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A

A SYSTEMATIC REVISION OF THE ELECTRIC RAY GENUS NARCINE HENLE, 1834 (CHONDRICHTHYES: TORPEDINIFORMES: NARCINIDAE), AND THE HIGHER-LEVEL PHYLOGENETIC RELATIONSHIPS OF THE ORDERS OF ELASMOBRANCH FISHES (CHONDRICHTHYES)

(Parts I and II)

by

Marcelo R. de Carvalho

VOLUME I (TEXT)

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

1999

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This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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ABSTRACT

A SYSTEMATIC REVISION OF THE ELECTRIC RAY GENUS NARCINE HENLE, 1834 (CHONDRICHTHYES: TORPEDINIFORMES: NARCINIDAE), AND THE HIGHER-LEVEL PHYLOGENETIC RELATIONSHIPS OF THE ORDERS OF ELASMOBRANCH FISHES (CHONDRICHTHYES)

(Parts I and II)

by

Marcelo R. de Carvalho

Advisor: Dr. John G. Maisey

In Part I of this study, the Recent electric ray genus Narcine Henle, 1834 is taxonomically reviewed and found to contain 20 species, of which 11 have been previously described and nine are described as new. Twenty six nominal species can be applied to Recent Narcine, of which 15 are here placed in synonymy, some for the first time. Narcine brasiliensis (von Olfers, 1831), the type-species, is restricted to the southeastern coast of Brazil from Espírito Santo south to Argentina, and Torpedo bancroftii Griffith, 1834 is resurrected from synonymy for specimens of Narcine ranging from North Carolina to northeastern Brazil

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including the Gulf of Mexico, Caribbean Sea and islands of the West Indies. Narcine brachypleura Miranda Ribeiro, 1923 is a junior synonym of Torpedo brasiliensis von Olfers, 1831. Torpedo ocellata Quoy and Gaimard, 1824 is a primary homonym of Torpedo ocellata Rafinesque, 1810, and is therefore not available, but is identified with N. brasiliensis. Torpedo pictus Gray, 1854, Narcine corallina Garman, 1881, Narcine punctata Garman, 1881 and Narcine umbrosa Jordan, 1884 are all placed in the synonymy of N. bancroftii (Griffith, 1834). Narcine entemedor Jordan and Starks, 1895 and Narcine vermiculatus Breder, 1928 are valid species from the eastern Pacific, but Narcine schmitti Hildebrand, 1948 is synonymized with N. vermiculatus for the first time. Narcine indica Henle, 1834, Narcine macrura Valenciennes, 1852, Narcine microphthalma Valenciennes, 1852 and Narcine brunnea Annandale, 1909 are all junior synonyms of Raja timlei Bloch and Schneider, 1801. Raja bicolor Shaw, 1804, Narcine maculata Duméril, 1852, Narcine firma Garman, 1913 and Narcine prodorsalis Bessednov, 1966 are considered junior synonyms of Raja maculata Shaw, 1804 (N. maculata Duméril, 1852 is also a secondary homonym), but N. prodorsalis may prove to be valid once more material is examined. Narcine brevilabiata Bessednov, 1966 is a valid species ranging from the Gulf of Thailand to southwestern China. Both previously described species from Australia (Narcine tasmaniensis Richardson, 1841 and Narcine westraliensis McKay, 1966) are valid. Heteronarce rierai Lloris and Rucabado, 1991, the only previously described species from the western Indian Ocean, is valid, and its allocation to Narcine is confirmed. Lectotypes are designated for T. ocellata, T. brasiliensis, N. corallina, N. umbrosa, R. timlei and N. brunnea. A neotype is chosen for N. brevilabiata. Extant type-specimens of all species were examined and are figured. In addition, nine new species are described, from the eastern Pacific

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Ocean, western Indian Ocean, gulfs of Oman and Aden, Bay of Bengal, Andaman Sea, and from off the Philippines, Indonesia and Australia. The western Indo-Pacifc region presents the highest diversity of species of Narcine. Characters used in the revision include proportional measurements, meristics, coloration and external and internal morphology. The separation of N. maculata and N. lingula, and the limits of certain other species of Narcine (including N. bancroftii) requires further research. Fossil electric rays known from more than isolated teeth are also reviewed. "Narcine" molini Jaekel, 1894 from the Eocene Monte Bolca formation (northeastern Italy) is redescribed on the basis of type- and new material, and cannot presently be allocated to Narcine. Other fossil narcinid electric rays from Monte Bolca, representing new taxa, are also described on the basis of previously unreported material. All nine other genera of Recent electric rays are demonstrably monophyletic, but the monophyly of Narcine is still currently being investigated. The genus is putatively monophyletic on the basis of presenting the following derived features: i) fused hypobranchial plates with sinuous external margins, articulating with ceratobranchials 2 – 4; ii) presence of facio-palatine foramen; iii) conspicuous shape of basibranchial copula that bears a well-developed and slender posterior process; iv) lack of contact between ceratohyal and "hypobranchial 1." Further characters supporting a monophyletic Discopyge and Diplobatis are discussed. Narcinidae is corroborated as monophyletic and includes Narcine, Discopyge, Benthobatis and Diplobatis.

In Part II, Recent higher-level elasmobranch taxa are subjected to a cladistic analysis to clarify the interrelationships of Compagno's (1973, 1977) superorders, to test the monophyly of the Squalea and the reported non-monophyly of Hexanchiformes, and to review the long suspected recognition that Squaliformes is also paraphyletic. A matrix containing 20 terminal

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taxa and 67 morphological characters was analyzed using computer-based parsimony procedures. This matrix includes characters also analyzed by recent authors including Shirai (1996), additional characters putatively incongruent with some of his components, and a differential coding for many features. The resulting single most parsimonious tree (L = 132 steps, Ci = 0.67, Ri = 0.80) further supports a monophyletic Squalea, but two of Shirai's higher-level nodes are falsified. Hexanchiformes is unambiguously defended as a monophyletic unit by seven morphological features (including the single dorsal fin, extra gill arch and extra column of heart valves in the conus arteriosus; the latter feature, however, needs more critical examination). The Squaliformes is also monophyletic but only if Echinorhinus is excluded. Echinorhinus is placed in its own order, which is in accordance with evidence presented by previous workers, and is the sister-group to a node composed of Squaliformes + Hypnosqualea. Resolution within galeomorphs indicates that Heterodontus is the sister-group to an Orectolobiformes + (Lamniformes + Carcharhiniformes) clade. The previously proposed sister-group relationship between Heterodontus and Orectolobiformes is therefore falsified, but due to the high amount of discordance, this node may eventually be supported if further characters, putatively homologous to Heterodontus and orectolobiforms, are included (e.g., the space between meso- and metapterygium, not considered here due to lack of evidence). Certain fossil taxa, especially the Jurassic Palaeospinax, play an important role in the optimization of some characters at the base of the phylogeny for living taxa. The high degree of misfit or homoplasy, the misleading effects of autapomorphy and the tardy application of more rigorous phylogenetic procedures have inhibited further progress in elasmobranch systematics when compared to Osteichthyes (bony fishes). Recent elasmobranchs are divided

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into two higher divisions, the Galeomorphii and Squalea, with 10 included monophyletic orders. The interrelationships of Compagno's four superorders, a problem that has persisted with little notice since 1973, is resolved and is in general agreement with Shirai's work concerning these higher-levels. The resulting classification, however, is intermediate between the schemes of Compagno and Shirai.

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For my parents, Sergio and Daisy, my grandparents, Eduardo and Aura, and my siblings, Adriana, Heloisa and Flavio – my role-models, personal cheerleaders, and heroes

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PART I

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INTRODUCTION

Systematic studies concerning elasmobranch fishes (sharks, skates and rays) are uncommon, or even rare, compared to research on their potential biomedical benefits. However, without the proper understanding of species limits, identification, distribution and interrelationships, the proper fruition of this biomedical (or any other) potential cannot be achieved. The same is true for any taxon, but elasmobranchs are perhaps especially notorious. Elasmobranchs are a large and diverse group of fishes with approximately 1050 Recent species by some estimates, yet they are primarily known as a result of the media-exploitation of a very small minority of species implicated in the anthropocentric phenomenon of "shark attack." Although elasmobranchs have been the subject of much anatomical research, dating at least from Aristotle (ca. 350 B.C.), it is only relatively recently that taxonomic revisions have led to a greater understanding of their true diversity. As a result, certain groups of elasmobranchs are now known to be much more speciose than previously understood (e.g., the Scyliorhinidae and Squalidae; Compagno, 1988, Last and Stevens, 1994). Regarding the Batoidea (comprising all the rays and their immediate relatives), this is particularly true for skates (e.g., McEachran and Miyake, 1990a, 1990b; McEachran and Dunn, 1998; Last and Stevens, 1994). Electric rays, however, with few exceptions, have not been the subject of taxonomic scrutiny.

Electric rays (Torpediniformes) are a relatively diverse and monophyletic group of small, medium or large-sized batoids that inhabit most tropical and temperate seas of the world, in depths ranging from one to more than 1000 meters. Currently 10 genera and some 50 species of electric rays are recognized from a large number of nominal species (many of which

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were described prior to 1850, see Tables 2 – 5), but the number of valid species will increase as revisionary studies are conducted and new species are discovered. Electric rays are divided into two principal groups, each with approximately one-half of the total number of electric ray species: the Torpedinoidea ("torpedo" and "coffin" rays) and the Narcinoidea ("lesser" electric rays or "numbfishes"). Members of the Torpedinoidea (Torpedo and Hypnos) are generally larger and more mobile, frequently swimming above the ocean floor in search for prey, and may inhabit distant oceanic islands (some species of Torpedo). The Narcinoidea features species that are generally smaller and more stationary, inhabiting primarily continental shelf and slope regions. Species of Torpedinoidea are common in temperate and sub-temperate waters (while species of Narcinoidea generally frequent warmer seas) and have a greater electrogenic capacity. This increased electrogenic potential, coupled with a more mobile mandibular architecture devoid of labial cartilages, permit species of Torpedo and Hypnos to use their electric organs to actively hunt for prey (e.g., Lowe et al., 1994). Electric rays are not of direct economic importance as they are not generally consumed as food.

Narcine Henle, 1834 is the most diverse genus of the "lesser" electric rays (Narcinoidea), with some 12 to 16 species currently recognized by most recent authors (e.g., Last and Stevens, 1994; Compagno, 1995). Narcine occurs in most tropical to sub-temperate oceans and seas, and around continental islands, generally in shallow in-shore to off-shore waters. Species of Narcine are conspicuously absent from the Atlantic coast of Africa, eastern Pacific coast of South America (south of northern Peru), the Mediterranean and Red seas, and off New Zealand. The taxonomic revision of Narcine below, comprising Part I of this thesis, was initiated in conjunction with large-scale revisionary work on all genera of electric rays.

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The objectives of this revision are to identify, describe, delimit, and provide full synonymies for all valid species of Narcine, and to review previous literature on the genus. This study is based on the examination of as many specimens of Narcine as possible, Recent and fossil, including almost all extant type-material.

The resulting identification of 20 valid species of Recent Narcine, of which 11 are previously described (from 26 nominal species that can be applied to Narcine) and nine are new, is a departure from recent consensus. Many taxonomic problems in Narcine are solved (e.g., the identification of problematic nominal species and their correct synonymization), but additional difficulties, or areas of future research, are diagnosed. Further work in delimiting certain species-limits is still necessary, and examination and collection of fresh specimens from many areas is imperative. The objectives of this revision are to document the morphological variation within Narcine, and to make taxonomic decisions on the basis of that variation.

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ID METHODS

Morphometrics

Specimens for taxonomic analyses were studied in museum and institutional collections, and were obtained on loan whenever possible and necessary. An attempt was made to study collections of as many insitutions as possible. However, the number of collections holding specimens of electric rays is high, which is expected with a group that is so widely distributed. Consequently, and regrettably, many collections (e.g., those bordering the Pacific coast of Central and South America, Argentina, eastern coast of Africa, India, Thailand and China) could not be studied (but hopefully will be in the fututre). Specimens from the full range of the recognized species were examined whenever available, to account for as much variation as possible for a given species.

Measurements were taken on preserved specimens to establish morphometric characters useful in discerning species limits. Each measurement is defined below and illustrated in Fig. 1. Measurements were modified primarily from Bigelow and Schroeder (1953), Rosa (1985), Miyake (1988) and Fechhelm and McEachran (1984), and are defined specifically for electric rays. Measurements were taken with electronic calipers in a straight line, point-to-point to the nearest tenth of a millimeter. When specimens were large or required measurements of approximately 150 mm or more, the aid of a steel ruler or tape measure was employed, and these measurements are expressed to the nearest millimeter. Measurements were chosen so as to convey a general notion of the size and shape of each specimen.

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Measurements are depicted in separate tables for each species in the taxonomic accounts, and were prepared using Systat (versions 5.01 and 6.1). In the tables, total length (TL) is given to the nearest millimeter, and all other measurements are expressed as percentages (%) of total length. Data is given for type and non-type specimens separately (for undescribed species [Narcine sp. nov. A, Narcine sp. nov. B, etc.] types are not specified). Ranges refer to minimum and maximum dimensions (in percentages). All percentages are rounded to the nearest decimal point. The calculation of means and standard deviations (SD) were generally based on all specimens examined, type and non-type, the number (N) of which is given in a separate column. Data were entered in Systat directly from specimen data sheets, measurement by measurement, prior to being transformed in percentages of total length (done automatically in Systat). The final tables were prepared in Word for Windows 98.

Electric rays can easily deform from their original shape after preservation (especially in the deep-sea genus Benthobatis; Carvalho, in press). Enhanced shrinkage of the disc and fins was observed in many specimens of various species, distorting proportional characters. For example, shrinkage of the disc and pelvic fins increases the space between them, a distance which has been used as a character to identify certain species of Narcine (e.g., Bianchi, 1985). Specimens that underwent noticeable post-mortem distortion typically have unusually shrunken and flattened eyes, shortened discs (disc width is more noticeably affected), pelvics heavily shrunken (leaving, in males, unusually protruded claspers), general all-around stiffness, and when left out of preservative for a short time, dorsal and caudal fins that quickly become brittle and dried. Specimens displaying these characteristics were excluded from the calculation of

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proportional measurements, once it was determined that they had indeed undergone deformation as a result of poor preservation.

Morphometric characters used to separate species are those deemed unequivocal, where proportional differences are obvious without the application of refined multi-variate techniques. This "descriptive" application of the measurements was sufficient for the taxonomic purposes of this paper. A similar situation is described by Fechhelm and McEachran (1984) in their revision of Diplobatis.

List of Measurements

1. Total length (TL): From tip of snout to posterior tip of caudal fin (independent variable for proportional measurements).
2. Disc width (DW): Measured at the widest lateral margins of disc.
3. Disc length (DL): Measured as the greatest distance from tip of snout to posterior margin of disc.
4. Preocular snout length (PCSL): Distance from anterior tip of eyeball to tip of snout.
5. Preoral snout length (POSL): Distance from mouth opening to tip of snout.
6. Prenasal snout length (PNSL): Distance from anterior tip of nostrils to tip of snout.
7. Snout to maximum disc width (SDW): Measured from tip of snout to maximum disc width, in a straight line over mid-disc.
8. Interorbital distance (IOD): Distance between inner margins of eyeballs.
9. Eye length (EL): Distance from anterior tip of eyeball to posterior tip of same.

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10. Interspiracular distance (ISD): Distance between inner margins of spiracles.
11. Spiracle length (SPL): Measured from anterior-most point of spiracle to posterior-most point of same.
12. Spiracle width (SPW): Measured as greatest distance between lateral margins of each spiracle.
13. Mouth width (MW): Measured as the greatest distance between outer-most jaw corners.
14. Upper tooth band width (UTBW): Width along widest lateral margins of upper tooth band, close to mouth opening.
15. Lower tooth band width (LTBW): Width along widest lateral margins of lower tooth band, close to mouth opening.
16. Nasal curtain width (NCW): Measured as the distance between outer margins of nasal curtain at posterior-most aspect, close to mouth opening.
17. Nasal curtain length (NCL): Measured from line between posterior margin of nostrils to center of nasal curtain at posterior-most point.
18. Distance between nostrils (DBN): Measured as distance between inner-most margins of nostrils.
19. Distance between first gill openings (DBFGO): Measured as distance between inner-most aspect of first gill openings.
20. Distance between last gill openings (DBLGO): Maximum distance between inner- most margins of last gill openings.
21. Branchial basket length (BBL): Measured from first gill opening to last gill opening.

