E. Koch, 1977: 166–172, figs 18, 47, 82, 83, maps 9a, b (part); Kamenz & Prendini, 2008: 11, 43, pl. 134.
Liocheles neocaledonicus: Monod, 2000: 102–107, pl. 41–45, map 13.

Type material

Holotype of *I. neocaledonicus*: NEW CALEDONIA (MNHN), could not be found in the collections of the MNHN, probably lost. **Paratype of *I. neocaledonicus***: NEW CALEDONIA, 20.VIII.1900, Bougier, 1 ♀ (ZMH). **Lectotype of *H. sarasini*** (designated by Forcart, 1961: 49): NEW CALEDONIA, Tchalabel, V.1911, F. Sarasin & J. Roux, 1 ♂ (NMB 56-a). **Paralectotypes of *H.sarasini***: Tchalabel, V.1911, F. Sarasin & J. Roux, 6 ♂, 27 ♀ (NMB 56-a); Tchalabel, II.1913, F. Sarasin, 1 ♂, 5 ♀♀, 1 juv. (ZMH).

Material examined

Paratype of *I. neocaledonicus*. **Paralectotypes of *H.sarasini***. **Additional material**: WITHOUT LOCALITY DATA: specimens examined by Vachon in 1981, 1 ♂, 1 ♀ (MNHN MF, VA 2660). NEW CALEDONIA: III–IV.1939, L. Macmillan (Acc 37523), 1 ♂, 3 ♀♀, 9 juv. (AMNH); J. & M. Sedlacek, 1 juv. (BPBM); P. Rougeot, 1 ♀ (MNHN); 14.I.1995, N. & B. Thibaud, 2 ♀♀, (MNHN); collection Simon, 9 ♂♂, 11 ♀♀, 21 juv. (MNHN-RS 0474); Germain, 1 juv. (MNHN-RS 0488); collection Simon no.1998, M. Bougier, 2 ♀♀ (MNHN-RS 0530); M. Plessis, 1 ♀, 1 juv. (MNHN-RS 4424); 1 ♀ (MNHN-RS 8253); 1 ♀ (MRHN); 1914, P. D. Montague, 1 ♀ (NHML 1924.II.1.1); 17.II.1977, B. Jamieson, 1 ♂ (QM-S 17097); 1 ♀ (ZMH). Bogui-Col des Rousettes, Station 26b,165°26'49''Ex21°24'55''S, 270 m, 4.V.1987, mesic forest, A. Mordan & S. Tillier, 1 juv. (MNHN-RS 8537). Bourail, 1902, H. Méray, 3 ♂♂, 1 ♀, 1 juv. (MNHN-RS 3240). Col des Rousettes: 490 m, 29.V.1987, dry forest, N. I. Platnick, R. J. Raven, 1 juv. (AMNH); 21°25'13''Sx165°27'53''E, 500 m, 29.V.1987, mesic forest, S. Tillier, 2 ♀♀, 2 juv. (MNHN-RS 8537); 21°27'Sx165°28'E, 11.II.1993, rainforest, M. S. Harvey, N. I. Platnick, R. J. Raven, 1 ♀ (WAM 98/1892), 1 juv. (WAM 98/1891); track, 21°25'08.0''Sx165°27'58.9''E, 427 m, 21. IX.2004, small patch of rainforest in between niaoulis savannah, in between stones in a scree covered by litter and tree roots, dryer habitat than previous specimens, D. Gaillard, L. Monod, 2 ♂♂, 3 ♀♀, 7 imm. (LM; LP 5544). Dothio, Col de Pétchékara, Station 287, 166°06'32''Ex21°34'32''S, 340 m,27.X.1986, mesic forest, A. & S.Tillier, 2 ♀♀, 13 juv. (MNHN-RS 8537). Farino, Louis Barbou forest exploitation, 7.X.2004, C. Mille, S. Cazeres & T. Nuques (I.A.C. Pocqueureux), L. Monod, (1) 21°36'50.4''Sx165°42'05.5''E, 383 m, degraded humid forest, near dry creek, under stones, 3 ♂♂, 4 ♀♀ (LM; LP 5547); (2) 21°37'03.7''Sx165°42'51.0''E, 477 m, degraded humid forest, under stones, 2 ♂♂, 3 ♀♀ (LM; LP 5548). Forêt nord, sud de Noumea, Kwa Neie transmitter station, forest mix-dry, 25.X.1988, T. C. (?) & R.Raven, 1 juv. (QM-S 23332). Goro, 3.IX.1975, mesic forest, P. Bouchet, 1 juv. (MNHN-RS 8349). S of Grand Lac, Station 235, 166°54'00''Ex22°16'31''S, 280 m, 26.XI.84, mesic forest on peridotites, A. & S. Tillier, P. Bouchet (MNHNP, Malacologie), 1 ♂, 1 juv. (MNHN-RS 8537). Hienghene, 10–50m, 14–17.VIII.1979, G. M. Nishida, 2 juv. (BPBM Acc. No. 1979.380). Koya Boa Forest (Poindimié), NE central coast, 16/22.X.1983 / Saint Louis (Noumea), 16.XI.1979, on the banks of a

creek, A. Renévier, 3 ♂♂, 17 ♀♀, 2 juv. (AMNH, AH 4622-4643). Ile des Pins, near Grotte de la 3ème, 22°37'Sx167°26'E, 19.III.1993, rainforest, M. S. Harvey, N. I. Platnick, R. J. Raven, 1 ♂, 1 juv. (WAM 98/1887-8). La Foa, IX.1976, M. Droin, 2 ♀♀ (MNHN-RS 7333). Grotte Le Cresson, 18.IX.65, 1 ♀ (MNHN-K 6, PNK 82/1). Chute de la Madeleine, 22°14'Sx166°52'E, 230 m, 12.XI.2000, P. Bouchard, C. Burwell & G. Monteith (9918), 2 ♀♀, 1 juv. (QM-S 39694). Mt Arago, P. D. Montague, 4 ♀♀ (NHML 1927.II.1.2-5). Mt Dor, 15 mi from Noumea, 22.X.1944, W. D. Crabb, 1 ♀, 1 juv. (USNM 00753). Mount Humbold, near mine, 21°54'24.4''Sx166°21'14.5''E, 505 m, 4.X.2004, degraded primary forest, vine thicket, in between stones in a scree covered by leaves litter and humus and under larger stones, L. Monod, 3 ♂♂, 2 ♀♀ (LM; LP 5546). Mt Koghis: 22°11'Sx166°31'E, 500 m, 2–3.XI.2002, rainforest, night collecting, Burwell, G. Monteith & Wright (11088), 1 ♀ (QM); start of tracks, 22°10'40.5''Sx166°30'28.6''E, 440 m, 26. IX.2004, rainforest, under rocks, D. Gaillard, L. Monod, 3 ♂♂, 3 ♀♀ (LM-LP 5545); Mount Koghis, ca. 20 km N Noumea, 4.XII.2004, S. Huber, 2 imm. (LP 6224). S.E. slope of Mt Koyoboa (390 m), Poindimié, elevation less than 500 ft, 3.VI.1985, L. Wishmeyer, 1 ♀, 2 juv. (CAS). Mt. Mé Ori, SE slope, Station 29 a, 165°40'22''Ex21°32'18''S, 530 m, 7.V.1987, forêt humide, A. Mordan & S. Tillier, 1 ♀, 19 pullus, 1 juv. (MNHN-RS 8537). Mt Pouédihi forest, 18.IV.65, 1 ♂, 2 ♀♀, 1 juv. (MNHN-K 8). Barrage de la Néaoua (Ouen Sieu), Station 210, 165°32'35''Ex21°21'57''S, 500 m, 20.XI.84- mesic forest, A. & S. Tillier, P. Bouchet, M.-P. Triclot (MNHNP, Malacologie), 1 juv. (MNHN-RS 8537). Road Nouméa - Rivière Bleue Forest Reserve, 22°12'47.2''Sx166°39'59.3''E, 177 m, 17.IX.2004, vine thicket, in rock crevices, D. Gaillard & L. Monod, 1 ♀ (LP 5542). Oua Tom, 130 m, 16.IX.1978, mesic forest, 5 juv. (MNHN-RS 8350). Vallée de la Ouen Nondoué, Station 205, 165°44'00''Ex21°22'36''S, 70 m, 20.X.84, *Nothofagus* forest, A. & S. Tillier, P. Bouchet, M.-P. Triclot (MNHNP, Malacologie), 1 ♀, 2 juv. (MNHN-RS 8537). Plaine des Lacs, 23.II.14, forest, under bark, D. Montague, 1 ♂, 1 ♀ (NHML 1924.II.1.6-7). Rivière Blanche, Parc Cagous, Station 256, 166°38'20''Ex22°08'09''S, 160/170 m, 1.IX.1986, mesic forest, A. & S. Tillier, 1 ♂, 1 ♀, 2 juv. (MNHN-RS 8537). Rivière Bleue Forest Reserve: 17.VIII.1965, 6 juv. (MNHN-K 2, PNK 52/2), 1 ♂, 1 ♀ (MNHN-K 3, PNK 52/3); 20.VIII.1965, 3 juv. (MNHN-K 1, PNK 56/1); 21.XI.1995, J. P. Hugot, 1 juv. (MNHN-KM 70), 1 juv. (MNHN-KM 71); 17.VII.1965, under bark, Stanniloner, 1 ♂ (MNHN-K 5); 280 m, 21.V.1987, wet forest, N. I. Platnick, R. J. Raven, 1 juv. (AMNH); 21.V.1987, N rainforest, R. Raven, 3 ♀♀, 3 juv. (QM-S 23328); 22°06'Sx166°39'E, 240 m, 9.III.1993, rainforest, M. S. Harvey, N. I. Platnick, R. J. Raven, 1 ♂, 1 ♀ (WAM 98/1885-6); trail between Pont Pérignon and Kaori gèant, 22°06'14.2''Sx166°41'12.8''E/22°06'31.8''S 166°41'35.6''E, 116–169 m, 18.IX.2004, rainforest, under stones and in rock crevices, D.Gaillard, L. Monod, 3 ♂♂, 3 ♀♀ (LM; LP 5543); Pic du Grand Kaori, 22°16.770'Sx166°53.691'E, 400 m, 11.V.2005, under dead wood branches, J. Murienne, 2 imm. (LP 4323). Rivière Bleue Forest Reserve, 166°39'16''Ex22°06'13''S, mesic forest/alluvia: Station 250, parcelle VI M, 160 m, 1.VIII.1986, A.& S. Tillier, 1 ♀, 1 juv. (MNHN-RS 8537); station 250 a, parcelle VI H, 160 m, 15.IX.1986, Y. Letocart, A. & S. Tillier, 1 juv. (MNHN-RS 8537); station 250 b, parcelle VI I, 160 m, 2.X.1987, A. & S. Tillier, 2 juv. (MNHN-RS 8537); station 250 d, parcelle VI I, 160 m, 4.XII.1987, A. & S. Tillier, 1 juv. (MNHN-RS 8537); station 250 e, parcelle VI J, 160 m, 5.I.1987, A. & S. Tillier, 1 juv. (MNHN-RS 8537); station 250 g, parcelle VI O, 160 m, 6.III.87, A. & S.Tillier, 1 ♂, 1 juv. (MNHN-RS 8537); station 250 h, parcelle VI O, 160 m, 6.IV.1987, A. & S.Tillier, 1 ♀ (MNHN-RS 8537); station 250 i, parcelle VI W, 160 m, 30.V.1987, A. Mordan, A. & S. Tillier, 1 juv. (MNHN-RS 8537); station 250 j, parcelle VI G, 160 m ,12.VI.87, A. & S.Tillier, 1 ♂ (MNHN-RS 8537). Rivière Bleue Forest Reserve, 166°40'01''Ex22°05'59''S, mesic forest: station 251, parcelle VII V, 170 m, 15.VIII.1986, A. & S. Tillier, 2 ♂♂, 2 juv. (MNHN-RS 8537); station 251 a, parcelle VII U, 165 m, 22.IX.1987, A. & S. Tillier, 2 juv. (MNHN-RS 8537); station 251 b, parcelle VII O, 170 m, 13.X.1986, A. & S. Tillier, 1 ♂, 1 ♀, 1 juv. (MNHN-RS 8537); station 251 d, parcelle VII U, 170 m, 11.XII.1986, A. & S. Tillier, 1 juv. (MNHN-RS 8537); station 251 e, parcelle VII U, 170 m, 13.I.1987, A. & S. Tillier, 4 juv. (MNHN-RS 8537); station 251 f, parcelle VII L, 170 m, 12.II.1987, A. & S. Tillier, 1 ♂, 2 ♀♀ (MNHN-RS 8537); station 251 g, parcelle VII K, 170 m, 16.III.1987, A. & S. Tillier, 1 juv. (MNHN-RS 8537); station 251 h, parcelle VII R, 170 m, 14.IV.87, A. & S. Tillier, 1 ♂ (MNHN-RS 8537); station 251 i, parcelle VII G, 170 m, 14.V.1987, A. Mordan, A. & S.Tillier, 1 ♂, 1 ♀, 2 juv. (MNHN-RS 8537); station 251 k, parcelle VII, Alt.170 m, 16.VII.1986, A. & S.Tillier, 1 ♂, 4 juv. (MNHN-RS 8537). Rivière Bleue Forest Reserve, 164°23'23''E 20°38'48''S, Station 255, Mt Kaala, S slope, dry forest, A. Chazeau & S. Tillier, 27.VIII.1986, 2 juv. (MNHN-RS 8537). Rivière Bleue Forest, Kaori geant, 22°06'Sx166°39'E, 11–12.XI.2000, P. Bouchard, C. Burwell & G. Monteith

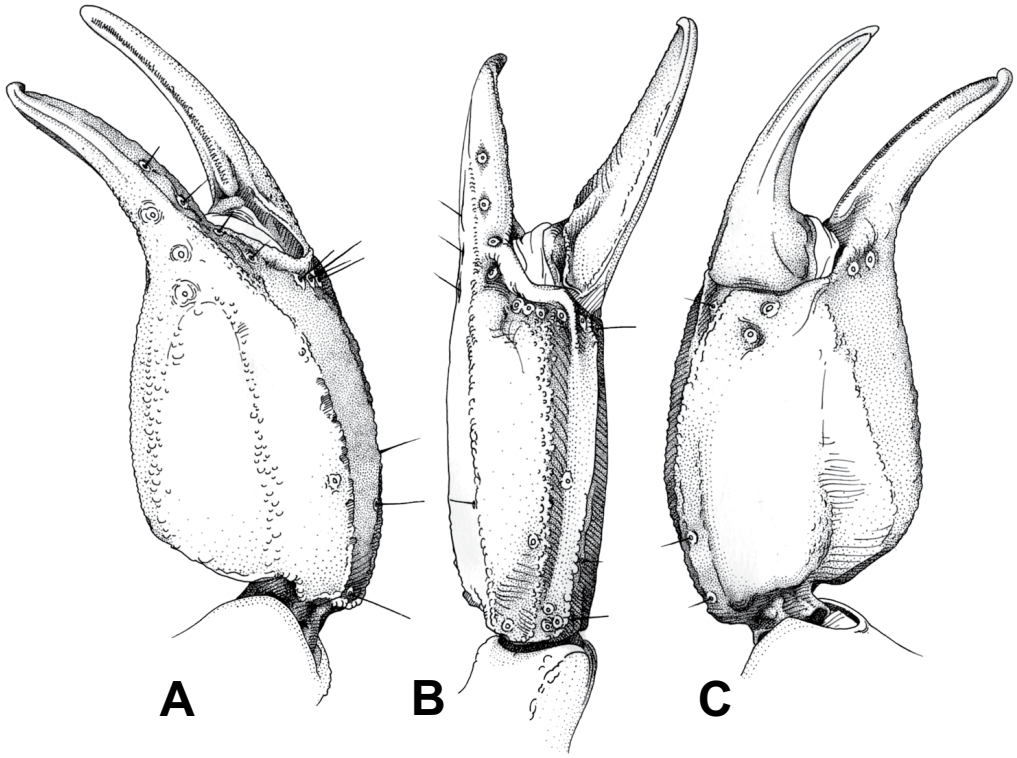
(9957), 1 ♂, 2 juv. (QM-S 39696). Riviere Bleue Reserve, near Kaori géant, 120 m, 25.V.1984, G. Monteith & D. Cook, 2 juv. (QM-S 23331). Riviere Bleue Forest Reserve, Panoramic track, 22°06'Sx169°39'E, 12.XI.2000, P. Bouchard, C. Burwell & G. Monteith (9951), 1 ♀, 1 juv. (QM-S 39711). Riviere Bleue Forest Reserve, Pic du Grand Kaori, 22°17'Sx166°54'E, 250 m, 16–18. XI.2002, S. Wright (11198), 1 ♂ (QM); 29.I.2002, G.B.Monteith (8922), 1 juv. (QM-S 59098). Riviere des Pirogues (headwaters), 350–400 m, 22.V.1984, G. Monteith & D. Cook, 1 ♀, 3 juv. (QM-S 23339). Thi Forest Reserve, 5.VIII.65, 1 ♂, 1 juv. (MNHN-K 7, PNK 38/2); 150 m, 21.V.1984, G. Monteith & D. Cook, 1 ♀ (QM-S 23330). Touaourou, 20.X.1959, under stones, B. Malkin, 2 juv. (AMNH); 25.XII.1960, J. P. E. Morrison (3927, gto VI), 1 ♀ (USNM 00753). 2 km N of Troulala, 20°38'Sx164°21'E, 14.III.1993, M. S. Harvey, N. I. Platnick, R. J. Raven, 1 ♀, 1 juv. (WAM 98/1889-90).

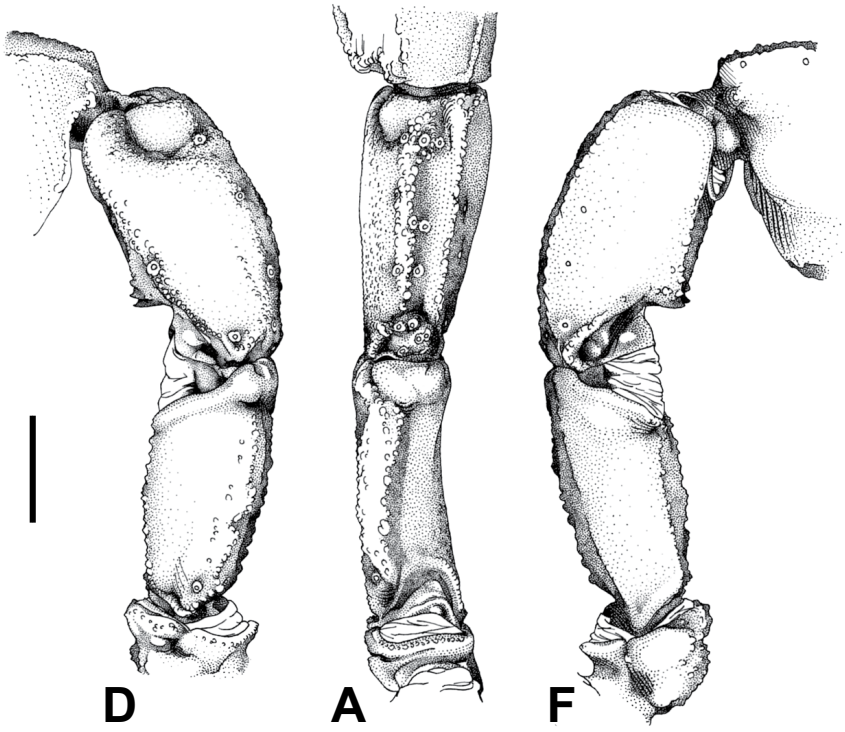
Distribution (fig. 120)
New Caledonia.

Notes
Given that the holotype of *I. neocaledonicus* is now lost, the paratype located in the collection of the Zoologisches Museum Hamburg is designated neotype.

DESCRIPTION. ADULT MALE
COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).
CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.
PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth; wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger, low hump with 2–3 larger conical teeth. Chela fixed finger, supra-basal lobe present and distinct, low/reduced; basal lobe absent. TRICHOBOTHRIOTAXY (fig. 116). Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est–esb* similar to distance *esb–eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb–et* axis; *esb* trichobothrium below *est–et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em–esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), Low, forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not

Fig. 116. *Hormurus neocaledonicus* (Simon, 1877), female, pedipalp with trichobothrial pattern.A, chela, dorsal aspect. B, idem, external aspect. C, idem, ventral aspect. D, femur and patella, dorsal aspect. E, idem, external aspect. F, idem, ventral aspect. Scale line, 2.5 mm.


A
B
C


D
A
F

expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in three distinct smooth depressions (one around each trichobothrium). Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

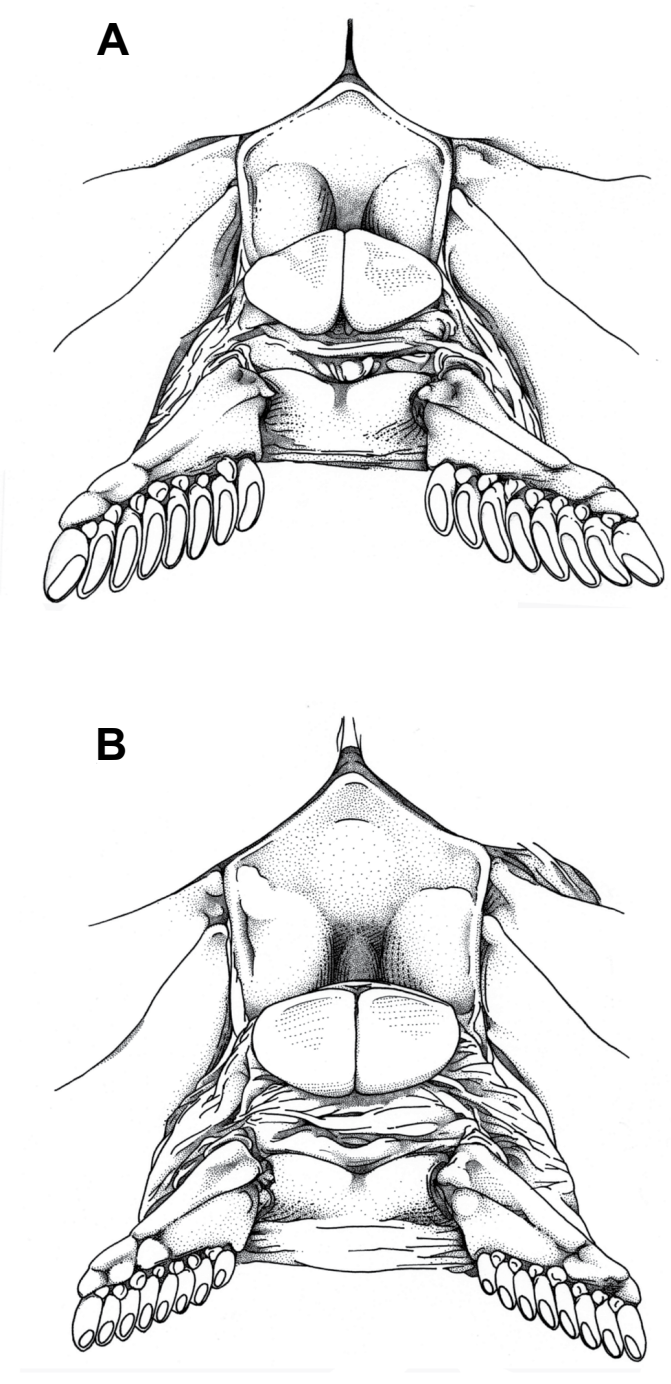
CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial; Medium-sized, ca. 1/7 of the carapace width, raised at least slightly; superciliary carinae present, with at least few granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules, evenly and sparsely distributed; anteromedian surface entirely granular at least sparsely; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM (fig. 117A), shape, anterior width approximately equal to slightly less than posterior width (1<pw/aw<1.5) [=subpentagonal]; length less than or equal to posterior width. PECTINES (fig. 117A), length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; nine pectinal teeth, short, curved, sensory papillae covering distal portion only. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA (fig. 118C). Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae absent or obsolete; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform

Fig. 117. *Hormurus neocaledonicus* (Simon, 1877), pectines and genital opercula, ventral aspect. A, male. B, female. Scale line, 1 mm.


A
B

granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, 1–3 pairs of well developed medial granules. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, one pair of well developed sub-posterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), one pair of well developed subposterior spiniform granules. Ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi (fig. 118B), two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 5/5; 5/5.

HEMISPERMATOPHORE (fig. 119). Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with base of lamellar hook, sometimes slightly below, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

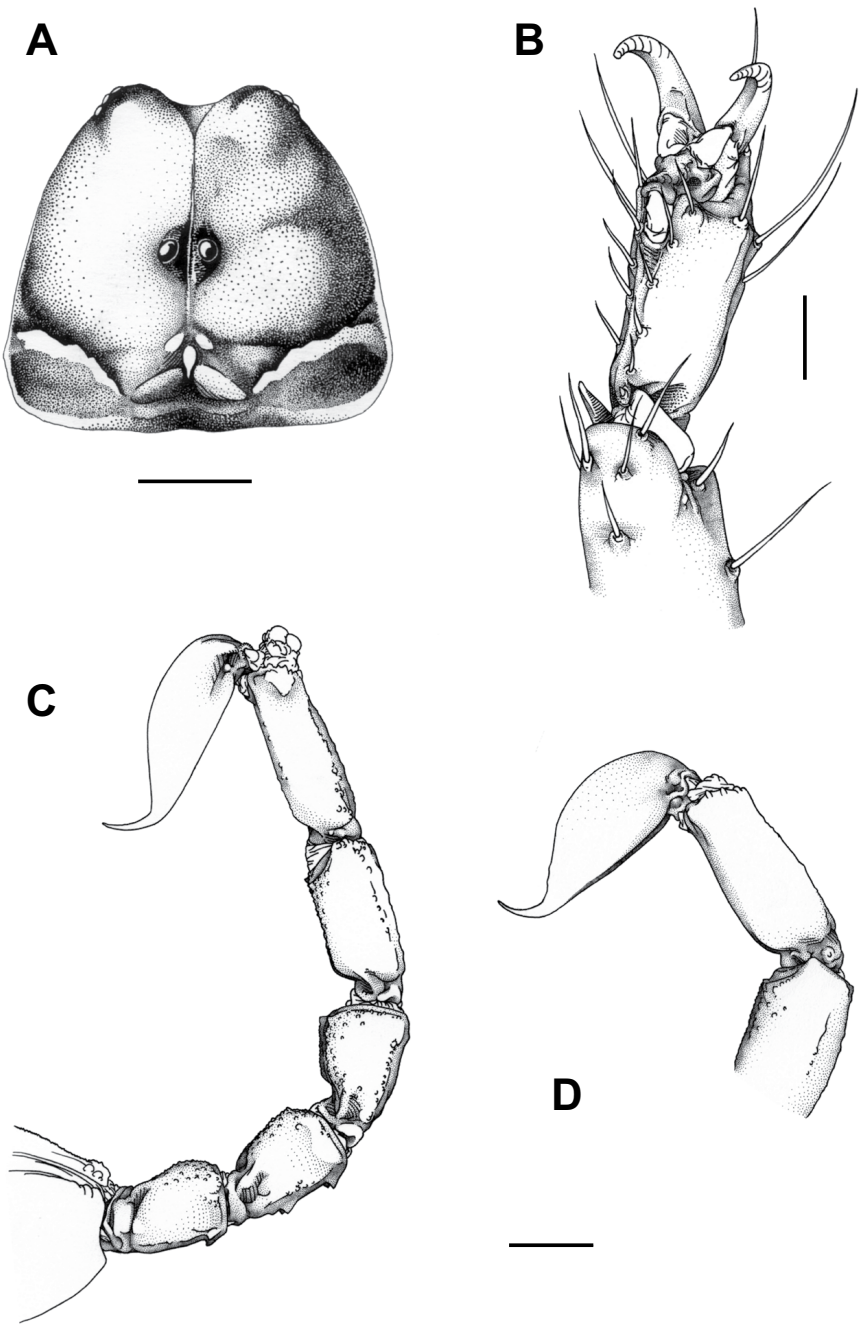
BOOK LUNGS. Lamellar surface with simple trabeculae, with arcuate bow-like structures. Posterior spiracle edge with chisel-like structures.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface entirely granular, at least sparsely; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface

Fig. 118. *Hormurus neocaledonicus* (Simon, 1877). A, carapace, dorsal aspect. B, left tarsus IV, ventral aspect. C, metasoma, lateral aspect, male. D, metasoma, lateral aspect, female. Scale lines, 2.5 mm (A), 2 mm (C, D), 0.5 mm (B).


A
B
C
D

at least sparsely granular; posterolateral surfaces at least sparsely granular.
MESOSOMA. Tergites I–III, post-tergites entirely granular; IV–VI, post-tergites, mesial and lateral surfaces granular; VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.
VENTRAL MORPHOLOGY (fig. 117B). GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa. Seven–eight pectinal teeth.
METASOMA (fig. 118D). Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 119. *Hormurus neocaledonicus* (Simon, 1877), male. Hemispermatophore. Scale line, 1 mm.

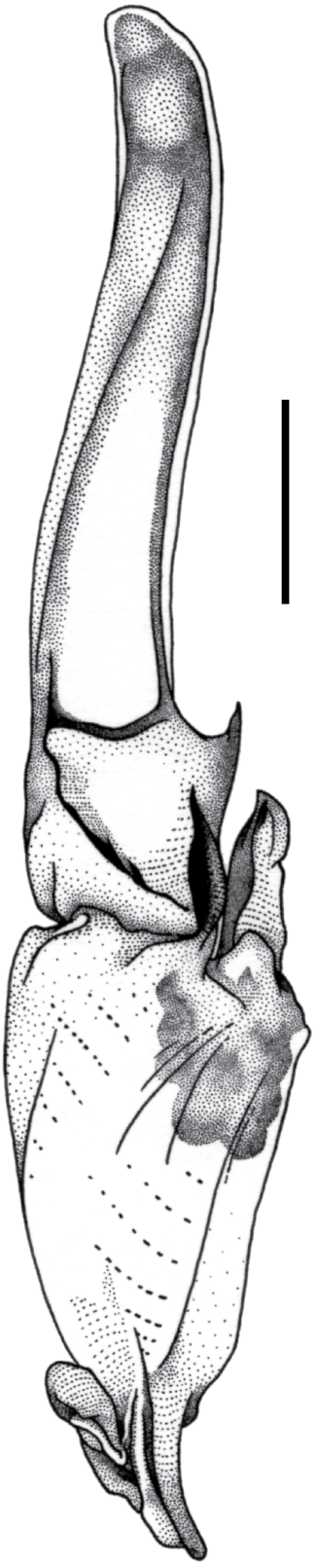
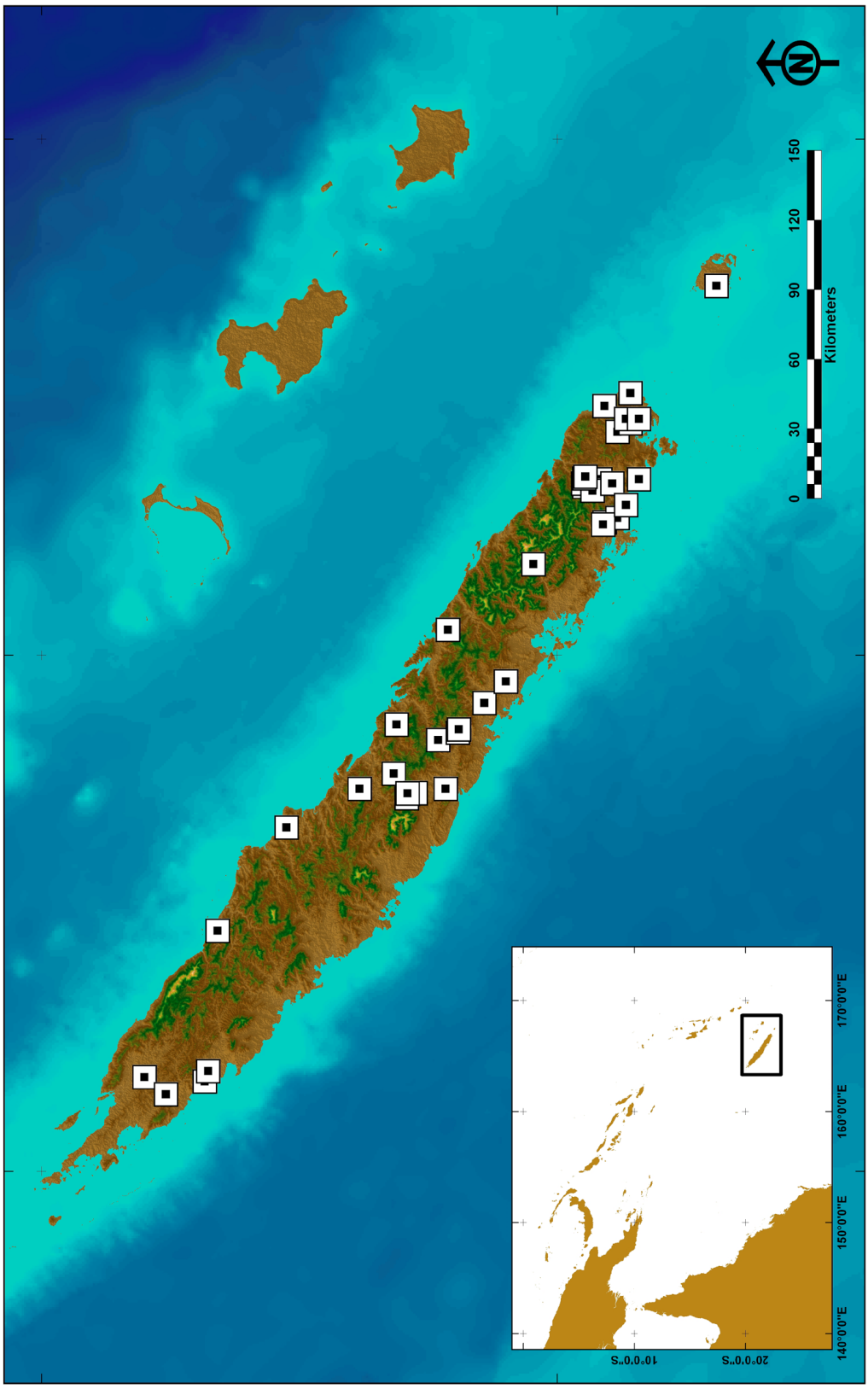


Fig. 120. Distribution map of *Hormurus neocaledonicus* (Simon, 1877).


N
0
30
60
90
120
150
Kilometers
140°0'0"E
150°0'0"E
160°0'0"E
170°0'0"E
10°0'0"S
20°0'0"S

Hormurus nesiotes n. sp.

References

Hormurus caudicula (nec C. L. Koch, 1867;MIS): Chapin, 1957: 69.

Material examined

Holotype: OCEANIA, PALAU, Peleliu, 21.IV.1936, Y. Kondo, 1 ♀ (USNM 04167). **Paratype**: same data as holotype, 1 imm. (BPBM).

Distribution (fig. 121)

Palau.

Etymology

The Greek word *nesiotes* [insular] is an invariable noun in apposition and refers to the distribution range of the species which is restricted to the remote Palau Islands.

Notes

Chapin (1957) believed that the species was introduced on Peleliu before 1936.