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22. Pelvic fin length (PFL): Measured in a straight line along body axis from anterior tip of pelvic fin to posterior tip of same.
23. Pelvic fin width (PFW): Distance between outer-most tips of pelvic fins, both fins measured together .
24. Length of anterior lobe of pelvic fin (ALPF): Measured from widest lateral margin of pelvic fin to anterior-most point of same.
25. Length of posterior lobe of pelvic fin (PLPF): Measured from widest lateral margin of pelvic fin to posterior-most tip of same.
26. Tail width (TW): Distance between lateral margins of tail, measured at axil of pectoral fins.
27. Height of first dorsal fin (HFD): Measured from base of first dorsal to heighest tip of same.
28. Length of first dorsal fin (LFD): Measured along tail from origin to posterior-most point of contact with tail.
29. Height of second dorsal fin (HSD): Measured from base of second dorsal to heighest tip of same.
30. Length of second dorsal fin (LSD): Measured along tail from origin to posterior-most point of contact with tail.
31. Length of dorsal lobe of caudal fin (LDLC): Measured from origin of dorsal lobe to posterior-most tip of same.
32. Length of ventral lobe of caudal fin (LVLC): Measured from origin of ventral lobe to posterior-most tip of same.

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33. Height of dorsal lobe of caudal fin (HDLC): Measured vertically from upper-most tip of caudal to origin of base on tail.
34. Height of ventral lobe of caudal fin (HVLC): Measured vertically from lowest tip of caudal to origin of base on tail.
35. Height of caudal fin (HC): Measured from dorsal-most point of caudal fin to ventral tip of same (not equal to measurements 33 + 34).
36. Distance between first and second dorsal fins (DBD): Measured from posterior-most point of first dorsal fin on tail to origin of second dorsal fin, along tail.
37. Distance between second dorsal fin and caudal fin (DSDC): Measured from posterior-most point of second dorsal fin to origin of caudal, along tail.
38. Snout to cloaca length (SCL): Measured from tip of snout to anterior tip of cloaca.
39. Cloaca to caudal fin (CLCF): Measured from posterior-most tip of cloaca to tip of caudal fin (equals "tail length" in species accounts).
40. Snout to first dorsal length (SFD): Measured as the distance between tip of snout to origin of first dorsal fin.
41. Electric organ length (EOL): Measured from anterior margin of electric organ to posterior margin of same.
42. Electric organ width (EOW): Measured as the distance between lateral margins of electric organ, close to level of third gill slit or at mid-organ length.
43. Clasper length (CL): Measured from posterior tip of cloaca to posterior tip of clasper.

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Meristics

Meristic data (counts of fin-radials, vertebrae, etc.) are defined below. Most counts were taken from radiographs (X-rays), sometimes placed under a stereomicroscope, but for the most part analyzed on a light-table with the aid of a loupe. The majority of specimens were radiographed in the Department of Ichthyology, AMNH. Specimens were placed on Kodak Industrex M film (25.4 x 30.5 cm or 20.3 x 25.4 cm) and exposed to X-rays from a Hewlett Packard 43807N Faxitron series machine at 35 KVP, 3.0 milliampères, for a period of 60 to 120 seconds, depending on the size of the specimen (the larger the specimen, the greater the necessary exposure). Anatomical data were gleaned, when possible, from X-rays as well.

The division of vertebrae into trunk and pre-caudal vertebrae was based on the position of the pelvic girdle: trunk vertebrae are counted from the first distinguishible entire vertebral centrum in the synarcual cartilage to the pelvic girdle, and pre-caudal vertebrae are those from the anterior border of the pelvic girdle to the beginning of the caudal fin. The transition between pre-caudal and caudal zones is delimited by the presence of elongated neural spines as of the beginning of the caudal fin (neural spines are conspicuously elongated at the beginning of the caudal fin). Using monospondyly and diplospondyly to indicate vertebral centra transitions was not always possible from radiographs. Caudal radial elements present between the upper and lower lobes of the caudal fin, at the posterior caudal tip, were counted as part of the lower caudal radial elements (counts 9 and 10 below). Caudal radial elements were counted from the origin of the caudal fin as determined by fin insertion on tail, and not by beginning of elongated neural and hemal elements only, as the hemal elements are elongated usually as of the second

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dorsal fin, and an obvious transition is not necessarily present at the beginning of the caudal fin. Elongated neural elements begin at the origin of caudal fin, thus also serving as a landmark for counting caudal radials; hemal arches (ventral radials) of the caudal fin were counted as of the beginning of the neural (dorsal) spines. Pectoral radials fused at base articulating with posterior aspect of mesopterygium (present in some species) were counted as two distinct radial elements (count 2 below). Likewise, dorsal fin radials fused basally were counted separately (counts 6 and 7 below). The greatly enlarged first pelvic radial, which articulates with the basipterygium, was counted as one single radial element, as it is not clear if this element is formed from the fusion of separate radials and, if so, how many radials are involved in the fusion. Clasper elements were not included in pelvic radial counts. Tooth counts were taken from preserved specimens under stereomicroscope and follow the method outlined by Stehmann (1978), where individual rows (or "columns") are counted following a cranial-caudal orientation. Only exposed tooth rows were counted, i.e., rows visible when mouth is closed. Horizontal rows (i.e., rows arranged following a lateral orientation) were not counted, although comments on the size of the exposed tooth rows (which may be correlated with the number of horizontal rows) may be included for certain species. Only exposed rows were routinely counted as dissection is necessary to count internal rows, and this was possible for only a very limited number of specimens. Tooth counts are expressed as fractions, where the numerator designates the number of exposed rows on the upper jaws, and the denominator indicates the same on the lower jaws (e.g., 12/14, 13/15 – 15/17).

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List of Counts

1. Propterygial radials (PROP): Pectoral fin radials articulating with propterygium, ranging from anterior-most visible radial element in pectoral fin to last radial prior to articulation with mesopterygium.
2. Mesopterygial radials (MESO): Pectoral fin radials articulating with mesopterygium.
3. Metapterygial radials (META): Pectoral fin radials articulating with the metapterygium, beginning with first radial posterior to articulation with mesopterygium to last visible radial element in pectoral fin (in many cases the metapterygium was not properly exposed in radiographs, therefore all radials occurring posterior to the mesopterygium, and not articulating with it, were counted as metapterygial radials).
4. Total pectoral radials (TPR): Addition of counts 1, 2 and 3.
5. Pelvic radials (PVR): All radials articulating with the basipterygium of the pelvic fin. The first enlarged radial is counted as a single radial element).
6. First dorsal fin radials (FDR): All radial elements present in the first dorsal fin, including the posterior extension of the basal elements which functions as the posterior-most radial.
7. Second dorsal fin radials (SDR): All radials present in the second dorsal fin, including the posterior extension of the basal elements as with the first dorsal fin.
8. Dorsal caudal radials (DCR): Radials present in the dorsal lobe of the caudal fin, the beginning of which is demarked by the upper fleshy lobe of the fin, and not necessarily by the presence of enlarged neural spines.

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9. Ventral caudal radials (VCR): Radials present in the ventral lobe of the caudal fin, the beginning of which is demarked by the fleshy lobe of the lower caudal fin, and not necessarily by the beginning of hemal spines (these occur anteriorly in relation to the caudal fin as well); the radials occurring on the same level as the vertebral column are counted as ventral caudal radials.
10. Total caudal radials (TCR): Addition of counts 8 and 9.
11. Upper exposed tooth rows (UTR): Exposed vertical rows of teeth present in upper tooth band (upper jaw), including symphyseal row.
12. Lower exposed tooth rows (LTR): Exposed vertical rows of teeth present in exposed lower tooth band (lower jaw), including the symphyseal row.
13. Trunk vertebral centra (TC): First whole and distinguishable vertebral centrum in synarcual cartilage to anterior border of pelvic girdle.
14. Precaudal centra (PC): First distinguishable vertebral centrum at anterior border of pelvic girdle (and overlying the girdle) to first centrum at beginning of caudal fin.
15. Caudal centra (CC): Vertebral centra from anterior margin of caudal fin to last distinguishable whole centrum in caudal fin.
16. Total vertebral centra (TV): Addition of counts 13, 14 and 15.
17. Ribs (R): Refers to number of extended ribs articulating with paired hemal spines (located posteriorly on disc, slightly dorsal to pelvic girdle area).

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Species descriptions, terminology, illustrations and miscellaneous

Male specimens were determined to be sexually mature or adult when their claspers were rigid and not very flexible. Data concerning sexual maturity is more complicated for females, as no evident external characteristic exists to separate juveniles from adults, and dissection to reveal ripe eggs and ovaries was not possible on a regular basis. Information given in this regard is based on gravid females, either from literature records (based on studies of reproduction) or from observations from dissections. The terms *late-term embryo* and *pup* are used interchangeably, while *juvenile*, *adolescent* and *adult* designate consecutive stages of development from young to old, respectively. *Pre-adult*, *immature* and *adolescent* are also used interchangeably.

Specimens were photographed by the author unless stated otherwise in the figure legend. Specimens were generally placed on black non-reflective velvet and exposed to 35 mm film through a 50 mm macro lens, using either slide film (Ektachrome or Fujichrome, 100 or 200 speed, occasionally 400 speed) or black and white print film (Kodak TMAX 100 was the most used print film). The exposure varied according to *in situ* lighting conditions, however a flash was regularly employed. All slides were professionally scanned onto a photo CD-ROM, and the final plates were mounted in PowerPoint, where they were properly sized and contrast and brightness were occasionally corrected. Illustrations were also scanned and the final composition was done in PowerPoint as well.

Species descriptions begin with an account of the type species of Narcine [N. brasiliensis (von Olfers, 1831)] followed by all other recognized species in alphabetical order.

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New species are not formally named herein, and are included after all previously described species as Narcine sp. nov. A, Narcine sp. nov. B, etc. Some of these are currently being prepared for publication elsewhere. An anatomical description is given for the skeleton of N. brasiliensis and is included in the generic account, based on cleared and stained specimens, dissected specimens, and radiographs. Although radiographs do not provide much detail for certain features (e.g., gill-arches), they are enough at least to corroborate the assignment of species to Narcine.

Diagnoses in the species accounts begin by strictly stating unique characters (autapomorphies) or unique combinations of characters that serve to distinguish each species. When species are diagnosed by unique combinations of characters (the majority of the species), alternative conditions for the character in question are given following the strict diagnosis, unequivocally identifying the species under consideration. Each species is hypothesized to be an independent evolutionary lineage, distinguished on the basis of morphological criteria. The diagnoses follow the style adopted by Schaefer (1997) and Reis and Schaefer (1998), among other authors.

Synonymies in the taxonomic sections are given in abbreviated form (author, date, page number and figures, when present); the complete citations are located in the references. A colon is placed between the taxonomic name and reference other than the original description. The synonymies include the original description, emendations, misspellings, new nomenclatural combinations and misidentifications. When a reference could not be verified, or it was unclear exactly what species the author(s) was referring to, a question mark ("?") is placed before the reference. Unfortunately, as is common with a revision encompassing a wide-ranging taxon,

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many references were probably overlooked. An attempt was made to find and obtain all pertinent references to all species. However, doubtlessly many citations in lesser-known foreign journals have not been included as these are not indexed in common zoological catalogs, or are generally unavailable to workers outside local circles. I would deeply appreciate having relevant references not included herein being brought to my attention. Nomenclatural discussions and decisions are based on the rules and guidelines outlined in the 5th edition of the International Code for Zoological Nomenclature (ICZN, 1985).

Species descriptions are given in a five-paragraph format. The first paragraph describes features of the disc region, including general features of the disc, snout, eyes and spiracles, electric organs and gill-slits. The second paragraph describes the mouth, teeth, nostrils and nasal curtain area – morphological components generally of importance for species identifications. The third paragraph is dedicated to features of the pelvic fins, claspers, tail region, dorsal and caudal fins. The fourth paragraph is generally more brief, focusing on the distribution of sensory pores (of both the ampullary and lateral-line systems, which do not vary greatly among species). The fifth paragraph describes coloration of both dorsal and ventral surfaces, making reference to both live and preserved coloration. The coloration becomes more drab when specimens are placed in preservative, as all colors become more faded, but the general color characteristics remain present (this is the case for chondrichthyans in general). The first three paragraphs also include more important proportional measurements from the tables. Means are represented either in text form (as "average" or mean) or symbolically by "x =" in the text.

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The section "Remarks" follows the species descriptions and includes information on the original species descriptions, type-specimens, synonymies, and what is known regarding reproduction and variation within each species. Information on relationships to other species of Narcine and further comments on identification are also included here.

Distributional maps (Figs. 102 – 106) contain occurrences for species based on first-hand specimen data or reliable literature records. Not included on the maps are recorded occurrences that seem counter-intuitive or are unconfirmed, but these are discussed under "Geographical Distribution" for each species when appropriate. Figure legends for the maps descibe included symbols.

Material examined is listed for each species separately, and may include not only specimens but photographs, radiographs, etc. Information concerning relevant biological parameters are included in this list for some species, but this could not be accomplished for all, and information on any given specimen will be provided upon request (information for all specimens is currently being added). The number in parenthesis after the museum acronym and specimen number refers to number of specimens included in the lot.

Terminology for external morphology is modified from various sources including Bigelow and Schroeder (1953) and Fechhelm and McEachran (1984), as well as the terminology employed by Compagno (1984) for sharks. Terminology for internal morphology follows Daniel (1934), Cappetta (1987), Miyake (1988), and Nishida (1990). Terms employed for the lateral-line and ampullary pores follows Chu and Wen (1982). Terms used herein not present in the above references are mentioned and explained in the text when necessary, most probably in the description of the type-species, N. brasiliensis.

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The phylogenetic analyses conducted for this thesis served primarily to further understand the relationships among the orders of elasmobranch fishes, a problem of current interest but, with few exceptions, highly neglected. Methodology employed and material used for these analyses are explained and listed in Part II (see "Methods" section of Part II below).

Institutional abbreviations

AMNH	American Museum of Natural History, New York
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia
BMNH	The Natural History Museum (ex- British Museum of Natural History), London
BPBM	Bernice P. Bishop Museum, University of Hawaii, Honolulu
CAS	California Academy of Sciences, Department of Ichthyology, San Francisco
CSIRO	Commonwealth Scientific Industrial and Research Organization, Hobart, Tasmania
DBAV-UERJ	Departamento de Biologia Animal e Vegetal, Universidade do Estado do Rio de Janeiro, Rio de Janeiro
FMNH	Field Museum of Natural History, Chicago
IIPB	Instituto de Ciencias del Mar, Barcelona
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels

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ISH	Insitut für Seefischerei (housed with ZMH), Hamburg
LACM	Los Angeles County Museum, Los Angeles
MB	Museo Bolca (includes private collection of Massimiliano Cerato), Bolca
MCSN	Museo Civico di Storia Naturale, Verona
MCP	Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre
MCZ	Museum of Comparative Zoology of Harvard University, Cambridge, Massachusetts
MNHN	Muséum National d'Histoire Naturelle, Paris
MNRJ	Museu Nacional do Rio de Janeiro, Rio de Janeiro
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo
NMNZ	National Museum of New Zealand, Wellington
NMV	Museum of Victoria, Melbourne
NNM	Nationaal Natuurhistorisch Museum, Leiden
NSMT	National Science Museum of Tokyo, Tokyo
NTM	Northern Territory Museum, Darwin
NTUM	Museum of Zoology, National Taiwan University, Taipei
QM	Queensland Museum, Brisbane
RUSI	J.L.B. Smith Institute of Ichthyology, Rhodes University of Grahamstown, Grahamstown, South Africa
SAM	South African Museum, Cape Town
SIO	Scripps Institution of Oceanography, San Diego

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SMF	Senckenberg Museum, Frankfurt
SU	Stanford University (collection presently housed in CAS)
TCWC	Texas Cooperative Wildlife Collection, Texas A & M University, College Station, Texas
UP	University of Padova, Padova
USNM	National Museum of Natural History, Smithsonian Institution, Washigton D.C.
WAM	Western Australian Museum, Perth
YPM	Yale Peabody Museum, Yale University, New Haven
ZMA	Institute for Systematics and Population Biology (ex- Institute of Taxonomic Zoology, Zoölogisch Museum), University of Amsterdam, The Netherlands
ZMB	Institut für Systematische Zoologie der Humboldt-Universität (ex-Zoologisches Museum), Berlin
ZMH	Zoologisches Institut und Zoologisches Museum, Hamburg
ZRC	Zoological Reference Collection, Department of Zoology, National University of Singapore, Singapore

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Anatomical abbreviations

AA	Articular facet for antorbital cartilage
ACV	Anterior cerebral vein foramen
AF	Anterior fontanelle
AFR	Articular facet for first radial element of pelvic fin
ANT	Antorbital cartilages
BB	Basibranchial plate or copula
BP	Basipterygium
CB1-5	Ceratobranchials 1 – 5
CC	Caudal centra
CO	Coracoid bar
CH	Ceratohyal
DPH	Dorsal pseudohyal
EB1	Epibranchial 1
EB5	Epibranchial 5
EF	Endolymphatic foramen
EHS	Enlarged hemal spine
ENS	Enlarged neural spine
EPA	Efferent pseudobranchial artery foramen
FP	Facio-palatine foramen
FPF	Fronto-parietal fontanelle

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GA	Gill arches
HA	Hemal arch
HB1?	Hypobranchial 1
HB4?	Hypobranchial 4
HBFN	Hyomandibular branch of facial nerve foramen
HBP	Hypobranchial plate
HF	Hyomandibular facet
HM	Hyomandibula
IC	Internal carotid foramen
IL	Illiac process
LC	Labial cartilages
LIP	Lip (upper or lower)
LRC	Lateral rostral cartilage
LRF	Lateral rostral fenestrae
LS	Lateral stays
LTB	Lower tooth band
MC	Mesocondyle
MESO	Mesopterygium
META	Metapterygium
MK	Meckel's cartilage
NC	Nasal capsule
NCAR	Narial cartilages

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NCH	Nasal capsule horn
NS	Neural spine
OBF	Obturator foramina
"OF"	"Orbital fissure"
ONC	Orbito-nasal canal
OR	Orbit
OS	Optic stalk
OT	Otic capsule
OTS	Subotic shelf
PAF	Parietal fossa
PAL	Palatine cartilages
PANT	Posterior process of antorbital cartilages
PB1-5	Pharyngobranchials 1 – 5
"PC"	"Preorbital canal"
PCC	Precaudal centra
PCF	Precerebral fontanelle
PFR	Pectoral fin radials
PIB	Puboischiadic bar
POP	Posterior pelvic process
PQ	Palatoquadrate
PROP	Propterygium
PRP	Pre-pelvic process

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PVR	Pelvic fin radials
PSC	Pre-spiracular cartilage
PSYN	Posterior extension of synarcual cartilage
R	Radial element of dorsal fin
RF	Rostral fontanelle
RO	Rostrum
SC	Supra-scapula
SNF	Spinal nerve foramina
SP	Scapular process
TP	Tooth patch
UTB	Upper tooth band
VC	Vertebral centra
VPH	Ventral pseudohyal

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HISTORY OF RESEARCH ON ELECTRIC RAYS

Early History

The electric ray was known for many centuries before formal taxonomic recognition, prior to the classificatory efforts of F. Willughby, P. Artedi and C. Linnaeus. The electric ray was commonly referred to as "torpedo," "narke" or "cramp-fish" in the early classical literature. Its torporific qualities were known to Hippocrates, and Plato has compared them in a humorous vein to Socrates (Pringle, 1774). Peripatetic philosophers, most notably Aristotle and his student Theophrastus, described many aspects of these "numbing" fish in the course of their attempts to understand and describe living organisms in general (Cuvier, 1828). These early authors were primarily interested in the electrogenic and medicinal properties of the electric ray.

In mid to late 17th century, F. Redi, his student S. Lorenzini, and other post-Renaissance investigators (e.g., J. Hunter, J. Walsh, H. Cavendish, L. Galvani, A. Volta and L. Spallanzani), demonstrated through elegant experiments the anatomical and electrical aspects of the electrogenic organs ("corpi falcati") and the currents they generated (e.g., Lorenzini, 1678; review in Moller, 1995). These studies helped to further understand the physiology of muscle activity by contributing data concerning the origin and regulation of electrical currents in muscle tissue (for a more recent study and references from a developmental perspective, see Mellinger et al., 1978). An extensive essay on many of these early experiments was published

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by Pringle (1774), and Pera (1992) provides an excellent account on the history of research concerning animal electricity.

The species of electric ray invariably used in these early experiments was either Torpedo torpedo (Linnaeus, 1758) or T. marmorata Risso,1810 the only species of electric rays known at the time to inhabit European (Mediterranean) seashores. These "classical" works therefore contributed little to understanding the actual diversity of electric rays.

Taxonomic History[1]

C. Linnaeus (1758), in the 10th edition of the *Systema Naturae*, placed the chondrichthyan fishes in the order "Nantes," a subgroup of the Amphibia (his "Classis III"), along with the sturgeon (Acipenser), angler-fish (Lophius) and lamprey (Petromyzon). In this class he also included 10 genera of various "reptilian" groups and the amphibians per se. Linnaeus, based almost exclusively on the work of his friend P. Artedi (1738), recognized 10 species of rays and 14 species of sharks (Artedi, according to Pietsch [1995: 112], recognized 11 species of rays). Linnaeus (1758) also included two species of chimaeroids, not mentioned by Artedi (1738). Linnaeus's system, however, allowed for only a single genus for each of these three groups (Raja, Squalus, and Chimaera, respectively – Raja and Squalus originated with Artedi).

[1] This section concerns mainly, but not exclusively, the genus Narcine. Electric rays have a long and sometimes complicated systematic history, such that sources of information other than primary species descriptions and revisional studies are not discussed here (these are restricted to the taxonomic sections for each species, when appropriate). The abbreviated nature of this chapter is necessary in light of the large number of nominal species, faunistic surveys, anatomical studies, etc., related to or including electric rays.

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Linnaeus' (1758) placement of the chondrichthyan fishes in the Amphibia in the tenth edition was a departure from Artedi (1738). Artedi classified the chondrichthyans as equal in rank with the three other major fish groups (and the marine mammals, order Plagiuri), as the order Chondropterygii (which also included Petromyzon and Acipenser). This arrangement was adopted by Linnaeus (1735) in the first edition, but later modified extensively, as seen in the tenth edition. Gmelin (1789), in editing the thirteenth edition of the *Systema Naturae*, finally returned the Chondropterygii to the fishes, following general opinion of the time (Cuvier, 1828).

The binomial history of electric rays began with Linnaeus (1758). Among Linnaeus' (and Artedi's) species of rays was Raja torpedo (= Torpedo torpedo), an electric ray from the Mediterranean Sea. This species is present in all editions of the *Systema Naturae*, including the first edition of 1735 (for a bibliographical synopsis of the 13 editions of the *Systema Naturae*, in tabular form, see Pietsch, 1995: 113). Prior to Linnaeus, one of the first descriptions of an electric ray in a "systematic" framework was given by Willughby (1686), who also published one of the first depictions of an electric ray (for T. torpedo). His work is considered to have had a major influence on Artedi, even though the nomenclature he adopted was not binomial (Cuvier, 1828).

Houttuyn (1764) was the first author to use Torpedo in generic form for Linnaeus' Raja torpedo (for an abbreviated synonymy of the genera of electric rays, see Table 1). By the end of the eighteenth century, three species of electric rays had been described. Along with the Linnean Raja torpedo were Raja capensis Gmelin, 1789 (= Narke capensis) and Lophius monopterygius Shaw and Nodder, 1795 (= Hypnos monopterygium). Bonaterre (1791),

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however, recognized solely the species R. torpedo, even though his work is comprehensive, generally diagnostic and well illustrated.

The first species presently referable to Narcine (which was not yet erected) were described in the beginning of the nineteenth century from the Bay of Bengal (northern Indian Ocean). Bloch and Schneider (1801) described Raja timlei (= Narcine timlei) from off the coast of Tranquebar, southeastern India (along with Raja dipterygia [= Narke dipterygia]). Shaw (1804), based on the "Temeree" and "Nalla Temeree" of Russell (1803), described Raja maculata (= Narcine maculata) and Raja bicolor (= Narcine bicolor), respectively, both from off Vizagapatnam, eastern India.

Rafinesque-Schmaltz (1810) described as new three species of Torpedo in his regional review of the fishes of Sicily (all presently referred to T. torpedo). Blainville (1816) erected the genus Narcobatus (as a subgenus of Raia [sic]), apparently unaware of the availability of Torpedo, and included in it 11 species of electric rays (including Raja maculata Shaw, 1804). Four of Blainville's (1816) species of Narcobatus were named by him for the first time but are unavailable as they lack descriptive qualities (published as name only). Cuvier (1817, 1829) listed only two valid species of electric rays, and mistakenly recognized Torpedo as originating with André Duméril (1806), not aware of Houttuyn's (1764) translation of, and additions to, Linnaeus (1758).

The next description of a species of electric ray belonging to Narcine Henle, 1834 appeared in 1824 (Torpedo ocellata Quoy and Gaimard, 1824), and was erroneously indicated as coming from the Cape of Good Hope (South Africa) (see section on Narcine brasiliensis below). von Olfers (1831) described Torpedo brasiliensis (= Narcine brasiliensis), from Rio de

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Janeiro, Brazil, and reviewed existing species of electric rays. He placed all four recognized species in Torpedo, apparently overlooking Kaup's (1826) description of Narke. von Olfers considered both Raja timlei and R. dipterygia as "species dubia," and possibly as synonyms of T. brasiliensis and R. capensis, respectively, even though R. timlei antedates T. brasiliensis. von Olfers (1831) recognized many "varieties" for T. marmorata including four that he described as new (T. panthera, T. pardalis, T. sinuspersici and T. gigantea, the last species a fossil taxon from Monte Bolca, Italy, presently referred to the genus Platyrhina, a guitarfish). Shaw's (1804) species R. maculata and R. bicolor (both belonging to Narcine) were considered varities of T. marmorata as well. His revision is very complete, covering most previous literature, and well organized.

Henle (1834) placed the classification of electric rays on a more modern level by erecting the genus Narcine (type-species: Torpedo brasiliensis von Olfers, 1831) for species of electric rays that differed from Torpedo in having a more rounded and extended snout, differently arranged teeth, distinct configuration of the mouth, among other characters (see character synopsis on p. 25 of his paper). Henle (op. cit.) described Narcine indica, also from off the Tranquebar coast, and like von Olfers (1831), reviewed the classification of existing species. However, he also overlooked Kaup's (1826) description of Narke. Henle transferred Raja capensis Gmelin, 1789 (which he erroneously attributed to Linnaeus) to Narcine, and considered Raja dipterygia Bloch and Schneider, 1801 as "species dubium." Henle's monograph is extensively detailed, and reviews previous literature, even though he was unable to properly identify three specific names then published for species of Narcine (Raja maculata Shaw, 1804, R. bicolor Shaw, 1804 and T. ocellata Quoy and Gaimard, 1824), and erected the

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junior synonym (of R. timlei) N. indica. Henle also provided more diagnostic characters for species than previous authors, illustrating for the first time the teeth, neurocranium and branchial arches of representative electric rays. Henle also cited time ranges for some forms, making reference to the Eocene electric ray (later described as Narcine molini Jaekel, 1894) of Monte Bolca, Italy.

With the publication of Henle (1834), Cuvier (1834) and Davy (1834), a total of 26 nominal species of electric rays were published. Of these, seven can presently be referred to Narcine, fifteen to Torpedo Houttuyn, 1764, two to Narke Kaup, 1826, and one each to Hypnos Duméril, 1852 and Temera Gray, 1831.

Müller and Henle's (1838-1841) formidable *Systematische Beschreibung der Plagiostomen* dealt more briefly with electric rays compared to the previous revisions of von Olfers and Henle. These authors had previously erected the genus Astrape (Müller and Henle, 1837) for species with a single dorsal fin, still unaware of Kaup's (1826) description of Narke. They recognized almost the same species of Narcine as did Henle (1834), but transferred N. capensis to Astrape. Müller and Henle's synonymy for at least one species of Narcine was more comprehensive than previous workers. For N. brasiliensis, they included as synonyms T. ocellata Quoy and Gaimard, 1824 and T. bancroftii Griffith, 1834, both for the first time. However, Müller and Henle failed to mention the species described by Shaw (1804), even though the species were cited previously by Henle (1834). Müller and Henle, following von Olfers (1831), divided electric rays into suprageneric groups on the basis of the number of dorsal fins (von Olfers used this character to separate species). Nine distinct species of electric

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rays were recognized. These authors also described, albeit informally, three distinct varieties of N. brasiliensis.

Müller and Henle's (1837) previous study of electric rays was more abbreviated, but included a total of 10 species (one more than in Müller and Henle, 1838-1841), in the same four genera (Torpedo, Narcine, Astrape and Temera). The species eventually left out in their later revision (1838-1841) is unknown, as only species numbers and not names are specified in Müller and Henle (1837).

In Bonaparte's (1838, 1839) *Selachorum Tabula Analytica*, the elasmobranchs are divided into two families, the Rajidae (including all the rays) and the Squalidae (all the sharks). The different groups of rays received subfamilial status, and five species of electric rays (in four genera) are recognized in the "Torpedinini." Bonaparte's shortcomings include using Astrape Müller and Henle, 1834 instead of Narke Kaup, 1826 and crediting Torpedo to Duméril, 1806. All supraspecific taxa are diagnosed and synonymies are included in Bonaparte (op. cit.). Bonaparte (1841) later adopted the same classification.

Richardson (1841) briefly described the very distinctive N. tasmaniensis from Hobart, Tasmania. The specific name was actually published in an earlier account (Richardson, 1840), but because that publication fails to diagnose in any way N. tasmaniensis, the authorship must be attributed to Richardson (1841). He later expanded his descriptions and included a color plate and an illustration of the teeth of this species (Richardson, 1849). Much later, Whitley (1940) erected the genus Narcinops for N. tasmaniensis.

Electric rays were again reviewed about a decade after Müller and Henle by Auguste Duméril (1852). Duméril's revision was very comprehensive, recognizing 18 species, of which

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five were newly described along with the new genus Hypnos. Four of the seven accepted species of Narcine were described as new in Duméril's monograph (two of these were credited to A. Valenciennes). The three distinct varieties of N. brasiliensis were again mentioned, but also without formal taxonomic recognition. Duméril discussed physiological aspects of the electric organs based on the existing literature, and provided identification keys for genera and species. However, he also neglected to include both of Shaw's (1804) available nominal species of Narcine and misidentified Bloch and Schneider's (1801) Raja timlei, thus creating the synonyms N. maculata (of N. maculata, also a secondary homonym, ICZN, 1985, Art. 57c [i]), N. microphthalma and N. macrura (of R. timlei). Duméril also overlooked Richardson's (1841, 1849) descriptions of N. tasmaniensis, and the description of Discopyge by J. Heckel (1846). One of Duméril's species of Narcine (N. nigra) belongs in Discopyge (see Table 4).

Gray's (1851) catalogue of the fishes of the British Museum (The Natural History Museum) included 12 species of electric rays recognized as valid (five of Narcine), in four genera. Gray's account included a synonymy, albeit incomplete, and diagnoses for genera, but the genus Discopyge Heckel, 1846 was overlooked. Gray (1854) published a manuscript by Gronovius in which a species of electric ray from the Antilles was described (first mentioned in Gronovius, 1763), for which Gray furnished the name Torpedo pictus (= Narcine pictus) (see also Wheeler, 1958). Gray (1831) had previously described the monotypic electric ray genus Temera from Malaysia.

André Duméril (1856), in his general classification of fishes, included five genera of electric rays and mentioned species only in a passing manner. Again, Discopyge was not included. Andre Duméril's work is much less complete than that of his son Auguste Duméril

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(1852, 1865), and, at least in relation to rays, was mostly compiled directly from Müller and Henle (1838-1841). Günther (1870) recognized 15 species in six genera of electric rays (repeated in his text-book, Günther, 1880). His 1870 account is similar to that of Gray (1851), but also provided diagnoses for species. Only four species of Narcine were included in Günther's 1870 compilation. All of these authors overlooked the available genus Narke Kaup, 1826, as did many previous workers, recognizing instead the junior synonym Astrape Müller and Henle, 1841 (a problem only addressed much later, by Gill, 1895).

Auguste Duméril (1865) produced an extensive revision of chondrichthyan systematics and anatomy, recognizing 20 species of electric rays in six genera. This work is doubtlessly one of the most complete accounts of the systematics of chondrichthyans of its time. Duméril (1865) synonymized Valenciennes' species (published in Duméril, 1852) N. microphthalma and N. macrura with N. indica and N. timlei, respectively, and again overlooked both Shaw's (1804) species of Narcine and Kaup's (1826) description of Narke. Duméril provided identification keys to all genera and species, along with extensive diagnoses of taxa. Many "varieties" of species were described, including those previously reported by Müller and Henle (1841) for N. brasiliensis. At the time of Duméril's monograph, over 50 nominal species of electric rays were available, many applicable to Torpedo, representing more than a two-fold increase since Henle'e (1834) revision of Narcine.