DESCRIPTION. ADULT FEMALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, dark (as dark as metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in a single group or in two groups [esb_2][esb_1/em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina costate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually

more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules, evenly and sparsely distributed; anteromedian surface entirely granular at least sparsely; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence. Tergites I–III, post-tergites, mesially smooth, laterally granular; IV–VI, post-tergites, mesially smooth, laterally granular; VII, posttergite granular at least posteriorly; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width approximately equal to slightly less than posterior width (1<pw/aw<1.5) [=subpentagonal]; length less than or equal to posterior width. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; three marginal lamellae; fulcrae present; Seven pectinal teeth, short, curved, sensory papillae covering distal portion only. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae absent or obsolete; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules,

medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial subposterior spiniform granules, medial spiniform granules absent. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

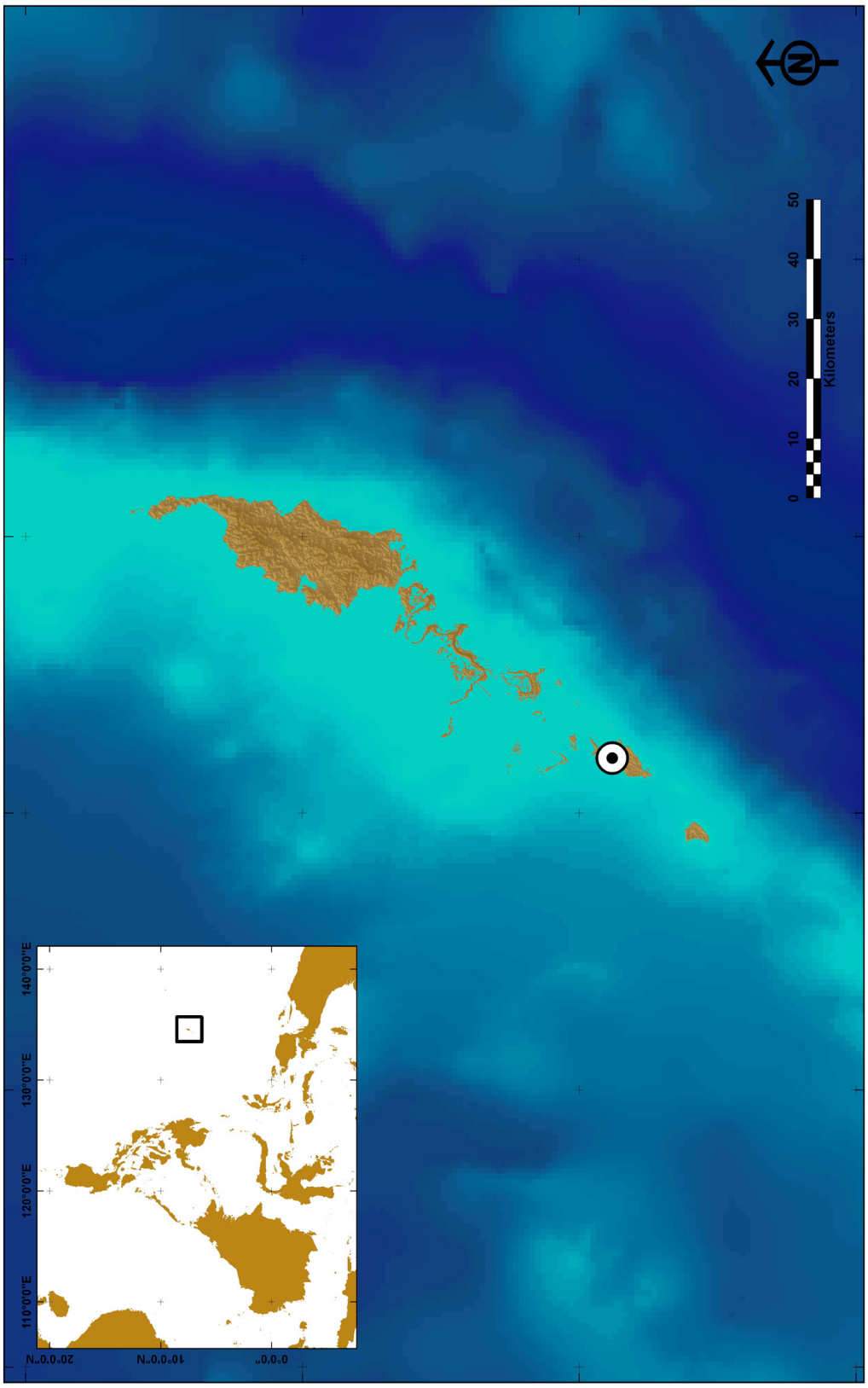
LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 5/5; 5/5.

JUVENILE MALE.

VENTRAL MORPHOLOGY. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; nine pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 121. Distribution map of *Hormurus nesiotes* n. sp.


N
0
10
20
30
40
50
Kilometers
110°0'0"E
120°0'0"E
130°0'0"E
140°0'0"E
20°0'0"N
10°0'0"N
0°0'0"

Hormurus papuanus Kraepelin, 1914

Hormurus papuanus Kraepelin, 1914: 333.

References

Hormurus papuanus: Kraepelin, 1914: 333; Kopstein, 1921: 138 (part); Kopstein, 1923: 186.
Hormurus caudicula papuanus : Giltay, 1931: 10–13, 18, 19 (part).
Hormurus caudicula (nec C. L. Koch, 1967; MIS): Kopstein, 1923: 185.
Liocheles caudicula papuanus: Takashima, 1945: 96.
Liocheles waigiensis (nec L. E. Koch, 1977; MIS): Kovařík, 1997: 184.
Liocheles papuanus: Monod, 2000: 113–117, pl. 51–55, map 15.

Material examined

Syntypes (not listed in Weidner, 1959): PAPUA NEW GUINEA, NEW BRITAIN, WEST NEW BRITAIN PROVINCE, S coast, Möwe Hafen (= Moewe Harbour), 13/14.XII.1908, 20/24. II.19009, lower reaches of waterfall, Dr. G. Duncker, 1 ♂ (ZMH 334); SW coast, Liebliche Inseln (= Arawe Islands), 11/12.XII.1908, 5.I.1908, 26/31.I.1909, Dr, G. Duncker, 2 ♂♂, 5 ♀♀, 13 juv. (ZMH 340). MOROBE PROVINCE, Sattelberg, near Finshhafen, IX.1908/IV.1909, Dr. G. Duncker, 2 ♂♂ (ZMH 924). **Additional material**: PAPUA NEW GUINEA, Operation Drake, 1 ♀, (NHML). MOROBE PROVINCE: Bukaua (Kap Arkona), Huon Gulf, 1909, Prof. Neuhauss S. G. (1287/09), 2 ♂♂, 3 ♀♀, 2 juv. (ZMB 15165). Buso River, 16.IX.1979, Operation Drake, 1 ♂ (NHML). Finshhafen, IV.1944, E. S. Ross, 3 ♂♂, 3 ♀♀, 1 ♂ sub., 5 juv., 7 pullus (CAS); 7.IV.1944, E. S. Ross, 1 ♂ (CAS); 12.IV.1944, E. S. Ross, 3 juv. (CAS); 21.IV.1944, E. S. Ross, 1 ♀ (CAS). Kamiali Guest House, 7.29934°Sx147.13435°E, 3 m, 12.X.2003, coastal forest, J.D. Slapcinsky & F. Kraus, 1 ♀ (LP 2718). Mt. Shungol, W of Apele, near junction of Kasang Creek and Ouz River, 6.82632°Sx146.69943°E, 860 m, broadleaf forest, arboreal 1–3 m on mossy tree trunks, 22.X.2003, J. D. Slapcinsky & F. Kraus, 2 ♂♂ (LP 2715), 1 ♀ (LP 2721). Mt. Shungol, W of Apele, Bwemamik, junction of Bwemamik Creek and Ouz River, 6.81543°Sx146.69282°E, 730 m, 17.X.2003, mature broadleaf forest, J.D. Slapcinsky & F. Kraus, 1 ♀ (LP 2725), 2 imm. (LP 2726), 1 imm. (LP 2727). Sattelberg near Finschhafen, Dr. Pöch, 1 ♀ (NHMW 8254); Dr. Neuhauss S.G., XII.1908 (684/09), 1 ♂, 1 ♀, 1 juv. (ZMB 15159).

Distribution (fig. 122)

Papua New Guinea, Morobe Province, West New Britain Province.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, dark (as dark as tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, conical (as high as wide or higher than wide), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch with a distinct posterior gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/ well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to $Eb_{1–2}$; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* tric*h*obothria.

Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em–esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules, granular (at least sparsely or faintly), equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) ca*rin*ae; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface smooth or nearly so; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, close together (less than a diameter), at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules, evenly and sparsely distributed; anteromedian surface entirely granular at least sparsely; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, post-tergites with minute spiniform granules, uniformly

and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; 8–9 pectinal teeth long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, 1–3 pairs of small/vestigial sub-posterior spiniform granules, medial spiniform granules absent. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; Vesicle smooth, without granules, unmodified.

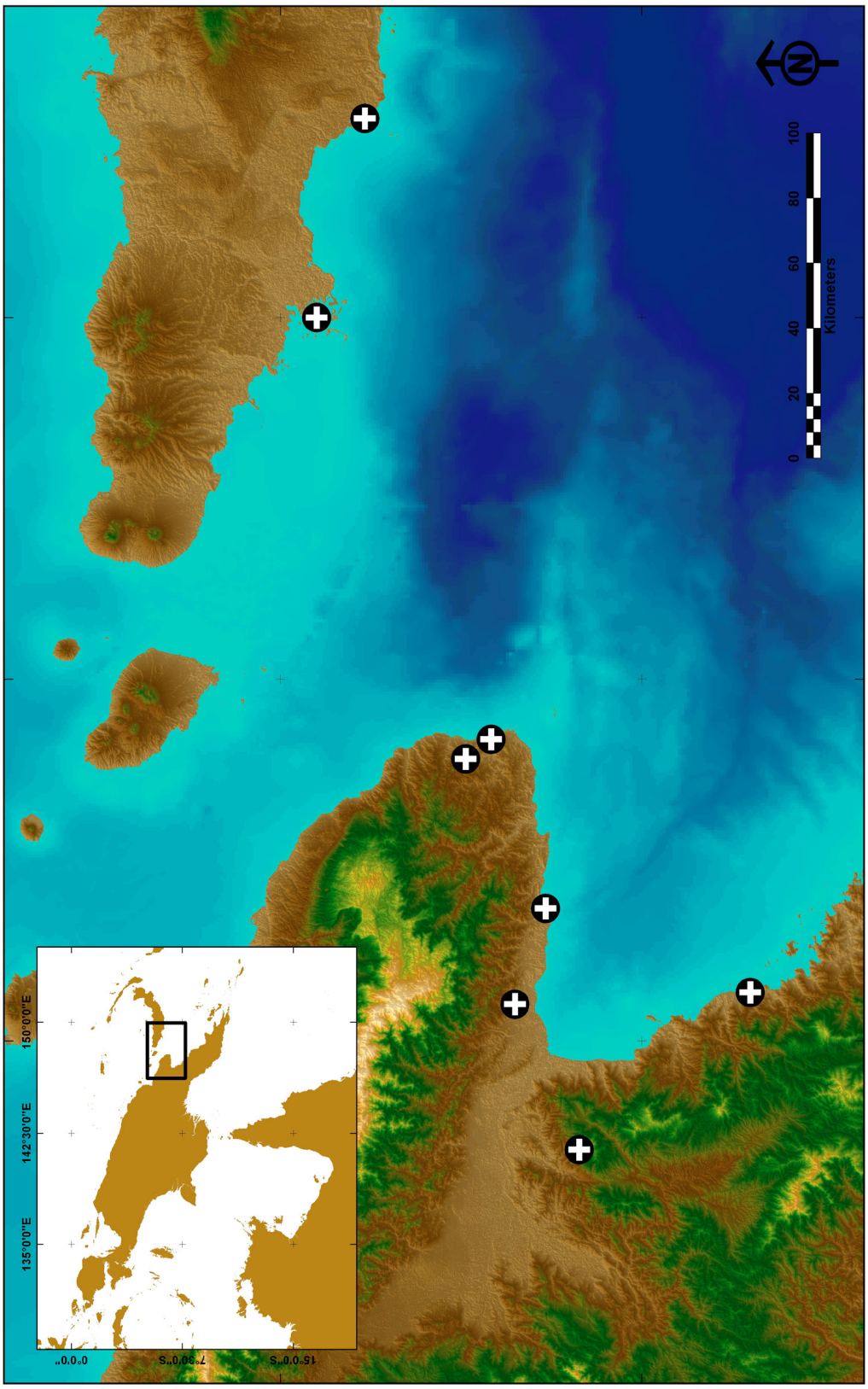
LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae present. Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 5/5; 5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, Distal, at least mid-lamella (usually in distal 1/3); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge below base of lamellar hook, below base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal ‘spine’ (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like

shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.
PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.
CARAPACE. Anteromedian surface entirely granular, at least sparsely; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.
MESOSOMA. Tergites I–III, post-tergites, mesially smooth, laterally granular; IV–VI, post-tergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, longer than wide, approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; 7–8 pectinal teeth.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 122. Distribution map of *Hormurus papuanus* Kraepelin, 1914.


0
20
40
60
80
100
Kilometers
150°0'0"E
142°30'0"E
135°0'0"E

Hormurus penta (Francke & Lourenço, 1991), **new combination**

Liocheles penta Francke & Lourenço, 1991: 200–203, figs 1–11.

References

Liocheles karschii (nec Keyserling, 1885; MIS): Browning & Hyatt, 1957: 71.

Liocheles penta: Kovařík, 1998: 134; Monod, 2000: 118–122, pl. 56–59, map 16; Monod & Volschenk, 2004: 677, 686; Prendini & Wheeler, 2005: tab. 5.

Type material (not examined)

Holotype: SOLOMON ISLANDS, RENNEL ISLAND, Hutuna, III.1965, 1 ♂ (UZM). **Paratypes**: SOLOMON ISLANDS, RENNEL ISLAND, Hutuna, 15.III.1965, Noona Dan Expedition, 1 ♂ (UZM); Tigoa, 22.III.1965, Noona Dan Expedition, 1 ♂, 2 ♀ (UZM); Niupani, 19.VIII.1965, Noona Dan Expedition, 1 ♂, 1 ♀ (UZM).

Material examined

SE PAPUA NEW GUINEA, 10.X.1914, 1 ♂ (QM-S 23254). Samarai, 10º36'Sx150º39'E, 5.VII.1937, S. Bemrose, 1 ♂ (WAM 37-2542). SOLOMON ISLANDS, GUADALCANAL, Cho-cho, ca. Tambea, 09°16'Sx159°40'E, 200 m, 27.I.1999, J. Lattke 2354, 1 ♂ (LP 1817-CAS). Mount Austen, 20.XII.1963, P. Greenslade (Royal Society B.S.I.P. 1965, 1446, Acc. No. 2182), 1 ♂, (NHML). San Jorge, IX.1965, *Casuarina* forest & fringing semb. (Royal Society Expedition 23/27), 1 imm. (NHML). SOLOMON ISLANDS, RUSSELL ISLANDS, XII.1944, Lt. R. B. Eads, Navy #60, 1 juv. (AMNH).

Distribution (fig. 127)

Solomon Islands.

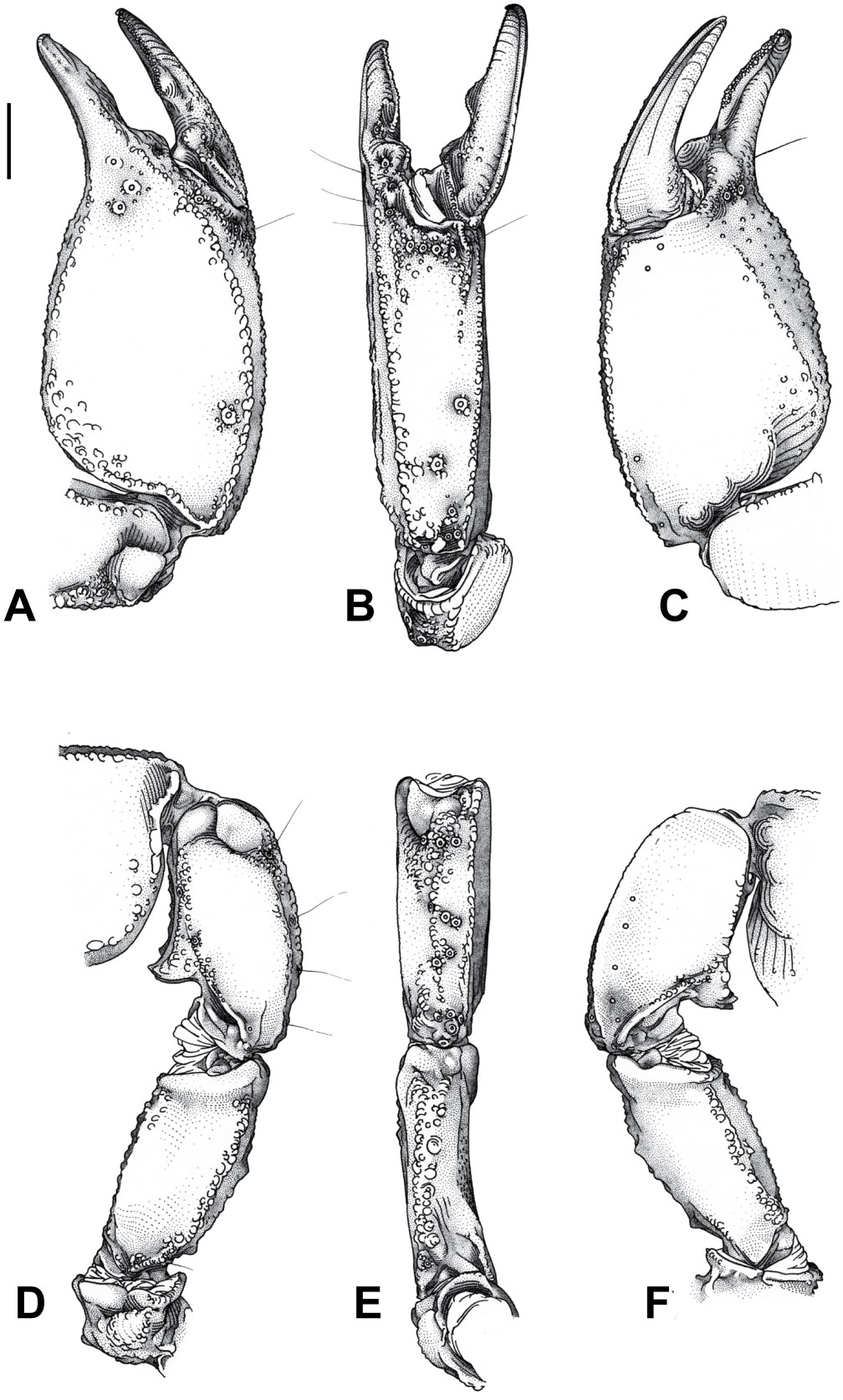
DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth; wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger, low hump with 2–3 larger conical teeth. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY (fig. 123). Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than *Eb* group, midway between *Eb* group and *Est*; Eb_3 trichobothrium distal to basal group [Eb_{1-2}]; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb*–*et* axis; *esb* trichobothrium below *est*–*et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; five *v* trichobothria (two accessory). CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian

Fig. 123. *Hormurus penta* (Francke & Lourenço, 1991), male, pedipalp with trichobothrial pattern.A, chela, dorsal aspect. B, idem, external aspect. C, idem, ventral aspect. D, femur and patella, dorsal aspect. E, idem, external aspect. F, idem, ventral aspect. Scale line, 1.5 mm.


A
B
C
D
E
F

(*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina costate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) ca*rin*ae; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in three distinct smooth depressions (one around each trichobothrium). Chela, dorsal intercarinal surface, macrosculpture limited to prolateral and retrolateral edges, absent from the median part, granulation vestigial, at most low granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation absent; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface smooth or nearly so; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

PROSOMAL CARAPACE (fig. 125A). Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial; Medium-sized, ca. 1/7 of the carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules, evenly and sparsely distributed; anteromedian surface entirely granular at least sparsely; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM (fig. 124), shape, anterior width approximately equal to slightly less than posterior width (1<pw/aw<1.5) [=subpentagonal]; length less than or equal to posterior width. PECTINES (fig. 124), length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; nine pectinal teeth, short,

Fig. 124. *Hormurus penta* (Francke & Lourenço, 1991), male, pectines and genital opercula, ventral aspect. Scale line, 1 mm.

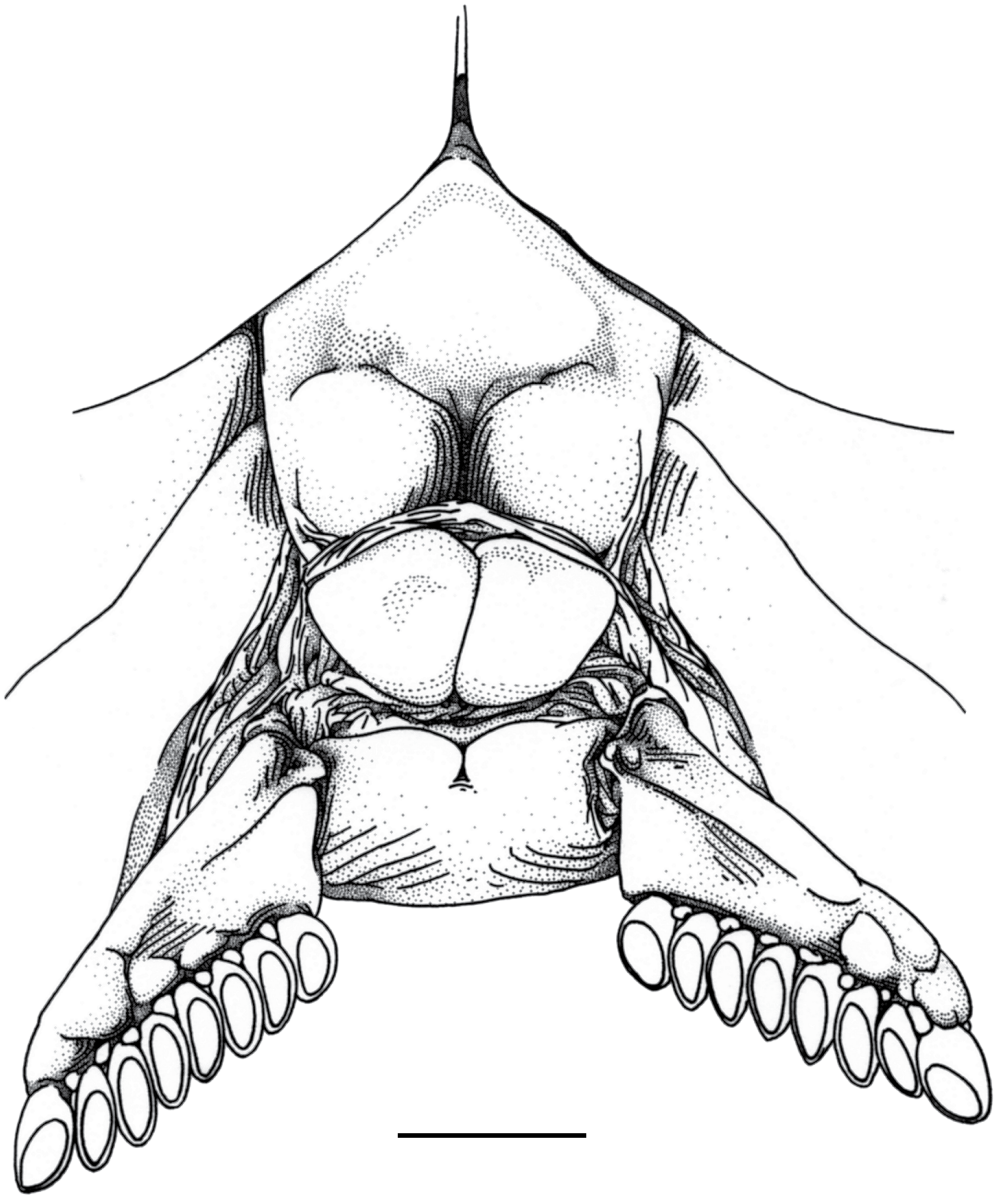
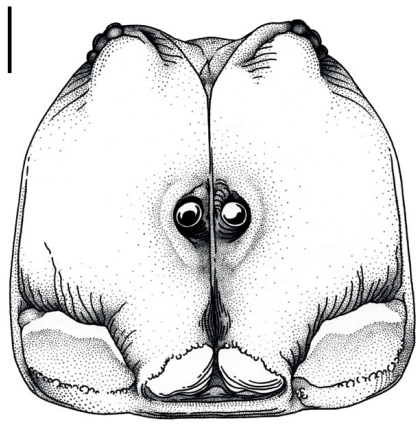
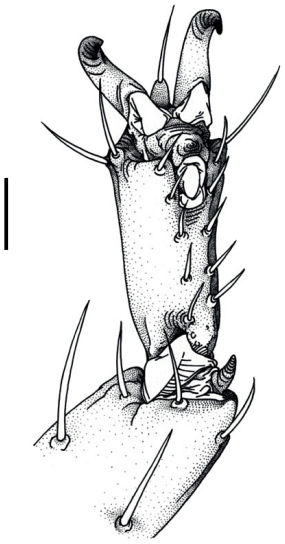


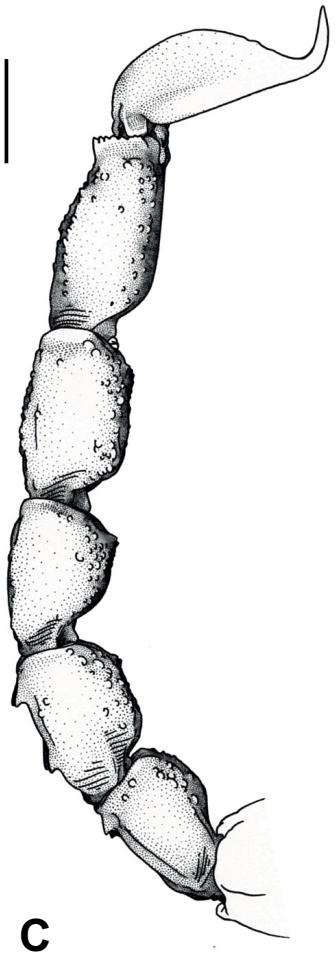
Fig. 125. *Hormurus penta* (Francke & Lourenço, 1991), male. A, carapace, dorsal aspect. B, right tarsus IV, ventral aspect. C, metasoma, lateral aspect, male. Scale lines, 1 mm (A), 1.5 mm (C), 0.3 mm (B).



A



B



C

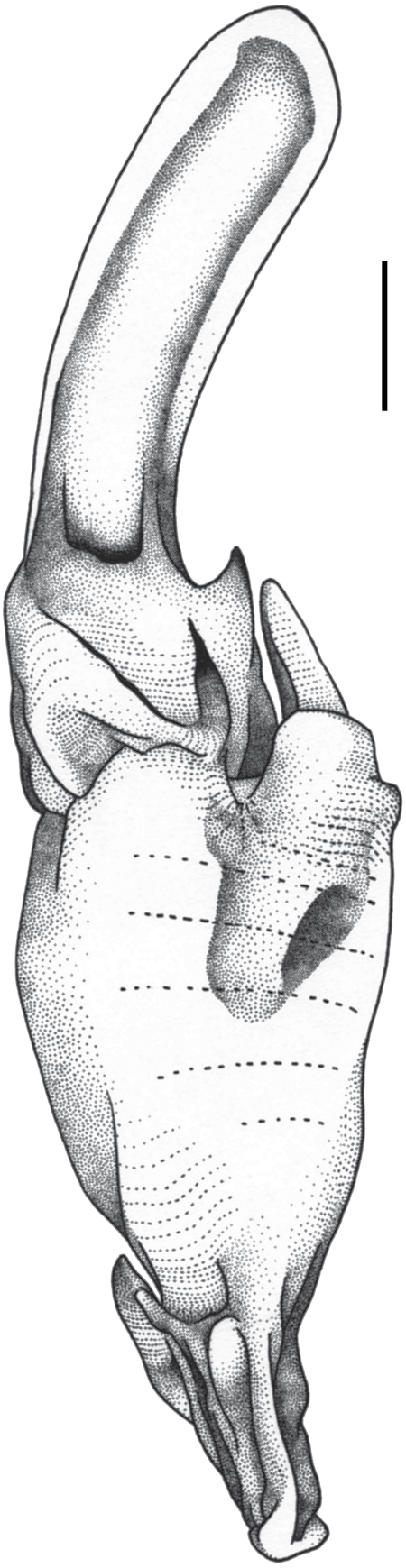
curved, sensory papillae covering distal portion only. STIGMA (spiracle), half-moon shaped (with a distinct curve), or round/oval; short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA (fig. 125C). Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae absent or obsolete; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules present, more strongly developed; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, one pair of well developed sub-posterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half with at least small spiniform granules, with medium spiniform granules more strongly developed than preceding granules (anterior half); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi (fig. 125B), two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/5; 4/5.

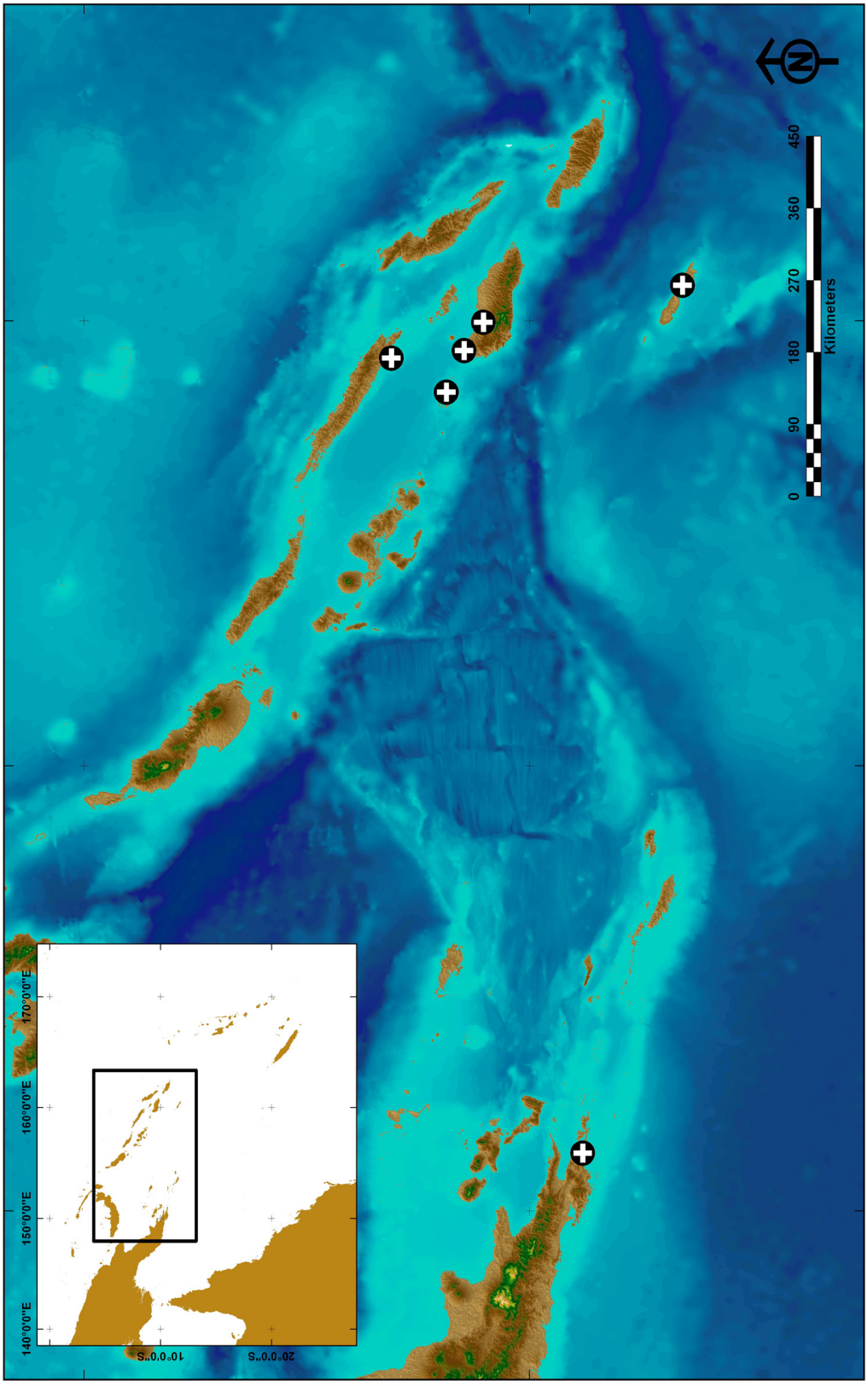
HEMISPERMATOPHORE (fig. 126). Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with base of lamellar hook, sometimes slightly below, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent. Accessory carinae and ccessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle

Fig. 126. *Hormurus penta* (Francke & Lourenço, 1991), male. Hemispermatophore. Scale line, 0.5 mm.



with lamella.

Fig. 127. Distribution map of *Hormurus penta* (Francke & Lourenço, 1991).


N
0
90
180
270
360
450
Kilometers
140°0'0"E
150°0'0"E
160°0'0"E
170°0'0"E
10°0'0"S
20°0'0"S

Hormurus polisorum (Volschenk, Locket & Harvey, 2001), **new combination**

Liocheles polisorum Volschenk, Locket & Harvey, 2001: 163–169, figs 1–16.

References

Liocheles polisorum: Humphreys & Eberhard, 2001: 62, pl. 1, tab. 3; Monod & Volschenk, 2004: 675, 686; Volschenk & Prendini, 2008: tab. 1.

Material examined

Holotype: CHRISTMAS ISLAND (Australian territory), INDIAN OCEAN, Bishops Cave, 10°27.99'Sx105°35.5'E, top of rock pile, first main chamber, 120 m from light, 11.VIII.1987, N. Plumley, 1 ♂ (WAM 97/2938). **Paratype**: CHRISTMAS ISLAND (Australian territory), INDIAN OCEAN, 10°25.04'Sx105°42'E, 19th Hole, Cave (CI-19), 30.III.1998, dark zone, wall, S. M. Eberhard (BES 5782), 1 ♀ (WAM 97/1624; LP 1614).

Distribution (fig. 128).
Christmas Island.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, conical (as high as wide or higher than wide), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch with a distinct posterior gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, low/reduced; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria. *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules, granular (at least sparsely or faintly), equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral

(*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) c*arina*e; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in three distinct smooth depressions (one around each trichobothrium). Chela, dorsal intercarinal surface, macrosculpture limited to prolateral and retrolateral edges, absent from the median part, granulation vestigial, at most low granules; retrolateral intercarinal surface: smooth or nearly so (only few scattered granules). Ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface: granulation absent or nearly so.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, raised at least slightly; superciliary carinae present, with at least few granules. Median ocelli absent. Lateral ocelli extremely reduced, vestigial; Two pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, extremely dense, giving tegument sand-like appearance; anteromedian surface entirely granular at least sparsely; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin crenulate (small spiniform granules). Tergites I–VI, post-tergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, post-tergites with minute spiniform granules, extremely densely distributed; III–VII, post-tergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length greater than posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; eight pectinal teeth, short, curved, sensory papillae covering distal portion only. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior

spiniform granules absent; ventrosubmedian carinae, sub-posterior spiniform granules weak to absent, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, sub-posterior spiniform granules absent, medial spiniform granules absent. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae, ridges with at least a few small/medium spiniform granules, subposterior spiniform granules absent; ventrolateral carinae with at least few minute/small spiniform granules. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae, ridges with at least few reduced spiniform granules distally; ventrolateral carinae with minute/small spiniform granules. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae present. Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4–5/4–5; 5/5; 5/5; 5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly; distinctly longer than basal part; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, below base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with base of lamellar hook, sometimes slightly below, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

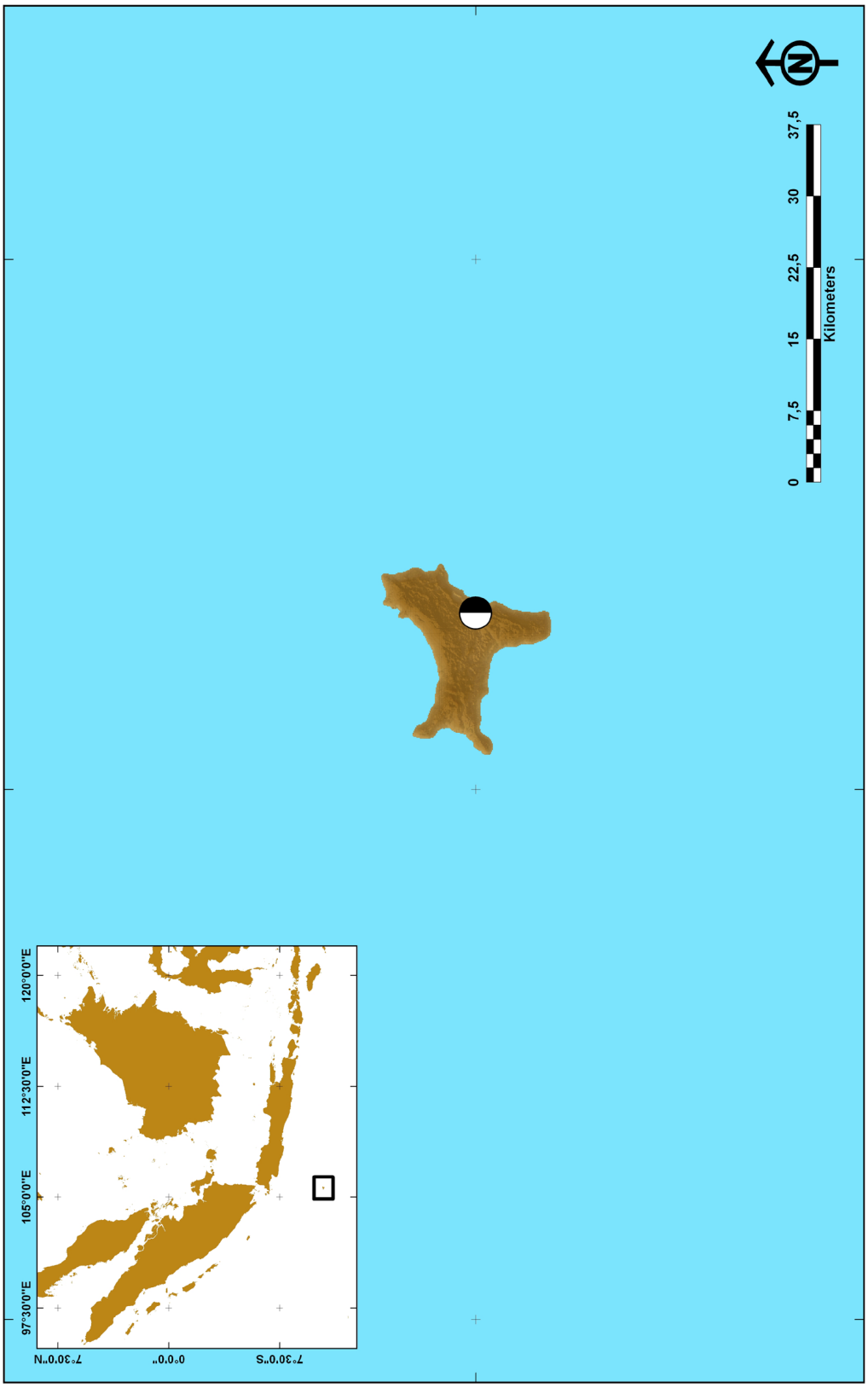
CARAPACE. Anteromedian surface entirely granular, at least sparsely; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–III, post-tergites entirely granular; IV–VI, post-tergites, mesial and lateral surfaces granular; VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.

VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal

edge of coxa; six pectinal teeth.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 128. Distribution map of *Hormurus polisorum* (Volschenk, Locket & Harvey, 2001).


N
0
7,5
15
22,5
30
37,5
Kilometers
120°0'0"E
112°30'0"E
105°0'0"E
97°30'0"E
7°30'0"N
0°0'0"
7°30'0"S

Hormurus solomonensis n. sp.

References

Hormurus karschii (nec .Keyserling, 1885; MIS): Pocock, 1898b: 458; Pocock, 1899: 97; Kopstein, 1921: 138 (part).

Hormurus caudicula karschi (UE) (nec Keyserling, 1885; MIS): Kraepelin, 1899: 155 (part), Giltay, 1931: 13, 18, 19 (part).

Hormurus karschi (UE) (nec Keyserling, 1885; MIS): Kopstein, 1921: 138 (part).

Liocheles waigiensis (nec Gervais, 1844; MIS): L. E. Koch, 1977: 172 (part); Kovařík, 2002: 15 (part).

Liocheles sp.: Soleglad *et al.*, 2003: 8, 69, 158.

Material examined

Holotype: Haruligo Village, Vatugulan area (NE coast), 09°19'03.4''Sx159°45'34.6''E, 5 m, 17.X.2004, rainforest, under stones, F. Tungale, M. R. & B. Tavalus, V. & F. Saurono, R. Wyss, L. Monod, 1 ♂ (LM/ LP 5549). **Paratypes**: same data as holotype, 1 ♂, 7 ♀♀, 1 imm. (LM/ LP 5549). **Additional material**: SOLOMON ISLANDS: R. A. Lever, 1 juv. (NHML 1933.11.24.1); 22.V.1976, Sofu Johnson, 1 ♂ immature (WAM 98/1893); Guadalcanal?, 67 area 1, 1.VI.1944, D. E. Beck, 1 ♀ (AMNH). CENTRAL PROVINCE, Ngella Islands, Tulaghi Island, 100', 25.XI.34, under log, R. A. Lever, 1 ♀ (NHML). Russel Islands, Pavuvu Island, 17.VIII.1964, R. Straatman, 2 ♀♀ (BPBM). GUADALCANAL PROVINCE, Guadalcanal Island: 1944, D. E. Beck, 1 ♀ (AMNH); Area 1, # 216, 23.VII.1944, D. E. Beck, 2 ♀♀ (AMNH); 1944, F. Cilley, 2 ♂♂, 2 ♀♀, 1 juv. (AMNH); VII.1945, F. Cilley, 3 ♂♂ (AMNH); I.1963, P. Greenslade (Royal Society B.S.I.P. 1965, 16 466), 1 ♂ (NHML, Acc. No. 2182); 3.VIII.1963, P. Greenslade (Royal Society B.S.I.P. 1965, 8393), 1 ♀ (NHML, Acc. No. 2182); 8.VIII.1963, P. Greenslade, (Royal Society B.S.I.P. 1965, 8466), 5 juv. (NHML, Acc. No. 2182). Honiara, 17.VII.1965, from G. Dennis garden (Royal Society B.S.I.P. 1965), 1 ♂ (NHML, Acc. No. 2182). Honiara Botanical Garden, 09°26'18.0''Sx159°56'25.7''E, 5 m, 14.X.2004, rainforest, under rotten logs, R. Wyss & L. Monod, 1 ♂, 1 ♀ (LM). Kukum, 22.IV.1963, P. Greenslade (Royal Society B.S.I.P. 1965, 5125), 1 ♂ sub. (NHML, Acc. No. 2184). Mt Austen, 12.VI.1963, P. Greenslade (Royal Society B.S.I.P. 1965, 6680), 2 juv. (NHML, Acc. No. 2182); 19.VI.1963, P. Greenslade (Royal Society B.S.I.P. 1965, collection no 6476), 1 ♂ (NHML, Acc. No. 2182); 21.VIII.1963, P. Greenslade (Royal Society B.S.I.P. 1965, 11 148), 1 ♂ (NHML, Acc. No. 2182); 22.VII.1963, P. Greenslade (Royal Society B.S.I.P. 1965, 11 307), 1 ♂ (NHML, Acc. No. 2182); 29.XI.1965, P. Greenslade (Royal Society B.S.I.P. 1965, 11 054), 1 ♀ (NHML, Acc. No. 2182). Mt Gallego, lower camp area (Royal Society B.S.I.P. 1965, H1), 1 ♂ (NHML, Acc. No. 2182). Approaches to Popomanasui via Nuhu, X.1965, J. Grant, (Royal Society B.S.I.P. 1965), 1 ♂ (NHML, Acc. No. 2182). ISABEL PROVINCE, Santa Isabel Island: "Albatros", 15.II.1857, 2 ♀♀ (NHMW 1738). Buala, 20–30 m, 29–31.X.1980, J. L. Gressitt, 1 ♀, 1 juv. (BPBM). Tatamba, 22.VIII.63, P. Greenslade (Royal Society B.S.I.P. 1965, 9585), 1 ♀ (NHML, Acc. No. 2184). Steep ridge side west of Tatamba Rest House, 4.X.65, humus on rotten logs (Royal Society B.S.I.P. 1965, KEL 288), 1 ♂ juv. (NHML, Acc. No. 2184). MAKIRA-ULAWA PROVINCE, San Cristoval Island (=Makira): Pue Pue River, 3 km S Kira Kira, 10°29'Sx161°55'E, 120 m, 20.I.1999, J. Lattke, 1 ♂ (LP 1818); Kira Kira, 10°28'Sx161°55'E, 22.I.1999, P. Gilbert & J. Lattke, 2 juv. (LP 1819). Ridge above confluence of Warahito and Pegato Rivers, 300', 22.VII.65, on rotten log, forest (Royal Society B.S.I.P. 1965, KEL 60), 1 ♀ (NHML, Acc. No. 2180). Wainoni Bay (Royal Society B.S.I.P. 1965, P3), 1 ♂ sub., 1 juv. (NHML, Acc. No. 2180). NE Wainoni, Huni River Estuary, 9.VIII.1965, hole in rotten log, Isiah (Royal Society Expedition Brit. Mus. 1966-1), 1 ♀ (NHML). Ca. 6 3/4 ml S Wainomi, 26.VII.1965, crevice in rotten stump, P. N. Lawrence (Roy. Soc. Exped. Brit. Museum 1966-1), 1 juv. (NHML). MALAITAI PROVINCE, Malaita Island: Nafinua, 27.IV.1885, under loose bark of coconut trunk, E.S.Brown, 1 ♂ (NHML); 27.V.1885, under loose bark of coconut trunk, E. S. Brown, O. E.Janson, 1 ♂ (NHML 1896.12.7.46-50). Near Riba Caves, Auki, 19.XI.1965, under litter, J. F. P. (Royal Society B.S.I.P. 1965, JP 107), 1 juv. (NHML, Acc. No. 2181). RENNEL-BELLONA PROVINCE, Rennel Island, Macanga (or Maranga), 24.XI.1955, E.S.Brown, 1 juv. (NHML). WESTERN PROVINCE: Baga Island (=Mbava Island), 5.XI.1929, 1 ♂ (AMNH, Acc. 275590). New Georgia Island: Munda, 31.XIII.1944, L. A. Conwell, 1 ♀ (USNM); Rubiana, 8.VI.1994, W., 2 ♀♀ (NHML). Vella Lavella Island, Bilua, E. G. Sayers, 2 ♀♀ (NHML 1953.2.24.5-6). Ranonga

Island, Niami Village, 08°02'44.0''Sx156°35'22.3''E, 22 m, 1.XI.2004, rainforest, under rocks and in rock crevices, near a creek, Veronika, Cherry, Ravia, R. Wyss, L. Monod, 3 ♂♂, 8 ♀♀, 28 imm. (LM; LP 5551); Rendova Island, Mbaniata Village, 08°37'46.1''Sx157°16'39.1''E, 62 m, 4.XI.2004, rainforest, under rotten logs, rocks and in rock crevices, usually near creeks, M. Vagi, J. Havea, R. Wyss, L. Monod, 1 ♀, 32 imm. (LM; LP 5552); 08°37'54.3''Sx157°16'36.2''E, 39 m, 5.XI.2004, in a garden, under bark and in rotten logs, D. Havea, L. Monod, 1 ♀, 1 juv. (LM); 08°37'49.9''Sx157°16'39.1''E, 10 m, 5.XI.2004, outskirts of rainforest, under logs, D. Havea & L. Monod, 1 ♂, 2 ♀♀, 1 sub. (LM). Tetepare Island, surroundings of WWF research station, around creeks, 08°43'15.4''Sx 157°27'10.7''N, 54 m, 7.XI.2004, rainforest, under rotten logs, rocks and in rock crevices, usually near creeks, R. Suka & L. Monod, 2 ♂♂, 8 ♀♀, 2 imm., 14 pullus (LM); 08°43'13.0''Sx157°27'25.6''E, 100 m, 8.XI.2004, rainforest, under stones and rotten logs, in rock crevices, near a creek, R. Suka, A. Fuhi & L. Monod, 2 ♂, 2 ♀♀ (LM). N coast, Raro Bay, Raro River area, 08°42'22.5''Sx 157°32'26.2''E/ 08°42'21.4''Sx157°32'33.0''E/ 08°42'37.5''Sx157°32'42.1''E, 4–133 m, 9.XI.2004, rainforest, under stones and rotten logs, lots of mud crabs, R. Suka, A. Fuhi, R. Wyss, L. Monod, 3 ♂♂, 7 ♀♀, 1 imm. (LM; LP 5554); Raro River area, 08°43'10.5''Sx157°33'08.3''E/ 08°43'01.1''Sx157°33'02.4''E, 343–287 m, 10.XI.2004, rainforest, under rocks and logs, A. Fuhi, R. Wyss & L. Monod, 3 ♂♂ (LM). Vella Lavella Island, S tip, Mbuna Poro Village, 25.X.2004, secondary rainforest, under stones and in rock crevices, around creeks, C. Sirno, R. Wyss, L. Monod, 1 ♂, 6 ♀♀, 2 juv. (LM; LP 5550).

Distribution (fig. 129)
Solomon Islands.

Etymology
The name *solomonensis* refers to the Melanesian archipelago where the species occurs.

DESCRIPTION. ADULT MALE
COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, dark (as dark as tergites). Telson, dark (as dark as metasoma).
CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.
PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth; wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in a single group or in two groups [esb_2][esb_1/em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina present at least as a

faint ridge or a distinct row of granules, granular (at least sparsely or faintly), equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface smooth or nearly so; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus markedly different with at least a few spines. MACROSCULPTURE. Carapace surfaces with large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules, evenly and sparsely distributed; anteromedian surface entirely granular at least sparsely; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) long, distal edge reaching beyond distal edge of coxa; three marginal lamellae; fulcrae present; ten pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow distinct on at least

segments I–IV, sometimes also in segment V, usually deep; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, sub-posterior spiniform granules weak to absent, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, sub-posterior spiniform granules absent, medial spiniform granules absent. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules present, well-developed. Basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/ 4; 4/5; 5/5.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, sub-distal, not more than mid-lamella; basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface entirely granular, at least sparsely; posteromedian surface

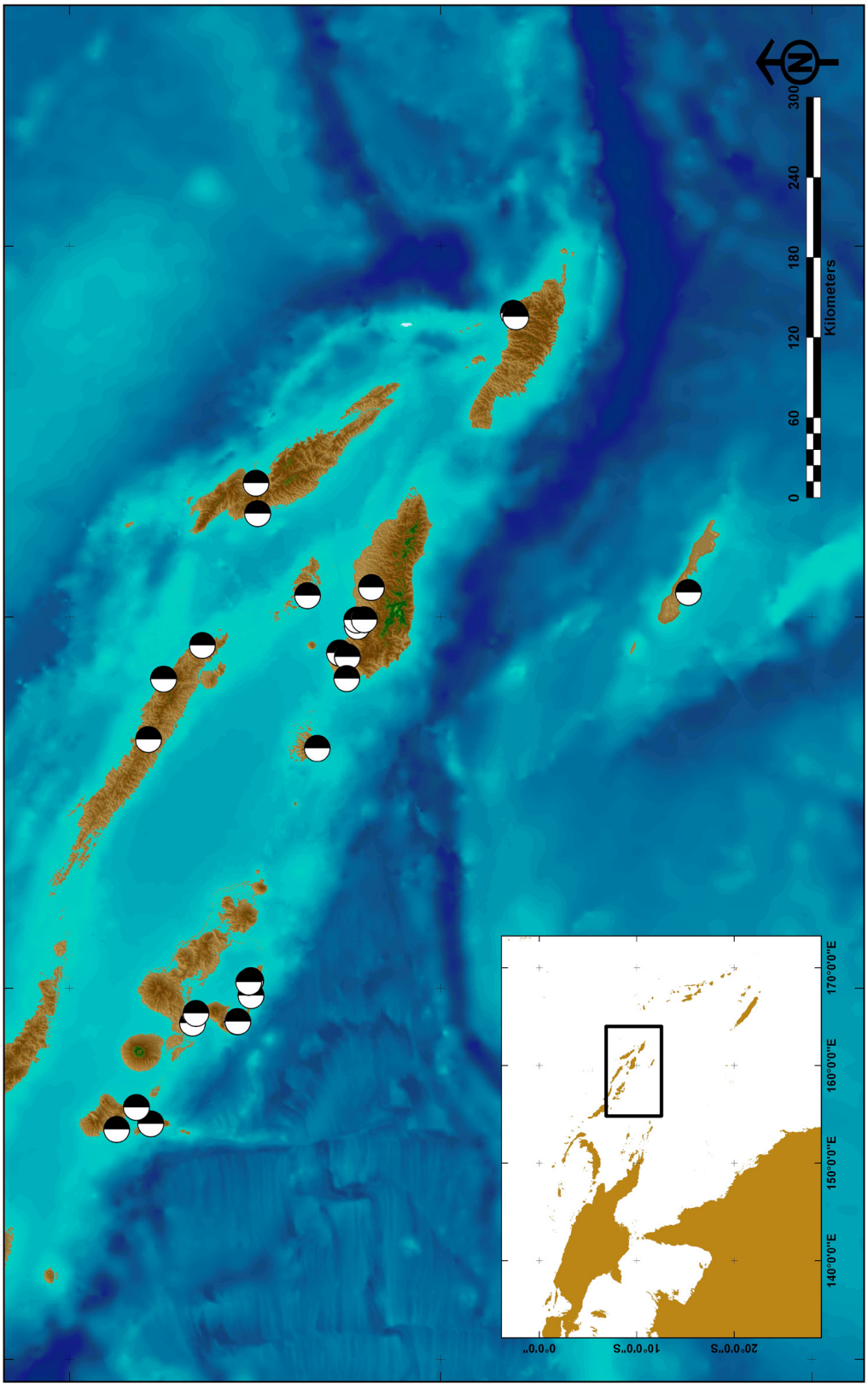
at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–III, post-tergites, mesially smooth, laterally granular; IV–VI, post-tergites, mesially smooth, laterally granular; VII, posttergite granular at least posteriorly; III–VII, reticulated network of ridges and dimples distinct, uneven surface.

VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa. Eight pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified

Fig. 129. Distribution map of *Hormurus solomonensis* n. sp.


N
0
60
120
180
240
300
Kilometers
140°0'0"E
150°0'0"E
160°0'0"E
170°0'0"E
20°0'0"S
10°0'0"S
0°0'0"

Hormurus waigiensis (Gervais, 1943), **new combination**

Scorpio (Ischnurus) waigiensis Gervais, 1843: 131.

References

Scorpio (*Ischnurus*) *waigiensis*: Gervais, 1844a: 237, pl. XII, figs 45, 46; Gervais, 1844b: 69.
Hormurus waigiensis: Thorell, 1888: 338, 427, 428.
Hormurus caudicula karschi (UE) (MIS): Kraepelin, 1899: 155, Kraepelin, 1901: 272 (part).
Hormurus caudicula: Kraepelin, 1901: 272 (part).
Hormurus karschi (UE) (nec Keyserling, 1885: MIS): Kopstein, 1921: 138 (part).
Liocheles waigiensis: Monod, 2000: 123–125, map 17.

Material examined

Holotype: INDONESIA, WEST PAPUA, RAJA AMPAT ARCHIPELAGO, Wiaigiou Island (= Waigeo Island), 1 ♂ (badly preserved) (MNHN-RS 0491). **Additional material**: INDONESIA, WEST PAPUA, RAJA AMPAT ARCHIPELAGO, Salawaty Island, A. Raffray, 1 juv. (MNHN-RS 0503).

Distribution (fig. 130)
Indonesia, West Papua.

Notes

Given the very poor preservation state of the holotype it was not possible to give a complete and accurate description of the species. Fresh material is critically needed to precisely characterize this species.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform.

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, conical (as high as wide or higher than wide), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est*–*esb* greater than distance *esb*–*eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, in line with *esb*–*et* axis; *esb* trichobothrium in line with *est*–*et* axis, in proximal region of fixed finger; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in a single group or in two groups [esb_2][esb_1/em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina present at least as a faint ridge or a distinct row of granules, granular (at least sparsely or faintly), equally or less strongly developed than

prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina distinct, at least a low ridge or a row of granules, costate or granular; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) c*arin*ae; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface, entire surface densely granular, distinct medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation distributed across entire surface; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with large spiniform granules at least on anteromedian surface (areas I–V), rest of prosoma usually with sparse smaller spiniform granules, evenly and sparsely distributed; anteromedian surface entirely granular at least sparsely; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

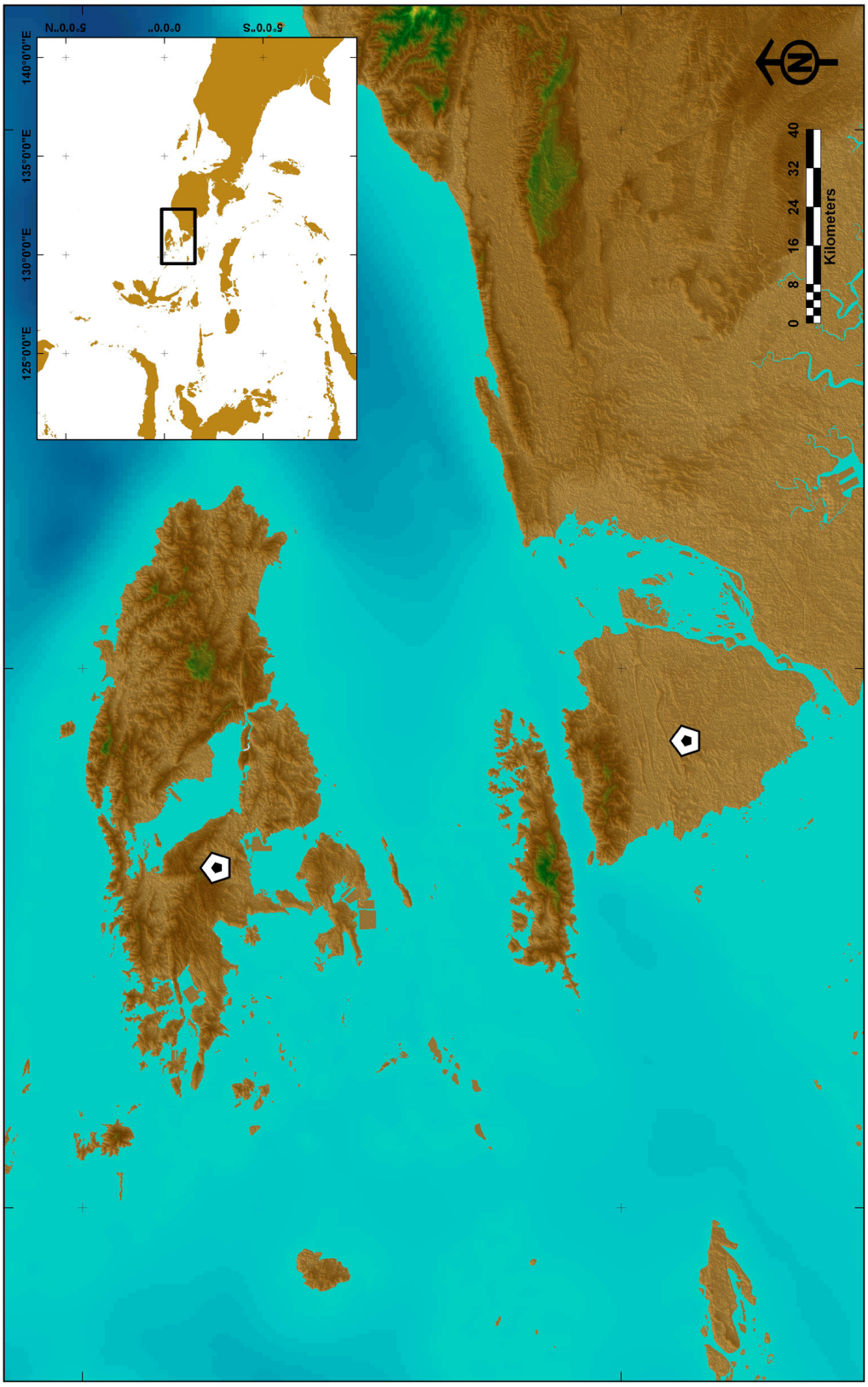
MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence. Tergites I–VI, post-tergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip with a distinct swelling/bulge oriented posteriorly, at least weak, usually more pronouced in ♂. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width).

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules); ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal

ventromedian spinules absent; ungues shorter than telotarsus.

Fig. 130. Distribution map of *Hormurus waigiensis* (Gervais, 1943).


N..0.0.S
..0.0.0
S..0.0.S
140°0'0"E
135°0'0"E
130°0'0"E
125°0'0"E
0
8
16
24
32
40
Kilometers

Hormurus weberi Pocock, 1894

Hormurus weberi Pocock, 1894: 97–99, pl. VI, fig. 7–7b.

References

Hormurus caudicula weberi: Kraepelin, 1894: 138; Kraepelin, 1899: 155; Giltay, 1931: 13, 18, 19 (part); Roewer, 1943: 235
Hormurus weberi: Kraepelin, 1914: 332; Kopstein, 1921: 139, 140; Kopstein, 1923: 186.
Liocheles caudicula weberi: Takashima, 1945: 96.

Material examined

Lectotype: INDONESIA, SULAWESI, Sulawesi Selatan, Luwu, Dr Max Weber, 1 ♂ (NHML 1896.10.6.6)**. Additional material**: INDONESIA, SULAWESI, Sulawesi Tengah, N of Guef Boni, Habland near Djaladja, 1 ♂ (NHML). Near Morowali, Ranu River Area, 27.I–20.IV.1980, 1 ♂ (NHML). Sulawesi Utara, Dumoga-Bone NP (=Bogani Nani Wartabone NP), 1985, 1 ♀ (NHML).

Distribution (fig. 131)
Indonesia, Sulawesi.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth, conical (as high as wide or higher than wide), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/ well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; our *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium more distal than Eb group, close to *Est*, sometimes slightly more distal than *Est*; Eb_3 trichobothrium close to $Eb_{1–2}$; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb*–*et* axis; *esb* trichobothrium below *est*–*et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two i tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in a single group or in two groups [esb_2][esb_1/$em_{1–2}$]; *eb* series with five trichobothria in two groups [eb_1] and [$eb_{2–5}$] or [eb_1/$eb_{4–5}$] and [$eb_{2–3}$]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not

expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae absent or obsolete; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina absent without spines or at most vestigial with a single spine at proximal extremity; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria granular (at least in the most proximal part), *db*/*dsb*/*dst* trichobothria in a single large smooth depression. Chela, dorsal intercarinal surface entirely and densely granular, distinct medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface entirely granular, at least a reticulated network of granules; retrolateral dorsal intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface entirely granular at least sparsely; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites entirely granular, at least sparsely in posterior half, granulation may be absent or vestigial on ridges; VII, posttergite entirely granular, at least sparsely; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples distinct, uneven surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) long, distal edge reaching beyond distal edge of coxa; three marginal lamellae; fulcrae present; 7–8 pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve), or round/oval; short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae present and distinct on at least some segments; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, posterior spiniform granules absent; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform

granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules absent; ventrosubmedian carinae, posterior spiniform granules absent, one pair of well developed subposterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae absent; ventromedian carina absent or obsolete, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half smooth or nearly so (rarely one pair of vestigial granules posteriorly); anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 3/4; 3/4; 4/4; 4/4.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, sub-distal, not more than mid-lamella; basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip below base of lamellar hook, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 135–150º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface entirely smooth or nearly so; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; mediolateral surface at least sparsely granular; posterolateral surfaces at least sparsely granular.

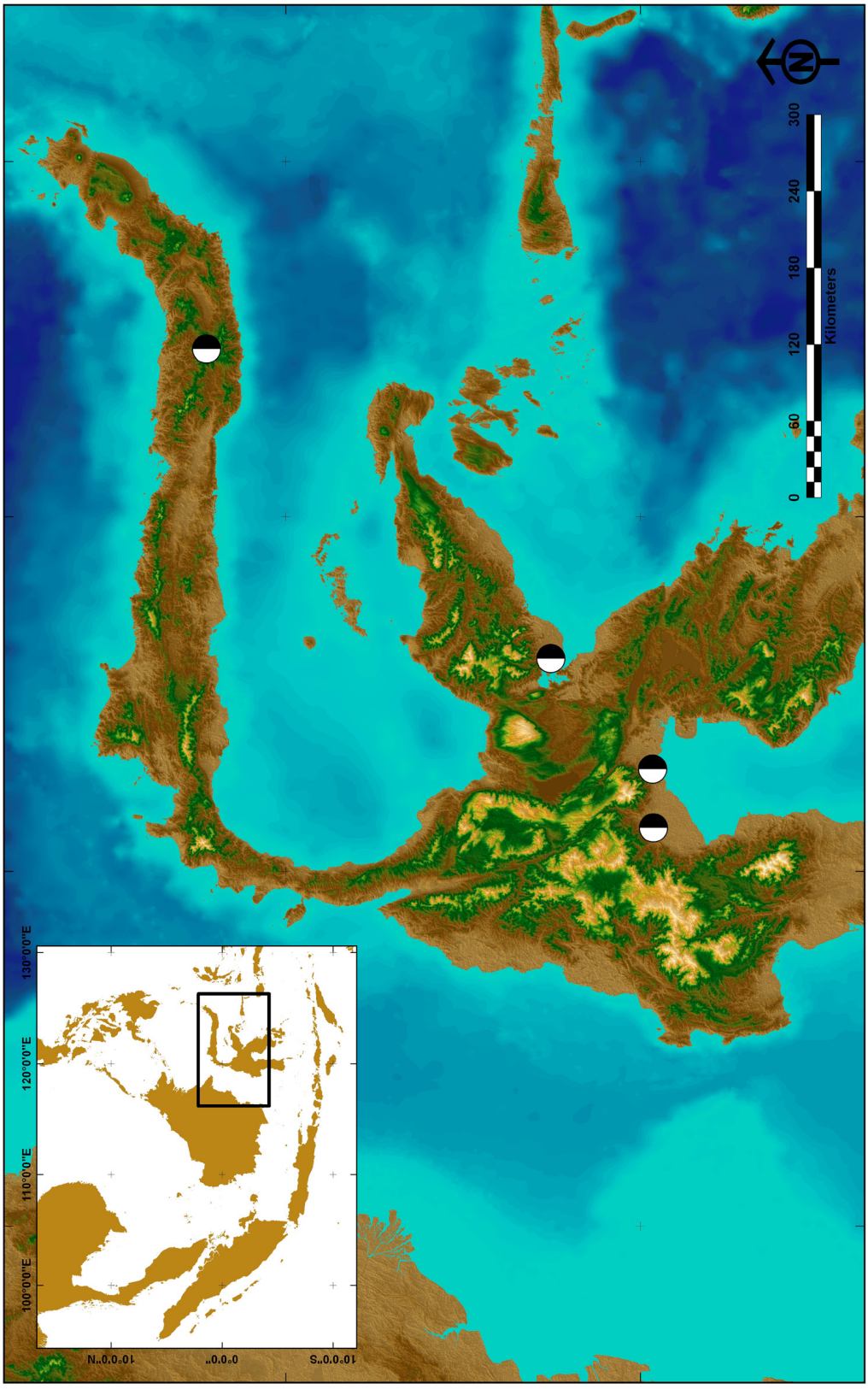
MESOSOMA. Tergites I–III, post-tergites, mesial and lateral areas smooth; IV–VI, post-tergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples distinct, uneven surface.

VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES,

length (expressed relative to length of coxa of leg IV) short, distal edge not reaching to distal edge of coxa; 5–6 pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. TELSON. Vesicle unmodified.

Fig. 131. Distribution map of *Hormurus weberi* Pocock, 1894.


N
0
60
120
180
240
300
Kilometers
100°0'0"E
110°0'0"E
120°0'0"E
130°0'0"E
10°0'0"N
0°0'0"
10°0'0"S

Genus ***LIOCHELES*** Sundevall, 1833

Scorpio (*Liocheles*) Sundevall, 1833: 31

Type species by monotypy *Scorpio australasiae* Fabricius, 1775 [= *Liocheles australasiae* (Fabricius, 1775)]

Synonyms

Ischnurus C.L. Koch, 1837b: 37, pl. VI, fig. 69

Type species by subsequent designation (Pocock, 1902: 364) *Ischnurus complanatus* C. L. Koch, 1937 [= *Liocheles complanatus* (C. L. Koch, 1837)] (synonymized with *Hormurus* Thorell by Pocock, 1902: 364).

References

Ischnurus: C. L. Koch, 1837a: 71–73; C. L. Koch, 1837b: 37 (part); Birula, 1917b: 162.

Sisyphus: C. L. Koch, 1837b, pl. VI, fig. 69 (*lapsus calami*; name created in the legend to fig. 69) (see Notes).

Hormurus: Thorell, 1876b: 249 (part); Keyserling, 1885: 21 (part); Thorell, 1888: 338, 419 (part); Kraepelin, 1894: 131–133 (part); Laurie, 1896a: 193; Laurie, 1896b: 128; Kraepelin, 1899: 153 (part); Pocock, 1900: 78, 79; Pocock, 1902a: 364; Kulczyński, 1910: 411; Kopstein, 1921: 135 (part); Giltay, 1931: 13 (part); Werner, 1934: 280 (part); Wu, 1936: 121; Kästner, 1941: 234 (part); Mello-Leitão, 1942: 125 (part); Roewer, 1943: 235 (part); Vachon, 1953: 8 (part); Chapin, 1957: 66, 67 (part); Pérez Minocci, 1974: 37 (part); Tikader & Bastawade, 1983: 499, 500 (part).

Liocheles: Karsch, 1880: 408; Takashima, 1945, 1948, 1949; L. E. Koch, 1977: 159, 160 (part); Lourenço, 1983: 404 (part); Francke, 1985: 9, 17 (part); Lourenço, 1985: 35, 47 (part); Lourenço, 1989: 171 (part); Stockwell, 1989: 87, 111, 116, 117, 119, 140, 169, 207, 212, 223, 236, 238 (part); Sissom, 1990: 126 (part); Nenilin & Fet, 1992: 19, 20 (part); Lourenço, 1996b: 40; Kovařík, 1995: 201 (part); Kovařík, 1998c: 133 (part); Fet & Bechly, 2000: 26, 27 (part); Kovařík, 2000: 60 (part); Monod, 2000: 58–62 (part); Volschenk *et al.*, 2001: 163 (part); Soleglad *et al.*, 2003: 19, 57–58, 67, 112, 113, 142, 146, tabs. 3/4/9 (part); Monod & Volschenk, 2004: 677 (part); Kamenz *et al.*, 2005: 107, 108; Prendini & Wheeler, 2005: tab. 5/10 (part); Soleglad *et al.*, 2005: 32, 34, tab. 6 (part); Kamenz & Prendini, 2008: 11, 30, 34, 35, 43 (part).

Idocheles (ISS): Nenilin & Fet, 1992: 20

Notes

C. L. Koch (1837) used the name *Sisyphus* C. L. Koch, 1837 instead of *Ischnurus* in a legend to the figure 69; the genus is called *Ischnurus* in the rest of the paper. Fet (2000) considered this name a *lapsus calami*.

Diagnosis

PEDIPALP. Chela fingers, dentition, inner accessory denticles (IAD) present. TRICHOBOTHRIOTAXY. Chela manus, *Esb* trichobothrium basal, in same axis as *Eb* group. Fixed finger, *db* trichobothrium on dorsal surface. ORNAMENTATION, CARINAE. Patella, dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae present at least as smooth ridge. Femur, prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with 2 large spines (one proximal and one midway). ORNAMENTATION, MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, *db*, *dsb* and *dst* trichobothria not in distinct depressions, surrounding areas smooth.

PROSOMAL CARAPACE: anterior furcated suture/sulci present and distinct; median occular tubercle raised at least slightly; superciliary carinae present; three pairs of lateral ocelli.

MESOSOMA: tergites I–VI with lateral transversal sulcus present; tergites III–VII, posttergites without reticulated network of ridges and dimples (even surface).

PECTINAL TEETH long, straight, sensory papillae entirely covering.

METASOMA not markedly flattened laterally (as thick as large or slightly thicker, more rounded). Segment I, ventral surface, 1–2 pairs of well developed of posterior spiniform granules. Segment V, ventral surface with a smooth shiny depression on posterior half between ventro-

lateral carinae; ventrolateral carinae, posterior half with strong conical tooth. Telson equal to or slightly longer than metasomal segment V,

HEMISPERMATOPHORE, lamella without longitudinal ‘spine’ (*ls*) on external surface absent; lamellar tip at approximately same level with apex of lamellar hook or slightly above. Distal lobe well developed, as a distinct hump. Basal lobe well developed (‘spoon’ shaped), merging with accessory anterior basal lobe; posterior edge of basal lobe forming a 90° angle with lamella.

Liocheles australasiae (Fabricius, 1775)

Scorpio australasiae Fabricius, 1775: 399.

Synonyms

Scorpio gracilicauda Guérin Méneville, 1843: 11 (synonymized with *Ischnurus complanatus* by Gervais, 1844: 69)

? Chactas brunneus Bellevoye, 1870: 113, 114 (synonymized by Fet, 2000: 396) (see notes).

Ischnurus pistaceus Simon, 1877a: 93 (synonymized by Simon, 1887: 113).

Buthus brevicaudatus Rainbow, 1897: 107, 108, pl. II, figs 1, 1c (synonymized by Pocock, 1898a: 323)

Liocheles australasiae brevidigitatus Werner, 1936: 190, **new synonymy**

References

Scorpio australasiae: Fabricius, 1781: 550; Fabricius, 1787: 348; Fabricius, 1793: 433; Herbst, 1800: 57, 58, tab. VI, fig. 1; Latreille, 1804: 124, 125; Chamisso, 1821: 159; Zimsen, 1964: 637.

Scorpio (*Liocheles*) *australasiae*: Sundevall, 1833: 31.

Ischnurus australasiae: C. L. Koch, 1837a: 71–73, pl. CXXVIII, fig. 294; Gervais, 1844b: 69; C. L. Koch, 1850: 89.

Hormurus australasiae: Thorell, 1876b: 251–254; Keyserling, 1885: 22–24; Thorell, 1888: 338, 419; Thorell, 1889: 525, 526, 590; Simon, 1893: 328; Kraepelin, 1894: 133–135, pl. II, figs 46/65; Pocock, 1894: 96, 97; Thorell, 1894: 15; Laurie, 1896a: 192; Laurie, 1896b: 127; Kraepelin, 1897: 1; Lönnberg (1897a): 187; Pocock, 1898b: 458; Kraepelin, 1899: 154, fig. 41; Pocock, 1899: 97; Simon, 1899: 120; Pocock, 1900: 79, 80; Flower, 1901: 36; Kraepelin, 1901: 272 (part); Simon, 1901: 79; Werner, 1902: 603; Borelli, 1904: 4; Iwakawa, 1906: 10; Kulczyński, 1910: 411; Simon, 1910: 83; Henderson, 1913: 133; Kraepelin, 1914: 328–330, 334; Werner, 1916: 91, 92; Lampe, 1917: 201; Kopstein, 1921: 135, 136; Kopstein, 1923: 185, 186; Pavlovsky, 1924: 79, pl. II, fig. 4; pl. III, figs 17–25; Pavlovsky, 1925: 177–179, 192, 193, pl. III, fig. 6; pl. IX, fig. 19; pl. X, figs 15–17; Kopstein, 1926: 109; Banks, 1928: 505; Kopstein, 1929: 124; Giltay, 1931: 9, 10, 18, 19; Meise, 1932: 269; Werner, 1932: 576; Fage, 1933: 27; Werner, 1934: 280; Giltay, 1935: 2; Kopstein, 1935: 210; Fage, 1936: 180; Pelt, 1936: 401–403; Wu, 1936: 121–123, fig. 4; Kästner, 1941: 234; Roewer, 1943: 235; Savory, 1943: 355; Fage, 1946: 71; Dammerman, 1948: 72; Sachet, 1953: 3–5; Chapin, 1957: 67–69, fig. 1a; Pérez Minocci, 1974: 37 (part); Kerr, 1991: 211.