Gill (1862), the first non-European student of Narcine, erected four new subgenera of electric rays, two for Torpedo (Narcacion and Tetronarce) and two for Narcine (Cyclonarce and Gonionarce). Because neither Klein's (1777) genera nor their revival by Walbaum (1792) are admissable according to the ICZN (Opinion no. 1938), Narcacion, which was original with

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Klein, must date from Gill (1862). Gill (1895) provided a synopsis of the genera of electric rays, noting the previous misuse of Astrape instead of Narke, and other nomenclatural problems related to various genera. According to Gill (1895), Tetranarce was the original intended spelling for Tetronarce, which was a misprint.

The most comprehensive and well illustrated study exclusive to electric rays from an anatomical, physiological and systematic standpoint, prior to the twentieth century, was Fritsch (1890). Fritsch reorganized the classification of electric rays by sorting the existing species of Torpedo into distinct subgenera, which he had established previously (Fritsch, 1884). Fritsch recognized nine species of Torpedo (divided among his subgenera Gymnotorpedo and Fimbriotorpedo, junior synonyms of Tetranarce Gill, 1862 and Narcacion Gill, 1862, respectively), five of Narcine, two of Astrape (again unaware of Narke Kaup, 1826), and one each for Discopyge, Hypnos and Temera. Many nominal species were placed in synonymy, such as those published by Auguste Duméril (1852), including some for the first time.

Garman (1881) named two "varieties" of N. brasiliensis, one from St. Vincent in the Lesser Antillies (N. brasiliensis punctata) and the other from Key West, Florida (N. brasiliensis corallina). These names are available at the specific rank (ICZN, 1985, Art. 45e). Garman (1881) overlooked the description of T. bancroftii by Griffith (in Cuvier, 1834), but later synonymized N. brasiliensis punctata with N. bancrofti in his more extensive revision (Garman, 1913). In the *Plagiostomia*, Garman (1913) summarized the systematics of electric rays, recognizing seven genera and 30 species, of which one was described as new (Narcine firma, from Colombo, Sri Lanka). Garman (op. cit.) provided synonymies, diagnoses, descriptions, ranges and identification keys for all species, but much of the information appears to be

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compiled from earlier accounts and he overlooked the available species N. entemedor Jordan and Starks, 1895.

The first more or less "complete" fossil of an electric ray to be described comes from the Eocene shallow-water marine environments of the Monte Bolca formation, Italy (Jaekel, 1894). Jaekel described the fossil species Narcine molini on the basis of a large, dorso-ventrally preserved specimen (in part and counter-part; this species is redescribed below on the basis of additional specimens).

Alcock (1898) described the deep-water genus Benthobatis for the very rare B. moresbyi, from off the southwest coast of India. Bean and Weed (1909) described B. marcida and its synonym B. cervina from deep waters of the tropical western Atlantic, considerably increasing the range of this genus. Benthobatis has remained poorly known and undercollected, until specimens were sampled from southwestern Brazil and southwestern Taiwan, in 1991 and 1970, respectively. Both new occurrences constitute new species. A synopsis of Benthobatis and a redescription of the type-species, B. moresbyi, is in press (Carvalho, in press).

Jordan (1884) described N. umbrosa from Key West, Florida, and Jordan and Starks (in Jordan, 1895) named the first species of Narcine from the eastern Pacific (N. entemedor). Jordan and Evermann (1896), in revising the species of marine and freshwater fishes in North and Central America, mention two species, N. brasiliensis and N. entemedor (the latter appeared only in Part 3). Jordan and Evermann placed as a junior synonym of N. brasiliensis Jordan's own species of Narcine (N. umbrosa). Four additional available specific names were

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also placed in synonymy of N. brasiliensis by these authors, including (erroneously) N. nigra Duméril, 1852. These authors overlooked N. punctata Garman, 1881.

Annandale (1909), Miranda Ribeiro (1923) and Breder (1928) published reviews of the elasmobranchs from the Bay of Bengal, southwestern Atlantic and from Panama to lower California, respectively, describing each a new species of Narcine. Regan (1921) described the electric ray genus Heteronarce for the new species H. garmani, and also included Narcine mollis Lloyd, 1906 (both from the western Indian Ocean). New species of Heteronarce were subsequently described by Fowler (1926), von Bonde and Swart (1923), Talwar (1981), and Baranes and Randall (1989). von Bonde and Swart (1923) also reviewed the batoid fauna of South Africa.

Liu (1932) reviewed the elasmobranch fishes from China, providing identification keys to species, and reporting new material from Tsingtao and other localities in the Yellow and East China Seas. Whitley (1940) is an extensive account on the chondrichthyan fishes of Australia and New Zealand, giving much anecdotal information, and describes Narcinops for N. tasmaniensis Richardson, 1941. Fowler (1941) reviewed the Indo-Pacific species of electric rays, and recognized eight genera (with many subgenera), and 20 species for the region. His review is primarily a compilation from published accounts, but includes identification keys, synonymies and citations for included taxa. Fowler erroneously synonymized N. firma Garman, 1913 with N. brunnea Annandale, 1909. Hildebrand (1948) described the third nominal species of Narcine from the eastern Pacific, N. schmitti (a junior synonym of N. vermiculatus).

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Bigelow and Schroeder (1948) erected the genus Diplobatis for Discopyge ommata Jordan and Gilbert, 1890 from off the Pacific coast of Central America. Diplobatis was later reviewed by Fechhelm and McEachran (1984) and found to include four species (as "subspecies"), three occurring off the northern coast of South America. Garrick (1951) reviewed the distinctive blind electric ray genus Typhlonarke Waite, 1909 from New Zealand, and recognized two distinct species (T. aysoni [Hamilton, 1902] and T. tarakea Phillipps, 1929).

The revision of Bigelow and Schroeder (1953), although primarily restricted to the northwestern Atlantic species, provides unparalleled synonymies and references for many electric rays. These authors also present identification keys to all accepted species of genera occurring in the area. In their Torpedinidae (i.e., electric rays with two dorsal fins) they included seven genera and 30 species (the Narkidae and Temeridae were not studied). Bigelow and Schroeder considered N. entemedor a junior synonym of N. brasiliensis, and doubted the validity of the previously described genus Heteronarce Regan, 1921, stating that it could be a synonym of Narcine. They synonymized Narcinops Whitley, 1940 with Narcine, and like Fowler (1941) considered Syrraxis Jourdan, 1841 a generic synonym as well. Their revision also covers aspects related to the physiology, electrogenic capacities, development and distribution of electric rays, in particular those reviewed.

After Bigelow and Schroeder's revision, the major taxonomic focus on Narcine shifted to the Indo-Pacific area, with the descriptions of two new species from the Gulf of Tonkin (Bessednov, 1966), and one each from the eastern Indian Ocean (McKay, 1966) and western Indian Ocean (Lloris and Rucabado, 1991). Numerous regional revisions have treated electric

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rays in the Indo-Pacific, normally in the context of revisions of elasmobranchs in general or of all fishes of a given region. Some of these revisions provide diagnoses to species, identification keys, synonymies and illustrations (Lindberg and Legeza, 1959 [translated 1967], for the Seas of Japan, Okhotsk and Yellow Sea; Zhu, 1962 for the South China Sea; Bessednov, 1969 for the Gulf of Tonkin; Misra, 1969 for India; Qureshi, 1972 for the Arabian Sea; Kyushin et al., 1982 for the South China Sea; Monkolprasit, 1984 for Thailand; Masuda et al., 1984 for Japan; Chen and Chung, 1971, Shen, 1984a and Chen and Joung, 1993 for Taiwan; Last and Stevens, 1994 for Australia; Moshin and Ambak, 1996 for Malaysia; Compagno, 1995 for the western Indian Ocean), and others are compilations and species lists (Senta and Min, 1975; Monkolprasit, 1977; Shen, 1984b). Carvalho et al. (in press) revised the Indo-West Pacific species of Narcine, with identification keys, illustrations and distributional maps for the majority of the species. However, nominal species were used as applied in the recent literature, which involves numerous misidentifications.

At the time of writing, about 101 nominal species of Recent electric rays are available, of which some 51 are synonymous (nominal species listed by family in Tables 2 – 5). According to Eschmeyer (1990: 437; also Eschmeyer, 1998: 2451), 33 nominal genera have been applied exclusively to the group, of which 30 are available. Of these, current consensus recognizes only 10 or 11 (Crassinarke Takagi, 1951 being the difference; Table 1). Five nominal genera have been proposed exclusively for species of Narcine, which is the oldest available generic name. Presently, 26 nominal species can be applied unequivocally to Recent Narcine (Table 5).

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Evolutionary Studies

Early anatomical studies of electric rays were primarily descriptive and served to establish the morphological distinctiveness of electric rays compared to other batoids (Henle, 1834; Gegenbaur, 1865, 1872; Haswell, 1885; Garman, 1913; Daniel, 1934; Edgeworth, 1935; see also de Beer, 1926, 1932, 1985; Goodrich, 1986 and references therein). Regan (1906) was one of the first to use these data in a classification. He reviewed the classification of chondrichthyan fishes and, very impressed with the anatomical peculiarities of electric rays, divided all rays into two groups of equal rank, the "Narcobatoidei" (for electric rays) and the "Batoidei" (for all the other rays). The latter taxon was diagnosed mainly by the absence of characters present in electric rays (lack of electric organs between the pectoral fins and head, antorbital cartilages not extending forward, etc.). This scheme was followed by White (1937), Berg (1947) and Lindberg (1971).

After Regan (1906), many authors advanced theories concerning the phylogenetic relationships of electric rays (Holmgren, 1940, 1941; Compagno, 1973, 1977; Heemstra and Smith, 1980; Maisey, 1984; Muñoz-Chápuli and Garrido, 1986; Nishida, 1990; McEachran et al., 1996; Shirai, 1996). These works attempt to phylogenetically position electric rays within the general context of batoids. The relationships among electric ray genera, however, have been comparatively neglected.

Holmgren's (1940, 1941) views were based on his extensive studies of the development of the head of chondrichthyan fishes. His comparisons also involved placoderms and acanthodians, as Holmgren (1942) advocated the separate origin of sharks, rays and

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chimaeroids from different placoderm ancestors. Holmgren (1941) compared the chondrocranium of Narke, Narcine, Torpedo and Hypnos, and concluded that electric rays are more closely related to stingrays than to any other batoid taxon.

Compagno (1973) regarded electric rays as the sister-group to all other rays except sawfishes (Pristiformes, his most basal group), although he recognized similarities in electric rays and "rhinobatoids" (which he believed are probably not homologous). Heemstra and Smith (1980) advanced a similar theory, which they expressed as a cladogram. In their scheme, electric rays shared with all other batoids except pristiforms the absence of the basal angle, elongate propterygia that extend to the nasal capsules, and plesodic pectoral and pelvic fins without ceratotrichia. To Heemstra and Smith (1980), skates, guitarfishes and stingrays were monophyletic on the basis of having suprascapulae fused or articulating with the vertebral column or synarcual, a feature absent in electric rays.

Compagno (1977) presented a different arrangement for electric rays, in which they represent the most basal group of batoids. His opinion was heavily influenced by the retention in one electric ray genus (Narke) of a strong ligamentous connection between the ceratohyals and hyomandibulae, a feature typical of sharks and lacking in other rays. Compagno (1977) regarded this as a primitive character for electric rays and for elasmobranchs in general, hence his placement of electric rays as the sister-group to all other batoids. Compagno (1977), however, considered some alternatives to this classification, but with much less conviction.

Maisey (1984) agreed with Compagno (1977), although his placement of electric rays as the sister-group to all other batoids was also based on what he believed was the primitive ("shark-like") arrangement of the hyobranchials, all of which are in contact with the

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basibranchial copula in Torpedo (a feature apparently shared by the Jurassic taxa Spathobatis and Belemnobatis as well).

Fechhelm and McEachran (1984) reviewed the taxonomy and anatomy of the electric ray genus Diplobatis and commented on the interrelationships within Narcinidae, considering the family to be monophyletic and concluding that Discopyge and Narcine form a monophyletic unit.

Muñoz-Chápuli and Garrido (1986) considered electric rays to be the sister-group of "Rajiformes" on the basis of shared vascular patterns. Their concept of Rajiformes is not clear as they report to follow Compagno (1973, 1977); however, Compagno's concept of Rajiformes is different in both papers (including skates [Rajoidei] and guitar-fishes [Rhinobatoidei], or just skates, respectively). Muñoz-Chápuli and Garrido (1986) did not examine any rhinobatoid, and their hypothesis is best understood as favoring the monophyly of electric rays and skates only. In any case, this theory of relationships for electric rays is novel, and is based on three characters that have gone generally unnoticed (as is true of characters related to the circulatory system in general). Their data are presented as being somewhat preliminary, and Muñoz-Chápuli and Garrido (1986) express the need to further test their hypothesis by studying the vascular system of more taxa.

Nishida (1990) placed the electric rays as the sister-group to a large component including many "rhinobatoid" genera, skates and stingrays (demonstrating that Rhinobatoidei as commonly used is not monophyletic). Nishida also considered the Narcinidae to be monophyletic, and that Torpedo was the most basal electric ray genus. At about this time anatomical data for rays in general were becoming more available, as very good descriptive

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studies on the ventral gill arch skeleton (Miyake and McEachran, 1991), rostral structures (Miyake et al., 1992) and cephalic musculature (Miyake et al., 1993) were published.

Shirai (1996) presented a hypothesis similar to Nishida's, disagreeing on the position of "rhinobatoids" (which he also considered paraphyletic), but followed Nishida in crediting narkids (also deemed paraphyletic, as in Nishida, 1990) as the sister-group to narcinids. This arrangement was challenged by McEachran et al. (1996), who placed the electric rays as the most basal batoid group, as did Compagno (1977) previously. McEachran et al.'s hypothesis is based on the presence of the jugal arch in pristiforms, rajoids and taxa traditionally placed in the Rhinobatoidei (of Compagno, 1973), non-horizontal arrangement of the pectoral pterygial condyles in electric rays and lack of the ethmoideo-parethmoidalis muscle in electric rays (these characters were hypothesized by McEachran et al. (op. cit.) to unite all groups of batoids to the exclusion of electric rays).

The above hypotheses are represented in Fig. 2. Two theories concerning the phylogenetic relationships of electric rays to other batoids prevail: one in which they are the sister-group to all other batoids (Regan, 1906; Compagno, 1977; Maisey, 1984a; McEachran et al., 1996), and the other in which they form a monophyletic group with skates, stingrays and some (Nishida, 1990), all (Heemstra and Smith, 1980) or without (Shirai, 1996) "rhinobatoids." Muñoz-Chápuli and Garrido (1986) are the only authors to defend a sister-group relationship exclusively between electric rays and skates.

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SYSTEMATIC ACCOUNTS

The Genera of Recent Torpediniformes

Table 1 is a summary of the genera of Recent Torpediniformes, indicating their taxonomic authority and present status. Nominal species of each genus are listed in Tables 2 – 5. A key to the genera of Torpediniformes is included below to allow for the quick identification of Narcine, and a taxonomic revision of Narcine is presented following the key.

Key to the Genera of Recent Torpediniformes

The following key has components that are also present in the identification keys of Fowler (1941) and Bigelow and Schroeder (1953). The usage of the number of dorsal fins as a character to isolate genera and form suprageneric groupings stems from von Olfers (1831). It has been used by many subsequent authors (e.g., Müller and Henle, 1841) and is followed here because it is reliable and simple, and is generally not subject to vagaries of preservation. Internal anatomical features are not used in the key but could easily be added to aid in identification of radiographs or skeletal material. Figures 3 – 6 provide outline illustrations of representative specimens (and their nasoral regions) of the families of electric rays.

1a. No dorsal fins on body (Narkidae in part). Temera Gray, 1831.

1b. One or two dorsal fins on body (Torpedinidae, Narcinidae, Narkidae in part). **2.**

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2a. One dorsal fin present (Narkidae in part). **3.**

2b. Two dorsal fins present (Torpedinidae, Narcinidae, Narkidae in part). **4.**

3a. Eyes functional and visible dorsally on disc; pelvic fins not greatly expanded antero-laterally, not continuous with ventral aspect of body posteriorly. Narke Kaup, 1826.[2]

3b. Eyes vestigial, not funcional and not visible dorsally on body; pelvic fins greatly expanded antero-laterally, and indistinct from disc posteriorly. Typhlonarke Waite, 1909.

4a. Tail much shorter than disc; disc anteriorly blunt in outline, not rounded; mouth widely distensible (Torpedinidae). **5.**

4b. Tail as long as or longer than disc; disc anteriorly rounded in outline; jaws not widely distensible (Narcinidae, Narkidae in part). **6.**

5a. Tail from cloaca to tip measuring roughly one-third the distance from cloaca to snout; teeth with more than one cusp. Hypnos Duméril, 1852.

5b. Tail from cloaca to tip measuring approximately one-half the distance from cloaca to snout tip; teeth with only one cusp[3]. Torpedo Houttuyn, 1764.

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[2] Crassinarke Takagi, 1951 is considered here a synonym of Narke Kaup, 1826. Bengalichthys was created by Annandale (1909) for B. impennis (= N. dipterygia), the type specimens of which (deposited in the Natural History Museum, London) seem to agree in general characteristics with those diagnostic of Crassinarke, as described by Takagi (1951). If this proves to be true upon further examination, then Bengalichthys must be used instead of Crassinarke if their included species are considered generically separate from Narke.

[3] This information was taken from Bigelow and Schroeder (1953: 87, 88), and was confirmed for Hypnos and many, but not all, species of Torpedo.

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6a. Eyes very minute, embedded in integument, probably not functional, and visible dorsally only as small dark spots if visible at all. Benthobatis Alcock, 1898.

6b. Eyes funcional, not embedded in integument, visible dorsally. **7**.

7a. Pelvic fins united posteriorly to form a continuous "apron"; joint nasal curtain with distinctive medial projection. Discopyge Heckel, 1846.

7b. Pelvic fins not united posteriorly to form "apron"; joint nasal curtain without distinctive medial projection. **8**.

8a. Nostrils divided into two separate openings by fused stiff strip of integument on inside of nostril. Diplobatis Bigelow and Schroeder, 1948.

8b. Nostrils not divided into two separate openings by fused stiff strip of integument on inside of nostril. **9**.

9a. Teeth concealed within mouth when latter is closed; joint nasal curtain studded with numerous pores; pores present on posterior aspect of nasal curtain close to mouth opening; nostrils elongated and slit-like, longer than wide. Heteronarce Regan, 1921.

9b. Teeth exposed in rows on outer surface of "lips" when mouth is closed; joint nasal curtain not studded with numerous pores; pores, if present, not continuing posteriorly on nasal curtain to close to mouth opening; nostrils circular, not elongated and slit-like, not longer than wide. Narcine Henle, 1834.

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TAXONOMIC REVISION OF NARCINE HENLE, 1834

Narcine Henle, 1834

Narcine Henle, 1834: 31 (original description; type-species: Torpedo brasiliensis von Olfers, 1831, by subsequent designation of Bonaparte, 1838 [according to Eschmeyer, 1990]; type-locality: Rio de Janeiro, Brazil); Bonaparte, 1838: 7 (listed); Muller and Henle, 1841: 129 (revision); Duméril, 1852: 51 (revision); Duméril, 1865 (compilation); Fritsche, 1890 (partial revision); Jordan and Evermann, 1896: 78 (diagnosis); Annandale, 1909: 43 (partial revision); Garman, 1913: 296 (revision); Fowler, 1941: 332 (compilation); Bigelow and Schroeder, 1953: 107 (diagnosis, description, key to species, illustrations); Compagno, 1973 (listed in a classification); Nelson, 1976 (listed); Compagno, 1977 (accepted as valid, anatomical illustrations); Fechhelm and McEachran, 1984 (comparisons, accepted as valid, illustration of skeleton); Nelson, 1984 (listed); Cappetta, 1987: 162 (compilation); Eschmeyer, 1990: 437 (listed); Eschmeyer and Bailey, 1990: 259 (compilation); Nelson, 1994 (listed); Compagno, 1995; McEachran et al., 1996 (listed in a classification); Eschmeyer, 1998: 2451 (compilation).

Syrraxis Jourdan, 1843 (no pagination given, original description, not illustrated; type-species: Narcine indica Henle, 1834, by monotypy; reference not seen, compiled from Bigelow and Schroeder, 1953 and Eschmeyer, 1990); Agassiz, 1846: 359 (unnecessarily

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emended to Syrrhaxis according to Bigelow and Schroeder, 1953; not seen); Bigelow and Schroeder, 1953: 107 (placed in synonymy of Narcine Henle, 1834); Eschmeyer, 1990: 437 (listed); Eschmeyer and Bailey, 1990: 397 (compilation); Eschmeyer, 1998: 2451 (compilation).

Cyclonarce Gill, 1862: 387 (original description, not illustrated; type-species: Raja timlei Bloch and Schneider, 1801, by original designation and monotypy); Jordan and Evermann, 1896: 78 (placed in synonymy of Narcine Henle, 1834); Fowler, 1941: 332 (compilation, placed in the synonymy of Narcine Henle, 1834); Bigelow and Schroeder, 1953: 107 (placed in synonymy of Narcine Henle, 1834); Cappetta, 1987: 162 (compilation); Eschmeyer, 1990: 437 (listed); Eschmeyer and Bailey, 1990: 112 (compilation); Eschmeyer, 1998: 2451 (compilation).

Gonionarce Gill, 1862: 387 (original description, not illustrated; type-species: Narcine indica Henle, 1834, by original designation and monotypy); Jordan and Evermann, 1896: 78 (placed in synonymy of Narcine Henle, 1834); Fowler, 1941: 332 (compilation, placed in the synonymy of Narcine Henle, 1834); Bigelow and Schroeder, 1953: 107 (placed in synonymy of Narcine Henle, 1834); Cappetta, 1987: 162 (compilation); Eschmeyer, 1990: 437 (listed); Eschmeyer and Bailey, 1990: 166 (compilation); Eschmeyer, 1998: 2451 (compilation).

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Narcinops Whitley, 1940: 164 (type-species: Narcine tasmaniensis Richardson, 1841 by original designation and monotypy); Bigelow and Schroeder, 1953: 107 (placed in synonymy of Narcine Henle, 1834); Eschmeyer, 1990: 437 (listed); Paxton et al., 1989: 60 (compilation, placed in synonymy of Narcine Henle, 1834); Eschmeyer and Bailey, 1990: 259 (compilation); Eschmeyer, 1998: 2451 (compilation).

DIAGNOSIS: A genus of narcinid electric ray distinguished from other narcinids (Discopyge, Benthobatis and Diplobatis) by the following combination of external features: joint nasal curtain lacking circular median posterior projection (present in Discopyge); pelvic fins not continuous posteriorly to form "apron" (present in Discopyge); eyes functional and clearly visible externally anterior to spiracles, normally about same size or slightly larger or smaller than spiracles (eyes externally not readily visible in Benthobatis); nostrils not subdivided into two distinct and discontinuous compartments by bridge of stiff integument between dorsal nasal curtain and ventral nasal flaps (nostrils fully divided in Diplobatis); claspers connected latero-externally to pelvic fins, not concealed in dorso-ventral view by pelvic fins (condition in Diplobatis and some species of Benthobatis); both lower and upper tooth bands exposed externally when mouth is closed (tooth bands not readily exposed in Diplobatis and Benthobatis); well developed lateral tail folds extending from lateral aspect of tail ventral to first dorsal fin and extending posteriorly to caudal peduncle (Benthobatis has inconspicuous lateral tail folds). Some of these features also separate Narcine from non-narcinid electric rays (discussed below). Additionally, Narcine can be further distinguished from other narcinids by skeletal differences, which are separately discussed below for each narcinid genus.

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Narcine is distinguished from Discopyge by not having its typically shaped posterior median projection of the nasal curtain, or continuous pelvic fins posteriorly ventral to tail ("apron"). The median projection of the nasal curtain in Discopyge is wider than long, with curved lateral margins, and partly covers the exposed upper tooth band. This projection is very distinct from any median lobe of the nasal curtain in Narcine, which is not as conspicuous. Additionally, Discopyge has relatively much smaller eyes and spiracles, the latter being regularly oval in shape with elevated, smooth margins (spiracular shape and condition of spiracular margins vary greatly in Narcine, see below). Both genera possess exposed tooth bands when the mouth is closed. Discopyge is generally purplish-gray dorsally, with small white specks delimiting sensory pores on outer disc margins, while Narcine varies greatly in dorsal coloration but is never purplish-gray with small white specks on outer disc margins. The pores of the lateral-line canals in Discopyge are diagnostically large, and their presence over the mid-disc region forming an upside-down horseshoe-shaped figure is diagnostic of Discopyge (no pores exist as such on the mid-disc region of Narcine). Discopyge is fleshy and somewhat soft, especially at its outer disc margins, and is relatively thick dorso-ventrally; Narcine is not as fleshy and soft normally and is not as thick dorso-ventrally. There are also anatomical distinctions between both genera: the shape of the scapular cartilages (stouter, with a more broad articulation with suprascapula in Discopyge), posteriorly directed projections from both sides of suprascapula in Discopyge (absent in Narcine), suprascapula very straight across in Discopyge (slightly curved in Narcine), distal spatulate tips of prepelvic processes (more developed or expanded in Discopyge), degree of anterior extension of mesopterygium (longer mesopterygium relative to prop- and metapterygium in Discopyge), branching of antorbital

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cartilages (more extensive branching on posterior portion of antorbitals in Discopyge, with different arrangement of antorbital foramina), absence of trochlear nerve and facio-palatine foramina in Discopyge (both present in Narcine), and ceratohyals contacting first hypobranchials (not contacting in Narcine).

Narcine is distinguished from Diplobatis by the fusion of dorsal side of the nasal curtain and ventral side of the posterior nasal flap in the latter genus (not fused in Narcine), the lack of basonasal fenestrae in the ventral rostral region of Narcine (uniquely present in Diplobatis), suprascapula projecting downwards laterally to connect with low scapula in Diplobatis, lack of facio-palatine foramen in orbit of Diplobatis, lack of small, posterior projection on antorbital cartilages in Diplobatis, and ceratohyals contacting first hypobranchials in Diplobatis. Also, the claspers in Narcine are not concealed dorsally by the pelvic fins as they are in Diplobatis (the pelvic fins adjoin the claspers laterally in Narcine, as the pelvics do not encase the claspers).

Narcine is easily separated from Benthobatis by the lack of developed eyes in the latter genus (well developed in Narcine), well developed lateral tail folds in Narcine (inconspicuous and barely noticeable in Benthobatis), conspicuous shape of anterior rostral region in Benthobatis (laterally expanded and sub-rectangular close to anterior disc margin, in Narcine the anterior rostral region is not expanded laterally to the same extent), lack of facio-palatine foramen in orbit of Benthobatis (present in Narcine), and ceratohyals also contacting first hypobranchials in Benthobatis. Also, specimens of Benthobatis are softer, generally more fragile than specimens of Narcine (Carvalho [in press] provides further diagnostic characters for Benthobatis).

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Narcine is distinguished from torpedinoid (Torpedo and Hypnos) and narkid (Narke, Heteronarce, Temera and Typhlonarke) genera by the following combination of internal and external characters: tooth bands are exposed and easily visible when mouth is closed in Narcine (tooth bands not exposed in any non-narcinid genus); nostrils not elongated antero-posteriorly running parallel to nasal curtain (a synapomorphy of narkids); nasal curtain usually without sensory pores posterior to nostrils, or, if sensory pores are present, not in great quantity throughout entire length of nasal curtain (characteristic of narkids); eyes developed and visible externally (eyes not externally visible in Typhlonarke); presence of two dorsal fins (one dorsal fin Narke and Typhlonarke, no dorsal fins in Temera); a deep groove surrounding the mouth and labial cartilages (not as complete and deep in other genera); a broad rostrum composed of a flattened, wide plate (no such rostrum present in any non-narcinid genus), supporting antler-like antorbital cartilages antero-laterally (antorbitals variously but differently configured in non-narcinids); wide and rectangular rostral fontanelle (absent in non-narcinids); flat and widened internasal region separating nasal capsules (internasal region reduced in non-narcinids); stout, protusile jaws (jaws either thin or not protrusile in non-narcinids); upper and lower jaws interconnected through two pairs of triangular labial cartilages giving support to "lips" surrounding exposed tooth bands (labial cartilages absent in torpedinids, and three pairs are present in narkids according to Holmgren, 1941: 60); large, heart-shaped basibranchial copula that is about as wide as long (wider and much shorter in narkids, rounder in torpedinoids); antero-posteriorly elongated and wide hypobranchial plate, articulating with three pairs of ceratobranchials laterally, and with wave-like external margin (hypobranchials not fused in torpedinoids to form elongated plate, and in narkids hypobranchials not as stout,

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separated by a wide gap); ceratohyals reduced, slender and rod-like, non-suspensory and therefore not directly connected with hyomandibulae (ceratohyals short and stout, suspensory and attached to hyomandibulae in Narke and Typhlonarke, absent or very reduced in torpedinoids).

SKELETAL ANATOMY: This section presents a description of the skeleton of Narcine based on the type-species, N. brasiliensis. The objective is to further provide a basis for the allocation of species to Narcine. Detailed descriptions of the skeleton were not attempted seperately for each species, because variation among species of Narcine in this regard is not great (variation, however, is significant in certain anatomical aspects, such as antorbital cartilage morphology). Statements concerning the distribution of characters within Narcinidae and Torpediniformes are included in this section for comparative purposes.

The following account is based primarily on a cleared-and-stained specimen (UERJ-DBAV 1176.4, 166 mm TL) of N. brasiliensis from the coast of Cananéia, off the state of São Paulo, Brazil, which is close to the type-locality of N. brasiliensis. Additional specimens used for the description are not necessarily of N. brasiliensis (as defined in this paper, see section on N. brasiliensis below). These specimens are as follows: a dissected specimen (N. brasiliensis, MCZ 644, from Rio de Janeiro), a dry skeleton (N. bancroftii, AMNH 218276SD, from the Gulf of Mexico, Alabama), a wet skeleton (N. bancroftii, AMNH 90769SW, from the Gulf of Mexico, Alabama), and other cleared and stained specimens (N. bancroftii, AMNH 2488CS, from Caximbas, Florida; N. cf. brasiliensis, DBAV-UERJ 776.3, from northeastern Brazil, Bahia state; N. cf. bancroftii USNM 216829, off northern Brazil, state of Maranhão).

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Statements regarding the distribution of features within Narcine are also based on other cleared and stained material (N. rierai, N. sp. nov. D, N. sp. nov. F; material listed in species accounts), dry skeletons (N. tasmaniensis) and radiographs (of all species).

Neurocranium: Neurocranium well calcified, with reinforcing prismatic calcification over most neurocranial regions (occasionally in more than one layer), except on distal tips of antorbital cartilages. Neurocranium about three times longer than wide (Fig. 7), with elongated and broad rostrum anteriorly occupying roughly 50 percent of neurocranial length. Neurocranium with ventro-laterally protruding nasal capsules (Fig. 7) articulating with stout antorbital cartilages (referred to only as "antorbitals" subsequently), and laterally bulging, longer-than-wide otico-occipital segment.

Post-rostral neurocranium widest at level of nasal capsules (Fig. 7), even when excluding antorbital cartilages. Rostrum elongated, widest at anterior disc tip, tapering only slightly towards level of nasal capsules. Rostral fontanelle (termed "precerebral fontanelle" by Miyake, 1988; Miyake et al., 1992) just wider than long and circular. Precerebral fontanelle situated posterior to rostral fontanelle. Precerebral fontanelle is sub-rectangular and widest anteriorly, with circular posterior border at level of nasal capsules, and straighter anterior border. Posterior border of precerebral fontanelle is close to mid-length of neurocranium. Lateral to anterior margins of rostral fontanelle are paper-thin extensions of cartilage, projecting as lateral rostral components on each side of main rostrum, connecting the rostrum to the antorbitals and giving support to anterior disc region (Fig. 7). These chondrifications (termed here "lateral rostral cartilages") are hialine, with little superficial calcification, stouter at anterior disc margin and conspicuously pointed posteriorly, extending to just beyond level of

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posterior margin of rostral fontanelle. The lateral rostral cartilages are connected to the rostrum by means of a small cartilaginous bridge, but are less strongly connected to antorbitals. There are no signs of paired basonasal fenestrae on the floor of the rostrum inside precerebral fontanelle as in typical Diplobatis (the basonasal fenestrae is considered here a synapomorphy for Diplobatis within Narcinidae; terminology for these fenestrae follows Fechhelm and McEachran, 1984: 184). In lateral view, rostral region of neurocranium is deepest posteriorly at level of nasal capsules (Fig. 7), and is very thin close to anterior disc margin. Lateral rostral fenestrae (termed "frontoparietal fenestrae" by Fechhelm and McEachran, 1984; "lateral fenestra of rostral cartilage" by Miyake, 1988) present on both sides of rostrum, extending from level of antorbitals to mid-rostral length, lateral to precerebral fontanelle. Lateral rostral fenestrae oval and elongated, relatively large compared to Diplobatis (fenestrae absent in both Discopyge and Benthobatis). Two strands of strong ligamentous tissue connect ventral side of posterior central rostral area with internasal space; both strands join to become one stouter ligament before connecting to internasal space.