Harmurus australasiae (ISS): Buxton, 1927: 13.

Hormurus australasiae brevidigitatus: Weidner, 1959: 101.

Liocheles australasiae: Karsch, 1880: 408; Karsch, 1881: 15; Simon, 1887: 113; Takashima, 1941: 279, 280; Takasima, 1942: 7; Takashima, 1945: 95; Takashima, 1948: 84–86; Takashima, 1949: 35; Takashima, 1950: 20; Takasima, 1952: 29; L. E. Koch, 1977: 160–166, figs 17/46/80/81, map 8a, b; L. E. Koch, 1981: 877; Makioka & Koike, 1984; Makioka & Koike, 1985; Vachon & Lourenço, 1985: 9; Lourenço, 1985: pl. 6, figs 6/13; Williams, 1987: 278; Paddy, 1988: 51, 53; Vachon & Abe, 1988: 27; Lourenço, 1989: pl. 5, figs 6/13; Stockwell, 1989: fig. 51; Francke & Lourenço, 1991: 200; Lourenço, 1991: 274; Goyffon, 1992: 18; Kovařík, 1992: 185; Makioka, 1992a; Makioka, 1992b; Makioka, 1993; Kovařík, 1994: 198; Lourenço & Cuellar, 1994: 20; Kovařík, 1995: 201, 202, fig. 20; Locket, 1995: 197, fig. 14b, tab. 1; Lourenço, 1996b: 40, figs 106/110/111; Kovařík, 1997: 184; Kovařík, 1998: 133; Fet & Bechly, 2000: 27; Monod, 2000: 63–71, pl. 17–21, maps 1–7; Kovařík, 2002: 15 (part); Soleglad *et al.*, 2003: 8, 59, 69, fig. 30; Monod & Volschenk, 2004: 675; Monod & Lourenço, 2005: fig. 35; Prendini & Wheeler, 2005: tab. 5; Kamenz & Prendini, 2008: 11, 43 (part).

Liocheles australasiae australasiae: Fet, 2000: 397; Monod & Volschenk, 2004: 686.

Liocheles australasiae brevidigitatus: Fet, 2000: 397; Monod & Volschenk, 2004: 686.

Type material (not examined)

Holotype of *Chactas brunneus*: sex unknown, CNHM, New Caledonia. **Syntypes of *Buthus brevicaudatus***: ELLICE ISLANDS (= TUVALU), Atoll Funafuti, 4 ♀ (AMS K2067).

Material examined

Type of *Scorpio australasiae*: in insuli Oceani pacifici (Zimsen, 1964: 637), formerly in NHML, now lost. **Type of *Scorpio gracilicauda***: INDONESIA, JAVA, formerly in MNHN, now lost. **Syntypes of *Ischnurus pistaceus***: PHILIPPINES, Manilla (Baer), formerly in MNHN, now lost. **Holotype of *L. australasiae brevidigitatus***: INDONESIA, JAVA, Buitenzorg, Botanical Garden, 21.I.1925, Dr. H. Winkler, 1 ♀ (ZMH). **Additional material**: WITHOUT LOCALITY DATA, 2 ♀♀ (BPBM); 3 juv. (BPBM); Gen.-R (?), 1 juv. (BPBM); 3 ♀♀, 3 juv. (MNHN-RS 0453); A.P.O. 40 (?), H. Spitzer, 1 ♀ (CAS); 1 ♀, 2 juv. (RMBR ZRC.ARA.438); 3 ♀♀ (RMBR ZRC.ARA.445); 2 juv. (RMBR ZRC.ARA.458); 27th Mal. S. Unit, A.P.O. 705, Acc 169081, Capt. M. C. Meyer, 1 ♀ (USNM 00310). MISLABELLED: CHILE, Koelbel's Nachlass, 1896.VIII.615, 5 juv. (NHMW 1754). UNCLEAR/UNREADABLE: dto ?, Otto ?, 1 ♀, 1 juv. (ZMB 4083). Banka?, Müller, 1 ♀ (ZMB 3024). Bigatyemangi?, in decaying coconut log, 26.XI.1948, No 34, 1 juv. (USNM 00310). Indes, Robie, 1 ♀ (MRHN). Jugend Willen? Oceans (Pacific Ocean?), 2 ♀♀, 3 juv. (NHML 1890.7.1.223-227). Limvens ?, VII.1878, 1 ♀ (ZMB 15141). Matupai?, DCXXXI, 1 ♀ (ZMB 7418). Nanvaro?, SMS Gazelle, 1 ♂, 1 ♀ (ZMB 7646). Ost Asien Expedition, Friedl, 1 ♀ (ZMB 7544). Südsee, Wagke, 4 ♀♀, 2 juv. (ZMB 15147). **AUSTRALIA,** N QUEENSLAND: Barcoo, Mrs McCarthy Metzger, 1 ♀, 1 juv. (AM KS 56793, KS 94921). Cairncross West Island, 12. VII.1969, H. Heatwole, 1 ♀ (WAM 98/1874). Cape York Peninsula, Rocky River, 100m, 1.V.1961, J. L. Gressitt, 1 juv. (BPBM). Iron Range, 50–75 ft, VI.1948, Archbold Expedition, 3 ♀♀, 1 juv. (AMNH). Noah Creek, 8km S of Cape Tribulation, 30.IX–7.X.1982, G. Monteith, D. Yeates & G. Thompson, 1 ♀ (QM-S 17211). Somerset, Finsch, 2 ♀♀, 1 juv. (ZMB 8292). Torres Strait Islands. Dauar Island (=Dowar Island), 29.VII.1974, under debris, H. Heatwole, 1 juv. (WAM 98/1875). Moa Island, 24.II.1975, closed forest, under and in logs, E. Cameron, 2 juv. (WAM 98/1876). Murray Island, VII–VIII.1974, H. Heatwhole & E. Cameron, 1 ♀ (USNM 00309); VII–VIII.1974, H. Heatwole, U.N.E, ARMIDALE, 2 juv. (WAM 98/1877-8); 21.VII.1974, under tree-bark, H. Heatwole & E. Cameron, 1 ♀, 1 juv. (WAM 98/1879-80). Saibai Island, 10–12 .VII.1975, H. Heatwole, 1 ♀ (WAM 98/1883); 14.VII.1975, under bark of dead mangrove tree, H. Heatwole, 2 juv. (WAM 98/1881-2). **BOUGAINVILLE ISLAND**, A98950, 1 ♀ (AMNH). Found in pineapple from Arawa market, IV.1989, C. Yule, 1 juv. (WAM 89/445). S part, Kokure, nr. Crown Prince Rn. ,900m, 10.VI.1956, J. L. Gressitt, 1 ♀, 1 juv. (BPBM). **BRUNEI**, Belait District: Andulau Forest Reserve, à 3.5 km S de Sungai Liang (39.5 km de Labi), forêt primaire (mixed dipterocarp forest), K-7 (Kompartment 7), 50 m, 19.XI.1988, B. Hauser, 12 juv. (MHNG, Bru-88/20); K-7 (Kompartment 7), 50m, 19.XI.1988, C. Lienhard, 1 ♀ (MHNG, Bru-88/22); K-8 (Kompartment 8), 70 m, 26.XI.1988, B. Hauser, 1 ♀, 2 juv. (MHNG, Bru-88/45). Labi Hills Forst Reserve, Teraja, 42 km S de Sungai Liang (12 km au sud de Labi), environs de Rumah Panjang, forêt primaire (mixed dipterocarp forest), 40 m, 22.XI.1988, C. Lienhard, 1 ♀, 3 juv. (MHNG, Bru-88/33). Près de Sungai Mau (14 km sur la route de Sungai Liang à Labi), 1.5 mille sur la route secondaire vers Badas, env. 50m, 16.XI.1988, B. Hauser, 1 ♀, 4 juv., 1 molt (MHNG, Bru-88/8). Sungai Liang, Arboretum Forest Reserve, forêt primaire (mixed dipterocarp forest), 20m, 25.XI.1988, B. Hauser, 6 juv. (MHNG, Bru-88/40). Brunei-Muara District: Bandar Seri Begawan, colline derrière Hôtel Sheraton, 30 m, 15.XI.1988, B. Hauser, 1 ♀, 1 juv. (MHNG, Bru-88/6). Forêt S de la route côtière, 38.5 km de Muara (83.5 km de Kuala Belait), 50 m, 25.XI.1988, leg. C.Lienhard, 1 ♀, 1 juv. (MHNG, Bru-88/44). Plage à 4 km de Muara (118 km de Kuala Belait), 0 m, 27.XI.1988, B.Hauser, 1 ♀, 2 juv. (MHNG, Bru-88/48). Temburong District: Peradayan Forest Reserve (Bukit Patoi), 14.5 km de Bangar (2.5 km de Labu), forêt primaire (mixed dipterocarp forest), 60–300m, 24.XI.1988, B. Hauser, 2 juv. (MHNG, Bru-88/37). Tutong District: petit marché sur la route venant de Muara, 77 km de Kuala Belait, ca. 40 m, 18.XI.1988, B. Hauser, 1 juv. (MHNG, Bru-88/16). **GUAM**, Latte Hts?, 1.III.1980, J. Schramal, 1 ♀ (BPBM). **HONK KONG** (New Territories): Tai Po Kau Nature Reserve, 100–200m, 1.XII.1988, leg. B. Hauser, 1 ♀ (MHNG Bru-88/54). **CAROLINE ISLANDS**. **FEDERATED STATES OF MICRONESIA**. CHUUK (=TRUK ISLANDS). Chuuk Atoll (= Truk Island), 28.XII.1935, Y. Kondo, 1 juv. (BPBM); 9.I.1936, Y. Kondo, 1 juv. (BPBM). Moen Island, 10 ft, V.31.1946, H. K. Townes, 1 juv. (USNM 00310, no 424); III.1949, D. Langford, 1 ♀, 3 juv. (USNM 00310). Natsushima? , 22.XII.1935, Y. Kondo, 1 ♀, 4 juv. (BPBM). Udot Islet, V.25.46, H. K. Townes, 1 juv. (USNM, no 255). Nama Island, 15.II.1949, R. W. L. Porns, 1 ♀ (BPBM). Namoluk Atoll, Namoluk Islet, 1971, in bird cage containing *Aplonus opacus angus*, MacMarshall (NK-60), 1 ♀ (BPBM). Nomwin Atoll, Nomwin Island, 17–18.II.1954, ex dead coconut,

drawn, J. W. Beardsley, 1 juv. (BPBM). Satawan Island, 22.IX.1952, N. H. L. Krauss, 1 ♀ (BPBM). KOSRAE. Innam Island?, 28.I.1953, J. F. G. Clarke, 1 ♀ (BPBM). Kosrae Island (= Kusaie), Hill 541, 31.I.1963, J. F. G.Clarke, 1 ♀ (BPBM). Hill 1010, 300m, 4.II.1953, J. F. G. Clarke, 1 ♀, 3 juv. (BPBM). Mutunlik, 22m, 27.I.1953, under bark dead bread fruit, J. F. G. Clarke, 1 ♀ (BPBM). POHNPEI, Kapingamarangi Atoll, Hare islet, 3.VIII.1946, H. K. Townes (1626), 1 ♀, 2 juv. (USNM 00310). Matiro Island, 13.VII.1954, under bark of decayed coconut logs of pig pen, W. A. Niering, 1 ♀, 5 juv. (BPBM). Werua Island, 21.VII.1954, decaying vegetate debris, W. A. Niering, 5 specimens badly preserved (BPBM). Nukuoro Atoll, Nukuoro Islet, VIII.6.46, H. K. Townes 1 ♀, 14 pullus (USNM 00310, 1600); 1 ♀, 2 juv. (USNM 00310, 1611). Pohnpei Island (= Ponape), 1913–14, Lederman (552/15), 1 juv. (ZMB 30878). Metalanim, 8.VIII.1989, P. A. Adams, 1 ♀ (BPBM). Mt Dolennankap, 1800ft, 11.VII.1946, H. K. Townes (no 1686), 1 ♀, 2 juv. (USNM). YAP: Elato Atoll, Elato Island, 24.IX.1952, 2 juv. (BPBM). Fais Island, 5.X.1952, N. L. H. Krauss, 2 juv. (BPBM). Faraulep Atoll, Faraulep Island, 21.IX.1952, N. Krauss, 1 ♀ (BPBM). Ifalik Atoll (=Ifaluk), 6.IV.1953, M. Bates, 1 ♀ (BPBM); 2.VIII.1953, under leaf, base of a young coconut tree, M. Bates, 1 juv. (BPBM). Ifalik Island, 25.IX.1952, N. L. H. Krauss, 2 ♀♀, 2 juv. (BPBM); 8.II.1953, J. W. Beardsley (M5866), 1 ♀ (BPBM). Falarik Islet, Rauan village, 13. IX.1953, F.M.B., A326, Pacific Science Board, 4th Pacific Atoll Survey Team 57-589, 1 juv. (USNM 00753, Acc No 200652). Ulithi Atoll, Mog Mog Island, V.1945, F. N. Young (57-805), 1 ♀, 1 juv. (USNM 00753); #8a, V.1945, F. N. Young (57-804), 1 ♀ (USNM 00753); #13, V.1945, F. N. Young (57-807), 1 ♀ (USNM 00753); V.1945, F. N. Young (57-808), 1 ♀ (USNM 00753); 6.X.1952, N. L. H. Krauss, 1 ♀ (BPBM). Potangeras Island, 16.VIII.1945, R. H. Baker, 1 ♀, 1 juv. (BPBM). Ngulu Atoll, Ngulu Island, 3.X.1952, N. L. H. Krauss, 1 juv. (BPBM). Rumung Island, S part, 8.VIII.1950, R. J. Ross, 1 juv. (BPBM); E part, 9.VIII.1950, R. J. Ross, 1 juv. (BPBM). Woleai Atoll, Falalais Island, 3.II.1953, J. W. Beardsley (M5867), 1 ♀ (BPBM). Yap Island, X/XII.1975, M. Lundgren, 1 ♀, 2 juv. (CAS); 8.VI.1950, R. J. Ross, 3 juv. (BPBM); 27. VI.1950, R. J. Ross, 2 juv. (BPBM); VII–VIII.1950, R. J. Ross, 3 juv. (BPBM); 2.VII.1950, R. J. Ross, 12 juv. (BPBM); 11.VII.1950, R. J. Ross, 3 ♀♀ (BPBM). N Yap Island, 14.VII.1950, R. J. Ross, 1 ♀ (BPBM). S Yap Island, 21.VIII.1950, R. J. Ross, 1 ♀ (BPBM). Colonia, 23.VI.1950, R. J. Ross, 1 juv. (BPBM). Rull district, 15.VIII.1950, R. J. Ross, 2 juv. (BPBM); 18.VIII.1950, R. J. Ross, 3 juv. (BPBM). So Map?, 3.VIII.1950, R. J. Ross, 1 juv. (BPBM). **CAROLINE ISLANDS. PALAU.** Badeldaob Island (= Babelthuap), E Egatpang, 65m, 7.XII.1952, J. L. Gressitt, 1 juv. (BPBM). Gakip, VII.19.1946, H. K. Townes 1416, 1 ♀, 5 juv. (USNM 00310). Galap, 18.VIII.1947, Y.K.Halbert, 1 juv. (BPBM). Ngiwal, Babelthuap, 21.VII.1951, J. L. Gressitt, 1 juv. (BPBM); 3.VIII.1951, J. L. Gressitt, 2 ♀♀, 1 juv. (BPBM); 5.X.1952, J. L. Gressitt, 1 ♀, 1 juv. (BPBM); 3.XI.1952, coconut trunk, J. L. Gressitt, 1 juv. (BPBM). Eil Malk Island, On path to JellyFish Lake, 2.X.1987, R. Van Syoc, 1 ♀ (CAS). Garakayo Island, 8.VIII.1945, E. Hagen, 3 juv. (BPBM). Koror Island, Ngerbeched, at Entomologic Laboratory, Oct. 26 1955, 1 ♀ (USNM 00753). Peleliu Island, E.Hagen, VII.1945, 1 ♀ (BPBM). **CHINA**, Hainan: H.Schoede, 10–25. III.1909 (801/09), 2 ♀♀ (ZMB 15131). Jaluit, 7.III.1894, Steinback (720), 4 ♀♀, 1 juv. (ZMB 7639); 7.XI.1900, holz bekamt umgeb., Dr Bartels, 2 ♀♀, 1 juv. (ZMB 15145). Liamin (Leng Moon), 3.VIII.1935, L. Gressitt, 3 ♀♀ (CAS). Taïwan (= Formosa) : S part, Kuraru, Koshun, 7.V/10.VIII.1934, L. Gressitt, 9 ♀♀ (CAS). **CHRISTMAS ISLAND (INDIAN OCEAN)**, IX.1967, on plateau and levels above shore terrasse, S.Slack-Smith & A.Patterson, 1 ♀, 3 juv. (WAM 72/326-329). Central Area Workshop, 25.VII.1996, in primary plateau rain forest, D. Metcalfe, P. Green, D. Wallace (via P. Meeks, Parks Australia Nth), 1 ♀ (WAMP 98/1873). Flying Fish Cove, VI.1961, Dr. G. F. Mees, 2 ♀♀, 3 juv. (WAM 66/321-326). **COOK ISLANDS**: NORTHERN COOK ISLANDS, Puka Puka Island, 9.IV.33, M. Willows Jr., Templeton Crocker Expedition 1933, 1 ♀ (CAS). SOUTHERN COOK ISLANDS, Aitutaki Atoll, Akaiami Island, II.1960, N. L. H. Krauss, under logs, 1 ♀, 7 juv. (AMNH). Rarotonga Island, Avarua, 3.III.1964, under bark of decaying log, N. L. H. Krauss, 1 juv. (BPBM). **FIJI**. Summer 1972, gift of University of Idaho, presented to CAS by W.F.Barr, 1 ♀ (CAS). Kadavu Island, waterfall, 2.5km E of Vunisea, 29–30. VI.1987, G. B. & S. R. Monteith, 50 m, 1 juv. (QM-S 23317). Lau Archipelago, Aiwa Island, W178: S18, 30.VIII.1924, E. H. Bryan Jr, 2 ♀♀, 2 juv. (AMNH); W178: S18, 30.VIII.1924, E. H. Bryan, 6 ♀♀, 5 juv. (AMNH). Kambara Island (=Kabara), Lau, W178: S19, 24.VIII.1924, E. H. Bryan Jr, 1 juv. (AMNH). Lakemba Island (= Lakeba), 1 ♀, 1 juv. (AMNH) Namuka Island (Nmauka-i-Lau), Lau, W178: S19, 13.VIII.1924, E. H. Bryan, 1 juv. (AMNH). Oneata Island, W178: S19, 18.VIII.1924, E. H. Bryan, 1 ♀ (AMNH). Ongea Island, W178: S20, 30.VII.1924, E. H. Bryan (R.H.Beck?), 1 ♀, 3 juv. (AMNH). Thikombia Island, W179: S16, 26.IX.1924, E. H.

Bryan Jr, 1 ♀ (AMNH). Ovalau Island, EI 79: S18, 15.X.1924, E. H. Bryan, 2 ♀♀ (AMNH). W side, 19.III.1929, under bark, K.P.S. Crane, Field Museum Pacific Expedition 1928–29, 1 ♀, 11 pullus (AMNH). Levuka, 0–200 m, XII.1969, N. L. H. Krauss, 3 ♀♀, 1 juv. (BPBM). Taveuni Island, L. Tagimancia track, 15.VII.1987, 500–600 m, G. Monteith & D. Cook, 1 ♀ (QM-S 23320); 17 .VII.1987, 300–400 m, G. Monteith & D. Cook, 1 ♀, 2 juv. (QM-S 23324). Vanua Levu, Mt Delaikoro, 600m, 21.VII.1987, G. Monteith & D. Cook, 2 ♀♀ (QM-S 23319). Savusavu/Labasa Divide, 20.VII.1987, 500 m, G. Monteith & D. Cook, 3 ♀♀ (QM-S 23312). Viti Levu Island, Colo-i-Suva Forest Park, EI 79: S17, 21.VI.1924, E. H. Bryan, 3 ♀♀, 5 juv. (AMNH). Embouchure de la Rewa (including Suva), G.Gilson, 3 juv. (MRHN). Namuamua (= Numuamua), Day-flying 1953, A. C. Smith, 1 juv. (USNM 00752) Savura Creek, Site 2, 30.V.1976, under bark of dead log, P. A. Maddison, M. Kirby, (Suva-Fiji, UNDP/FAO, Mr.G.Stride), 1 ♀ (NHML). 9 mi from Suwa, 14.III.1929, on tree, K. P. S. Crane, Field Museum Pacific Expedition 1928–29, 1 ♀, 9 pullus (AMNH). **FRENCH POLYNESIA**. SOCIETY ISLANDS, Mc Javisch, 1 juv. (AMNH). Leeward Islands, Raiatea Island, Uturoa, 10.XI.1927, J. Morgan Clements, 1 ♀ (USNM 00310). Windward Islands.Moorea, XII.1908, 3 ♀♀ (CAS). Tahiti, Mc Javisch, 1 ♀, 5 juv.; Novara Expedition, Zelebor leg., I.1970, 2 juv. (NHMW 1741); 2 ♀♀, 1 juv. (NHMW 1753); 13.VIII.1919, 2 ♀♀ (AMNH); ca. VII.1959, S. J. Cox, Collection Stahnke, 28 ♀♀ (CAS 60-193); 6.VI.1906, O. V. Bremer, 1 juv. (USNM 00310). Cascade de Fautaua, 4.IX.1961, J. F. G. Clarke (ic60-20), under rock, 1 juv. (USNM 00753). Fautaua Valley, 9.IX, 2 juv. (AMNH, A5514). Plateau de Papenoo, 1905, G. Seurat, 26 ♀♀, 38 juv. (MNHN-RS 0456). TUAMOTU ISLANDS, Fakarava Atoll, 22.IV.1923, Whitney South Sea Expedition, 4 ♀♀ (AMNH). Kaukura Atoll, 15.VII.1923, 2 ♀♀ (AMNH). Makemo Atoll, 21.V.1923, AMNH Whitney South Sea Expedition, 3 ♀♀ (AMNH). Raroia Atoll, Oteteu Island, 21.VIII.1952, J. P. E. Morrison, 5 juv. (USNM 00753). Opakea I., 16.VIII.1952, J. P. E. Morrison, 1 ♀, 1 juv. (USNM 00753). Tikehau Atoll, 22.VI.1923, 1 ♀ (AMNH). Toau Atoll, 6.VII.1923, 2 ♀♀ (AMNH). **INDONESIA, BALI.** Sangen, 30.VII.1980, E. Heiss, 1 juv. (MHNG). W part, Tjandi Koesoema, 27.IV.1932, S.A.R.le Prince Léopold, 2 ♀♀ (MRHN No 9.796). N part, Jankait?, 13.III.1927, Dr Rensch, Sunda Expedition (2820/28), 2 juv. (ZMB 15137). **INDONESIA, KALIMANTAN (BORNEO).** Dr. Schmidt (M142), 1 ♀ (ZMB 15134); Borneo, 25.I.1875, Plason, 1 ♀ (NHMW 1744); Boran?, 11.V.1929 (no D29), 1 ♀ (ZMB 30858). W/SW Borneo, S.Bilis?, V.1932, S.A.R.la Prince Léopold, 2 ♀♀, 1 juv. (MRHN No 9.796). KALIMANTAN BARAT PROVINCE (W Borneo). Martens, 1 ♀, 1 juv. (ZMB 7227). Sintang, Martens, 8 ♀♀ (ZMB 7296, 7549). KALIMANTAN TENGAH PROVINCE, Kuala Kapuas, F. Grabowsky, 2 juv. (ZMB 7327); 4.X.1887, unter Baumrinde, F. Grabowsky, 2 juv. (ZMB 4264). Permantang (Sampit River region, S of Kuala Kajan), Borneo, 28.I.1954, A. H. G. Alston, 1 juv. (NHML). **INDONESIA, JAVA.** 3 ♂♂, 2 ♀♀ (ZMB 7219); Novara Expedition, Frauenfeld, 1 ♀, 1 juv. (NHMW 1742, 1866.I.71); Meyer, 1 ♀ (ZMB 31082); Prof. Strubell (378 D), 8 ♀♀, 2 juv. (ZMB 15126), 1 ♀, 31 pullus (ZMB 15127). BANTEN PROVINCE, Unjung Kulon NP, Cibunar, 6°48'Sx105°17'E, 20.VIII.1984, under bark, 18.C, Zoological Expedition Krakataus 1984, 1 juv. (WAM). JAKARTA PROVINCE, Jakarta (= Batavia), A. G. Vorderman, 1 ♂, 3 ♀♀ (MRHN). JAWA BARAT PROVINCE, Bogor (= Buitenzorg), D. G. Fairchild, 3 ♀♀ (USNM 00310); D. M. Fleischer, 1 ♀, 3 juv. (ZMB 15129); VIII.1964, N. L. H. Krauss, 1 ♀ (BPBM); Jardin Botanique, env. 250 m, 23.XI.1987, B. Hauser, 1 juv. (MHNG, Sar-87/6). Mt Patoeha (=Mt Patuha), A. G. Vorderman, 1 ♀ (MRHN). **INDONESIA, MALUKU.** 1 ♀ (MHNG, MNHNP leg.); III.1962, Martens, 1 ♀ (ZMB 8291). Ambon Island, 1858, Doleschal, 2 ♀♀, 1 juv. (NHMW 1740, Acqu. No 1858.I.54); 25.XII.1858 (1858.I.49), Doleschal, 3 ♀♀ (NHMW 1739); 70 m, 22.XI.1961, coll. at light, A. M. R. Wegner, 1 ♀ (CAS). Kali Tua R., 12.XI.1964, J.R.Winkler, 1 ♀ (BPBM). Wahai, XI.1964, S. R. Winkler, 6 juv. (BPBM); 8.XI.1964, S. R. Winkler, 2 juv. (BPBM); 15.XI.1964, S. R. Winkler, 1 juv. (BPBM). **INDONESIA, EAST NUSA TENGARRA PROVINCE**, Flores, Rana Mêsé, 25.VI.1927, Sunda Expedition, Rensch, 1 ♀ (ZMB 15135). W part, Mboera, X.1929, de Jong, Mus. Buitenzorg, 1 ♀ (ZMB 31083). Timor, Kupang, V.Ma.?, 1 ♀ (ZMB 30857). **INDONESIA, WEST NUSA TENGARRA PROVINCE**, Lombok Island, Narmada, 18–21.IV.27, Rensch (Sunda Expedition), 1 juv. (ZMB). Swela, 22–25.II.27, Sunda Expedition, Rensch, 2 ♀♀ (ZMB 10498). Tetebatu, 6–10.VIII.1979, Winkler et récolte à la main, A. de Chambrier, 1 ♀ (MHNG, AC/52); 6–10.VIII.1979, A. de Chambrier, 14 ♀♀, 59 juv. (MNHN-AC 025). Sumbawa Island, W part, Dompoe, Dr Rensch, Sunda Exp., 24–25.V.27 (2820/28), 2 ♀♀ (ZMB 15136). **INDONESIA. PAPUA BARAT PROVINCE,** Biak Island, Vogelpark, Marau Beach, 10m, 20.IV.1998, 14–16 Uhr, N. Naidenow, 5 ♀♀, 7 juv. (PHY, BM 20/4). Cyclops Mountain, 750 m, Dr Mayr, IX.1928 (470/29), 1 ♀ (ZMB 31087). Jayapura (= Hollandia), VII.1945, B. Malkin, 1 juv.(AMNH);

25.V.1945, in a coconut palm, B. Malkin, 3 ♀♀, 7 juv. (AMNH); IV.1945, B. Malkin, 1 juv. (AMNH); 1–9.VII.1945, B. Malkin, 1 ♀ (AMNH); under moist dead bark, 15.XII.1945, T. Aarons, 1 ♀ (CAS); 24.I.1960, TMP 2216-25, T. C. Maa, 1 ♀ (BPBM). Ifar (near Sentani Lake), 350m, 25. VI.1962, J. Sedlacek, 1 juv. (BPBM). Lake Sentani, Jayapura, VIII–IX.1945, Markos, Hart, 1 juv. (AMNH). **INDONESIA. WEST PAPUA PROVINCE,** 10 km W Manokwari, kleiner Bach, 30 m, 24.V.1998, 11–15 Uhr, N. Naidenow, 1 juv. (PHY, M 24/5 T). Manokwari, 1.VII.1929, K. P. S. Crane, Field Museum Pacific Expedition 1928–29, 1 ? (badly preserved) (AMNH); 2.VII.1929, K. P. S. Crane, Field Museum Pacific Expedition 1928–29, 3 ♀♀, 18 juv. (AMNH). W part, Mar Village, X–XII.1944, V. Standish Mallory, 1 ♀ (AMNH). Salawati Island (Raja Ampat Islands), SMS Gazelle, 2 juv. (ZMB 7413). Sansapor, XII.1944, A.P.O. 159, R. B. Burrows, 1 ♂, 1 ♀, 3 juv. (AMNH). Segaar Bay, SMS Gazelle, 1 juv. (ZMB 3153), 1 ♀ (ZMB 7414). M. Siwi (Arfak Mountains), Dr Mayr, 17.V.28 (470/29), 1 juv. (ZMB 31086). **INDONESIA, RIAU ISLANDS PROVINCE**. Lingga Island, waterfall ca. 7km N of Daik, 00°08'53.3''Sx104°36'13.2''E, 60m, 13–15.VI.2001, rainforest along stream, P. Schwendinger, 3 ♀♀ (LM, SIM-01/03), 4 juv. (MHNG, SIM-01/03). **INDONESIA, SULAWESI.** SULAWESI SELATAN PROVINCE, Makassar, 9.I.1900, D. G. Fairchild, miscellaneous coll., 1 ♀ (USNM 00309). Près de la perte de Gua Salukkan Kallang Kappang (gua signifie grotte), Maros, sous une pierre, 21. VII.1986, P. Leclerc, 1 ♀ (MNHN). Flanc du Lompobattang, Malino, région de Maros, écorces de pins, ca. 930 m, 6. VII.1986, P. Leclerc, 1 ♀, 2 juv. (MNHN). SULAWESI TENGAH PROVINCE, near Morowali, Ranu River Area, 27.I–20.IV.1980, 1 juv.(NHML). SULAWESI UTARA PROVINCE, Dumoga-Bone N.P., Project Wallace 1985, R.D.Buxton and N.M.Collins, 10.10.85, under bark of a fallen tree, 1 ♀ (NHML). Pulau Lembeh, 21.VI.1929, K. P. S. Crane, Field Museum Pacific Expedition 1928–29, 1 ♀, 1 juv. (AMNH). Slope of Mt Tongkoko, 20.VI.1929, K. P. S. Crane, Field Museum Pacific Expedition 1928–29, 1 ♀, 1 juv. (AMNH). **INDONESIA, SUMATRA.** Maass, 1 juv. (ZMB 8234); Weyers, 2 ♀♀ (MRHN). Patai? (vloedbosch, op drÿvend hout, in 't water), 26.IV.1929, S.A.R.le Prince Léopold, 1 ♀ (MRHN No 9.223). ACEH PROVINCE: Babahrot, 27.VII.1983, J. Klapperich, 1 juv. (MHNG). Réserve du Mt Leuser, Lawe Gurah, au bord de la rivière Alas, 9. VII.1984, J. Robert (chasse), 3 juv. (MHNG, 5); Mt Leuser NP, 300–500 m, Ketambe, 23–30. XI.1989, I. Löbl, D. Agosti, D. Burckhardt (#25a), 1 juv. (MHNG). Paya Laot, 100 m, 2.VII.1983, B. Meulabon, J. Klapperich, 1 juv. (MHNG). BENGKULU PROVINCE, Kepahiang, 1960 ft., XI.1925, Eclipse Expedition, 2 ♀♀ (USNM 00309). LAMPUNG PROVINCE. Wai Lirua Z.? (Waiharoe?), Lampungas, XI–XII.1921, Karney & Sirben, 3 ♀♀ (AMNH). 7 km W of Lima, 5°04'Sx104°03'E, 640m, 1.IX.1984, 71.I, Zoological Expedition Krakataus 1984, 1 juv. (WAM). Pulau Panjang (Krakatau Islands), 6°05'Sx105°28'E, 17.VIII.1985, under bark, 237.I, Zoological Expedition Krakataus 1985, 5 juv. (WAM); 17.IX.1985, under bark, 237.JA, Zoological Expedition Krakataus 1985, 1 juv. (WAM). Pulau Rakata (Krakatau Islands), 18.IX.1996, under bark of tree, B. S. Scott, 1 ♀ (ESV 3377). South Bay, 6°09'Sx105°28'E, 18.IX.1984, under logs, 130. IA, Zoological Expedition Krakataus 1984, 1 ♀ (WAM); 19.IX.1984, under bark, Zoological Expedition Krakataus 1984, 1 ♀, 1 juv. (WAM); 130. 2A, Zoological Expedition Krakataus 1984, 1 juv. (WAM). Pulau Sertung (Krakatau Islands), 6°04'Sx105°24'–25'E, IX.1984, Spit, bark of ficus, 151.S, Zoological Expedition Krakataus 1984, 1 juv. (WAM). 6°05'Sx105°23'E, 18. VIII.1985, forest, under logs, litter, PJV.247.CB, Zoological Expedition Krakataus 1985, 1 ♀, 2 juv. (WAM); 18.VIII.1985, forest II near spring, under logs, 247. LA, Zoological Expedition Krakataus 1985, 3 juv. (WAM); 18.VIII.1985, forest, under logs, 247.ZA, Zoological Expedition Krakataus 1985, 1 ♀ (WAM); forest II, near spring, 19.VIII.1985, under logs, litter, PJV.247.DC, Zoological Expedition Krakataus 1985, 1 juv. (WAM). SUMATERA BARAT PROVINCE: Padang, H. Schoede, 7.XII.1908 (801/09), 2 ♀♀ (ZMB 15132). Région de Payakumbuh, environs de la grotte "Ngalau Lintau", près de Lintau Buo, 200 m, 24.XI.1985, B. Hauser, 2 juv. (MHNG, Sum-85/56). SUMATERA SELATAN PROVINCE, Palembang, forêt de Niroe, 1902, M. Bouchard, 3 ♀♀, 3 juv. (MNHN-RS 1542); 14.IV.1929, S. A. R. le Prince Léopold, 2 ♀♀ (MRHN No 9.223). SUMATERA UTARA PROVINCE: Garonggong, sur le versant du Lac Maninjau (36 km de Bukittinggi), 22.VII.1984, J. Robert (chasse, 17), 2 ♀♀, 3 juv. (MHNG); 22.VII.1984, J. Robert (Winkler, 18), 1 juv. (MHNG). Langkat, Réserve naturelle de Bukit Lawang, près de Bohorok, forêt primaire le long de la rivière, 180 m, 20.XI.1985, B. Hauser, 2 juv. (MHNG, Sum-85/48). Langkat, Bohorok, Bukit Lawang, centre de réhabilitation des orang-outans, intérieur de la réserve, randonnée d'environ 5 km, 6.VII.1984, J. Robert (chasse, 17), 1 juv. (MHNG). Lawang, à environ 5 km de Maninjau, au bord du Lac Maninjau (36 km de Bukittinggi), 21.VII.1984, J. Robert (chasse, 16), 2 juv. (MHNG). Medan, Sel Rampah, 15.VI.1996, H. H. Tan *et al.* (THH

9659), 1 juv. (RMBR ZRC.ARA.430). Parapat, Lac Toba, 20.VII.1980, E. Heiss, 2 juv. (MHNG). Pulau Nias, S. Rapp und G. Knuth, 1896 (5705-37), 3 ♀♀, 6 juv. (ZMB 30856). Siantar, Kamrulhag?, 2 ♀♀, 1 juv. (USNM 00309). Simalungun, route de Pematangsiantar, 18 km avant Prapat, lieu-dit "Ainuli", Bukit Parasat, derrière la station "Holzweg Nr. 2 du Dr Diehl", forêt primaire, 1000 m, 14.XI.1985, B. Hauser, 1 juv. (MHNG, Sum-85/28). Bord du Lac Toba; Prapat, sur les hauteurs, dans une petite plantation de pins, 15.VII.1984, J. Robert, 2 ♀♀, 2 juv. (MHNG, 11). **LAOS**, 30.IV.1965, P. Vanttana, 2 ♀♀ (ZMB 31085). **EAST MALAYSIA (BORNEO)**. SABAH. Darvel Bay (= Lahad Satu Bay), 1909, Dr med. Pagel (271/09), 1 ♀ (ZMB 15133). Ranau (vicinity), R. Traub (57-736), 1 ♀ (USNM 00752, 8-1953); R. Traub (57-737), 1 ♀ (USNM 00752, 8-1953); R. Traub (57-738), 1 ♀ (USNM 00752, B-1953 NO); VIII.1953, R. Traub (57-735), 1 ♀ (USNM 00752). Sandakan, 10.VII.1929, mile eight, K. P. Schmidt, 2 ♀♀ (AMNH). Sandakan Bay (SW), Sapagaya Lumber, Camp 2–20m, 7.XI.1957, J. L. Gressitt, 1 juv. (BPBM). Sandakan Residency, Batu Putih, massif rocheux peu avant le bac sur le fleuve Kinabatangan, 20 m, 25.III.1983, C. Lienhard, 1 ♀ (MHNG, Pal-83/53); sous des écorces, 20 m, 27.III.1983, B. Hauser, 1 juv. (MHNG, Pal-83/61). Mt Kinabalu, Poring Hot Springs (43 km à l'est de Park Headquarters), "Langanan Trail", sentier des "Kipungit Falls" aux "Bat Caves", 530–650 m, 21.III.1983, B. Hauser, 2 juv., 1 molt (MHNG, Pal-83/42). Poring Hot Springs, 500m, 6/9.V.1987, D. Burckhardt & I. Löbl, 1 ♀, 1 juv. (MHNG); 6.V.1987, D. Burckhardt & I. Löbl, 1 juv. (MHNG), 1 juv. (MHNG, 14a). Poring, 2000 feet, 20.VI.1989, E. D. Ross, 1 ♀ (CAS). SARAWAK: 1958, T. Maa, 1 ♀ (BPBM). Parc National de Bako, début du chemin Jalan Lintang, ca. niveau mer, 15.VII.1982, dans bois pourri, M. Freiburghaus, 1 juv. (MHNG). Bau, près de Fairy-Cave II, sous écorces, 10m, 3.XII.1987, C. Lienhard, 4 juv. (MHNG, Sar-87/44). Bau, environs de la grotte Gua Puang, près du Kampong Pelaman Sekiang dans un escarpement du Gunung Jambusan, sous écorces, 10–30.XII.1987, C. Lienhard, 2 juv. (MHNG, Sar-87/52). Bau, environs de la grotte Gua Sireh, près du Kampong Pelaman Sekiang dans un escarpement du Gunung Jambusan, 20–40 m, sous écorces, 5.XII.1987, C. Lienhard, 2 juv. (MHNG, Sar-87/59). Serian District, Penrissen Road 12 miles de Kuching, Semongok Wildlife Rehabilitation Centre: Nursery Centre of the Forest Department, 4.XII.1987, B. Hauser, 1 juv. (MHNG, Sar-87/53). Route Kuching–Matang, Mont Gunung Serapi, Sungai Cina, 80 m, 9.XII.1987, surtout sous écorces, B. Hauser, 1 juv. (MHNG, Sar-87/69). Route Kuching–Matang, Mont Gunung Serapi, surtout sous écorces, 670 m, 9.XII.1987, B. Hauser, 1 juv. (MHNG, Sar-87/69). Route Kuching–Serian, près de Kampong Kuap (à 18 km de Kuching), forêt secondaire, battage, 30 m, 13.XII.1987, C. Lienhard, 1 juv. (MHNG, Sar-87/88). Semengoh forest reserve, H.N.67.5, 14.IX.1966, J. F. G. Clarcke, 1 ♀ (USNM 00752); 16.IX.1966, J. F. G. Clarcke & T. M. Clarke, 1 juv. (USNM 00752), 1 ♀ (USNM 00752). SE de Serian, Sabal (= Forest Research Station), surtout sous écorces, 180 m, 10.XII.1987, B. Hauser, 4 juv. (MHNG, Sar-87/71). **WESTERN MALAYSIA (= PENINSULAR MALAYSIA)**. FEDERAL TERRITORY OF KUALA LUMPUR, NE Kuala Lumpur, 600 m, 9.VI.1962, D. E. Ross & D. Q. Cavagnaro, 1 ♀ (CAS). Kuala Lumpur, VIII.1958, under log, N. L. Krauss; 1 juv. (USNM 00752); 90 m, E. S. Ross & D. Q. Cavagnaro, 1 ♀ (CAS); 90 m, 7.VI.1962, E. S. Ross & D. Q. Cavagnaro, 1 ♀ (CAS). JOHOR, Gunung Arong, 15 km N Mersing, 2°33'12.1"Nx103°45'20.5"E, 20 m, 29–30.V.2004, rainforest, P. Schwendinger, 1 ♀ (MHNG, MAL-04/06). Pulo Bezar, Weltreise Erzherz. Franz. Ferdinand 1892/93, 3 ♀♀, 1 juv. (NHMW 977). Pulau Pisang, 1/34, 3 ♀♀, 6 juv. (RMBR ZRC.ARA.439). Pulau Tioman, footpath from Tekek to Juara (02°48'39.4"Nx104°10'36.6"E), 240–300 m (disturbed rain forest), 29.VI.2001, P. Schwendinger, 2 ♀♀ (MHNG, SIM-01/08). MALACCA, Saida Expedition, A.Wolf (1886.V.22), 3 ♀♀, 1 juv. (NHMW 1745). PAHANG, Rompin, Sg. Kinchin, 20.VII.1989, H. K. Lua, 1 ♀, 1 juv. (RMBR ZRC.ARA.431). Tasek Bera, 2.X.1992, D. Chia & M. Y. Yeo, 1 ♀ (RMBR ZRC.ARA.434). Pulau Tioman, Paya, 23.VI.1999, H. H. Tan, 1 ♀ (RMBR ZRC.ARA.433). PENANG: Penang, 1500–2428', V.1917, 3 juv. (RMBR ZRC.ARA.442); Tanjong Bungah, 28.X.1960, Univ Malaya, 1 ♀, 2 juv. (RMBR ZRC.ARA.437). Penang Hill, 100 m, 26.VI.1962, E. S. Ross & D. Q. Cavagnaro, 1 ♀ (CAS). PERAK, II.1925, 1 ♀, 11 pullus (NHML). SELANGOR: near Klang, coast, VI.1956, deep inside fungus gardens of termitarium, J. R. Audy, 1 ♀ (NHML). Sekinchang, 4.VI.1947, collected on coconut, H. T. Pagden (CM 67), 2 ♀♀, 1 juv. (NHML, G 5588). Sungei Butoh/Kuala Lumpur, 27.VII.1972, T. Jaccoud, 2 ♀♀, 2 juv. (MHNG). TERENGGANU, S Kelembang, 102 40'Ex05 28'N, 140 ft, 3.III.1974, under rotten log, N. Gunong Lawit Expedition, 1974-2, 1 juv. (NHML). **MARSHALL ISLANDS**. O. Finsch, 1682 ?, 2 juv. (ZMB 3682). Ailinglaplap Atoll, Bigatyelang Islet, VIII.25.1946, H. K. Townes (1973), 1 juv. (USNM 00310). Arno Atoll, Arno Island, 19.VIII.1950, I. LaRivers, 1 ♀ (BPBM). Bikarey Island, 15.VII.1950, I. LaRivers, 1

♀, 6 juv. (BPBM). Ine Island, 14.VI.1950, I. LaRivers, 2 ♀♀, 4 juv. (BPBM); 14.VI.1950, R. L. Usinger, 1 juv. (BPBM) 17.VI.1950, I. Larivers, 1 juv. (BPBM); 2.VIII.1950, I. LaRivers, 3 ♀♀, 6 juv. (BPBM). Bikini Atoll, 1.IV.1946, J. P. Morrison (R 4181), 1 ♀ (USNM 00310, Acc no 172224). S half of Bikini id, 11.III.1946, J. P. E. Morrison (R4052), 1 juv. (USNM 00311, Acc#172224). Namu islet, 1.III.1946, J. P. E. Morrison (R4011), 1 juv. (USNM 00310, Acc#172229). Romuk Islet, 9.IV.1946, L.P . Schultz, 1 juv. (USNM 00310); 5.IV.1946, J. P. Morrison (R 4242), 2 ♀♀ (USNM 00310, Acc no 172224). Jaluit Atoll, Elizabeth Island, 26.IV.1958, J. L. Gressitt, 1 juv. (BPBM). Lae Atoll, Enemanman Islet, 9.I.1952, F. R. Fosberg (638), 1 juv. (USNM 00310). Lae Islet, 6.I.1952, F. R. Fosberg (566), 1 ♀ (USNM 00310); 7.I.1952, F. R. Fosberg (579, 573), 1 ♀, 6 juv., 16 pullus (USNM 00310). Lwajap Islet, 9.I.1952, F. R. Fosberg (610), 1 juv. (USNM 00310). Ujae Atoll, Bock Islet, 10.II.1952, F. R. Fosberg (935, 959), 4 juv. (USNM 00310). Ebeju Islet, 8.III.1952, F. R. Fosberg (1032), 5 juv. (USNM 00310). Wotho Atoll, Kabben Islet, 20.III.1952, F. R. Fosberg (865), 1 juv. (USNM 00310). Wotho Islet, 12–15.II.1952, F. R. Fosberg (774), 2 ♀♀, 2 juv. (USNM 00310); 12–15.II.1952, F. R. Fosberg (815), 1 ♀, 17 pullus (USNM 00310); 20.X.1953, rotten wood, J. W. Beardsley, 1 juv. (BPBM). **NEW CALEDONIA**. III–IV.1939, L. Macmillan, 1 ♀ (AMNH, Acc 37523). LOYALTY ISLANDS PROVINCE: Lifu Island, NW, Chepinehe, I.1950, behind bark of *Hibiscus tilliaceus*, Miss L. E. Cheesman (S 61), 1 juv. (NHML 1952.9.2.76); near We (Oue), 2–35 m, 26–28.III.1968, Sapium, J. L. Gressitt, 2 ♀♀, 6 juv. (BPBM). Maré Island, Ceingeite, 13.X.1958, under bark, B. Malkin, 3 ♀♀, 2 juv. (AMNH). Ouvéa Island, Fayaoue, 0–50m, I.1969, N. L. H. Krauss, 2 juv. (BPBM). NORTHERN PROVINCE: Oubatche, 15.IX.1965, 1 ♂, 4 ♀♀ (MNHN-K13, PNK 75/3). Touho, 8.IX.65, Umgeb, 2 ♀♀, 3 juv. (MNHN-K16). **NORTHERN MARIANA ISLANDS**. 1888, M. Marche, 30 ♀♀, 8 juv. (MNHN-RS 0497). PAGAN ISLAND, Laguna Sonhavon, 23.IX.1951, Y. Kondo, 3 juv. (BPBM). Dirt bank on side of ravine, western side of central part of island, 1.4 Miles south of farmer village of Shomushon, 2002 (9), 369 (3), 8.31.54, Corwin coll. 57-1041, 1 ♀ (USNM 00753). SAIPAN ISLAND, VIII.1904, Fritz, angek. 27.IX.05 (750/05), 1 ♀ (ZMB 15150). E Hagen, 26.I.1945, #76 APO 244, 1 ♀, 2 juv. (BPBM). AGUIJAN ISLAND (= AGIGUAN), 27.V.1952, R. P. Owen (M4519), 1 ♀, 10 juv. (BPBM); 31.V.1952, G. D. Peterson, 3 ♀ (BPBM). N side, 7. VI.1952, Y. Kondo, 1 ♀, 8 juv. (BPBM). **PAPUA NEW GUINEA**, 1 ♀ (ZMB 15143); Dr. Werner, 2 ♀♀, 1 juv. (ZMB 15144); R. Rohde, 5 ♀♀, 3 juv. (ZMB 7295, 7315, 7348, 7417); 13.IV.1889, R. Rohde, 2 ♀♀, 3 juv. (ZMB 7342, 7416); 16.IX.1896, Kunzemann, 1 ♀ (ZMB 15142); But?, Schoede, II.1910 (961/1910), 6 ♀♀, 3 juv. (ZMB 15156); A.P.O. 159, X.1945, R. Burrows, 2 ♀♀ (AMNH); Operation Drake, Strick 5, 2 ♀♀ (NHML). BISMARCK ARCHIPELAGO, 1909, R. Thurmwald (1235/09), 2 ♀♀ (ZMB 15152). CENTRAL PROVINCE, Bisianumu, E of Port Moresby, 500m, 23.IX.1955?, J. L. Gressitt, 1 juv. (BPBM). Brown River, 5 m, 22.X.1960, broadleaf *Calamus*, J. L. Gressitt, 1 ♀, 1 juv., 11 pullus (BPBM). Mt Victoria,O. E. Janson, 2 juv. (NHML 1896.12.7.42-45). Neneba (Orangerie Bay), XI.1896, 1 juv. (QM-S 23256). Rigo, 21. VI.1969, P.Jolivet, 7 ♀♀, 10 juv. (MNHN-RS 5316). EAST SEPIK PROVINCE. Village Kambot by the Keram River (Sepik area), 12.VII.1995, F. Klausen, 1 ♀ (LM). May River Stn. 100m S, 30.V.1963, under bark, *Sago* forest, R. Straatman, 2 ♀♀, 1 juv. (BPBM). MADANG PROVINCE, Alexishafen, 8.V.1929, K. P. S. Crane, Field Museum Pacific Expedition 1928–29, 2 juv. (AMNH). Astrolabe Bay, 1889?, R. Rohde, 2 ♀♀, 1 juv. (ZMB 7203). Bogadjim (= Stephansort), V.1904, Preuss S., angek, 16.IX.1904 (J. No 1184/04), 3 ♀♀, 4 juv. (ZMB 15155). Baiteta Road, 2.2 km W of North Coast Road, Stop #89/86, 60 m, 22.IV.1989, Papua New Guinea Expedition 1989, D. H. Kavanaugh, G. E. Ball & N. D. Penny (Cal. Acad. Sci.), 1 juv. (CAS). Boven?, Ramu River Expedition, V.1878, 1 ♀, 5 juv. (ZMB 15130). Jagei Fluss (Ramu River Area), K. W. L. E., 2 .VIII.1896, Dr Lauterbach, 3 ♀♀, 4 juv. (ZMB 15157). Mt Hanseman, NE of Nobanob Mission, stop #89/11, 300/350 m, 4.III.1989, Papua New Guinea Expedition 1989, N. D. Penny & P. A. Meyer, 2 ♀♀, 1 juv. (CAS). Nagada Harbor, Christensen Research Institute, Stop #89/6, 3 m, 1–9.III.1989, Papua New Guinea Expedition 1989, D. H. Kavanaugh, G. E. Ball, N. D. Penny & P. A. Meyer (Cal. Acad. Sci.), 1 juv. (CAS). Ramu River Expedition, 29.VI.1899, 1 ♀ (ZMB 15146). MILNE BAY PROVINCE. Camp 2, Baiawa, Moi Biri Bay, Collingwood Bay, 6–10.V.1953, G. Tate, Archbold Expedition, 3 ♀♀ (AMNH). D'Entrecasteaux Islands, Normanby Island, Waikaiuna, 3 mi S of entrance of Seva Bay, 0–50 m, Camp #1 1956, 5th Archbold Expedition to New Guinea (Papau), L. J. Brass, 1 ♀, 11 pullus (AMNH). MOROBE DISTRICT, Bulolo, 800m, 14.II.1961, J. H. Sedlacek, 1 juv. (BPBM). Finschhafen, IV.44, E. S. Ross, 1 ♀ (CAS); 6.V.1944, E. S. Ross, 1 ♀, 3 juv. (CAS). Camp 1, Menapi, Cape Vogel Peninsula, 21.III–4.V.1953, Geoffrey Tate, Archbold Expedition, 7 ♀♀ (AMNH). Wandumi, Wau Valley, 15.XII.1968, 920 m, un-

der loose bark of dead tres and branches, secondary scrub vegetation and native gardens, R.C.A. Rice, 6 ♀♀ (AMNH). Wau, Bulolo Gorge, 5.IX.1971, G. Coleman, 1 ♀ (QM-S 17210); Maus Bokis in old water race tunnel, 750 m, 12.V.1973, Thomer & W. Davies, 1 ♀ (CAS). Wau, 1200–1300m, C. J. & M. Sedlacek, varia, 1 juv. (BPBM); XII.196?, J. H. Sedlacek, 1 juv. (BPBM). NEW BRITAIN (= NEU POMMERN): H. W. Lix (Kauf), 1892.I.1, 6 ♀♀, 1 juv. (NHMW 1748). EAST NEW BRITAIN PROVINCE. Duke of York Islands, Mioko island, 18.XI.1896, Dahl, 1 juv. (ZMB 7990). Gazelle Peninsula, Gaulim, 140m, 19–28.X.1962, J. Sedlacek, 2 ♀♀, 6 juv. (BPBM). Kokopo (= Herbertshöhe), XII.1900–V.1901, Heinroth, 11 ♀♀, 5 juv. (ZMB 15139); Dempwolff, II.1903, 1 ♀ (ZMB 15154); Rechinger 1906, 1 juv. (NHMW 1751). Malmalu, Vunaka, Nau, 8.V.1956, Cacao Tolera, J. L. Gressitt, 1 ♀ (BPBM). Mt. Sinewit, 900m, 5–14.XI.1962, J. Sedlacek, 1 ♀ (BPBM). Rabaul, 26.IV.1929, K. P. S. Crane, Field Museum Pacific Expedition 1928–29, 1 juv. (AMNH). Ralum, 29.V.1896, 1 ♀ (ZMB 7992); 11.VI.96, Dahl, 1 ♀ (ZMB 7994); 12.VI.1896, Dahl, 2 ♀♀, 7 juv. (ZMB 7993); VII.1896, Dahl, 1 juv. (ZMB 7991); 5.IX.1896, Dahl, 2 ♀♀, 13 juv. (ZMB 7995); 27.I.1897, *Ficus*, Dahl, 7 ♀♀, 20 juv. (ZMB 7996). Toma, II.1903, Dr. Dempwolff S., angek. 11.III.04 (J. No 341), 1 ♀, 2 juv. (ZMB 15153). Upper Warangoi, Illugi, 8–11.XII.1962, J. Sedlacek, 1 ♀ (BPBM); 230m, 8–16.XII.1962, J. Sedlacek, 1 juv. (BPBM); 1250m, 1–5.XII.1962, J. Sedlacek, 1 juv. (BPBM). NEW IRELAND PROVINCE, New Ireland Island, SMS Gazelle, 1 ♀ (ZMB 3023). SANDAUN PROVINCE. Aitpe, Finsch Coast, Fall 1944, W. R. Enns (705), 3 ♀♀, 1 juv. (AMNH). Camp by Chambri Lake (= Rosensee), 13.II.1913, Dr. Bürgers (I.259) (595/1913), 1 ♀, 1 juv. (ZMB 30859). Top Camp by Keram River (= Töpferfluss), Dr Bürgers (I.318), 24.IV.1913 (880/1913), 1 ♀ (ZMB 30861). Top camp near Malu, III–IV.1912 (742/1912), Dr. Bürgers, Kaiserin Augusta Fluss Expedition, 1 juv. (ZMB 30879) 3.II.1913 (595/1913), Dr Bürgers (I.254), Kaiserin Augusta Fluss Expedition, 1 ♀ (ZMB 30860). Pionierlager, 30.IV–14.V.1912, Dr. Bürgers (1086/1912), Kaiserin Augusta Fluss Expedition, 1 juv. (ZMB 30842); 30.IV–14.V.1972 (1016/1912), Ledermann (I.52 siche List), Kaiserin Augusta Fluss Expedition, 1 ♀ (ZMB 30862). WESTERN (DARU) PROVINCE, Daru Island, 24.X.1960, Pupa in Cocos, J. L. Gressitt, 1 juv. (BPBM); Oriomo G. St., 27.X.1960, J. L. Gressitt, 4 ♀♀, 3 juv. (BPBM). **PHILIPPINES**: In Orchids from Philippines, Quar., Hawaii #2508, 1 juv. (USNM 00309). 1 juv. (NHML 1913.9,1.72). C. S. Banks, 1 ♀, 1 juv. (USNM 00310); N. Banks, 2 juv. (USNM 00309); Cuming, 1 ♀ (ZMB 49); Edmüller, 2 ♀♀, 4 juv. (ZMB 7253); 1.VI.1961, H.Torrevillas, 1 ♀ (BPBM); 23.IV.1962, H. Torrevillas, 1 ♀ (BPBM). BASILAN, XII.1914, S. Böttcher & V. Heyne, 5 ♀♀, 3 juv. (ZMB 30869); 12.XII.1914, S. Böttcher & V. Heyne (137 D/24), 1 juv. (ZMB 30868). LEYTE, 29.IV–7.V.1915, S. Böttcher & V. Heyne (137 D/24), 2 ♀♀, 1 juv. (ZMB 30875). Near Dulag, 100', 8.IV.1945, L. W. Saylor, 1 ♀ (AMNH). Silago, VIII.1877, 1 ♀, 1 juv. (ZMB 15140). Tacloban, XI.1944, E. S. Ross, 2 ♀♀, 1 juv. (CAS); XI.1945, E. S. Ross, 1 ♀, 3 juv. (CAS). LUZON: Aurora province, Jilla, Alltop L. B. C 199, 1.17.58, 1c59-40, AS-5, 1 ♀ (USNM 00752). Bantos Province, N part, Polis, 2400', II.1917, S. Böttcher & V. Heyne (137 D/24), 1 ♀ (ZMB 30872). Benguet Province, Camp John Hay, Baguio, Mt Province, 15.II.1950, H. L. Keegan/ Dau, Pampanga, F. Endriga, 1 ♀ (USNM 00309). Camarines Sur Province, Mt Iriga, 500–600m, 21–24.III.1962, H. M. Torrevillas, 1 ♀ (BPBM); 500–600m, 13.IV.1962, H. M. Torrevillas, 1 ♀, juv. (BPBM); 14.IV.1962, H. M. Torrevillas, 2 juv. (BPBM); 21.IV.1962, H. M. Torrevillas, 1 ♀, 1 juv. (BPBM). Mt Isarog, 500m, 5.IV.1963, H. M. Torrevillas, 2 juv. (BPBM); 500–600m, 13.IV.1963, H. M. Torrevillas, 1 juv. (BPBM). Sagnay, Atulayan Island, 8–10.V.1992, D. M. General, 1 ♀ (CAS). Ilocos Norte Province, Bangui, XI.1923, R. C. McGregor, 1 juv. (USNM 00309). Ilocos Sur Province, Vigan, Schadenberg don, 1891.II.2, 1 ♀ (NHMW 1746). Isabela Province, Mt Moises, G. Taquibao, K. C. McGregor, 1 ♀ (USNM 00309). Laguna Province, Los Banos, 20.IX.1916, S. Böttcher & V. Heyne (137D/24), 3 ♀♀, 6 juv. (ZMB 30870); 20.X.1945, B. Malkin, 1 juv. (AMNH). Mt Makilling (= Mt Maquiling), ca. 150 m, Baker, 1 specimen badly preserved (AMNH); 1949, C. F. Baker, Chapin, 11 ♀♀, 21 juv. (USNM 00309); 1100–1400 ft, 29.IX.1945, B. Malkin; 1 ♀ (AMNH); 600–1200 ft, 13.X.1945, B. Malkin; 1 ♀ (AMNH). Laguna/Quezon Provinces, Mt Banahao (=Mt Banahaw), 2000', 20.IX.1916, S. Böttcher & V. Heyne (137D/24), 3 ♀♀ (ZMB 30871). Manila Province, Manila, 3 ♀♀ (MNHG); Bavuil?, 11.XI.1913 (2718/22), M. Deglau, 4 ♀♀, 5 juv. (ZMB 15138); Mindanao Estates Co., plantation, various times, E. H. Oesch?, 2 ♀♀ (AMNH). Nueva Ecija Province, 25 mi N San Jose, 1945? Capt. Tymiak, 2 ♀♀, 1 juv.(AMNH). Pampanga Province, Mt Arayat, under dead tree bark, near peak, 12.I.1984, C. K. Starr, 2 ♀♀, 6 juv. (USNM). Pangasinan Province, Binalonan, 13.XI.1913–12.I.1914 (no 2710/22), 2 juv. (ZMB 31088). Quezon Province, Balesin Island, I.1981, A. L. Grandt, 1 ♀ (NHML). Quezon Peak, Tayabas, 26.X.1931, F. C. Hadden, 1 ♀ (CAS). Sorsogon

Province, Inang, Pilar, 5.IV.1985, C. K. Starr, 3 juv. (USNM 00752); 6.IV.1985, in pineapple plant, C. K. Starr, 1 ♀, 10 juv. (USNM 00752). Tayabas Province, Dolores, 1200 ft, 13.XI.1945, B. Malkin, 1 ♀, 1 juv. (AMNH). MINDANAO: Agusan del Sur Province, Los Arcos, 19-23.XI.1959, L. W. Quate, 3 ♀♀, 3 juv. (BPBM). Davao del Norte Province, N part, Mamangan (transfered to San Isidro Municipality), II.1915, S. Böttcher & V. Heyne (137D/24), 1 ♀, 11 pullus (ZMB 31084); 17.II.1915, S. Böttcher & V. Heyne (137D/24), 2 ♀♀, 6 juv. (ZMB 30866). Lanao del Norte Province, Iligan, 3.II.1915, S. Böttcher & V. Heyne (137 D/24), 1 ♀ (ZMB 30874). N part, Kolambugan, I.1905, Böttcher S & Heyne V. (137 D/24), 1 ♀ (ZMB 30865). Misamis Oriental Province: Bal-ason, 4.IV.1960, H. M. Torrevillas, 1 ♀, 7 juv. (BPBM); 9.IV.1960, H. M. Torrevillas, 2 juv. (BPBM). Minalwang, 25.III.1961, H. M. Torrevillas, 1 juv. (BPBM); 27.III.1961, H. M. Torrevillas, 2 ♀♀, 1 juv. (BPBM); 30.III.1961, H. Torrevillas, 1 ♀, 1 juv. (BPBM). Min-ubanan, 6.IV.1961, H. M. Torrevillas, 1 juv. (BPBM). Mt Empagatao, 13.IV.1961, H. M. Torrevillas, 1 juv. (BPBM). Mt Kibu-ngol, 16–17.IV.1960, H.M.Torrevillas, 2 juv. (BPBM). South Catabato Province, S part, Port Banga, I.1915, S. Böttcher & V. Heyne (137 D/24), 2 ♀♀ (ZMB 30864). S part, Zambanuga, XII.1914, S. Böttcher & V. Heyne (137 D/24), 1 ♀ (ZMB 30863). Surigao del Norte Province, Lake Mainit, 23.XI–1.XII.1959, L. Quate & C. Yoshimoto, 1 ♀, 9 juv. (BPBM). N part, Surigao, V.1915, S. Böttcher & V. Heyne (137 D/24), 2 ♀♀(ZMB 30867). Zamboanga del Norte Province, Manucan, 30km S Kerosene H., 19.X.1959, L. W. Quate, 1 ♀ (BPBM). MINDORO, Bougalow, 20.I.1908, Schultze, 1 ♀ (USNM 00309). Occidental Mindoro Province, San Jose, Mindoro Island, X.1945, E. S. Ross, 8 ♀♀, 7 juv. (CAS). Oriental Mindoro Province, Calapan, II.1916, Böttcher S. & Heyne V. (137D/24), 1 ♀, 1 juv. (ZMB 30873). Puerto Galera, 0 à 300m, plus haut que le gouffre de Tabinay, 27–29.XII.1979, forêt primitive, bois pourri, appareil Berlese, L. Deharveng & J. Crousset, 1 juv. (MHNG, PHI-79/122). NEGROS: Negros Oriental Province, L.Balinsastao, 1–6.X.1959, Quate & Yoshimoto, 1 ♀ (BPBM). Dumaguete ravine, Camp lookout, 1300', 10.III.1961, T. Schneirla, 1 juv. (AMNH). PALAWAN, Surigao?, XII.1914 (137D/24), S. Böttcher & V. Heyne, 5 ♀♀, 11 juv. (ZMB 30867). Bugsuk, Balabac, 25.V.1982, birth 8. VI.1982, C. K. Starr, 1 ♀, 16 pullus (USNM 00752). PANAY ISLAND: Aklan Province, Buruanga, NW-Panay mountain range, low elevation rainforest, research station Sibaliw, in wood crevice next to station, 1.12.2007, H. Krehenwinkel, 1 ♀ (HK 133). Tibiao, 12.V.1918, 1 ♀, 4 juv. (USNM 00309). Antique Province, Culasi, Flores, central Panay mountain range, under stone next to ricefields, 11.11.2007, H. Krehenwinkel, 1 ♀ (HK 4). Tarumpitao, 12 miles S, 5–11.I.1960, 500m, I. L. Quate, 1 juv. (BPBM). SAMAR ISLAND, no date, 1 ♀ (AMNH); IV.1945, J. R. Stuntz, 1 ♀ (CAS). **AMERICAN SAMOA**. Tau Island, Maru Group?, Tavalagi Summit, 19.X.1936, 500m, under stones, native forest, dry, top and Fairarao cliff, Chas. Wilspe, 1 ♀ (BPBM). **WESTERN SAMOA**. Upolu Island, Mus. Godeffroy, 1 ♀, 1 juv. (NHMW 2503); G. G. Lister, 1 ♀ (NHML 1897.1.223-8); Rechinger 1906, 2 juv. (NHMW 1752). Afiamalu, 10.VI.1940, 2200 feet, O. H. Swezey, 3 ♀♀, 3 juv. (BPBM). Apia, Gouvernent Sekretär G. Klinkmüller (1063/1911), 1 ♀ (ZMB 30877); Friedländer, 4 juv. (ZMB 8293). **SINGAPORE**: 1898, H.N.Rialey (rec. X.1898), 3 juv. (NHML 1898.10.18.46-48); X.1913, H. Hoverbock, 3 ♀♀, 8 juv. (RMBR ZRC.ARA.447). Botanic Gardens, XI.1965, forest, under stones, forest, D. H. Murphy, 1 ♀ (RMBR ZRC.ARA.436) 21.V.1990, in rotting wood, K. Lim, 1 ♀ (RMBR ZRC.ARA.432). Bukit Timah, VI.1933, 3 juv. (RMBR ZRC.ARA.446); 100 feet, 4.VI.1962, E. S. Ross & D. Q. Cavagnaro, 1 ♀ (CAS). **SOLOMON ISLANDS**, 29.V.1976, S. Johnson, 11 ♀♀, 11 juv. (WAM 98/1894-1915). CENTRAL PROVINCE. Ngella Islands (= Florida Islands), III.1945, J. R. Stuntz, 1 ♀ (BPBM). Nggela Sule Island, Mboromole, 200m, 28.X–1.XI.1981, J. L. collector, 1 ♀ (BPBM). Russel Islands, Lingatu, 24.8.1936, R. A. Lever, 1 ♀ (NHML 1937.4.22.5). CHOISEUL PROVINCE. Choiseul Island, Malagona SL., 30.II.1944, P. Shanahan, 5 ♀♀, 5 juv. (BPBM). Sirovanga, 0–100 m, XI.1972, N. L. H. Krauss, 1 juv. (AMNH); 9.XI.1972, N. L. H. Krauss, 3 ♀♀, 2 juv. (AMNH). GUADALCANAL PROVINCE. Guadalcanal Island, XI.1920, J. A. Kusche, 1 ♀ (CAS); APO 709, 1943, A. B. Gurney, 1 ♀, 1 juv. (USNM 00310); Area #1 47, 24.IV.1944, D. E. Beck, 1 ♀ (AMNH); VII.1945, F. Cilley, 3 juv. (AMNH); 16.VIII.63, P. J. M. Greenslade, (Royal Society B.S.I.P. Expedition 1965, 9602), 1 ♀ (NHML, Acc. No. 2182); 1.XII.1963, under bark of log, P. J. M. Greenslade (Royal Society B.S.I.P. Expedition 1965, 20852), 7 juv. (NHML, Acc. No. 2182); 11.II.1965, P. Greenslade, (Royal Society B.S.I.P. Expedition 1965, 16953), 1 ♀, 1 juv. (NHML, Acc. No. 2182); 3.III.1965, P. J. M. Greenslade (Royal Society B.S.I.P. Expedition 1965, 20814), 5 ♀♀, (NHML, Acc. No. 2182); II.1966, P. J. M. Greenslade (Royal Society B.S.I.P. Expedition 1965, 21058), 1 juv. (NHML, Acc. No. 2182). Kaibia, Honiara, 18.V.1976, S. Johnson, 4 juv. (WAM 98/1916-1919); 29.V.1976, S. Johnson, 19 juv. (WAM 98/1920-1938). Kukum, 29.X.1963, P. J. M. Green-

slade (Royal Society B.S.I.P. Expedition 1965, 9754), 2 ♀♀, 2 juv. (NHML, Acc. No. 2182); 9.XII.1965-13.I.1966, P. J. M. Greenslade (Royal Society B.S.I.P. Expedition 1965, 19800), 4 juv. (NHML, Acc. No. 2182). Sahalu Area, 200–400 m, I.1973, N. L. H. Krauss, 1 juv. (AMNH). ISABEL PROVINCE. Santa Isabel Island. 2 mls W of Andraogu? opposite Codiatoo Island?, 20.IX.1965, *Casuarina* forest, under bark of dead tree, Royal Society Expedition, 1 ♀ (NHML). Ridge behind Huali Village, Tatamba Bay, 2.X.1965, secondary forest, rotten logs, P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. Exp. 1965, KEL 277), 2 ♀♀ (NHML, Acc. No. 2184). Ca 1 mile W of Tatamba Rest House, 6.X.1965, rainforest, rotten logs on alluvial flat beside large stream, P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. Expedition1965, no KEL 295), 1 ♀ (NHML, Acc. No. 2184). Tatamba Bay, IX–X.1965, J. Grant (Royal Society B.S.I.P. Expedition 1965), 3 ♀♀ (NHML, Acc. No. 2184). Tunnibuli, Ysabel, 19.IV.1929, K. P. S. Crane, Field Museum Pacific Expedition 1928–29, 1 ♀ (AMNH). St George Island, *Casuarina* forest, leg. J. F. P., P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. 1965, no CCCI), 1 juv. (NHML, Acc. No. 2184). MAKIRA-ULAWA PROVINCE. Makira (= San Cristoval Island), Kirakira, 0–100m, XI.1970, N. L. H. Krauss, 1 ♀, 1 juv. (BPBM). Ridge above confluence of Warahito e Pegato rivers, Alt. 300', 22.VII.1965, forest, on rotten log, P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. 1965, KEL 60), 1 ♀ (NHML, Acc. No. 2180). Turn up Warahito River from Warahito/Pegato confluence, 26.VII.1965, forest, logs on very wet alluvial flat, P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. Expedition 1965, KEL 97), 4 juv. (NHML, Acc. No. 2180). Ca. 7 ml S Wainomi, 31.VIII.1965, lurking around sample boxes, P. N. Lawrence, Royal Society Expedition B.M. 1966-I, 1 juv. (NHML). Wainoni Bay, 20.VII.1965, in logs, P. J. M. Greenslade (Royal Society B.S.I.P. 1965), 1 juv. (NHML, Acc. No. 2180). MALAITA PROVINCE. Malaita Island, Auki, 0–20 m, I.1972, N. L. H. Krauss, 3 juv. (BPBM). Opposite Lialasi, Langa Langa Lagoon, 20.XI.1965, coconut palm, on mainland, P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. 1965, J.P. 109), 1 ♀, 14 pullus (NHML, Acc. No. 2181). Wailulu, Maramasike, 28.XI.1965, village garden, leg. J. F. P., P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. Expedition 1965), 1 juv. (NHML, Acc. No. 2181). Ndai Island, Bethlehem, 0–5 m, 21.XII.1972, N. L. H. Krauss, 1 ♀ (AMNH). ONTONG JAVA ATOLL. Avaha Island, 0–10 m, 18.XII.1972, N. L. H. Krauss, 1 ♀ (AMNH). Liuanua?, 0–10 m, XII.1972, N. L. H. Krauss, 1 juv. (AMNH). Pelau Island, 0–10 m, 17.XII.1972, N. L. H. Kraus, 2 ♀♀, 5 juv. (AMNH). TEMOTU PROVINCE, Duff Islands, Taumako Island, 0–10m, 20.XI.1933, N. L. H. Krauss, 3 ♀♀ (BPBM). WESTERN PROVINCE. 28.XII.1964, P. J. M.Greenslade (Royal Society B.S.I.P. Expedition 1965, 16191), 1 ♀ (NHML, Acc. No. 2183). Gizo Island, 17–19. IV.1964, J. H. Sedlacek, 1 ♀ (BPBM); 6.XII.1965, L. Bengough, (Royal Society B.S.I.P. Expedition 1965, 13014),1 juv., (NHML, Acc. No. 2183); 3.I.1966, leg. L. Rengough, P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. 1965, 13092), 1 juv. (NHML, Acc. No. 2183); 14.III.1966, P. J. M. Greenslade (Royal Society B.S.I.P. Expedition 1965, 13224), 1 ♀ (NHML, Acc. No. 2183). Kolombangara Island (= Kulambungra). Base Camp, C 75', leg. various, P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. Expedition 1965, XXI), 1 ♀ (NHML, Acc. No. 2183). Lower Camp area, P. N. Lawrence, P. J. M.Greenslade & J. F. Peake (Royal Society B.S.I.P. Expedition 1965, JJI), 1 juv. (NHML, Acc. No. 2183). 1000', trunk covered with moss, under moss, leg. J. F. P., P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. Expedition 1965, Collection no SS23), 2 juv. (NHML, Acc. No. 2183). 2500', 25.VIII.1965, moss forest, moss and humus on rotten logs, (Royal Society B.S.I.P. Expedition 1965, Collection no KEL 182), 1 juv. (NHML, Acc. No. 2183). Near Kuzi, *Pandanus* crown, on ground, leg. J. F. P., P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. Expedition 1965, VV14), 1 juv. (NHML, Acc. No. 2183). S of Kuzi, 1000', 3.IX.1965, logs, leg Isiah, P. J. M. Greenslade (Royal Society B.S.I.P. Expedition 1965), 1 juv. (NHML, Acc. No. 2183). Kuzi, base camp, 1.IX.1965, leg. P. Naturaga, P. N. Lawrence, P. J .M. Greenslade & J. F. Peake (Royal Society B.S.I.P. Expedition 1965), 1 juv. (NHML, Acc. No. 2183); 2.IX.1965, logs, leg. P. Naturaga, P. N. Lawrence, P. J. M. Greenslade & J. F. Peake (Royal Society B.S.I.P. 1965), 2 ♀♀, 6 juv. (NHML, Acc. No. 2183). Papele, 30 m, 9.II.1964, P. Shanahan, 4 ♀♀, 7 juv. (BPBM). Webster Cove, 22.IV.1929, K. P. S. Crane, Field Museum Pacific Expedition 1928–29, 4 ♀♀, 5 juv. (AMNH). New Georgia Island. Munda, 1944, L. A. Conwell, 1 ♀ (USNM 00310), 1 ♀ (USNM 00311); 15.II.1945, L. A. Conwell, 1 ♀ (USNM 00310). Rendova Island, Hopongo, 0–200 m, XI.1972, N. L. H. Krauss, 1 ♀, 1 juv. (AMNH). Shortland Islands. Fauro Island, 1. XII.1927, AC 27590, 1 ♀ (AMNH). Laminiai Island, 12.X.1936, on *Locas* crown, R. A. Lever, 1