Nasal capsules sub-circular (Fig. 8), with large, triangular protuberances (termed here "nasal capsule horns") lateral to "preorbital canals" on dorsal aspects, adjacent to articulation between nasal capsules and antorbitals (nasal capsule horns present in Discopyge, Diplobatis and Benthobatis as well, but not as developed in Benthobatis as in other narcinids). Articulation for antorbitals on lateral aspects of nasal capsules large and irregularly shaped. Antorbitals with postero-ventrally directed processes before mid-length (termed "posterior processes of antorbital cartilages"), which are heavily branched distally close to disc margins. Typical narcinid "antler-like" shape of antorbitals very conspicuous. Distal tip of antorbitals

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fibrous and hialine in nature, not heavily calcified, even though small prismatic calcifications are present. Antorbitals covered by tight connective tissues, and strong connective fibres are present between lateral aspect of rostrum and each antorbital cartilage. Three small foramina are present on antorbitals laterally, the largest foramen is more posterior, the smallest is more anteriorly located. All foramina are situated mesially in relation to terminal branching of antorbitals, and are readily visible in dorsal view; in ventral view only one foramen on left side and two on the right are visible. Antorbitals typically bifurcate at slightly less than two-thirds distance between articulation with nasal capsules and disc margins. Antorbitals stout at bases, becoming progressively more flattened toward disc margins; more calcification is present proximally. Nasal apertures covered with highly curved nasal cartilages that are fibrous and weakly calcified (Fig. 8); nasal cartilages provide support for narial flaps.

No supraorbital crest on neurocranium overlying orbital region (as with all Torpediniformes; Compagno, 1973). Orbital region relatively elongated, occupying close to one-half of post-rostral neurocranial length (Fig. 8). Fronto-parietal fontanelle elongated, very narrow, especially at its mid-length, and very shallow, without distinct anterior margin. Fronto-parietal fontanelle beginning just posterior to precerebral fontanelle (separated from it by the narrow epiphysial bar) and terminating at level of (and medial to) otic capsules, anterior to parietal fossa. Parietal fossa triangular, with separate endolymphatic and perilymphatic foramina. Both pairs of foramina opening mesially, and not strictly dorsally, into parietal fossa (especially endolymphatic foramina). No suborbital ridge underlying orbit, although well-defined subotic shelf is present (further detailed below).

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The identity of the "preorbital canal" is questionable in narcinids and perhaps in all torpediniforms. The preorbital canal proper typically bears two distinct foramina, one for the entry of the associated nerves at the preorbital wall area (orbital foramen), and one for the exit of the nerves anterior to the preorbital wall (external foramen; terminology here is that of Compagno, 1988). However, at least in narcinids, the nerves typically associated with the preorbital canal run over the nasal capsules and into the rostral region, thus not entering and exiting the preorbital wall area as in other elasmobranchs. Therefore, the identity of the large fenestra or foramen antero-dorsally positioned on the nasal capsules (termed "preorbital canal" for Diplobatis by Fechhelm and McEachran, 1984) is uncertain. The orbital foramen is absent in narcinids. These terms are here applied for convenience (in quotation marks). In N. brasiliensis, the "preorbital canal" (corresponding to the "external foramen") lies on the antero-dorsal aspect of each nasal capsule, is circular and large, and bears a close relationship to the superior oblique muscle of the eye, which originates from its superior border and may have fibres originating from slightly inside the foramen.

In lateral view (Fig. 7), the anteriormost foramina visible in the orbital region are the antero-medial orbitonasal canal (for the passage of veins into the nasal capsules), and, just dorsal to the orbitonasal canal, the anterior cerebral vein foramen. The former is relatively larger than the latter. A small, inconspicuous foramen lies underneath the orbitonasal canal, has a ventral orientation, and seems to be connected to the orbitonasal canal by means of a vertical passage or tunnel (not visible in Fig. 7A). Just posterior to these foramina is the central, large and circular optic (II) nerve foramen, situated just anterior to mid-orbit. Postero-dorsal to the optic nerve foramen is the small foramen for the trochlear (IV) nerve, which lies more or less in

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between the optic nerve foramen and the hialine optic stalk (or pedicle), but situated very dorsally, close to the cranial roof. Just above the optic stalk is a small foramen for the oculomotor (III) nerve, and below and slightly posterior to the optic stalk is the small foramen for the efferent pseudobranchial artery.

The very large foramen termed "orbital fissure" by Fechhelm and McEachran (1984; "trigeminal lateralis foramen" of Miyake, 1988) is the dominating foramen in the orbit (Fig. 7A), from which many nerve masses exit the neurocranium to pass both anteriorly and ventrally within the orbit. The "orbital fissure" is larger than the optic nerve foramen, and located towards the posterior orbital wall, at the junction between the otic and orbital regions of the neurocranium. According to Miyake (1988), the "orbital fissure" serves as the exit from the neurocranium for the following rami (terminology as in Miyake, 1988: 316): ramus ophthalmicus lateralis, ramus buccalis lateralis, ramus oticus lateralis, ramus ophthalmicus superficialis V, ramus mandibularis V, ramus profundus V, and the ramus maxillaris V. My specimens seem to show four distinct nerve bundles exiting the "orbital fissure," but it is not certain which rami of the trigeminal (V) and facial (VII) nerves are bundled together. Miyake's seven rami may be partitioned into the four observed nerve bundles, but in which specific pattern is presently unclear. At least the superficial ophthalmic trunk, composed of both trigeminal (V) and facial (VII) components, is readily observed leaving the "orbital fissure" and running anteriorly in between the eyes and orbits, overlying the optic muscles, passing dorsal to the nasal capsules and branching distally to innervate anterior disc regions lateral to the rostrum. The superficial ophthalmic trunk probably is composed of the ramus ophthalmicus lateralis and ramus ophthalmicus superficialis V. Another nerve bundle runs antero-ventrally to

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innervate areas lateral and ventral to the rostrum, and is composed probably of rami from both the trigeminal (r. maxillaris V) and facial (r. buccalis lateralis) nerves as well. The remaining two nerve masses innervate the jaws (ramus mandibularis V) and the rostral region (ramus profundus V). A smaller branch does not leave the neurocranium but instead passes dorso-laterally to innervate sensory regions of the membranous labyrinth and semicircular canals (auditory [VIII] nerve). "Orbital fissure" is the term retained here, although this does not necessarily imply that the orbital fissure of other elasmobranchs is the same structure. The nerves exiting the orbital fissure of carcharhinoid sharks, for example (Compagno, 1988), differ from the pattern observed here for N. brasiliensis. There is also a positional difference as the orbital fissure is more dorsally situated in narcinids compared to carcharhinoids, and the narcinid "facio-hyomandibular lateralis foramen 2" (of Miyake, 1988; = hyomandibular branch of facial nerve foramen here) probably corresponds more with the orbital fissure of other elasmobranchs positionally. However, "orbital fissure" is retained here for narcinids until further work clarifying the topographical and nerve-mass similarities can be done.

Posterior to the "orbital fissure" is the large foramen for the hyomandibular branch of the facial nerve (termed "facio-hyomandibular lateralis foramen 2" by Miyake, 1988). Two separate nerves exit this foramen, which correspond to the "r. mandibularis lateralis" and "r. hyomandibularis VII" (= hyomandibular branch of facial nerve), according to Miyake (1988). These nerves innervate the hyomandibular-spiracular region. A small foramen ventral to and in between the "orbital fissure" and the hyomandibular branch of the facial nerve foramen is the "facio-palatine foramen" (sensu Miyake, 1988), from which the palatine branch of the facial nerve exits the orbit to innervate the mouth area ("r. palatinus VII" of Miyake, 1988) (Fig. 7A).

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This foramen is not present in Temera, Discopyge, Benthobatis and Diplobatis, and has been reported as absent in Narke and Typhlonarke as well (Miyake, 1988). I have seen it in Torpedo torpedo, but the condition in Hypnos and Heteronarce is still unknown. The presence of the facio-palatine foramen in Narcine may be unique within the Narcinidae and therefore a defining character of the genus, but its universal distrubution among Narcine species is also still under investigation. Also, because the facio-palatine foramen apparently is present in at least some species of Torpedo, a generic-level phylogeny for electric rays is necessary before this character can be used as a defining feature of Narcine.

Posterior to the orbit and situated laterally and slightly posteriorly on the otic region of the neurocranium are the well developed glosspharyngeal (IX) and vagus (X) foramina. Both are exits for stout nerve bundles and occur close together. The otic region has a bulging shape in general aspect. Ventrally on the neurocranium (Fig. 8A), the paired foramina for the internal carotid arteries are situated at close to the posterior one-third of neurocranium (as measured from rostrum), lying ventral on the same plane as the "orbital fissure." The neurocranial floor projects slightly laterally as a small shelf (subotic shelf) lateral to the glosspharyngeal and vagus nerve foramina.

Mandibular, hyoid and branchial arches: Jaws stout, lower jaws thicker than upper jaws. Both lower and upper jaws are not fused at mid-line, and are closely held together by two pairs of labial cartilages (Fig. 9). Labial cartilages triangular in outline, with portions distal to mouth opening terminating in a weakly bifid fashion. Labial cartilages provide support for the "lips" surrounding the exposed tooth bands. Mesial to the spiracular cartilages, and dorsal to the upper jaws, are a pair of triangular, calcified cartilages (termed "basihyoids" by

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Compagno, 1977 and Fechhelm and McEachran, 1984). The identity of these cartilages remains unknown, but it is probable that they are not basihyoids as they seem to be situated too far anteriorly in the pharyngeal cavity to be of hyoid-arch origin. They may represent additional labial cartilages displaced dorsally, as their shape is very similar to that of the two pairs of labials articulating with the jaws. However, as they lie dorsal to the integument of the mouth cavity, this possibility is very remote. It is more likely that these cartilages are related to the spiracular cartilages, due to shape and positional similarities. I do not believe in the interpretation of previous authors who considered these cartilages basihyoids, as they lie *dorsal* to the mouth. Further work is needed for a more reliable inetrpretation. These cartilages were first described by Henle (1834) as "palatine cartilages" (see also Holmgren, 1941: 62), and this is the terminology retained here.

The hyomandibulae articulate with the neurocranium from the posterior orbital area to the anterior otic region via a relatively long, curved, hyomandibular facet on the neurocranium. The beginning of this facet is situated ventral to the hyomandibular branch of the facial nerve foramen, and the facet terminates anteriorly and ventrally to the glossopharyngeal foramen in the otic region. Small triangular processes protruding laterally from the neurocranial floor abutt with the hyomandibulae at their posterior ends. The hyomandibulae themselves are stout (Fig. 9), dorso-ventrally flattened, and wider closer to the neurocranium. Hyomandibulae articulate with jaws by strong connections with the lower jaws, by means of ligaments throughout their length and through a stronger terminal ligament. Anterior to the hyomandibulae are calcified, sub-triangular, pre-spiracular cartilages, giving support to the anterior spiracular wall (hyomandibulae support the posterior spiracular wall).

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The ventral gill arches are composed primarily of five pairs of stout ceratobranchials, one pair of well-developed hypobranchial elements and a large basibranchial copula (Fig. 9B). The unique pair of hypobranchials are long, slightly oval in outline, contact the basibranchial plate posteriorly and articulate entirely with ceratobranchials 1 – 3 laterally, and partially with ceratobranchial 4. These paired hypobranchials are probably formed of fused hypobranchials 2 – 4 (Miyake and McEachran, 1991), and have processes branching laterally that contact the second and third ceratobranchials, giving the hypobranchials a wave-like outer margin. This particular hypobranchial configuration is unique to Narcine, as in all other genera within Narcinidae and Torpediniformes the hypobranchials do not present a sinuous latero-external margin which articulates with ceratobranchials 2 – 3, even when the hypobranchials are similarly elongated cartilages formed of fused individual hypobranchials (hypobranchials are fused into one large element in Narke, Typhlonarke, and Diplobatis; other genera present more than one hypobranchial element that may involve fusion to a lesser extent: Hypnos, Benthobatis and Discopyge). Anteriorly, each hypobranchial contacts a smaller, curved "hypobranchial 1" cartilage (also identified in the literature as "basihyal" by Shirai, 1992). This cartilage is paired, therefore it cannot be the basihyal which is single in elasmobranch taxa that possess it. Perhaps these cartilages are hypohyals, but I retain the previous usage of "hypobranchial 1" for consistency. A small, semi-circular element is present in between the elongated hypobranchial and ceratobranchial 4, perhaps representing a vestigial hypobranchial 4 or 5. Basibranchial plate large, flattened and somewhat heart-shaped, with a central, circular area of reduced calcification posteriorly. Ceratobranchials stout and flattened; last ceratobranchial distinct in morphology, and articulating with scapulo-coracoid posteriorly. Ceratobranchials 1 – 4 stouter

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at articular area with epibranchials. Ceratobranchials 1 – 4 with anterior, elongated ridge throughout most of their length (Fig. 9B).

Anterior to first ceratobranchial is the slender ceratohyal, which does not contact the "hypobranchial 1" cartilage, and is positioned adjacent to the stouter ventral pseudohyal cartialge (Miyake et al. [1991] believed the ceratohyal to be lacking in Narcine brasiliensis, but this is contradicted by my specimens). According to my specimens, the ceratohyals contact "hypobranchial 1" in Discopyge, Diplobatis and Benthobatis within the Narcinidae. Miyake et al. (1991) interpreted the ceratohyal as the pseudohyal in Discopyge, thus failing to recognize the ceratohyal – "hypobranchial 1" contact in this genus. My distinction between ceratohyal and pseudohyal (in this case ventral pseudohyal) depends not only on topographic considerations, but also on the presence or absence of gill-rays, which are not present on the ceratohyal but occur invariably within Torpediniformes, as far as known, on the pseudohyal bar (more on the identity of these cartilages can be found in Krivetsky, 1917; de Beer, 1932; Hamdy and Khalil, 1963; cf. Gegenbaur, 1872). Dorsal pseudohyal slightly stouter than ventral pseudohyal. Both pseudohyal cartilages occur between ceratohyal and first ceratobranchials, and are more slender than ceratobranchials. Occasionally present between ceratobranchials 4 and 5 on each side is a slender and weakly calcified unidentified cartilage, running parallel to ceratobranchials (not shown in Fig. 9B).

The dorsal gill arch elements are composed of four stout and uniform epibranchials, one modified epibranchial (epibranchial 5), and four separate, highly curved pharyngobranchials (Fig. 9B). The epibranchials have processes on their external aspect (on the side of gill-rays) projecting postero-laterally. Epibranchials 1 – 4 with a small foramen close to articulation with

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ceratobranchials. Epibranchials not as long as ceratobranchials, and with a slightly elevated ridge at anterior margins. Epibranchials 1 – 4 more or less equal in size and shape, being elongated and flattened. Epibranchial 5 semi-circular, not elongated and articulates with scapulo-coracoid posteriorly. The first three pharyngobranchials are sub-triangular, with posteriorly directed extensions that contact succeeding pharyngobranchials. Shirai (1992) labeled this posterior extension the "process of pharyngobranchial for joint with succeeding epibranchial" and illustrated the condition for "Narcine timlei." However, in N. brasiliensis, the posterior extension articulates almost exclusively with the succeeding pharyngobranchial, and not the succeeding epibranchial. The last pharyngobranchial is different in shape, being highly arched and contacting the penultimate pharyngobranchial and last epibranchial. Epibranchial 1 articulates partly with pharyngobranchial 2, as there is no separate pharyngobranchial 1. If the first pharyngobranchial is missing, or if the last pharyngobranchial represents a compound element formed by the fusion of the two last pharyngobranchials, remains to be clarified.

All ceratobranchials and epibranchials, along with the pseudohyal arch, are associated with gill-rays on their external surfaces. These gill-rays expand distally into flattened, plate-like elements that provide much support for the gill lamellae, and can sometimes be fused proximally to give the impression that a continuous gill "basket" supports the gills. The expanded distal sections of the gill-rays in torpediniforms have been called "extrabranchials" by previous authors, probably in error (e.g., Wiedersheim, 1886; Shirai, 1992; cf. Foote, 1897).