juv. (NHML 1937.4.22.6-5) Vella Lavella Island, IX.1936, R. J. A. W. Lever, 1 juv. (NHML 1937.4.22.9). Barakoma, 0–50 m, XI.1972, N. L. H. Krauss, 1 ♀, 3 juv. (BPBM). Tamaneke, 0–100 m, II.1987, N. L. H. Krauss, 1 ♀, 1 juv. (WAM 98/1939-40). **THAILAND**: Sonpayang?, N.Siam, 20.XII.1932, 1 ♀, 1 juv. (USNM 00309) Chanthaburi Province, Chanthaburi Khao Sabap NP, 150–300 m, 23–24.XI.1985, D. Burckhardt & I. Löbl. (no 27), 1 juv. (MHNG). Chiang Mai Province, Chiangdao, Chianomai, Prov; NW Thailand, 6–10.IV.1958, T. Maa, 1 ♀ (BPBM). Doi Chiang Dao, 29.I.1932, H. M. Smith, 2 ♀♀ (USNM 00309). Chumphon Province, Lang Suan (9°56'60''N 99°04'00''E), 30 m (garden in the city), 16.VII.2002, P. Schwendinger, 1 ♀ (MHNG, TH-02/07). Ranong Province, Ranong/Suden, 21.1–1.III.1987, Lehmann (Thailand Expedition, achat Bâle 1987), 1 ♀ (MHNG). Trang Province, Krachong Forest near Trang, 100 m, 8.VIII.62, E. S. Ross & D. Q. Cavagnaro, 1 juv. (CAS). Nakhon Phanom Province, Nakhon Phanom, 29.X.65, J. E. Foote, Stahnke collection, molt, 24.V.1966, 1 juv. (CAS). Trat Province, Ko Chang N.P., 12°03'Nx105°18'E, 50–200 m, 3–23.XII.1999, A. Schulz, 1 juv. (MHNG). **VANUATU (= NEW HEBRIDES)**: MALAMPA PROVINCE: Ambrym Island, Ranon to Mt. Toyo, 0–500 m, 2.IX.1979, W. C. Gagne, G. M. Nishida, G. A. Samuelson, 1 ♀ (BPBM, Acc. No. 1979.380); from dead wood, W. C. Gagne, G. M. Nishida, G. A. Samuelson, 1 juv. (BPBM, Acc. No. 1979.380). Malakula Island, Amok, 15–18.IX.1958, B. Malkin., 2 juv. (AMNH). Lakatoro, 0–200 m, II.1963, N. L. H. Krauss, 1 ♀ (AMNH). Lamap, 9.IX.1967, J. & M. Seldacek, 1 ♀ (BPBM); 13.IX.1967, J. & M. Seldacek, 1 ♀ (BPBM). PENAMA PROVINCE: Aoba Island (=Ambae Island), Bankaharijitoa, near Dunduy, 400–600 m, 8.IX.1958, rainforest, B. Malkin, 3 ♀♀, 2 juv. (AMNH). Dunduy, 6–7.IX.1958, under bark, B. Malkin, 1 ♀, 2 juv. (AMNH). Ndui Ndui, 0–200m, II.1974, N. L. H. Krauss, 3 ♀♀, 1 juv. (BPBM). Maewo Island, Kerepai (Kerepal?), 0–200 m, XII.1983, N. L. H. Krauss, 3 ♀♀, 2 juv. (BPBM). Above Nasaua, over 200 m, 4.IX.1958, under bark, B. Malkin, 1 ♀, 1 juv. (AMNH). Nasaua, 30.VIII.1958, B. Malkin, under bark, 1 ♀, 11 pullus (AMNH). SANMA PROVINCE: Santo Island (= Espiritu Santo Island), 3 ♀♀ (AMNH); IX–XII.1943, G. Brenner, 2 ♀♀, 1 juv. (AMNH). Baldwin Bay, 24–26.IX.1958, B. Malkin, 1 ♀ (AMNH). Hog Harbor, 5.IV.1929, K. P. S. Crane (Field Museum Pacific Expedition 1928–29) 2 ♀♀, 7 juv. (AMNH); 1.IV.1929, from tree stump, K. P. S. Crane (Field Museum Pacific Expedition 1928–29) 1 ♀, 1 juv.(AMNH). 15km N of Luganville, 100m, 12.IX.1979, W.C.Gagné, 1 juv. (BPBM, Acc. #1979.380). Luganville, E de Santo, 20–21.VI.1979, récolte à la main, A. de Chambrier, 1 juv. (MHNG, AC/48). SW part, Below Namatasopa, 250 m, 2.IX.1957, J. L. Gressitt collector, 1 ♀, 1 juv. (BPBM). SHEFA PROVINCE: Efate island (=Vate Island), SW Coast, 3m, 13.VIII.1957, J. L. Gressitt, 1 ♀, 3 juv. (BPBM). Devil's Point, 21.VIII.1958, B. Malkin, 1 ♀ (AMNH). 40 km NE Vila, 14.VIII.1967, J. & M. Seldacek, 1 ♀ (BPBM). Port Vila, II.1959, N. L. H.Krauss, 1 ♀, 1 juv. (BPBM); 0–100 m, III.1980, N. L. H. Krauss, 1 ♀ (BPBM, Acc. No. 1980.178), 1 ♀, 4 juv. (BPBM, Acc. No. 1978.114); II.1978, N. L. H. Krauss, 1 ♀ (BPBM); 24.VI.1979, A. de Chambrier, 1 ♀ (MNHN-AC 023). Epi Island, Vaemali, Ed, 10.VIII.1961, J. & M. Sedlacek, 1 ♀ (BPBM). TAFEA PROVINCE: Aneityum Island (= Anatom Island), 14–24.VIII.1937, L. Macmillan, 3 ♀♀, 4 juv. (AMNH). Erromango Island, III–IV.1937, L. Macmillan, 4 ♀♀, 1 juv. (AMNH); 15–30.V.1937, L. Macmillan, 4 ♀♀, 7 juv. (AMNH); 200–300 m, II.1981, N. L. H. Krauss, 2 juv. (BPBM). Dillon's Bay, 0–100 m, I.1984, N. L. H. Kraus, 1 ♀, 1 juv. (BPBM). Futuna Island, 10–15.VII.1937, L. Macmilla, 27 ♀♀, 11 juv. (AMNH). Tanna Island, 2km S Ipeukeul, 25 m, 23.VIII.1979, W. C. Gagne, 1 ♂, 1 ♀ (BPBM, Acc. No. 1979.380). Lerakel, 0–300 m, Att. R. & J. Gregory, 1 ♀, 1 juv. (BPBM Acc. No. 1977.196); 0–100m, I.1973, N. L. H. Krauss, 1 ♀, 1 juv. (BPBM). White Sands, 29.IX.1936, L. Macmillan, 6 ♀♀, 5 juv. (AMNH); 21.X.1937, L. Macmillan, 3 ♀♀, 2 juv. (AMNH). TORBA PROVINCE: Banks Islands, Vanua Lava Island, Sola, 5–11.VIII.1958, under bark, B. Malkin, 2 ♀♀ (AMNH); Winkler et récolte à la main, 10–20.VI.1979, A. de Chambrier, 3 ♀♀, 6 juv. (MHNG, AC/49). **VIETNAM**: Dak Lak Province: 10 km E Ban Me Thuot (= Buon Ma Thuot), stop 16, 1900', 11.V.1960, R. E. Leech, 1 ♀ (BPBM). Dak Song, 76 km SW of Ban Me Thuot, 870 m, 19–21.V.1960, S. & L. Quate, 1 juv. (BPBM). Lam Dong Province, Province du Haut-Donai, Col de Blao, Annam, 800 ft, 22.VI.1933, M. Poilane, 1 ♀ (USNM 00309). Dambri Waterfall, ca. 18 km N of Bao Loc, 11°38'42.0''N 107°44'36.6''E, 850 m (old secondary forest, roadside), 1–2.IX.2003, P. Schwendinger, 1 ♀ (MHNG, SV-03/18). 6 km SE Dilinh (= Djiring), stop 14, 3300', 2.V.1960, R. E. Leech, 4 juv. (BPBM); 3200', 3.V.1960, R. E. Leech, 1 juv. (BPBM). 24 km E Dilinh (= Djiring), 3000', 25.IV.1960, R. E. Leech, 2 ♀♀, 1 juv. (BPBM); stop 9, 29. IV.1960, R. E. Leech, 1 ♀ (BPBM). Dilinh (= Djiring), 25.IV.1960, L. Quate, 1 ♀, 1 juv. (BPBM). Fyan (near Lieng Khuong), 900–1000 m; 11.VII–9.VIII.1961, N. R. Spencer, 1 ♀, 12 juv., 10 pullus (BPBM). **TONGA ISLANDS**: Moa Tonga Tabu, B. Friedländer, 3 ♀♀ (ZMB 15149). Ton-

GATAPU ISLANDS, EUA ISLAND, Pangai, 0–50 m, I.1979, under bases of leaves of coconut, N. L. H. Krauss, 2 ♀♀ (BPBM, Acc. No. 1979.153); 0–100m, I.1979, N. L. H. Krauss, 1 juv. (BPBM, Acc. No. 1979.153). NINAFOON ISLAND, D. Friedländer, 3 ♀♀, 1 juv. (ZMB 15148); September, Dr D. Friedländer (Formalin ?), 1 ♀, 2 juv. (ZMB 15151).

DISTRIBUTION (fig. 132)
Australia (N Queensland), Bougainville Island, Brunei, Honk Kong, Federated States of Micronesia, Palau, China (Hainan), Christmas Island (Indian Ocean), Cook Islands, Fiji, French Polynesia, Indonesia, East Malaysia (Borneo), Western Malaysia (= Peninsular Malaysia), Marshall Islands, New Caledonia, Northern Mariana Islands, Papua New Guinea, Philippines, American Samoa, Western Wamoa, Singapore, Solomon Islands, Thailand, Vanuatu, Vietnam, Tonga Islands.

NOTES
Fet (2000) reported that Birula (1917b: 90) stated that *Chactas brunneus* described from New Caledonia by Bellevoye (1870) belongs to the genus *Hormurus* and tentatively put it in synonymy with *L. australasiae*. The types of Bellevoye were not examined in the course of this study but the species might refers to one of the two hormurid species occuring in New Caledonia, i.e. *L. australasia*e and *H. neocaledonicus*. As concluded by Fet after comparison of the original description and diagnoses of both species, the true identity of *Chactas brunneus* most likely is *L. australasiae*. Therefore the species is left in synonymy with *L. australasiae*.

DESCRIPTION. ADULT MALE
COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).
CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.
PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth; wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium basal, in same axis as *Eb* group; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb*–*et* axis; *esb* trichobothrium below *est*–*et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina costate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; prodorsal (*pd*) carina

distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrol*at*eral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrol*at*eral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) ca*rina*e; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria smooth (trichobothria not in distinct depressions). Chela, dorsal intercarinal surface, macrosculpture limited to prolateral and retrolateral edges, absent from the median part, granulation vestigial, at most low granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation absent; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface smooth or nearly so; retrolateral dorsal intercarinal surface smooth or nearly so; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface smooth or nearly so, sometimes with few scattered bigger spiniform granules proximally. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface, frontal lobes (area I) smooth, granular along median longitudinal sulci and anterior furcated sulci (areas II–IV); median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites, median area smooth, lateral areas at least sparsely granular posteriorly; VII, posttergite anteromedian area smooth; lateral and posteromedian areas granular; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples absent, even surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width approximately equal to slightly less than posterior width (1<pw/aw<1.5) [=subpentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; 6–7 pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae absent or obsolete; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median

lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, 1–2 pairs of well developed posterior spiniform granules; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, 1–3 pairs of well developed medial granules. Segment II, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules well developed; ventrosubmedian carinae, 2–3 pairs of well developed posterior spiniform granules, one pair of well developed sub-posterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae present; ventromedian carina absent or obsolete, partial, expressed only in posterior half, with distinct spiniform granules, at least distally; ventrolateral carinae present and distinct, diverging on distal part, anterior half with at least few small spiniform granules, posterior half with strong conical tooth; anal arch with few large conical teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae present. Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules absent; terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/4; 4/4.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with apex of lamellar hook or slightly above, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 90º angle with lamella.

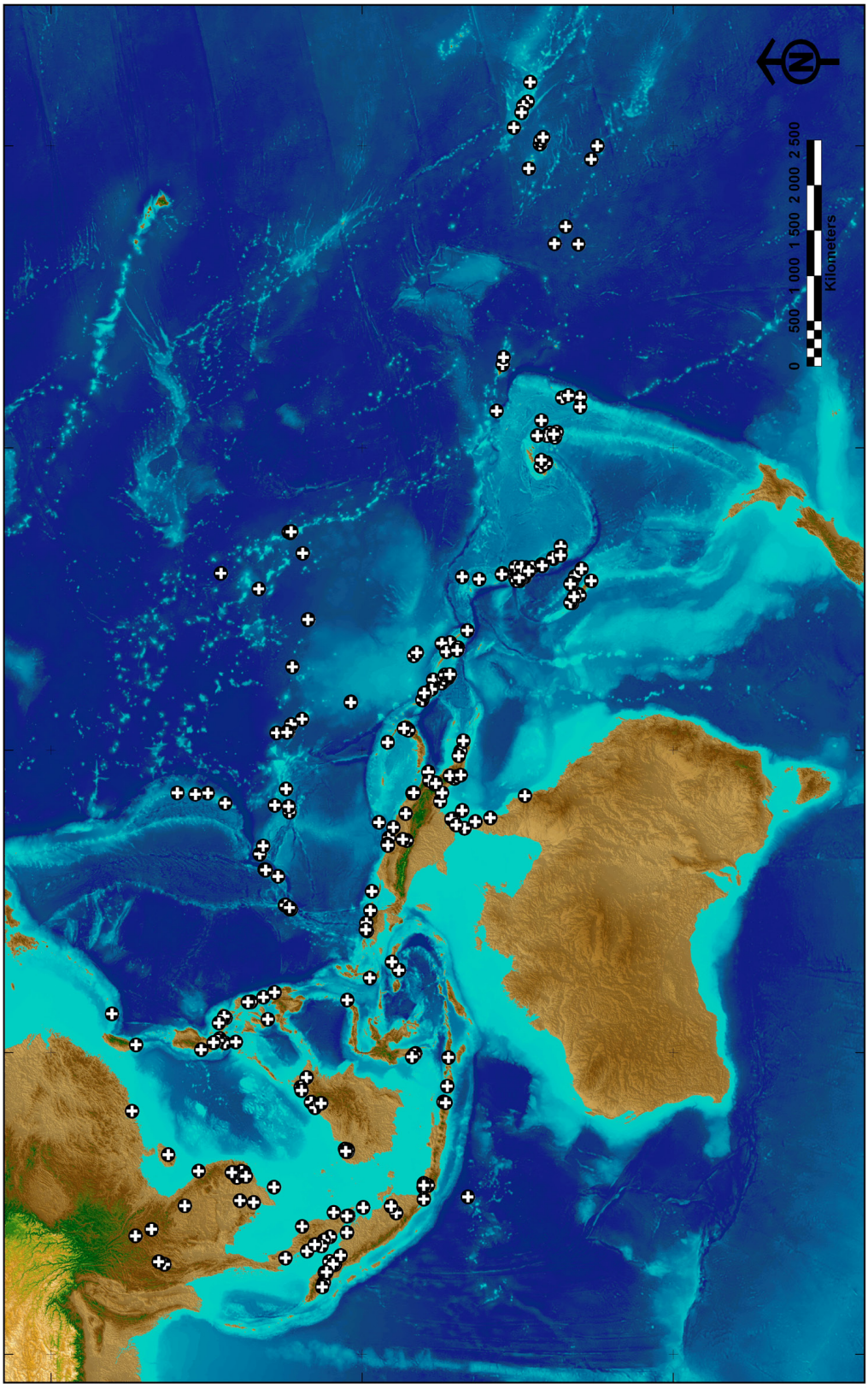
ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface entirely smooth or nearly so; posteromedian surface smooth or nearly so; anterolateral surfaces smooth or nearly so; mediolateral surface smooth or nearly so; posterolateral surfaces smooth or nearly so.

MESOSOMA. Tergites I–III, post-tergites, mesial and lateral areas smooth; IV–VI, post-tergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples absent or vestigial, even surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; 5–6 pectinal teeth.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 132. Distribution map of *Liocheles australasiae* (Fabricius, 1775).


0 500 1 000 1 500 2 000 2 500
Kilometers

Liocheles complanatus (C. L. Koch, 1837), **new combination**

Ischnurus complanatus C. L. Koch, 1837c: 37

References

Sysiphus complanatus: C. L. Koch, 1837b: 37.
Ischnurus complanatus: Gervais, 1844b: 69; C. L. Koch, 1850: 89; Doleschall, 1857: 405; Cambridge, 1871: 617.
Liocheles complanato: Simon, 1887: 113.
Hormurus australasiae: Kraepelin, 1901: 272 (part); Pérez Minocci, 1974: 37 (part).
Hormurus australasiae complanatus: Thorell, 1888: 329, 420; Thorell, 1889: 526, 590.

Material examined

Holotype: INDIA, Himalayas, Keys, 1 ♀ (Holotype, NHML 13.9.1.71 TYPE). **Additional material**: EAST PAKISTAN (= BANGLADESH), Lawa Chera Forest, Srimangal, IX.27.61, 110 m, E. S. Ross & D. Cavagnaro, 1 ♀ (CAS); Harbang Forest, 6 miles N Chiringa, IX.18.61, 50 ft., E. S. Ross & D. Cavagnaro, 2 imm. (CAS). INDIA, Himalayas, Keys, 1 ♀ (NHML 1890.7.1.228).

Distribution (fig. 133)
India, Pakistan.

DESCRIPTION. ADULT FEMALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpal; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium basal, in same axis as *Eb* group; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est–esb* similar to distance *esb–eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb–et* axis; *esb* trichobothrium below *est–et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em–esb* series with four trichobothria in 2 groups [esb_{1-2}] [em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina costate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrolateral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrolateral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than

dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) c*arin*ae; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria smooth (trichobothria not in distinct depressions). Chela, dorsal intercarinal surface entirely and densely granular, medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation absent; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface smooth or nearly so, prolateral edge and proximal end may be weakly granular; ventral intercarinal surface smooth or nearly so; retrolateral dorsal intercarinal surface smooth or nearly so; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface smooth or nearly so, sometimes with few scattered bigger spiniform granules proximally. Femur, dorsal intercarinal surface, granulation absent or limited to the proximal and retrolateral edges, when present granulation dense; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface smooth or nearly so; retrolateral ventral intercarinal surface smooth or nearly so; ventral intercarinal surface, granulation absent or vestigial and limited to the retrolateral edge; prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Anteromedian surface entirely smooth or nearly so; posteromedian surface smooth or nearly so; anterolateral surfaces smooth or nearly so; mediolateral surface smooth or nearly so; posterolateral surfaces smooth or nearly so.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence. Tergites I–III, post-tergites, mesial and lateral areas smooth; IV–VI, post-tergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples absent or vestigial, even surface; I–VI, lateral transversal sulcus present.

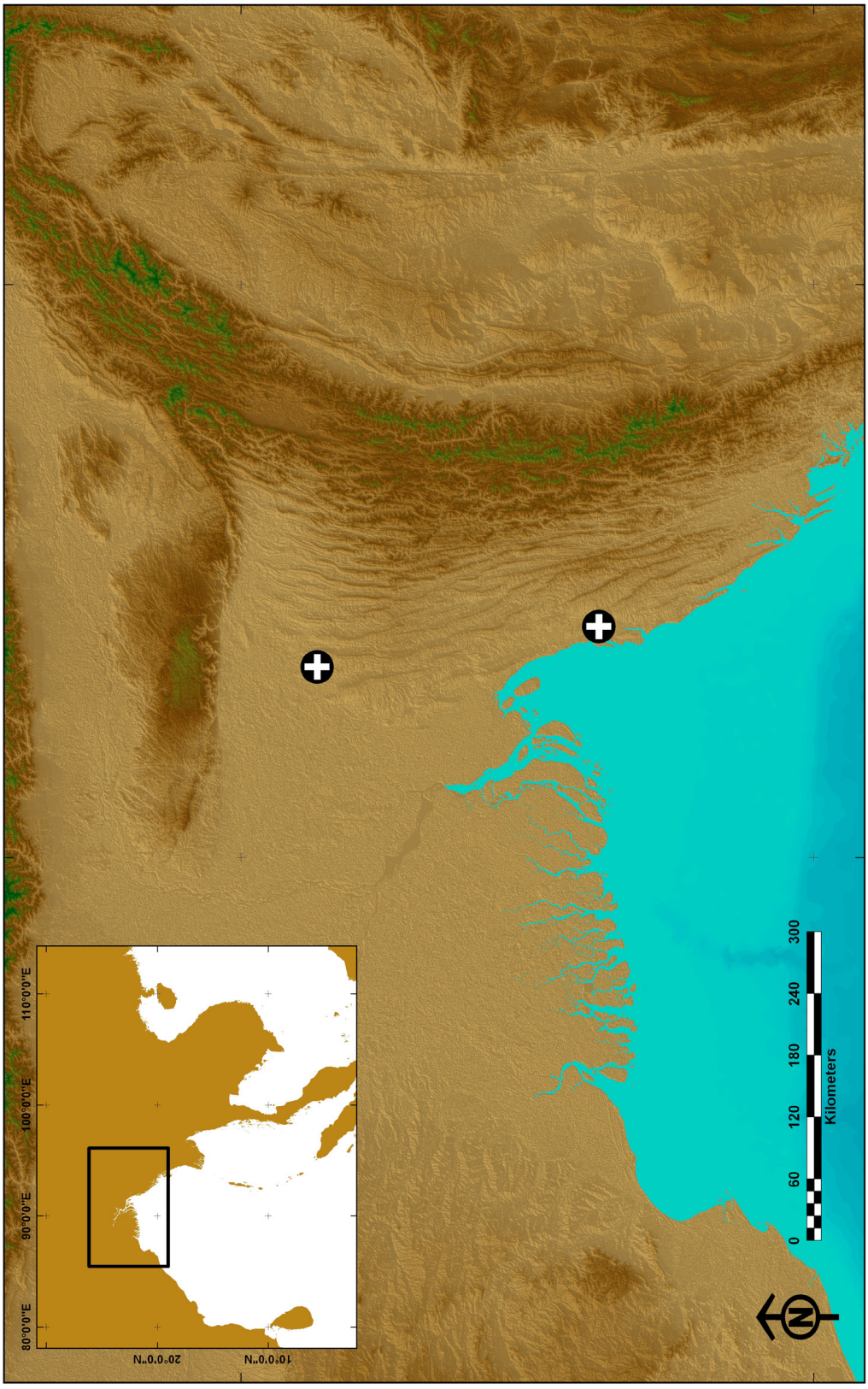
VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; six pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae absent or obsolete; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, 1–2 pairs of well developed posterior spiniform granules; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, 1–3 pairs of well developed medial granules. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent;

ventrolateral carinae, posterior spiniform granules well developed; ventrosubmedian carinae, 2–3 pairs of well developed posterior spiniform granules, one pair of well developed subposterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae, ridges with at least few reduced spiniform granules distally; ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae present; ventromedian carina absent or obsolete, partial, expressed only in posterior half, with distinct spiniform granules, at least distally; ventrolateral carinae present and distinct, diverging on distal part, anterior half with at least few small spiniform granules, posterior half with strong conical tooth. Telson, total length equal to or slightly longer than metasomal segment V; anal arch with few large conical teeth; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/4; 4/4.

Fig. 133. Distribution map of *Liocheles complanatus* (C. L. Koch, 1837).


80°0'0"E
90°0'0"E
100°0'0"E
110°0'0"E
20°0'0"N
10°0'0"N
0
60
120
180
240
300
Kilometers

Liocheles longimanus (Werner, 1939), **new combination**

Hormurus australasiae longimanus Werner, 1939: 362.

References

Liocheles australasiae longimanus: Locket, 1997: 331; Fet, 2000: 397; Monod & Volschenk, 2004: 686.
Liocheles longimanus: Monod, 2000: 97–101, pl. 36–40, map 12.

Material examined

Lectotype: INDONESIA, SUMATRA, SUMATERA UTARA PROVINCE, Montes Battak, H. Fruhstorfer, 1 ♂, (ZMAK, alte Trockenpräparate 111). **Paralectotype**: same data as holotype, 1 ♀ (ZMAK, alte Trockenpräparate 110). **Additional material**: INDONESIA. SUMATRA. Kenandam?, III.1913, Buxton, 1 ♀ (MNHN-RS 3477). Kenandam?, Kanamelean?, 1913, Buxton, 2 ♂♂, 4 ♀♀, 4 juv. (MNHN-RS 3471). SUMATERA BARAT PROVINCE, Harau Canyon, N of Payakumbuh, 0°05'46''Sx100°39'58''E, 750 m, 7.VI.2006, old secondary forest, P. Schwendinger, 1 ♂ (LP 6388). Lubuk Sikaping (Sumatra's Westkust), 450 m, 1926, E. Jacobson, 1 ♂ (NNHM). Mangani, mine near Kota Tingge, 700 m, 21.VII.1983, E. S. Ross, 1 ♂, 1 ♀, 1 ♂ sub. (CAS). Ngalau Kamang Cave, near Bukittinggi (Central Sumatra), 20.VII.1979, J. Balazuc, 1 ♀, 1 juv. (MNHN-RS 7417).

Distribution (fig. 138)
Indonesia, Sumatra.

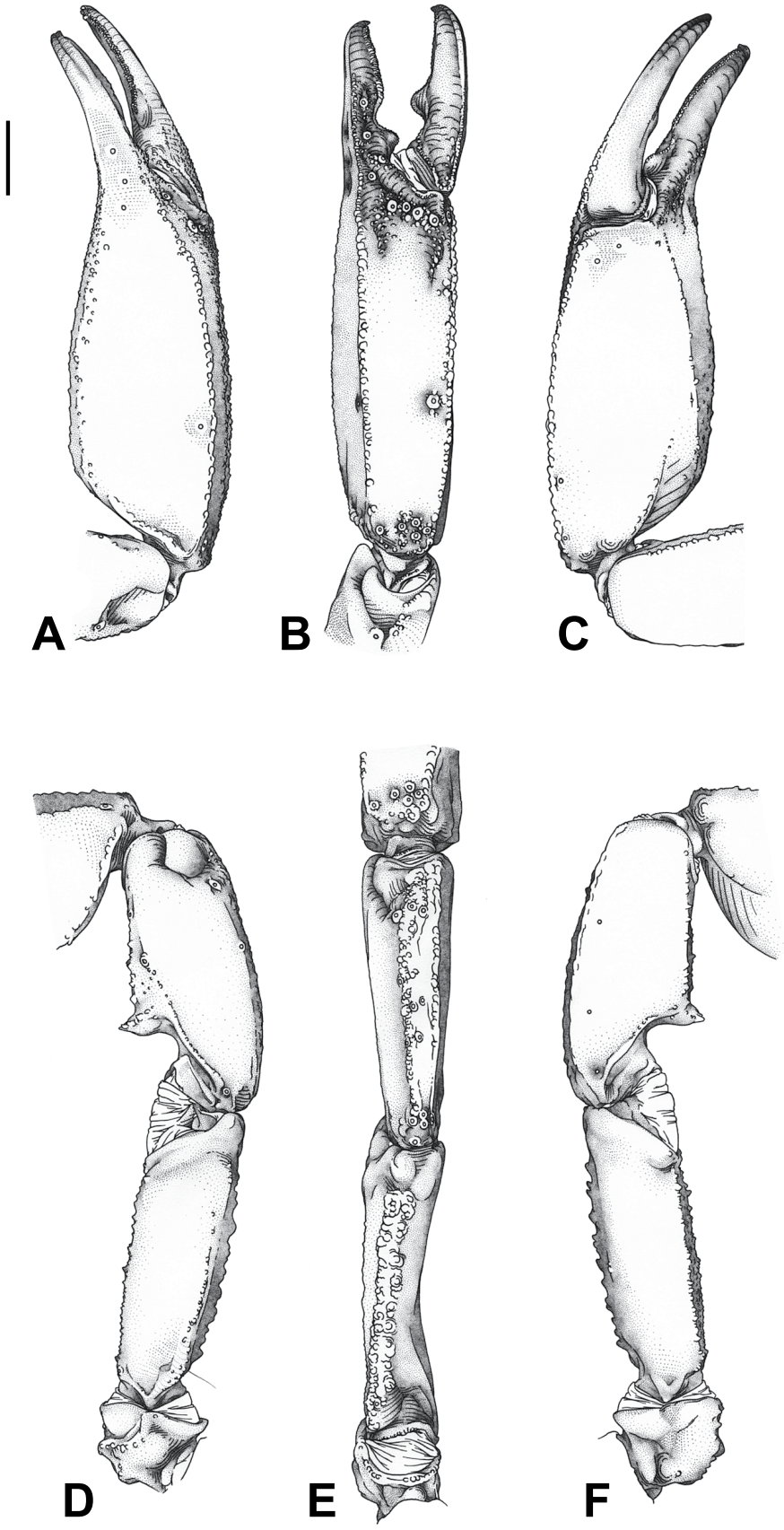
DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur longer than carapace, up to twice longer. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth; wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY (fig. 133). Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 close together, proximal part of manus; *Esb* trichobothrium basal, in same axis as *Eb* group; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est–esb* similar to distance *esb–eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb–et* axis; *esb* trichobothrium below *est–et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* trich*o*bothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em–esb* series with four trichobothria in 2 groups [esb_{1-2}] [em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrol*at*eral (*drl*) carina distinct, costate or granular; dorsal retrol*at*eral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina costate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian

Fig. 134. *Liocheles longimanus* (Werner, 1939), male, pedipalp with trichobothrial pattern.A, chela, dorsal aspect. B, idem, external aspect. C, idem, ventral aspect. D, femur and patella, dorsal aspect. E, idem, external aspect. F, idem, ventral aspect. Scale line, 2 mm.


A
B
C
D
E
F

(*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrol*at*eral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrol*at*eral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) c*arin*ae; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface*,* area around *db*/*dsb*/*dst* trichobothria smooth (trichobothria not in distinct depressions). Chela, dorsal intercarinal surface, macrosculpture limited to prolateral and retrolateral edges, absent from the median part, granulation vestigial, at most low granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation absent; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface smooth or nearly so, prolateral edge and proximal end may be weakly granular; ventral intercarinal surface smooth or nearly so; retrolateral dorsal intercarinal surface smooth or nearly so; retrolateral ventral intercarinal surface smooth or nearly so; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface, granulation absent or limited to the proximal and retrolateral edges, when present granulation dense; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface smooth or nearly so; retrolateral ventral intercarinal surface smooth or nearly so; ventral intercarinal surface, granulation absent or vestigial and limited to the retrolateral edge; prolateral intercarinal surface at least sparsely granular.

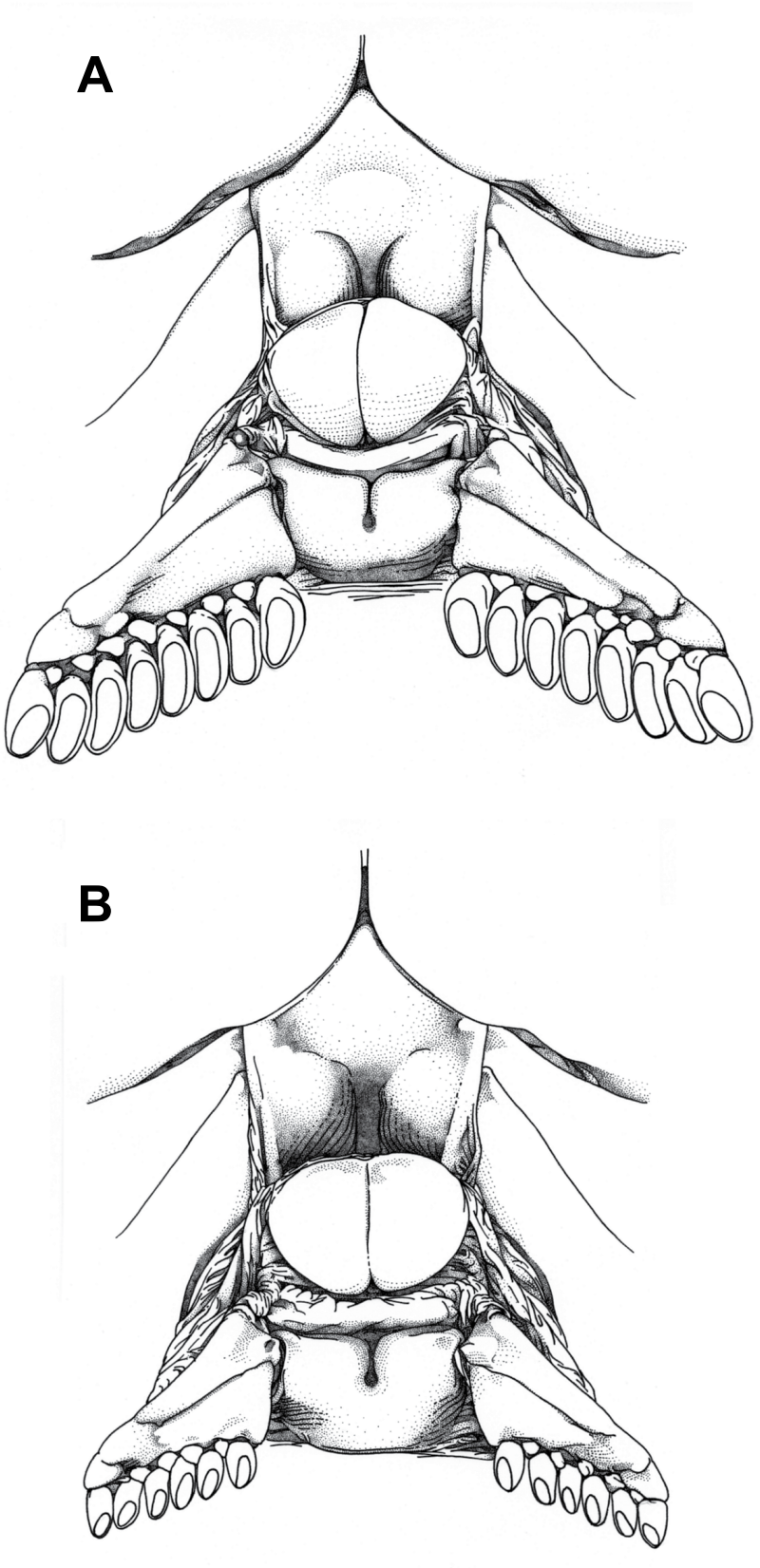
CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Anteromedian surface entirely smooth or nearly so; median surface smooth or nearly so; posteromedian surface entirely smooth or nearly so; anterolateral surfaces smooth or nearly so; posterolateral surfaces smooth or nearly so.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites, median area smooth, lateral areas at least sparsely granular posteriorly; VII, posttergite anteromedian area smooth; lateral and posteromedian areas granular; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples absent, even surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM (fig. 135A), shape, anterior width approximately equal to slightly less than posterior width (1<pw/aw<1.5) [=subpentagonal]; length less than or equal to posterior width. PECTINES (fig. 135A), length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; 7–8 pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA (fig. 136C). Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae absent or obsolete; ventrolateral and paired ventrosubmedian carinae

Fig. 135. *Liocheles longimanus* (Werner, 1939), pectines and genital opercula, ventral aspect. A, male. B, female. Scale line, 1 mm.