Axial and appendicular skeleton: The vertebral column of Narcine articulates with the neurocranium through a well-developed cervico-thoracic synarcual cartilage (Fig. 12A) (a posterior, thoraco-lumbar synarcual cartilage is absent in Torpediniformes). The synarcual

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cartilage is composed of fused vertebrae, and bears well-developed triangular lateral projections (lateral stays) at just posterior to its mid-length. The lateral stays are thin and overlie the articulation between the last pharyngobranchial and synarcual base. Pharyngobranchials contact synarcual cartilage laterally, fitting into small articular facets. Lateral stays continue posteriorly as long, thin segments past level of individual vertebrae (termed "posterior extension of synarcual" in Fig. 12A) . Individual vertebrae, and foramina through which spinal nerves exit, are noticeable mesially along the synarcual cartilage axis. Individual vertebrae begin at level of approximately mid-lateral stays. Spinal nerve foramina are situated dorsal to lateral stays. Ventrally the synarcual cartilage is a flat, uniform cartilage up to level of individual vertebrae, which is close to lateral projections of lateral stays. The synarcual cartilage articulates with the occipital condyles of neurocranium through a small peg-like ventral process. The suprascapula does not articulate with the synarcual laterally as in most other batoids, instead both antimeres contact each other dorsally where they are fused, but posterior to the synarcual cartilage.

Small, non-calcified neural spines are present as of the level of the lateral stays in the synarcual cartilage. Neural spines become more calcified closer to first dorsal fin, but are still thin, not plate-like, with individual neural spines for each vertebral centra (Fig. 12B). Neural spines enlarge and are more plate-like close to dorsal fin bases, where they provide support for dorsal fin radials. For both dorsal fins a set of three enlarged basal elements (enlarged neural spines) prevail: the anteriormost in taller than wide, followed by a central low and very wide neural spine, and the third and most posterior is shorter than the first but not nearly as wide as the second basal. These basals articulate with dorsal fin radials. Neural spines are also

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elongated as of level of caudal fin, providing it with endoskeletal support. Close to posterior two-thirds of caudal fin and in between elongated neural spines are shorter, more fibrous elements that are positioned as are neural spines, one for each vertebra. Hemal arches are conspicuous just posterior to lateral stays (Fig. 12A) as short, paired extensions articulating with lateral aspects of vertebral centra, and not as long as neural spines of same vertebrae. Hemal arches continue caudally up to level of first dorsal fin, where they become ventrally oriented as hemal spines (Fig. 12B). Hemal spines continue caudally, and provide endoskeletal support to the caudal fin. At the (ventral) beginning of the caudal fin, hemal spines are closely set and widened, plate-like.

The scapulocoracoid is thin and laterally expanded, arching slightly posteriorly to the extent that the articulation with pectoral basal cartilages lies at same level as the scapular process and suprascapula (Fig. 10). Latero-posteriorly directed segment of scapulocoracoid is stout. Procondyle is anteriorly oriented in relation to the lateral face of the scapulocoracoid, mesocondyle is laterally directed and the metacondyle is latero-posteriorly situated on the scapulocoracoid. All three articular surfaces for pectoral basals are sub-circular in shape and more or less equidistant. Suprascapula flatenned and well-calcified, as is scapulocoracoid generally. Anterior fontanelle triangular in frontal view and relatively large. Coracoid bar with small, central patch of hialine cartilage. Scapular process directed dorsally in a more or less straight fashion, not posteriorly directed as in Diplobatis. Propterygium stout, subdivided into six segments, the first being much longer than the rest. Mesopterygium anteriorly directed as a small, slender cartilage, situated slightly parallel to propterygium. Anterior to and almost contacting mesopterygium is a proximally expanded radial element. Metapterygium slightly

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longer than mesopterygium, and generally subdivided posteriorly. Both pro- and mesopterygium have sinuous external margins for articulation with radials. Radial elements occur in far greater number for the propterygium. Radials divided into four to six segments before becoming distally branched: more anterior radials in four segments, and more posterior radials in six segments. Two rows of branched radials contact unbranched radials distally. Radials occur between pro- and mesopterygium and between meso- and metapterygium. Radials for metapterygium are placed at a greater distance than for pro- and mesopterygium. Four nerve foramina are present on each side of scapulocoracoid, surrounding articular facets for basal cartilages. The predorsal and preventral foramina are situated, respectively, above and below the procondyle, and are large, about as large as the procondyle itself. The postdorsal and postventral foramina are dorsal and ventral, respectively, to the intersection between the meso- and metacondyles, and are smaller than the predorsal and preventral foramina.

Pelvic girdle with two pre-pelvic processes projecting anteriorly from both sides of puboischiadic bar (Fig. 11). Prepelvic processes with expanded, sub-triangular and flatenned distal tips that are not markedly calcified. Pelvic girdle generally well calcified. Four pairs of obturator foramina are present at both corners of puboischiadic bar, just mesial to long, filiform illiac processes which project dorsally. Sub-triangular post-pelvic processes are present at corners of puboischiadic bar. Posterior margin of puboischiadic bar slightly curved, with an almost inconspicuous central depression. Enlarged first radial element articulates with puboischiadic bar on its ventral surface, is shorter than succeeding radials, and is not distally

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branched as are succeeding radials. Metapterygium curved inward, also with sinuous external margin for articulation with radial elements.

REMARKS: As presently understood, Narcine is separated from other narcinid genera by a combination of characters mainly from external morphology. Benthobatis, Discopyge and Diplobatis all have unique defining features either of the skeleton or from external morphology, but Narcine has never been clearly demonstrated to be monophyletic (for characters corroborating the monophyly of Benthobatis, see Carvalho [in press]; for Diplobatis see Fechhelm and McEachran, 1984, and this study (above); for Discopyge see section above separating it from Narcine). However, the following characters are potential synapomorphies of Narcine, but are not yet confirmed as such as more species need to be studied, and a generic level phylogeny within Torpediniformes is currently in progress: i) fused hypobranchial plate with sinuous external margin, articulating with ceratobranchials 2 – 4; ii) presence of facio-palatine foramen; iii) conspicuous shape of basibranchial copula that bears a well-developed posterior process; iv) lack of contact between ceratohyal and "hypobranchial 1." These characters are discussed above in the section "Skeletal Anatomy." Further putative characters in the dorsal gill-arch elements are presently being studied.

Narcine is by far the largest genus of the Narcinoidea (Narcinidae and Narkidae) in numbers of species (Table 5 is a summary of nominal species of Narcine; cf. Tables 3 and 4). The revision below includes nine new species in addition to the 11 previously described that are presently recognized as valid. Species of Narcine are restricted to tropical and warm-temperate waters (less common in strictly temperate areas), occurring mainly on near-shore continental

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shelf regions, although some species inhabit continental slope areas as well. Although most species occur in shallow waters and are not collected from below 80 m in depth, some species may reach depths of more than 200 m on the continental slope, and one species has been recorded from a depth of more than 550 m (N. tasmaniensis, off the coast of New South Wales, Australia). Species of Narcine are widespread, having been collected from most oceans roughly in between the latitudes of 38°N and 38°S. No species of Narcine occur, as far as is known, off western Africa, in the Mediterranean and Red seas, off New Zealand, off the west coast of South America south of northern Peru, and off oceanic islands. The absence of Narcine from western Africa is probably related to the cold water of the Benguela current which is the dominant water mass in the region. Torpedo, a more temperate genus, is common in western Africa and in the Mediterranean Sea, and seems to occur in greater diversity in areas in which Narcine is not so prevalent. The absence of Narcine from the western coast of South America is probably also related to the predominantly colder waters of that region. A photograph of a putative Narcine specimen provides circumstantial evidence of its presence in New Zealand (Paulin, 1996; also C. Roberts, personal commun.). However, it is not clear that the specimen is unequivocally of Narcine, and its origin is not known but assumed to be from the vast continental shelf of New Zealand. Narcine has yet to be reported from there, even though abundant collections of the benthic electric ray genus Typhlonarke exist from New Zealand.

Stomach contents have revealed that species of Narcine eat a wide variety of invertebrates as well as bony fishes. Various polychaete species and small crustaceans are commonly encountered in stomach contents. Ctenoid and cycloid scales were observed

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frequently in the mouths of many species of Narcine, and dissections have revealed that they are capable of swallowing prey larger than would be expected given the constraints of their mouth architecture with strong, stout labial cartilages.

Key to Species of Narcine Henle, 1834

1a. Spiracles with warty, knob-like papillae on entire spiracular border (papillae more slender in smaller specimens). **2.**

1b. Spiracles smooth, devoid of any papillae on spiracular border. **4.**

2a. Dorsal coloration with entire preocular snout region devoid of conspicuous markings of any sort; generally with four or five distinct and circular ocelli on disc region (ocelli about equal to interocular distance in diameter), ocelli with outlines lighter than dorsal background color, and centers darker than dorsal background color. Narcine entemedor Jordan and Starks, 1895 (eastern Pacific coasts of Mexico, Central America and northern South America).

2b. Dorsal coloration with distinct dark brown to purplish-brown antorbital blotches or broad horizontal stripes occupying most of preocular snout region; dorsal disc region without four or five distinct and circular ocelli with outlines lighter than background color, and centers darker than background color. **3.**

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3a. Dorsal coloration with incomplete circles and ocelli formed by small brown spots (smaller than eye-diameter) over disc and tail regions; teeth in adult specimens of around 380 mm total length in no more than 22/23 rows (very rarely more – specimens larger than 480 mm total length may exceptionally have 27/28 rows). Narcine bancroftii (Griffith, 1834) (northern west Atlantic from North Carolina, Gulf of Mexico, Caribbean Sea and West Indies).

3b. Dorsal coloration without incomplete ocelli, composed generally of dark brown to blackish-brown horizontal stripes over disc and tail regions; teeth in 31/32 rows in large adults of around 380 mm total length. Narcine brasiliensis (von Olfers, 1831) (southwestern Atlantic, from southeastern Brazil to northern Argentina).

4a. Tail length as measured from cloaca to caudal fin tip is subequal to, and generally less than, disc width or length (tail length usually about 48 percent of total length, vs. disc width and length more or less 50 percent of total length). **5.**

4b. Tail length as measured from cloaca to caudal fin tip is much greater than disc width or length (tail length about 53 to 54 percent of total length, vs. disc width and length averaging usually about 40 percent of total length). **15.**

5a. Upper and lower tooth bands more or less of same size (both wide), or upper tooth band is just slightly wider; tooth bands broadly circular in outline and similar in shape. **6.**

5b. Upper tooth band much wider than lower tooth band; both tooth bands sub-triangular in shape. **14.**

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6a. Dorsal coloration uniform brown or light brown, to greyish-brown, without distinct reticulations, spots, blotches and horizontal stripes of any kind. Narcine timlei (Bloch and Schneider, 1801) (northern Indian Ocean to South China Sea).

6b. Dorsal coloration not uniform brown, composed of varying reticulations, spots, blotches and horizontal stripes over background color. **7.**

7a. Dorsal coloration composed of irregular, horizontal white stripes and vermiculations over brown to purplish-brown background. Narcine vermiculatus Breder, 1928 (eastern Pacific from Mexico to Costa Rica).

7b. Dorsal coloration not composed of horizontal white stripes and vermiculations over brown to purplish-brown background (dorsal coloration variously spotted, blotched and ocellated). **8.**

8a. Dorsal coloration composed of small white spots (roughly size of eye-diameter or smaller) in specimens up to 200 mm total length, or ocelli in larger specimens (close to length of dorsal fin base in diameter), over brown to purplish-brown background. Narcine sp. nov. F (eastern Pacific coast of Colombia).

8b. Dorsal coloration composed of various patterns of spots, reticulations and blotches, but without distinct small white spots or ocelli over brown to purplish-brown background. **9.**

9a. First dorsal fin clearly taller and with longer base than second dorsal fin. **10.**

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9b. First and second dorsal fins equal in height and length of base, or second dorsal fin slightly taller and with longer base than first dorsal fin. **12.**

10a. Dorsal coloration composed of few large, faint blotches and numerous small dark spots (smaller than eye-diameter) scattered over disc and tail, and even inside spiracles. Narcine sp. nov. I (Gulf of Oman and Bay of Bengal).

10b. Dorsal coloration without small dark spots over disc and tail and within spiracles. **11.**

11a. Disc averaging 44.9 and 43.8 percent of total length in width and length, respectively; branchial basket length always clearly greater than distance between last gill openings; 64 to 68 precaudal vertebral centra (only one specimen with 68), and 109 to 119 total vertebral centra. Narcine sp. nov. D (Gulfs of Oman and Aden).

11b. Disc averaging 48.0 and 47.5 percent of total length in width and length, respectively; branchial basket length subequal to distance bewteen last gill openings; 68 to 71 precaudal vertebral centra (only two of seven specimens with less than 70), and 119 to 127 total vertebral centra. Narcine sp. nov. E (southwestern Indian Ocean).

12a. Dorsal coloration composed of few dark large blotches and irregular smaller spots with slender white reticulated network over disc; preoral snout greater than preocular snout, preocular and prenasal snout regions about equal in length. Narcine sp. nov. G (Indonesia)

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12b. Dorsal coloration composed of dark spots and ovoid blotches, sometimes with dark elongated markings, but without network of slender, white reticulations over disc; preoral and preocular snout regions more or less equal, preocular snout always greater than prenasal snout area. **13.**

13a. Mouth width less than distance between outer margins of nostrils; nostrils prominent and relatively very large. N. maculata (Shaw, 1804) (Indo-Pacific).

13b. Mouth width equal to distance between outer margins of nostrils; nostrils not prominent and relatively small. N. lingula Richardson, 1846 (Indo-Pacific).

14a. Dorsal coloration with numerous small dark spots, smaller than eye-diameter, over most of disc and tail regions; preocular snout with same background coloration and generally with small spots present. N. brevilabiata Bessednov, 1966 (South China Sea and Gulf of Thailand).

14b. Dorsal coloration with less numerous small to medium-sized dark spots, greater than eye-diameter, over most of disc and tail regions; preocular snout with grey to brownish-grey coloration, lighter than background color of disc and tail regions, and generally without spots. Narcine sp. nov. H (from off Myanmar and the Philippines).

15a. Dorsal coloration with spots or horizontal stripes. **16.**

15b. Dorsal coloration uniform, without any spots or horizontal stripes. **17.**

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16a. Dorsal coloration with brown horizontal stripes over postocular disc and tail regions. N. westraliensis McKay, 1966 (western Australia).

16b. Dorsal coloration without horizontal stripes, and composed of large spots or variously-shaped blotches surrounded by smaller spots, smaller than eye-diameter, over disc and tail regions. Narcine sp. nov. A (northern Australia).

17a. Nasal curtain longer than wide. N. rierai (Lloris and Rucabado, 1991) (western Indian Ocean).

17b. Nasal curtain wider than long. **18.**

18a. Dorsal coloration dark brown; lateral tail fold well-developed and flap-like. N. tasmaniensis Richardson, 1841 (southern and southeastern Australia).

18b. Dorsal coloration light brown or yellowish-brown; lateral tail fold not flap-like, reduced to a slight ridge. **19.**

19a. Dorsal coloration yellowish-brown; disc width and length averaging 40.3 and 42.1 percent of total length, respectively. Narcine sp. nov. B (western Australia).

19b. Dorsal coloration light brown; disc width and length averaging 38.4 and 40.2 percent of total length, respectively. Narcine sp. nov. C (eastern Australia).

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Narcine brasiliensis (von Olfers, 1831)

Figs. 13 – 17, Tables 6 – 7

Torpedo ocellata Quoy and Gaimard, 1824: 199 (original description, not illustrated; type-locality: "Le Cap" [= Cape of Good Hope, South Africa], believed to be given in error, see discussion below; name unavailable as, and primary homonym of Torpedo ocellata Rafinesque, 1810); Duméril, 1865; Sérèt and McEachran, 1986 (in MNHN type-catalog).

Torpedo brasiliensis von Olfers, 1831: 19, pl. 2, fig. 4 (original description, illustrated; type-locality: Rio de Janeiro, Brazil).

Narcine brasiliensis: Henle, 1834: 31, pl. 1, figs. 1 – 2 , pl. 4, figs. 1 – 4, 8 (original description of Narcine, T. brasiliensis allocated to Narcine); Muller and Henle, 1841; Duméril, 1852; Duméril, 1865; Miranda Ribeiro, 1923: 37, pls. 18 – 19 (description, photograph; Rio de Janeiro); Bigelow and Schroeder, 1953: 107 – 123, figs. 24 – 25 (diagnosis, description, distribution, comparisons, numerous references in synonymy, in part); Eshmeyer et al., 1998 (compilation).