A
B

present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, 1–2 pairs of well developed posterior spiniform granules; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules well developed; ventrosubmedian carinae, 2–3 pairs of well developed posterior spiniform granules, one pair of well developed sub-posterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae present; ventromedian carina absent or obsolete, partial, expressed only in posterior half, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, anterior half smooth or nearly so, posterior half with strong conical tooth; anal arch crenulate, at least with few reduced teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi (fig. 136B). Two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules absent; terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/4; 4/4.

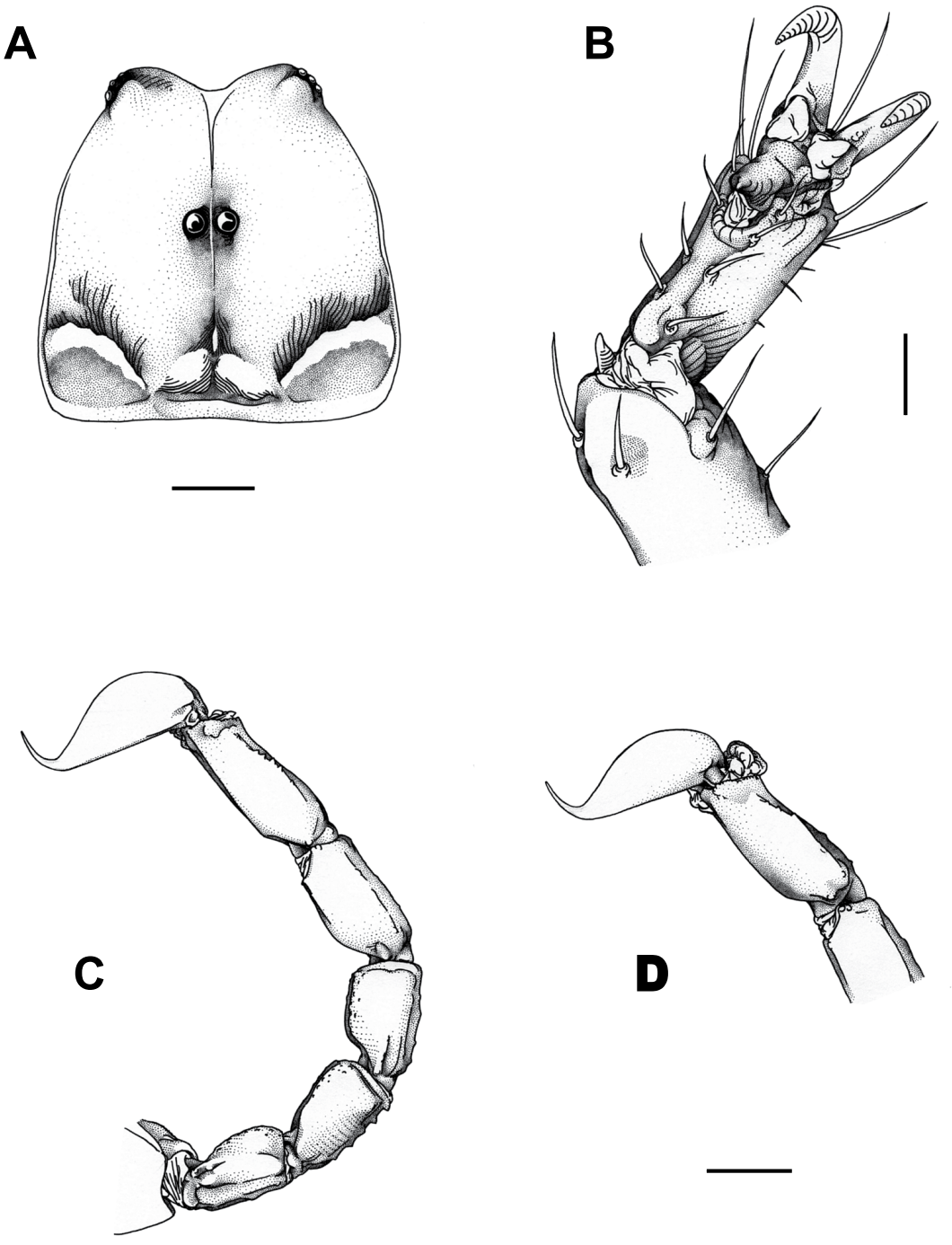
HEMISPERMATOPHORE (fig. 137). Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with apex of lamellar hook or slightly above, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 90º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface entirely smooth or nearly so; posteromedian surface smooth or nearly so; anterolateral surfaces smooth or nearly so; mediolateral surface smooth

Fig. 136. *Liocheles longimanus* (Werner, 1939). A, carapace, dorsal aspect. B, right tarsus IV, ventral aspect. C, metasoma, lateral aspect, male. D, metasoma, lateral aspect, female. Scale lines, 2 mm (A, C, D), 0.5 mm (B).


A
B
C
D

or nearly so; posterolateral surfaces smooth or nearly so.
MESOSOMA. Tergites I–III, post-tergites, mesial and lateral areas smooth; IV–VI, post-tergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples absent or vestigial, even surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM (fig. 135B) oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES (fig. 135B), length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; seven pectinal teeth.
METASOMA (fig. 136D). Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 137. *Liocheles longimanus* (Werner, 1939), male. Hemispermatophore. Scale line, 1 mm.

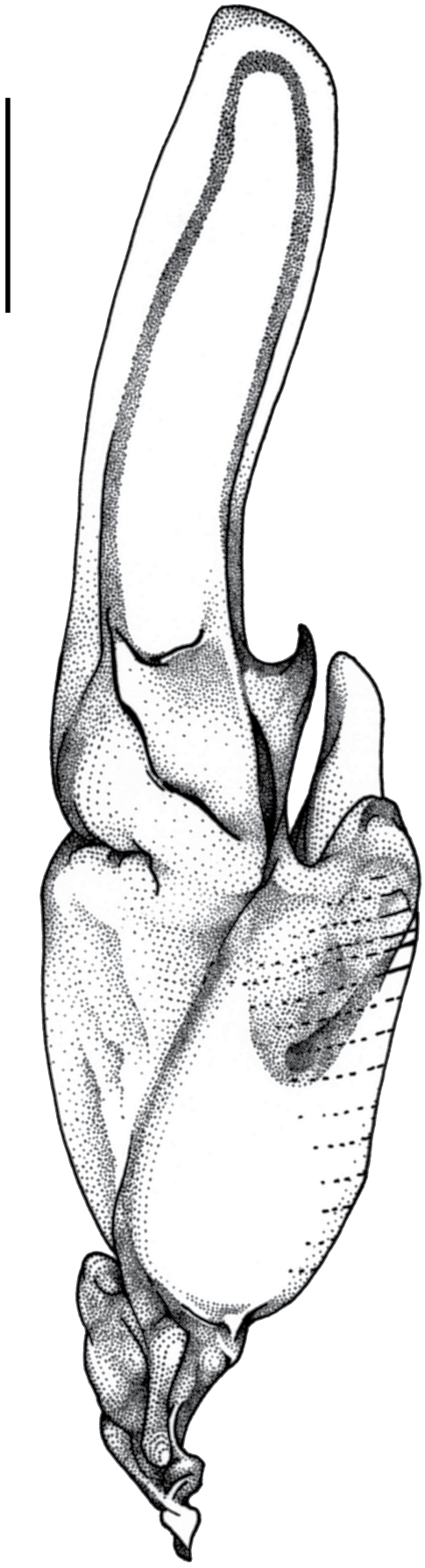
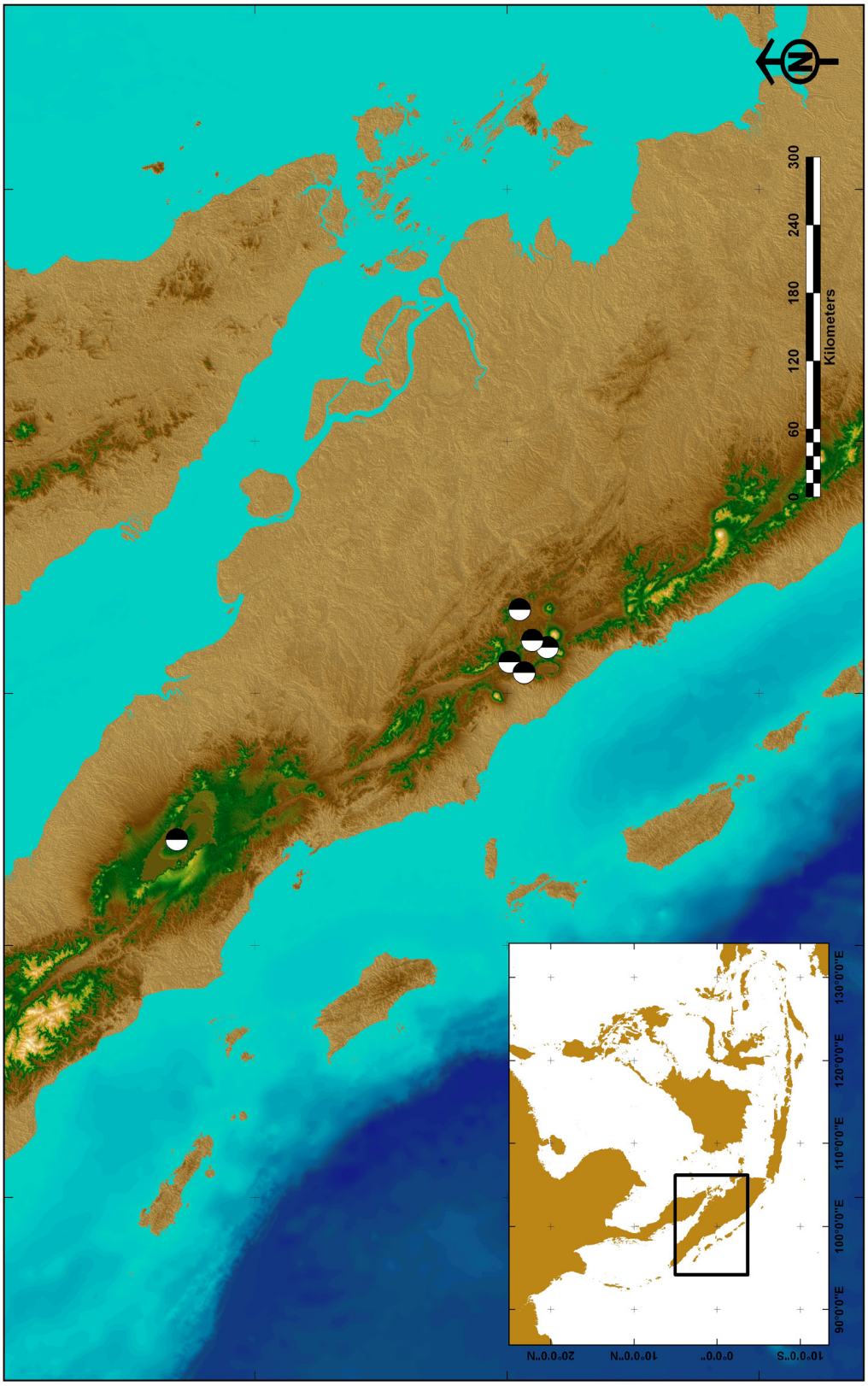


Fig. 138. Distribution map of *Liocheles longimanus* (Werner, 1939).


N
0
60
120
180
240
300
Kilometers
90°0'0"E
100°0'0"E
110°0'0"E
120°0'0"E
130°0'0"E
10°0'0"S
0°0'0"
10°0'0"N
20°0'0"N

Liocheles malaya n. sp.

Reference

Liocheles nigripes (nec Pocock, 1893; MIS): Kovařík, 2000: 58–63, figs 8–14.
Liocheles australasiae (nec Fabricius, 1775; MIS): Kamenz & Prendini, 2008: 11, 43, pl. 132.

Material examined

Holotype: WESTERN MALAYSIA (= PENINSULAR MALAYSIA), Perak, Maxwell Hill (= Bukit Larut), E of Taiping, 950–1250m, 21–25.XI.1999, G. Cuccodoro & Y. Löbl, 1 ♂ (MHNG). **Paratypes**: WESTERN MALAYSIA (= PENINSULAR MALAYSIA), PERAK, Kaki Bukit, foothills of Bukit Larut, start of track, 04°51.812'Nx100°45.716'E, 191 m, 25.IX.2001, rainforest, under bark of rotten logs, L. Monod, 1 ♀ (LM) Maxwell Hill (= Bukit Larut), 9.VII.1983, under bark in forest, E. S. Ross, 1 ♀ (CAS). **Additional material**: WESTERN MALAYSIA (= PENINSULAR MALAYSIA): 2 ♂♂ sub. (8/8), 1 ♀ sub. (7/7), 1 juv. (NHML). Federal territory of Kuala Lumpur, 22 mi NE Kuala Lumpur, 600 m, 9.VI.62, E. S. Ross, D.Q.Cavagnaro, 1 ♂ (CAS). Johor: Endau-Rompin National Park, between Kuala Jasin and Kuala Marong (02°31'44.2''N, 103°22'01.9''E), 40m (rain forest along stream), 3–5.VII.2001, P. Schwendinger, 1 ♀ immature (MHNG, SIM-01/10). Gunong Pulai, MWF Tweedie, IV.1934, 1 specimen (RMBR ZRC. ARA.449). Johore Bahru, D. Abdullah, 28.I.1904, 1 ♀, 1 ♀ sub., 6 juv. (L. sp.), 3 ♀♀, 3 ♀♀ sub. (RMBR ZRC.ARA.450). Malacca, V. Jachan, 2 ♂♂, 1 ♀, 2 sub., 2 ♀♀ (ZMB 15128). Pahang: Kuala Tahan, King George V National Park, 28.II.1958, Transect sq.3, 1 ♂ immature (BPBM). Kuala Terla, Telom Valley, 3/35, 4000'–4500', 1 ♂, 1 ♀ (RMBR ZRC.ARA.435); 3 ♂♂, 5 ♀♀, 2 juveniles (RMBR ZRC.ARA.453). Perak, Banding Island, Tasik Temengor, 14.IV.2001, under lumber, damp, R. West, 1 ♀ (LP 1909). Selangor, Bukit Kutu, 4/15, 3400', 3 ♂♂, 2 imm. (RMBR ZRC.ARA.451). SINGAPORE, Bukit Timah (2. Österr. Weltumseglung 1868–69), 1871.I.25, Ransonnet, 1 ♂ (ZMW 1743).

Distribution (fig. 139)

Western Malaya.

Etymology

The name *malaya* refers to "British Malaya", comprising the Malay Peninsula and the Island of Singapore that were colonized by the British from the 18th to the 20th Centuries before the formation of the Malayan Union in 1946. "British Malaya" corresponds to the distribution range of the species as currently known.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth; wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch contiguous (adjoin) or at most with a reduced gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/ well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* trichobothria; V_3 and V_4 separate; *Esb* trichobothrium basal, in same axis as *Eb* group; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est–esb* similar to distance *esb–eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between

fixed and movable fingers, above *esb*–*et* axis; *esb* trichobothrium below *est*–*et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur*; et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothri; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrol*at*eral (*drl*) carina distinct, costate or granular; dorsal retrol*at*eral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina granular or crenelate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming a single large spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrol*at*eral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrol*at*eral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, less strongly developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) c*arin*ae; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria smooth (trichobothria not in distinct depressions). Chela, dorsal intercarinal surface, macrosculpture limited to prolateral and retrolateral edges, absent from the median part, distinct medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation absent; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface smooth or nearly so, prolateral edge and proximal end may be weakly granular; ventral intercarinal surface smooth or nearly so; retrolateral dorsal intercarinal surface smooth or nearly so; retrolateral ventral intercarinal surface smooth or nearly so; prolateral intercarinal surface smooth or nearly so, sometimes with few scattered bigger spiniform granules proximally. Femur, dorsal intercarinal surface, granulation absent or limited to the proximal and retrolateral edges; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface smooth or nearly so; retrolateral ventral intercarinal surface smooth or nearly so; ventral intercarinal surface, granulation absent or vestigial and limited to the retrolateral edge; prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli, third ocellus apart from first and second ocelli. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Anteromedian surface entirely smooth or nearly so; median surface smooth or nearly so; posteromedian surface entirely smooth or nearly so; anterolateral surfaces smooth or nearly so; posterolateral surfaces smooth or nearly so.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites, median area smooth, lateral areas at least sparsely granular posteriorly; VII, posttergite anteromedian area smooth; lateral and posteromedian areas granular; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples absent, even surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width approximately equal to slightly less than posterior width (1<pw/aw<1.5) [=subpentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) long, distal edge reaching beyond distal edge of coxa; three marginal lamellae; fulcrae present; eight pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae absent or obsolete; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, 1–2 pairs of well developed posterior spiniform granules; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, medial granules weak to absent, or 1–3 pairs of well developed medial granules. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules well developed; ventrosubmedian carinae, 2–3 pairs of well developed posterior spiniform granules, one pair of well developed sub-posterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae present; ventromedian carina absent or obsolete, partial, expressed only in posterior half, as a double ridge, ridges absent/smooth or nearly so; ventrolateral carinae present and distinct, diverging on distal part, anterior half with at least few small spiniform granules, posterior half with strong conical tooth; anal arch with few large conical teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

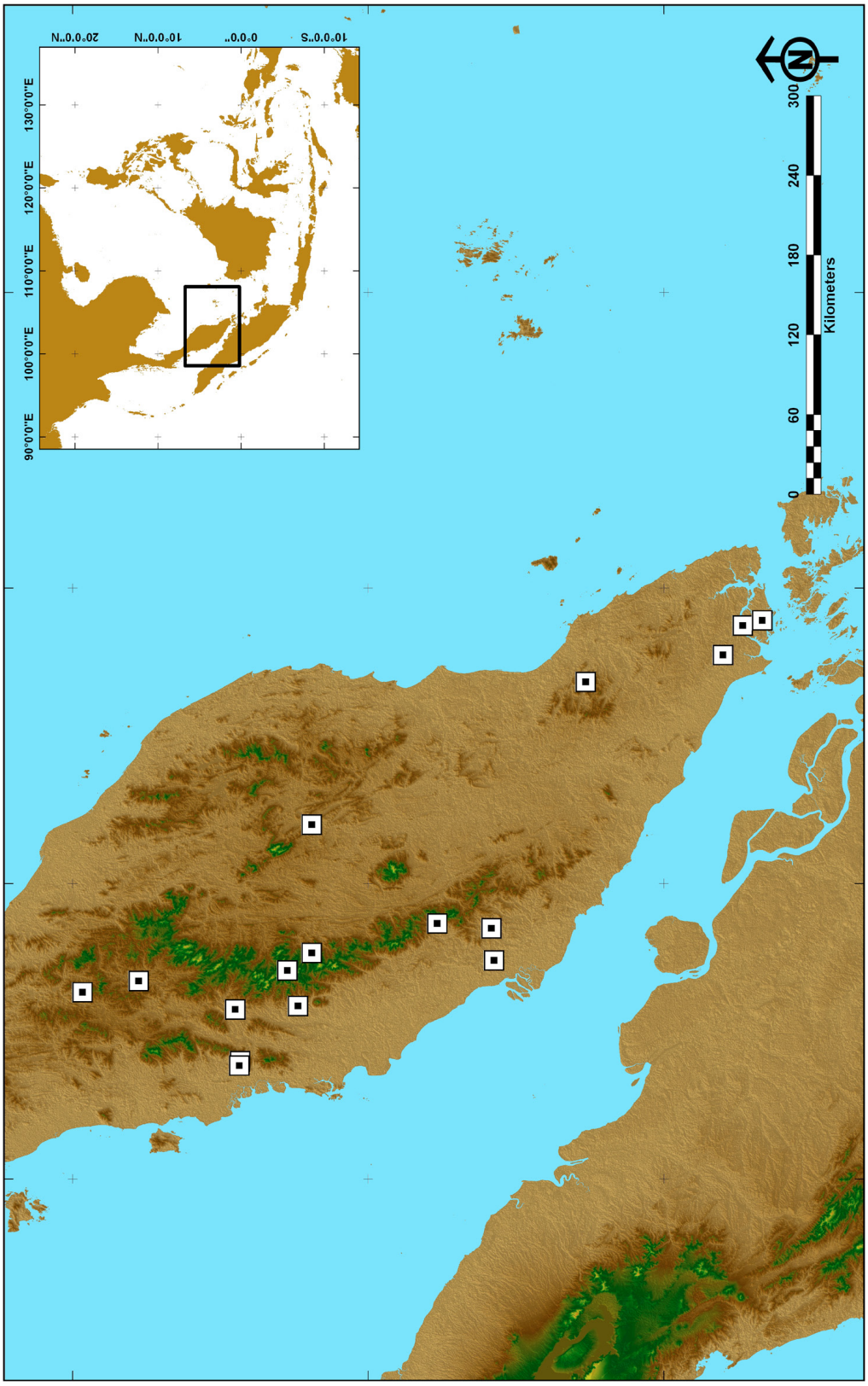
LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues shorter than telotarsus. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/4; 4/4.

HEMISPERMATOPHORE. Distal lamina curved at least slightly, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with apex of lamellar hook or slightly above, above tip of distal lobe.

Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 90º angle with lamella. **BOOK LUNGS**. Lamellar surface with simple trabeculae, with arcuate bow-like structures. Posterior spiracle edge with chisel-like structures.

ADULT FEMALE. Same characters as in ♂ except as follows.
PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.
CARAPACE. Anteromedian surface entirely smooth or nearly so; posteromedian surface smooth or nearly so; anterolateral surfaces smooth or nearly so; mediolateral surface smooth or nearly so; posterolateral surfaces smooth or nearly so.
MESOSOMA. Tergites I–III, post-tergites, mesial and lateral areas smooth; IV–VI, post-tergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples absent or vestigial, even surface.
VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; seven pectinal teeth.
METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 139. Distribution map of *Liocheles malaya* n. sp.


90°0'0"E
100°0'0"E
110°0'0"E
120°0'0"E
130°0'0"E
10°0'0"S
0°0'0"
10°0'0"N
20°0'0"N
N
0
60
120
180
240
300
Kilometers

Liocheles nigripes (Pocock, 1897), **new combination**

Hormurus nigripes Pocock, 1897d: 117.

Synonym

Tibetiomachus himalyensis Lourenço & Qi, 2006: 291–294.

References

Hormurus nigripes: Kraepelin, 1899: 155; Pocock, 1900: 80; Kraepelin, 1913: 163, 164, fig. 7a; Giltay, 1931: 13; Fage, 1933: 27; Fage, 1936: 180; Caius, 1942: 112; Fage, 1946: 71; Tylak, 1970: figs 1–3; Tikader & Bastawade, 1983: 506–510, figs 1376–1389.

Liocheles nigripes: Takashima, 1945: 95; Pérez Minocci, 1974: 37; L. E. Koch, 1977: 160; Kovařík, 1995: 202; Locket, 1995: 197; Kovařík, 1998: 134; Monod, 2000: 108–112, pl. 46–50, map 14; Monod & Volschenk, 2004: 686; Maqsood Javed *et al.*, 2010.

Type material

Holotype of *Hormurus nigripes*: INDIA, GUJARAT, Panch Mahals, Bombay Natural History Society (P.), W. A. Wallinger Esq., 1 ♀ (NHML 1896.9.26.84). **Holotype of *Tibetiomachus himalyensis***: CHINA, TIBET, High Plateau, Gurla Mandhata, ca. 4600 m, VII.1939, in soil under rocks, Italian Expedition, 1 ♀ (MNHN).

Material examined

Holotype of *Hormurus nigripes*. **Additional material**: INDIA. WEST BENGAL: 6 mi. N.E. Borio, 220 m, 30.X.1961, E. S. Ross & D. Cavagnaro, 1 ♀ (CAS). Janida, Jhargram, Midnapore, 17.VIII.65, C. L. Kau (H. L. Stahnke collection), 1 ♀ juv. (CAS ASU 65-0329 #1), 1 ♂ (CAS ASU 65-0330 #1), 1 ♀ (CAS ASU 65-0331 #1), 1 ♀ (CAS ASU 65-0333 #1), 1 ♂ (CAS ASU 65-0334 #1), 1 ♀ juv. (CAS ASU 65-0335 #1), 1 ♂ (CAS ASU 65-0336 #1), 1 ♀ juv. (CAS ASU 65-0337 #1), 1 ♂ (CAS ASU 65-0338 #1), 1 ♀ (CAS ASU 65-0339 #1), 1 ♂ (CAS ASU 65-0340 #1), 1 ♀ (CAS ASU 65-0341 #1), 1 ♀ juv. (CAS ASU 65-0342 #1); 30.VIII.1965, C. L. Kau (H. L. Stahnke collection), 1 ♀ (CAS ASU 65-0343 #1), 1 ♀ (CAS ASU 65-0344 #1), 1 ♂ (CAS ASU 65-0345 #1), 1 ♂ (CAS ASU 65-0346 #1), 1 ♂ (CAS ASU 65-0347 #1), 1 ♀ (CAS ASU 65-0348 #1), 1 ♀ juv. (CAS ASU 65-0349 #1), 1 ♂ (CAS ASU 65-0350 #1), 1 ♀ (CAS ASU 65-0351 #1), 1 ♀ (CAS ASU 65-0352 #1), 1 ♀ (CAS ASU 65-0353 #1), 1 ♀ (CAS ASU 65-0354 #1), 1 ♂ (CAS ASU 65-0355 #1), 1 ♀ (CAS ASU 65-0356 #1), 1 ♂ (CAS ASU 65-0357 #1), 1 ♂ juv. (CAS ASU 65-0358 #1), 1 ♀ (CAS ASU 65-0359 #1), 1 juv. (badly preserved) (CAS ASU 65-0360 #1), 1 ♂ juv. (CAS ASU 65-0361 #1), 1 ♂ (CAS ASU 65-0362 #1), 1 ♀ (CAS ASU 65-0363 #1). GUJARAT, Panch Mahals, Bombay Natural History Society (P.), W. A. Wallinger Esq., 2 ♀♀ (NHML 1897.9.17.21-22). MADHYA PRADESH, Sutna (= Satna), Central India, R. C. Wroughton (p.), Surg. Maj. Gimlette (c.), 1 ♀ (NHML 1896.8.15.6).

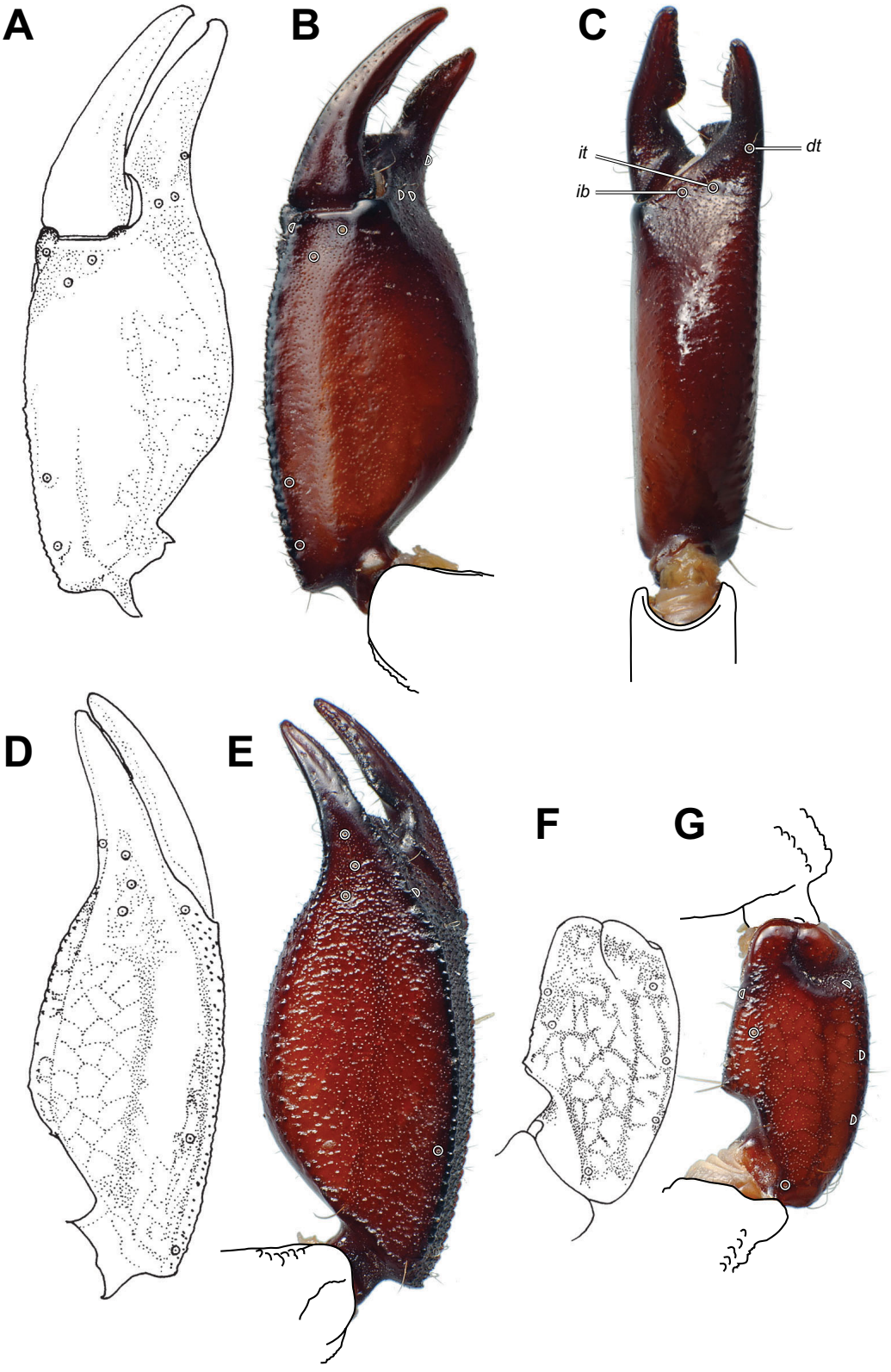
Distribution (fig. 145)

China (Tibet), India.

Notes

Lourenço & Qi (2006) recently described a new liochelid genus from Tibet, i.e. *Tibetiomachus*. Although the type specimens were not examined, the illustrations provided by the authors permit to unambiguously place the type species *Tibetiomachus himalayensis* Lourenço & Qi, 2006 in synonymy with *Liocheles nigripes* (Pocock, 1897). The establishment of the genus *Tibetiomachus* was based on only three diagnostic characters. One of these characters, i.e. the absence of trichbobothium *dt* on the pedipalp chela manus, is not valid: figures 20 and 21 of the original publication (here reproduced without modification as figs 140A and 140D) clearly show that the trichbobothium *db* is present on the dorsal surface of the pedipalp chela. Although the remaining two characters (shape of the ♀ genital operculum and chelicerae dentition) allows to distinguish *Tibetiomachus* from the genus *Iomachus*, they are not sufficient to separate *Tibetiomachus* from the genus *Liocheles*. Thus, *Tibetiomachus* is considered here as a junior synonym of *Liocheles*. Morevoer, *T. himalayensis* is placed in synonymy with *L. nigripes* for the following reasons: (1) Both species share the same unusual basally truncated pedipalp chela manus (fig. 140A–E), and a a poorly developed patellal prolateral spur (fig. 140F, G). (2) *L.*

Fig. 140. Comparison of the trichobothrial pattern and shape of the pedipalp chela manus and patella of *Liocheles nigripes* (Pocock, 1897) and *Tibetiomachus himalayensis* Lourenço & Qi, 2006. A, *T. himalayensis*, pedipalp chela manus, ventral aspect. B, *L. nigripes*, pedipalp chela manus, ventral aspect. C, *L. nigripes*, pedipalp chela manus, prolateral aspect. D, *T. himalayensis*. pedipalp chela manus, dorsal aspect. E, *L. nigripes*, pedipalp chela manus, dorsal aspect. F, *T. himalayensis*, pedipalp patella, dorsal aspect. G, *L. nigripes*, pedipalp patella, dorsal aspect. A, D and F are the unmodified illustrations from the original publication by Lourenço & Qi (2006).


A
B
C
it
ib
dt
D
E
F
G

nigripes is widespread in northern India with records as far north as Almora, a cantonment town located on the foothills of the Himalaya Mountain Range in the state of Uttarakhand (Caius, 1942). Therefore a record in southern Tibet is congruent with the known distribution range of the species.

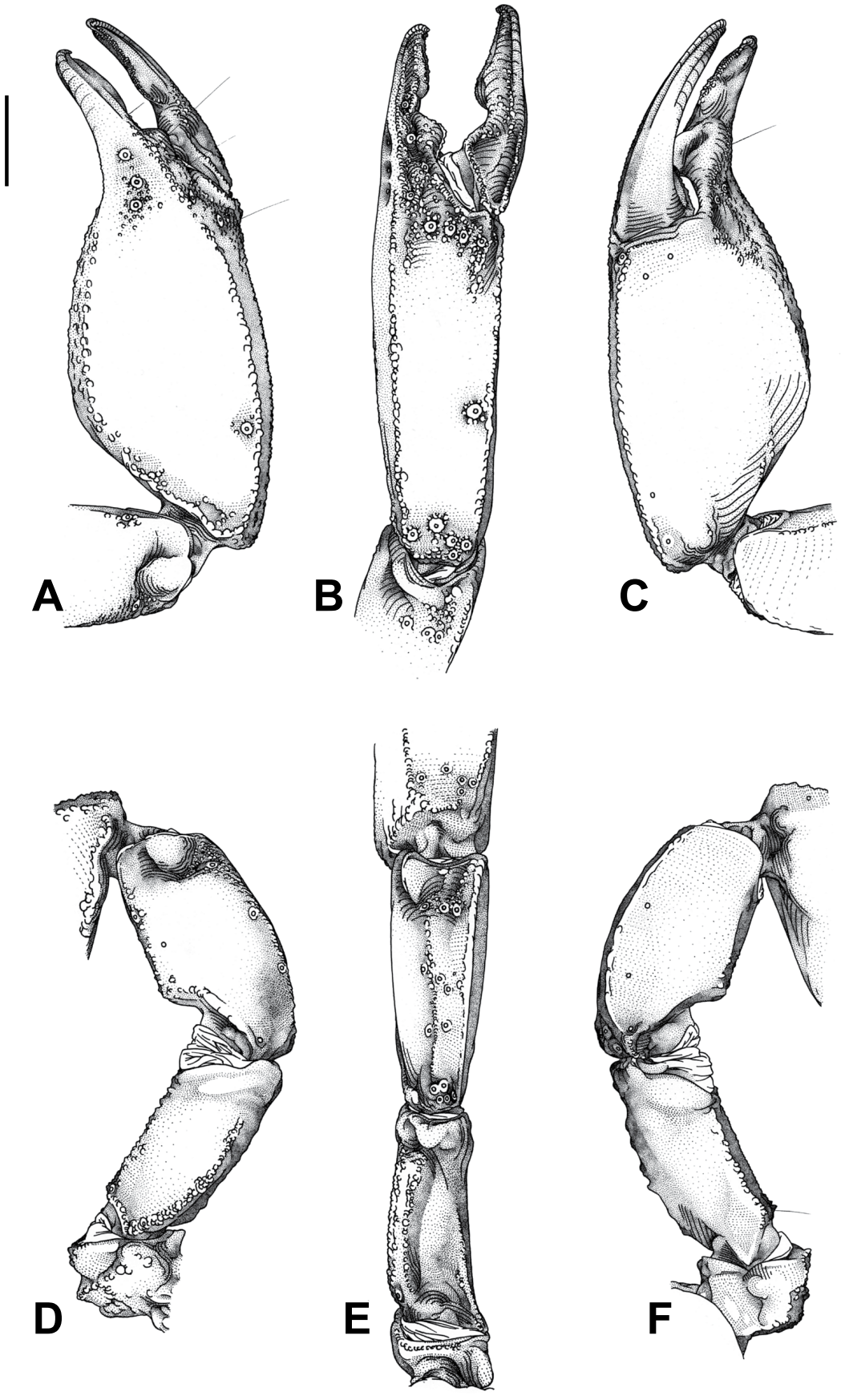
DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface dark (manus as dark as or darker than carapace). Legs, dark (as dark as tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth; wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep. Supra-basal lobe and corresponding notch with a distinct upper/anterior gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY (fig. 141). Chela manus, no accessory trichobothria; *Dt* trichobothrium midpalm or slightly less than midpalm; four *V* tri*c*hobothria; V_3 and V_4 close together, proximal part of manus; *Esb* trichobothrium basal, in same axis as *Eb* group; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb*, *eb*, *est*, *et* ca. equidistant (distance *est*–*esb* similar to distance *esb*–*eb*) or *est* closer to *esb*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb*–*et* axis; *esb* trichobothrium below *est*–*et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* tric*h*obothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em*–*esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrol*at*eral (*drl*) carina distinct, costate or granular; dorsal retrol*at*eral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina costate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*) carina; prolateral ventrosubmedian (*plvs*) carina absent or obsolete. Patella, prolateral process present (distinct); low, forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrol*at*eral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), as smooth ridge or faintly costate. Femur, dorsal retrol*at*eral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) ca*rin*ae; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface, area around *db*/*dsb*/*dst* trichobothria smooth (trichobothria not in distinct depressions). Chela, dorsal intercarinal surface, macrosculpture limited to prolateral and retrolateral edges, absent from the median part, granulation vestigial, at most low granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation absent; prolateral ventral intercarinal surface

Fig. 141. *Liocheles nigripes* (Pocock, 1897), male, pedipalp with trichobothrial pattern.A, chela, dorsal aspect. B, idem, external aspect. C, idem, ventral aspect. D, femur and patella, dorsal aspect. E, idem, external aspect. F, idem, ventral aspect. Scale line, 2 mm.


A
B
C
D
E
F

granular at least along prolateral edge. Patella, dorsal intercarinal surface smooth or nearly so, prolateral edge and proximal end may be weakly granular; ventral intercarinal surface smooth or nearly so; retrolateral dorsal intercarinal surface smooth or nearly so; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface smooth or nearly so, sometimes with few scattered bigger spiniform granules proximally. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface, granulation absent or vestigial and limited to the retrolateral edge; prolateral intercarinal surface at least sparsely granular.

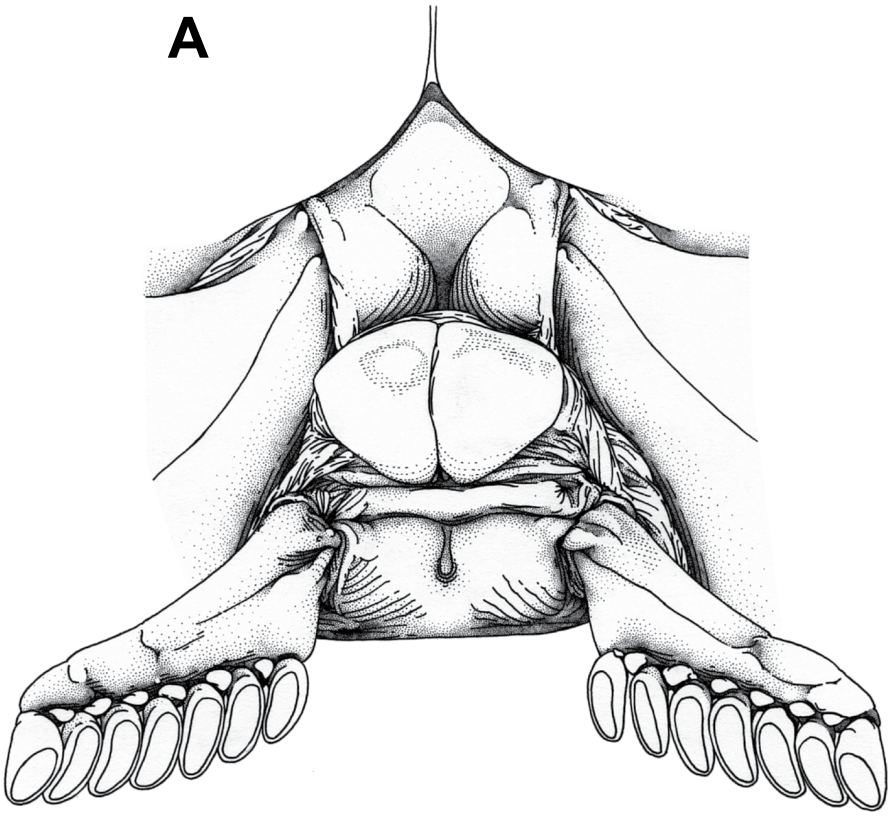
CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci present, distinct. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus smaller than first and second ocelli (2 anterior eyes in a cluster), third ocellus apart from first and second ocelli. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface entirely smooth or nearly so; median surface at least sparsely granular; posteromedian surface entirely smooth or nearly so; anterolateral surfaces at least sparsely granular; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites, median area smooth, lateral areas at least sparsely granular posteriorly; VII, posttergite anteromedian area smooth; lateral and posteromedian areas granular; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples absent, even surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM (fig. 142A), shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES (fig. 142A), length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; three marginal lamellae; fulcrae present; 6–7 pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae absent or obsolete; ventrolateral and paired ventrosubmedian carinae present and distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, 1–2 pairs of well developed posterior spiniform granules; ventrosubmedian carinae, sub-posterior spiniform granules weak to absent, medial granules weak to absent. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules well developed; ventrosubmedian carinae, 2–3 pairs of well developed posterior spiniform granules, sub-posterior spiniform granules absent, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventrosubmedian carinae with no visible ridge, when visible ridges smooth or nearly so (sometimes with a few reduced spiniform granules), subposterior spiniform granules absent; ventrolateral carinae with no visible ridges, when visible ridges smooth or nearly so. Segment IV, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae with no ridges visible, when visible ridges smooth or nearly so (sometimes with few reduced spiniform granules on posterior half); ventrolateral carinae with no ridges visible, when visible ridges smooth or nearly so. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny

Fig. 142. *Liocheles nigripes* (Pocock, 1897), pectines and genital opercula, ventral aspect. A, male. B, female. Scale line, 1 mm.


A

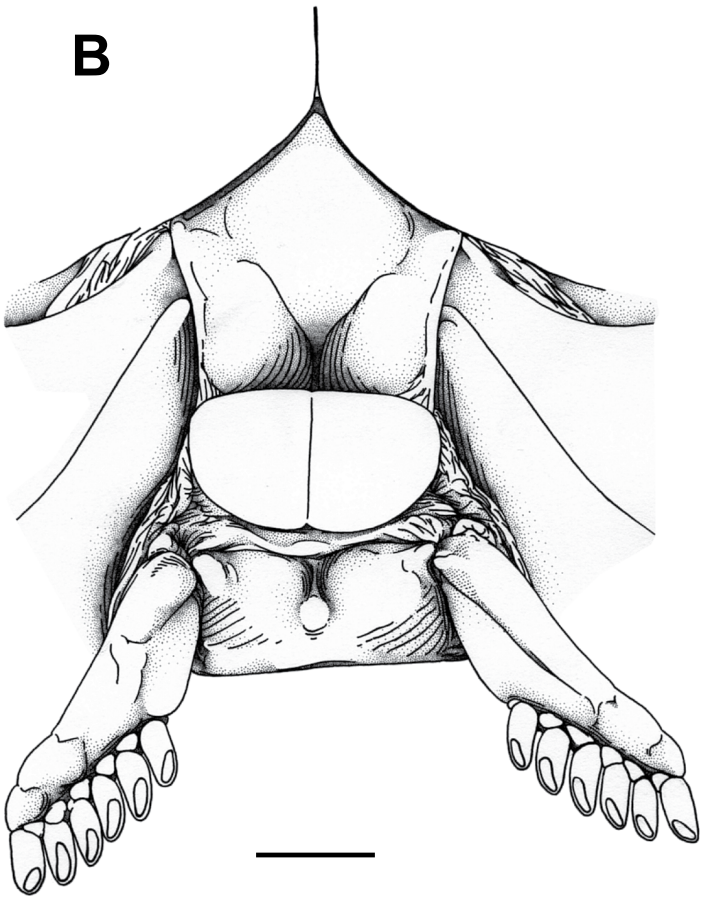
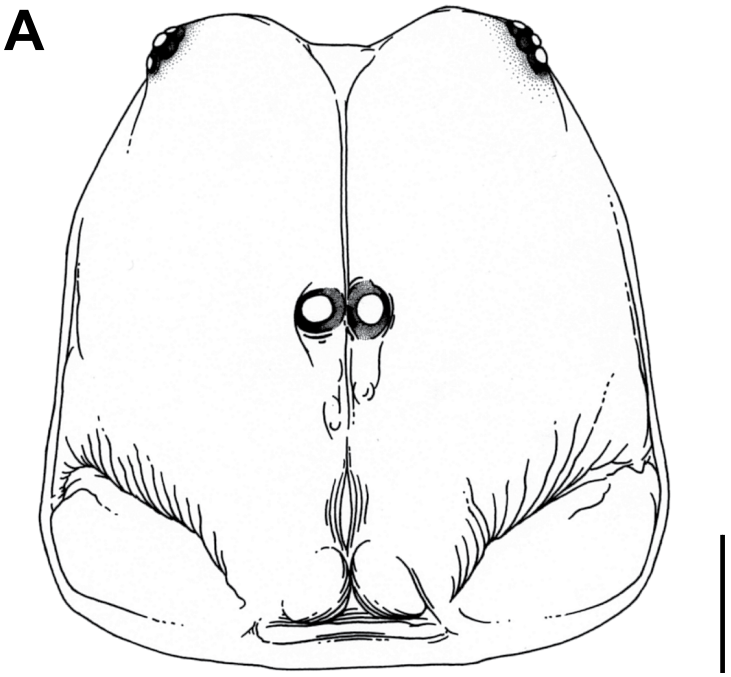
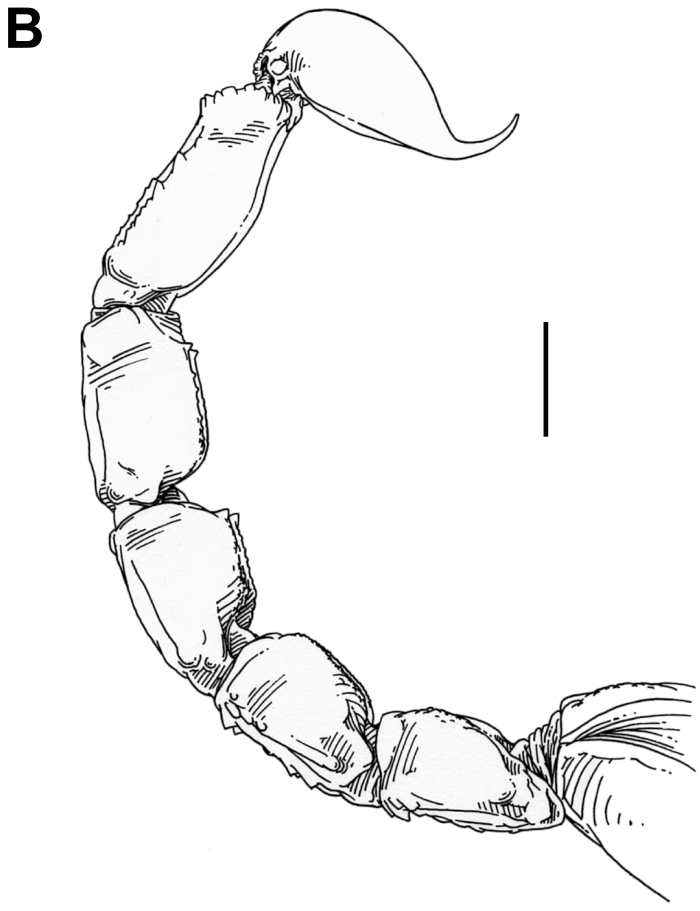

B

Fig. 143. *Liocheles nigripes* (Pocock, 1897). A, carapace, dorsal aspect. B, metasoma, lateral aspect, male. Scale lines, 1.5 mm.


A


B

depression on posterior half between ventrolateral carinae present; ventromedian carina absent or obsolete, partial, expressed only in posterior half, with distinct spiniform granules, at least distally; ventrolateral carinae present and distinct, diverging on distal part, anterior half with at least few small spiniform granules, posterior half with strong conical tooth; anal arch with few large conical teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues approximately the same size as telotarsus or longer. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/4; 4/4.

HEMISPERMATOPHORE (fig. 144). Distal lamina straight or nearly so, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with apex of lamellar hook or slightly above, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 90º angle with lamella.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface entirely smooth or nearly so; posteromedian surface smooth or nearly so; anterolateral surfaces smooth or nearly so; mediolateral surface smooth or nearly so; posterolateral surfaces smooth or nearly so.

MESOSOMA. Tergites I–III, post-tergites, mesial and lateral areas smooth; IV–VI, post-tergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples absent or vestigial, even surface.

VENTRAL MORPHOLOGY (fig. 142B). GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; 5–6 pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 144. *Liocheles nigripes* (Pocock, 1897), male. Hemispermatophore. Scale line, 2 mm.

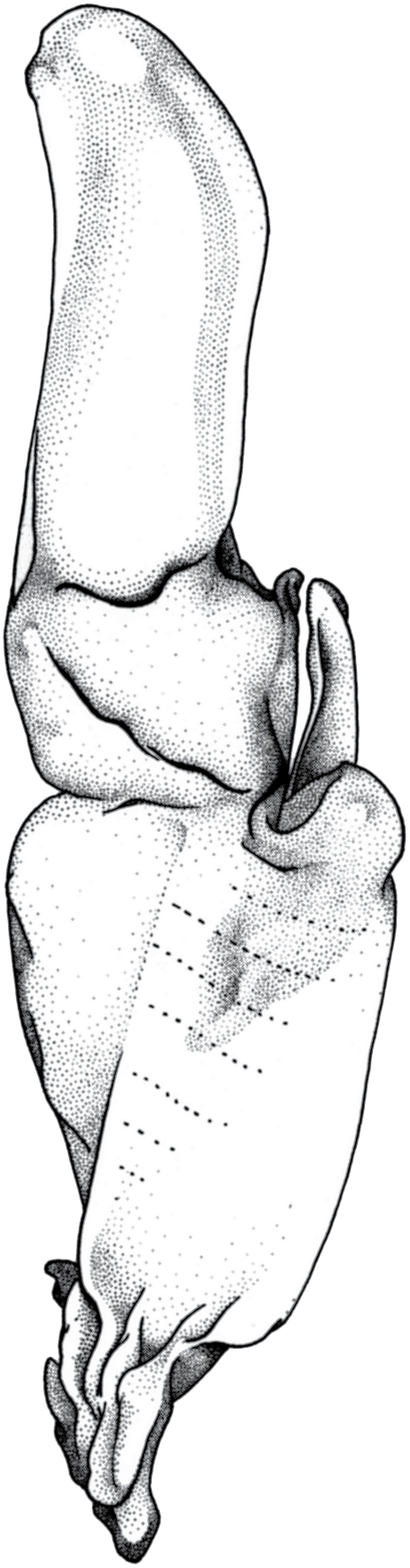
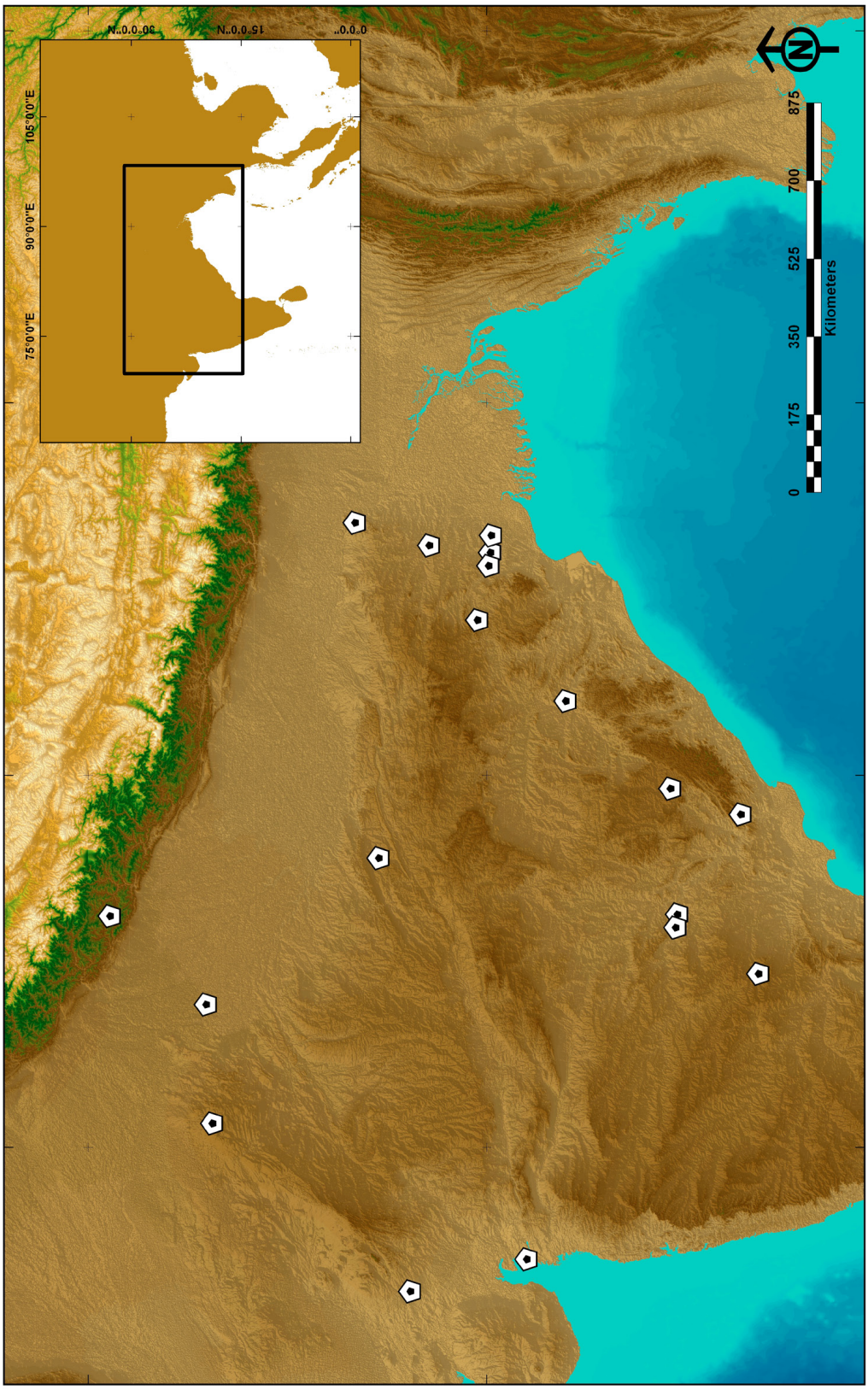


Fig. 145. Distribution map of *Liocheles nigripes* (Pocock, 1897).


N
0
175
350
525
700
875
Kilometers
75°0'0"E
90°0'0"E
105°0'0"E
0°0'0"
15°0'0"N
30°0'0"N

Liocheles suspectus (Thorell, 1888), **new combination**

Hormurus australasiae var. γ suspectus Thorell, 1888: 420–422.

References

Hormurus australasiae suspectus: Thorell, 1889: 590; Pocock, 1900: 80; Kraepelin, 1913: 163.
Hormurus australasiae suspecta: Kraepelin, 1899: 154.
Hormurus australasiae: Kraepelin, 1913: 163–165, fig. 7b (MIS); Tikader & Bastawade, 1983: 501–505, fig. 1362–1375 (MIS).
Liocheles australasiae: L. E. Koch, 1977: 161.
Liocheles australasiae (nec Fabricius, 1775; MIS): Kovařík, 2002: 15 (part); Kamenz & Prendini, 2008: 11, 43, pl. 131.

Type material (not examined)

Holotype: MYANMAR, 1 ♂ (MCSNG).

Material examined

MYANMAR, BAGO DIVISION, Pegu Hills/Mountains (= Bago Yoma), 2 ♂♂ (NHML 1897.5.10.193). RAKHINE STATE, Gwa Township, Kan Thar Yar Resort, along creek near Kan Thar Yar, beach area, NW of Gwa, 17º43.5Nx094º32.5'E, 28.XI–6.XII.2000, K. J. Ribardo, 1 ♂, 1 ♀, 1 imm. (LP 2796-CAS).

Distribution (fig. 146)

Myanmar.

DESCRIPTION. ADULT MALE

COLORATION. Tergites, uniform. Chelicerae, dorsal surface pale or nearly so, fingers may be very slightly infuscated (manus similar to or paler than carapace). Legs, pale (as pale as as or paler than tergites). Telson, pale (as pale as or paler than metasoma).

CUTICLE. ORNAMENTATION. Non-granular surfaces of mesosoma, metasoma, prosoma, legs and pedipalp finely punctated.

PEDIPALP. Femur equal to or shorter than carapace. Chela virtually asetose. CHELA FINGERS MORPHOSCULPTURE. Dentition, inner accessory denticles (IAD) present; denticulate edge even distally, without enlarged granules; double row of primary denticles often fused at the base. Chela movable finger, supra-basal lobe well-developed (if dentate margin markedly scalloped, first lobe disproportionately developed), gently rounded dorsally and lacking a sharp conical tooth; wider than high (low), not overlapping with fixed finger; supra-basal notch distinct and deep; supra-basal lobe and corresponding notch with a distinct posterior gap; basal lobe and corresponding notch in fixed finger absent or at most 2–3 small spiniform granules. Chela fixed finger, supra-basal lobe present and distinct, conical/well developed; basal lobe absent. TRICHOBOTHRIOTAXY. Chela manus, no accessory trichobothria; *Dt* trichobothrium on proximal 1/3; four *V* trichobothria; V_3 and V_4 close together, proximal part of manus; *Esb* trichobothrium basal, in same axis as *Eb* group; Eb_3 trichobothrium close to Eb_{1-2}; *Est* trichobothrium midpalm or nearly so. Chela fixed finger, *db* trichobothrium on dorsal surface; *esb* closer to *eb* and *est* closer to *et* (distance *est–esb* greater than distance *esb–eb*) or *est* closer to *et*; *eb* trichobothrium at base of finger, behind point of articulation between fixed and movable fingers, above *esb–et* axis; *esb* trichobothrium below *est–et* axis, at base of finger, behind point of articulation between fixed and movable fingers; two *i* trichobothria. Patella, d_2 trichobothria distal to patellal spur; *et* series with three trichobothria; *est* series with one trichobothrium; *em* series with two trichobothria; *esb* series with two trichobothria; *em–esb* series with four trichobothria in 2 groups [esb_{1-2}][em_{1-2}]; *eb* series with five trichobothria in two groups [eb_1] and [eb_{2-5}] or [eb_1/eb_{4-5}] and [eb_{2-3}]; three *v* trichobothria. CARINAE. Chela manus, dorsal prosubmedian (*dps*) carinae absent or obsolete; dorsal median *(dm*) carina obsolete; dorsal retrolateral (*drl*) carina distinct, costate or granular; dorsal retrolateral (*drl*) carina stronger than [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carina; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae absent or obsolete; ventral retrolateral (*vrl*) carina costate; ventral median (*vm*) carina absent or obsolete; ventral prolateral (*vpl*) carina absent or obsolete, equally or less strongly developed than prolateral ventrosubmedian (*plvs*)

carina; prolateral ventrosubmedian (*plvs*) carina present, granular (at least sparsely or faintly). Patella, prolateral process present (distinct), strongly developed, forming 2 distinct spiniform processes (bifid), sometimes fused but not forming a large median spine; prodorsal (*pd*) carina distinct; dorsal prosubmedian (*dps*) carina distinct; dorsal retrol*at*eral (*drl*) carina absent or obsolete; [retrolateral median (*rlm*) + retrolateral ventrosubmedian (*rlvs*)] carinae granular or costate; ventral retrolateral (*vrl*) carina present and distinct (sometimes not expressed on proximal and distal extremities), costate or granular. Femur, dorsal retrol*at*eral (*drl*) carina present and distinct, at least as a ridge usually more distinct in proximal half, equally developed than dorsal prosubmedian (*dps*) carina; dorsal prosubmedian (*dps*) carina present and distinct; [prolateral subdorsal (*pls*) + prolateral median (*plm*)] carinae present and distinct, or at least marked by several larger granules; prolateral subdorsal (*pls*) carina absent without spines or granules (or with a single basal spine); prolateral median (*plm*) carina vestigial with two large spines (one proximal and one midway); prolateral subdorsal (*pls*) and prolateral median (*plm*) median carina oriented parallel to prodorsal (*pd*) and prolateral ventrosubmedian (*plvs*) ca*rin*ae; ventral retrosubmedian (*vrs*) carina absent or obsolete; ventral prolateral (*vpl*) carina present. MACROSCULPTURE. Chela fingers granular (at least sparsely on proximal half). Chela fixed finger, dorsal surface*,* area around *db*/*dsb*/*dst* trichobothria smooth (trichobothria not in distinct depressions). Chela, dorsal intercarinal surface entirely and densely granular, distinct medium-sized spiniform granules; retrolateral intercarinal surface granular; ventral intercarinal surface, granulation present along prolateral and retrolateral edges only, smooth medially; prolateral ventral intercarinal surface granular at least along prolateral edge. Patella, dorsal intercarinal surface entirely granular, at least a reticulated network of granules; ventral intercarinal surface smooth or nearly so; retrolateral dorsal intercarinal surface smooth or nearly so; retrolateral ventral intercarinal surface at least sparsely granular; prolateral intercarinal surface, proximal half at least sparsely granular, distal half usually less granular. Femur, dorsal intercarinal surface densely granular except distal end; dorsal and prolateral intercarinal surfaces with small to medium-sized spiniform granules; dorsal retrolateral intercarinal surface at least sparsely granular; retrolateral ventral intercarinal surface at least sparsely granular; ventral intercarinal surface granular proximally, distal part without granulation (sometimes reduced to the extremity); prolateral intercarinal surface at least sparsely granular.

CARAPACE. Anterior margin, median notch almost absent. Anterior furcated suture/sulci vestigial or absent. Median ocular tubercle anteromedial, small, ca. 1/9 of carapace width, raised at least slightly; superciliary carinae present, without granules. Median ocelli present, separated by at least half diameter of median ocellus, at least twice the size of lateral ocelli. Lateral ocelli present and distinct; three pairs, first ocellus equal in size to second or second and third ocelli, third ocellus equal to or larger than first and second ocelli; ocelli equidistant, close together, almost touching each other. Margin behind lateral ocellus not markedly different, without any spines. MACROSCULPTURE. Carapace surfaces with minute spiniform granules, evenly and sparsely distributed; anteromedian surface entirely smooth or nearly so; median surface at least sparsely granular; posteromedian surface at least sparsely granular; anterolateral surfaces smooth or nearly so; posterolateral surfaces at least sparsely granular.

MESOSOMA. Tergites I–VII, posterior margins straight or nearly so, without distinct prominence; pretergites, posterior margin smooth. Tergites I–VI, post-tergites, median area smooth, lateral areas at least sparsely granular posteriorly; VII, posttergite entirely granular, at least sparsely; I–VII, post-tergites with minute spiniform granules, uniformly and sparsely distributed; III–VII, post-tergites, reticulated network of ridges and dimples absent, even surface; I–VI, lateral transversal sulcus present.

VENTRAL MORPHOLOGY. COXAE III, antero-distal tip without swelling or bulge. STERNUM, shape, anterior width slightly greater than posterior width (pw/aw<1) [=equilateral pentagonal]; length less than or equal to posterior width. PECTINES, length (expressed relative to length of coxa of leg IV) long, distal edge reaching beyond distal edge of coxa; three marginal lamellae; fulcrae present; seven pectinal teeth, long, straight, sensory papillae entirely covering. STIGMA (spiracle), half-moon shaped (with a distinct curve); short (less than 1/3 of sternite width). STERNITE VII, longitudinal carinae absent or vestigial.

METASOMA. Segments I–V, length similar to or slightly longer than ♀; not modified (as thick as large or slightly thicker, more rounded). Segments I–IV, median furrow shallow, weak to absent or only visible on segments I–III; dorsosubmedian carinae absent or obsolete; dorsolateral carinae absent or obsolete; ventrolateral and paired ventrosubmedian carinae present and

distinct on at least some segments. Segment I, width less than or equal to height; median lateral carina present and distinct; dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventral surface, 1–2 pairs of well developed posterior spiniform granules; ventrosubmedian carinae, 1–2 pairs of moderate to strong sub-posterior spiniform granules, 1–3 pairs of well developed medial granules. Segment II, dorsosubmedian carinae, posterior spiniform granules weak to absent (not noticeably larger than preceding granules); dorsomedian posterior spiniform granules weak to absent; ventrolateral carinae, posterior spiniform granules well developed; ventrosubmedian carinae, 2–3 pairs of well developed posterior spiniform granules, one pair of well developed sub-posterior spiniform granules, 1–3 pairs of well developed medial spiniform granules. Segment III, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventrosubmedian carinae, ridges with at least a few small/medium spiniform granules, subposterior spiniform granules absent; ventrolateral carinae with at least few minute/small spiniform granules. Segment IV, dorsosubmedian carinae, posterior spiniform granules moderate to strong (distinctly larger than preceding granules); ventromedian carinae, subposterior spiniform granules absent; ventrosubmedian carinae, ridges with at least few reduced spiniform granules distally; ventrolateral carinae with minute/small spiniform granules. Segment V, dorsal surface smooth; dorsolateral carinae absent or obsolete; smooth shiny depression on posterior half between ventrolateral carinae present; ventromedian carina absent or obsolete, partial, expressed only in posterior half, with distinct spiniform granules, at least distally; ventrolateral carinae present and distinct, diverging on distal part, anterior half with at least few small spiniform granules, posterior half with strong conical tooth; anal arch with few large conical teeth. Telson, total length equal to or slightly longer than metasomal segment V; vesicle smooth, without granules, unmodified.

LEGS. Femora, ventromedian surfaces bicarinate, distinct ventromedian surfaces as well as anterior and posterior surfaces marked by macrosetae and, usually, granules, although anterior carinae often weakly developed. Femora IV, ventromedian carinae absent or vestigial (only expressed distally) or no distinct carinae (only scattered granules). Tibia I and II, retrolateral margins without spiniform macrosetae. Basitarsi I, prolateral margin with few spiniform macrosetae [1–4]; retrolateral margin with few spiniform macrosetae [1–5]. Telotarsi, two ventrosubmedian rows of macrosetae, secondarily setiform (not including distal pair); one pair of distal setiform macrosetae in ventrosubmedian rows; ventromedian row of spinules absent or vestigial; basal spinules present (at least one, usually a short row); terminal ventromedian spinules absent; ungues approximately the same size as telotarsus or longer. Telotarsi I–IV, prolateral and retrolateral rows of spiniform macrosetae: 4/4; 4/4; 4/4; 4/4.

HEMISPERMATOPHORE. Distal lamina straight or nearly so, approximately same size as basal part or slightly longer; distal crest absent; single lamellar hook, basal (in basal 1/3 of distal lamella or below, at least less than mid-length); basal extrusion absent; transverse ridge present and distinct, merging with anterior edge above base of lamellar hook, at approximately same level as base of lamellar hook. Lamella thin, folded only proximally and unfolded to flattened distal extremity (tip and base approximately same width); longitudinal 'spine' (*ls*) on external surface absent to weak; accessory hook (*lah*) on distal part of external surface, oriented toward basal part absent; accessory lobe (*Lac*) on basal part of posterior surface absent; lamellar tip at approximately same level with apex of lamellar hook or slightly above, above tip of distal lobe. Distal lobe well developed, as a distinct hump, without distinctive hook-like shape; accessory hook on anterior surface absent; accessory carinae and accessory crest absent. Basal lobe well developed ('spoon' shaped), merging with accessory anterior basal lobe; anterior edge without accessory fold toward posterior part, forming 90º angle with lamella; posterior edge without accessory fold (no groove), forming 90º angle with lamella.

BOOK LUNGS. Lamellar surface with simple trabeculae, with arcuate bow-like structures. Posterior spiracle edge with hillocklike structures.

ADULT FEMALE. Same characters as in ♂ except as follows.

PEDIPALP. Chela movable finger, supra-basal lobe absent or at most weakly developed, close to base of movable finger; basal lobe and corresponding notch in fixed finger absent. Chela fixed finger, supra-basal notch absent; supra-basal lobe absent.

CARAPACE. Anteromedian surface entirely smooth or nearly so; posteromedian surface

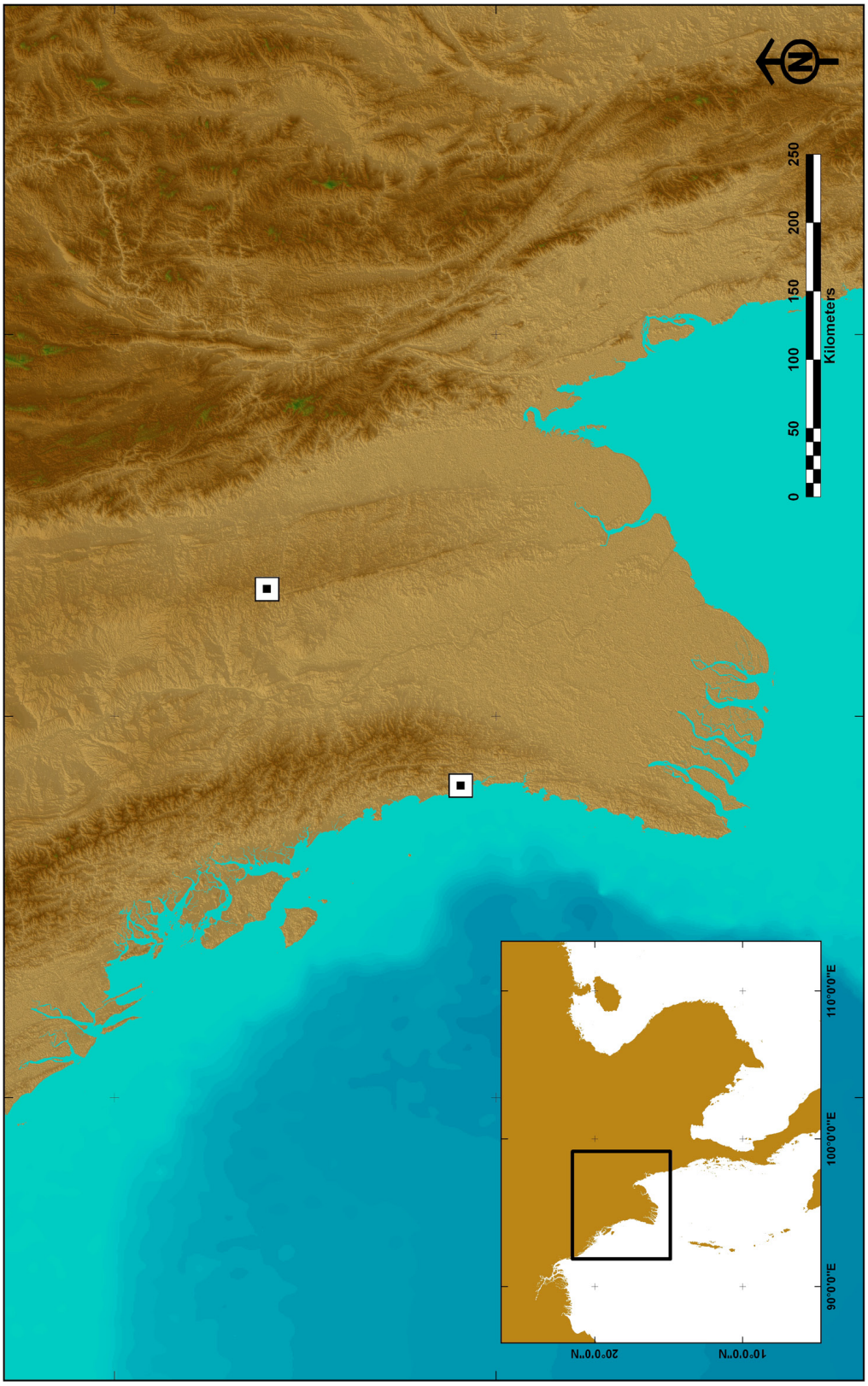
smooth or nearly so; anterolateral surfaces smooth or nearly so; mediolateral surface smooth or nearly so; posterolateral surfaces smooth or nearly so.

MESOSOMA. Tergites I–III, post-tergites, mesial and lateral areas smooth; IV–VI, post-tergites, mesial and lateral surfaces smooth (or nearly so); VII, posttergite entirely smooth or nearly so; III–VII, reticulated network of ridges and dimples absent or vestigial, even surface.

VENTRAL MORPHOLOGY. GENITAL OPERCULUM oval to semi-oval, as wide as long (or wider than long), approximately same width as sternum, maybe slightly narrower; sclerites partly fused, clear median suture; posterior notch present, at least weakly developed. PECTINES, length (expressed relative to length of coxa of leg IV) moderate, distal edge reaching to, but not beyond distal edge of coxa; six pectinal teeth.

METASOMA. Segment I, median lateral carina present and distinct. Telson, vesicle unmodified.

Fig. 146. Distribution map of *Liocheles suspectus* (Thorell, 1888).


N
0
50
100
150
200
250
Kilometers
110°0'0"E
100°0'0"E
90°0'0"E
20°0'0"N
10°0'0"N

NOMINA DUBIA

Hormurus cumingii (Gervais, 1844), **new combination**

Scorpio (*Ischnurus*) *cumingii* Gervais, 1844a: 236, 237.

SYNTYPES: sex unknown, MNHN, Philippines. Probably lost.

NOTES

In his description, Gervais (1844) mentioned the absence of spines on dorsal carinae and on the ventral and ventrolateral carinae of the metasoma in this species: 'point de crénelures distinctes à la face supérieure de la queue qui présentre une rainure médiane' (p. 69) and 'point de crénelures inférieures' (p. 70). Therefore, *Ischnurus cumingii* is not a synonym of *L. australasiae* which possess strong terminal spines on dorsal carinae of metasomal Segments II and III and a series of strong spines on ventral and ventrolateral carinae of metasomal Segments I, II and V. On the other hand, the species is potentially conspecific with *Hormurus boholiensis* and *Hormurus dechangei* which also occur in the Philippines and have no spines on the metasoma or at most very reduced spiniform granules. Both *H. boholiensis* and *H. dechangei* were described earlier than *I. cumingii* and may thus be junior synonyms of the latter. Unfortunately, the holotype of *I. cumingii* could not be found in the collection of the Museum National d'Histoire Naturelle (Paris) and is considered lost. Therefore, *I.cumingii* is placed in the genus *Hormurus* and regarded here as a *nomen dubium*. *H. boholiensis* and *H. dechangei* are maintained as valid species.

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