Narcine brachypleura Miranda Ribeiro, 1923: 36, pls. 16 – 17 (original description, illustrated; type-locality: Rio de Janeiro, Brazil); Bigelow and Schroeder, 1953: 123 (considered probable junior synonym of N. brasiliensis); Eschmeyer et al., 1998 (compilation).

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DIAGNOSIS: The possession of a uniform brown to greyish dorsal background coloration, with strong, dark antorbital patches and dark, undefined horizontal streaks over disc and tail (without incomplete ocelli over disc), in combination with 25/26 – 32/34 exposed vertical tooth rows in specimens over 340 mm total length, is unique to N. brasiliensis. N. brasiliensis can also be identified by the presence of spiracles with warty, knob-like papillae on entire spiracular border (spiracles smooth in all species of Narcine except N. bancroftii and N. entemedor). The latter two species differ in coloration from N. brasiliensis: N. bancroftii has small brown spots scattered on disc and tail base regions, with spots sometimes outlining ocelli and circular areas on disc; N. entemedor generally possesses a very clear set of four or five circular, small ocelli on disc, without antorbital blotches. Also, specimens of N. bancroftii have from four to six less rows of exposed teeth in specimens over 340 mm total length (teeth usually ranging between 21/22 – 24/25, some very large specimens over 450 mm total length may have a few more rows, but teeth typically in four, five or six more rows in specimens of same size of N. brasiliensis).

DESCRIPTION: Measurements and counts are given in Tables 6 and 7, respectively. Disc oval to broadly rounded in outline, with width and length more or less equal, even though both measurements somewhat variable in specimens (disc width ranges from 43.7 to 55.3 percent of total length [x = 51.0], disc length is between 45.7 to 56.0 percent of total length [x =50.2]). Greatest disc width at just anterior to two-thirds of disc length. Disc overlapping origin of pelvic fins posteriorly, and projecting forward before contacting trunk, leaving a slight notch at

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pectoral axil. Snout rounded to angular (especially angular in some large adult specimens). Preocular snout length variable, but moderately elongated, ranging from 8.9 to 14.2 percent of total length, and occupying around one-fourth of disc length. Electric organs relatively long, occupying between 21.5 and 32.3 percent of total length, and wide, ranging from 7.5 to 13.4 percent of total length. Electric organs originate dorsally at close to level of eyes on disc and continue caudally to more or less posterior one-fifth of disc. Gill-slits broad, more or less straight (not greatly semi-circular), and with slight median posterior projection. Branchial basket length proportionally small, as gill-slits appear relatively close together. Mesially, gill-slits are slightly directed anteriorly, and situated progressively closer to mid-line from first to last gill-slit. Eyes and spiracles adjacent, without significant gap in between. Eyes large and bulging in fresh or well-preserved specimens (for eye length, x = 3.1 percent of total length), and larger than spiracles (eyes may be shrunken more than spiracles in poorly preserved material, giving the impression that spiracles are greater). Spiracles more or less circular to ovoid, not situated at a slight angle in relation to eyes. Spiracles with thickly elevated borders, and with papillae on entire spiracular margin. In juvenle and smaller specimens (less than around 180 mm total length), papillae appear as slender, disjunct projections, but in larger adults papillae are thick and rounded, with a warty-like aspect.

Nasal curtain relatively short and very wide (nasal curtain about three times as broad as long), and without pronounced lateral lobes (but slight triangular lateral projection below nostrils may be present). Posterior margin of nasal curtain with more or less straight posterior margin, but slight curvature may be present mesially, and with minute fringes adjacent to its center. Nasal curtain only partially covering upper exposed tooth band in some specimens, and

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devoid of sensory pores posterior to level of nostrils. Nostrils small and circular, with small and slightly variable elevated borders posteriorly. Prenasal snout length averaging about one-tenth in disc length. Mouth slightly wider than distance between nostrils, but outer margin of nostrils generally situated lateral to vertical through mouth corners. Upper tooth band slightly broader than lower tooth band, but both tooth bands relatively long antero-posteriorly, appearing as wide as, or wider than, adjacent lips. Tooth bands with circular to sub-rectangular profiles. Teeth in 17/18 – 25/26 vertical exposed tooth rows in pre-adult to adult specimens ranging from 225 to 340 mm in total length (specimen 356 mm total length has 25/29); specimens of close to 400 or over 400 mm total length with 30/31 – 32/34 exposed tooth rows; smaller specimens of 110 mm total length with 12/13, and juvenile specimens of about 190 mm total length with 18/19 rows. Many specimens conspicuously with more rows of exposed teeth (generally only one or two more rows) in lower tooth band. Teeth closely packed together, but generally more so in lower tooth band. Teeth with very long and pointed cups in specimens reaching sexual maturity and in larger adults (both in males and females), on both exposed and (especially) not exposed rows (cusps when very pronounced ususally overlie bases of teeth in row closer to mouth opening). Teeth on exposed rows sometimes heavily worn down and blunt. Teeth with diamond-shaped to circular bases.

Pelvic fins broad and long; pelvic fin width ranges from 24.9 to 38.4 percent of total length ($x = 33.1$), pelvic fin length ranges from 15.4 to 31.2 percent of total length ($x = 24.0$). Pelvic fins begin just underneath posterior aspect of disc and extend caudally to level of first dorsal fin origin. Pelvic fins have a prominent free lobe at their posterior insertion to ventral aspect of tail in females. In male specimens, posterior free lobe of pelvic fins is smaller where

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pelvics adjoin to claspers, but still moderately expanded). Pelvic fins with proportionally large posterior margins. Laterally, pelvics vary from rounded to sub-angular, and without thick, fleshy lateral lobes. Claspers elongate and straight, not tapering from base to tip of clasper glans. In adult males, claspers project caudally to level of posterior first dorsal fin base, and are free from distal tip of pelvics by as much as one-third of their length. Tail length slightly less than disc width or length, averaging 46.3 percent of total length. Tail width measured at base averaging just more than 20 percent of total length; tail tapers significantly from base to tip of caudal fin. Lateral tail folds originate on lateral aspect of tail at vertical through mid-base or posterior two-thirds of first dorsal fin base, and extend caudally to insert on lateral portion of caudal peduncle. Lateral tail folds appear more prominent in smaller specimens where it is proportionally wider. Dorsal fins large and variable in shape. Both dorsal fins similar in height and length, but generally second dorsal fin slightly taller and longer at base. First dorsal fin originates over posterior lobes of pelvic fins, over pelvic connection to trunk at pelvic axil, but in some specimens first dorsal originates slightly posterior to pelvic axil. Dorsals with variably developed free lobes above base. Dorsals with sloping anterior margins, but more sloping in second dorsal than in first. Dorsals sub-acute to roundish at apex, and with more or less straight or upright posterior margins. Caudal fin tall and conspicuously fan-shaped; ventral surface of caudal fin more rounded in profile, while dorsal surface is more sloping and straight. Caudal fin with relatively straight posterior margin, and acute at both dorsal and ventral corners, but more acute at dorsal apex. Ventral lobe of caudal fin originates generally just anterior to dorsal lobe on caudal peduncle. Height of caudal fin just greater, in average, to

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height of both first and second dorsal fins. Distance between dorsals and distance between second dorsal and caudal fin more or less equal.

Pores of lateral-line and ampullary systems present both dorsally and ventrally (lateral-line pores absent on ventral surface, as with all electric rays examined). Pores of supraorbital lateral-line canal running in a straight line from anterior disc margin to posterior to eyes, just mesial to eyes. Posterior to eyes, the supraorbital canal continues as the postorbital canal, but few pores are present. Pores of infraorbital canal somewhat obvious, running in between eyes and spiracles and continuing anteriorly to disc margin. The hyomandibular canal is located at mid-distance between eyes and anterior disc border, and is a continuation of the infraorbital canal, branching laterally from it. The hyomandibular canal has pores lateral to, and outlining, electric ogans. Pores of the posterior extension of lateral canal run in a more or less straight or sinuous line just dorsal to lateral tail fold, from dorsal disc area (at junction with scapular segment) posteriorly towards caudal peduncle. Pores of lateral canal arch dorsally underneath first and second dorsal fin. Ventrally, scattered pores of ampullary system not occuring posterior to level of nostrils. Pores on ventral snout area in not well-defined rows, scattered from anterior snout border to nasal curtain. A small group of pores is present postero-lateral to each nostril.

Dorsal coloration somewhat variable, but generally with drab brown to chocolate brown background and distinct darker brown blotches over antorbital, mid- and lateral-disc, pelvic fins, tail and dorsal and caudal fins. Blotches of varying shape, but generally horizontally eleongated, without sharply defined margins. Antorbital blotches cover the anterior (preocular) snout region, and in some specimens follow the contours of antorbital cartilages. Antorbital

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blotches are connected posteriorly to dark streaks that cover antero-lateral disc margins in many specimens. Some specimens present over mid-disc region, a central, poorly-defined and circular blotch or spot posterior to interocular space. Streaks over disc region appear as horizontal, blurry stripes in many specimens, and occur from antorbital blotches anteriorly to base of tail region posteriorly. Streaks over base of tail may continue laterally onto pelvic fins. Lateral streaks are present at base of dorsal fins, more or less covering anterior portions of dorsal fins, and also at caudal peduncle and posterior caudal fin. Degree of develpoment of lateral streaks over tail and dorsal and caudal fins somewhat variable, as in preservative many specimens, including lectotype of T. brasiliensis von Olfers, 1831 (ZMB 4577), have faded color pattern over tail region. Many blotches and streaks are faded over disc region as well in many preserved specimens. Dorsal color pattern more vivid and strong in smaller, recently free-swimming specimens (around 110 mm total length). In these specimens, laterally expanded blotches over antorbital area and most of disc and tail regions appear as weak ocelli, as borders of blotches and streaks are somewhat more defined and darker in color. Ventrally specimens are uniform white to creamy-white, but some dark grey to brown blotches may be present posterior to electric organs or scattered on ventral disc region. These blotches are generally isolated and not numerous. Postero-lateral margins of disc and pelvic fins may be covered by grey to brown streaks.

REMARKS: von Olfers (1831) described Torpedo brasiliensis on the basis of two specimens from Rio de Janeiro, Brazil. One specimen was located and is in relatively good condition. It is therefore designated the lectotype of T. brasiliensis (ZMB 4577; Fig 13). The lectotype is a

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pre-adult or adult male (if pre-adult, it is very close to sexual maturity judging from the rigidity of its claspers), of 235 mm total length. It agrees very closely with specimens of similar size from Rio de Janeiro and southeastern Brazil in coloration, proportional measurements (Table 6), meristics (Table 7), and dentition. The lectotype is slit-open ventrally at mid-line, is only slightly shrunken, and has very long cusps on teeth close to mouth opening from both upper and lower tooth bands. The specimen contains original label information that indicates it was one of von Olfers (1831) original specimens (also Paepke and Schmidt, 1988). The second syntype (now paralectotype) is reportedly lost (Paepke and Schmidt, 1988). It was reported to be from the Anatomical Museum kept by J. Muller, and was collected by Sello in Rio de Janeiro (as was the lectotype; H.-J. Paepke, personal commun.). One specimen examined, ZMB 32753, is from the Anatomical Museum and dissected by J. Muller (as by arterial and venous preparations, H.-J. Paepke, personal commun.). This specimen fits the dimensions given to von Olfers' second specimen by Henle (1834; 260 mm total length), and may be the lost syntype. It is heavily dissected on its right side, but agrees with N. brasiliensis in general morphology of neurocranium, lateral sensory pores of tail, and in proportions. The spiracles appear to be papillated, but this is difficult to determine with certainty. Further investigation is required before this specimen is regarded as the paralectotype of T. brasiliensis von Olfers, 1831.

Torpedo ocellata Quoy and Gaimard, 1824 is preoccupied by Torpedo ocellata Rafinesque, 1810 (= Raja torpedo Linnaeus, 1758), and is permanently invalid as a primary homonym as long as Rafinesque's nominal species remains available. Torpedo ocellata Quoy and Gaimard, 1824 was described from three small specimens credited as from Table Bay, just

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north of the Cape of Good Hope (South Africa). All three specimens are extant (MNHN 7891 [2 specimens], MNHN 7516; Figs. 14 and 15), but are poorly preserved, and their proportional measurements are generally not very indicative of their original dimensions (Table 6). However, all three can be identified as N. brasiliensis (von Olfers, 1831) on the basis of coloration (similar to specimens of N. brasiliensis of around same total length), and in presenting clearly papillated spiracles (present only in N. brasiliensis, N. bancroftii [see below] and N. entemedor [see below]). Their proportions, although not very reliable, generally agree with specimens of N. brasiliensis of same size, as do positions of dorsal fins, pores on lateral aspect of tail and lateral tail fold. MNHN 7516 is designated lectotype, as it is the best preserved of the three specimens.

The original locality of the type-series of T. ocellata, however, is problematic, as no specimens of Narcine have been collected from South Africa (N. rierai, known from Mozambique, may extend into eastern S. Africa, but this is speculative), and extensive surveys have been conducted in S. African waters (papers reviewing electric rays from S. Africa include von Bonde and Swart, 1923; Wallace, 1967; Compagno, 1995). The waters off the Cape of Good Hope (western S. Africa) are probably below the normal temperature tolerance of Narcine, as the predominant water influx is from the relatively cold Benguela current. Quoy and Gaimard's (1824) account of T. ocellata is rather brief, but the description given matches the three syntypes identified above (there is no doubt concerning the composition of the original type-series). Quoy and Gaimard (1824) describe a number of new species of fishes from all over the world, so it is possible that original labels or localities were confused, as the "Uranie" collected from wide-ranging areas.

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Miranda Ribeiro's (1923) description of Narcine brachypleura is based on a single specimen from off Rio de Janeiro, an adult male of 321 mm total length (MNRJ 548; Fig. 16). It agrees in every character with typical specimens of N. brasiliensis from southeastern Brazil. Miranda Ribeiro's only defining character is the relatively more slender disc, a character somewhat variable and preservation-dependent. Disc length and width for the holotype of N. brachypleura fall within the range accepted for N. brasiliensis (Table 6). The holotype is well-preserved, permitting N. brachypleura Miranda Ribeiro, 1923 to be clearly synonymized with T. brasiliensis von Olfers, 1831.

N. brasiliensis is very similar to N. bancroftii from the northwestern Atlantic, Gulf of Mexico and Caribbean Sea. Both species have been referred to as N. brasiliensis, as previous authors have stressed the similarities of both species as an indication of their conspecificity (e.g., Bigelow and Schroeder, 1953). The separation of both species is difficult, but is here recognized primarily on the basis of numbers of tooth rows in adult and/or close to adult specimens (along with color pattern). The following account is a comparison of large specimens from throughout the range of Narcine in the western Atlantic. A large female (441 mm total length) from Rio de Janeiro (MCZ 643) has 31/32 exposed tooth rows, which is typical for specimens of that size from southeastern Brazil (some specimens with 32/34), while a 442 mm total length female female from Florida (USNM 66986) has 24/24 exposed tooth rows (MCZ 39898, 439 mm TL, from Florida, has 22/24). A female 403 mm TL specimen from North Carolina similarly has 23/23 exposed tooth rows (USNM 222486), compared to a 395 mm TL female specimen from Rio de Janeiro (MCZ 655) that has 30/31. A 376 mm TL female from Texas (Port Isabel) has 21/22 exposed rows, while a specimen of similar size from

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southeastern Brazil (374 mm TL, MCZ 308, male) has 31/31 (a 356 mm TL specimen from Rio de Janeiro has 26/29; MCZ 645). A 509 mm TL female specimen from Belize (USNM 301384) has 26/25 exposed rows. A 384 mm TL female specimen from Colombia (ANSP 103930) has 22/21. A 391 mm TL female from Venezuela (MCZ 51034) has 19/20 exposed rows. Two large Venezuelan specimens are slightly exceptional in that they have a higher number of exposed rows (ANSP 120022, 435 mm TL with 28/28; ANSP 120033, 452 mm TL, 26/29), however the number is still lower than specimens of similar size from southeastern Brazil. A 479 mm TL specimen from Jamaica has 24/25 exposed rows (BMNH 1879.7.1.31), and a 389 mm TL specimen from Jamaica has 20/21 (FMNH 2805). A very large specimen of N. bancroftii from Martinique in the Lesser Antilles (MNHN 7886) has 28/29 rows, but is 561 mm TL, some 120 mm larger than the largest specimen examined of N. brasiliensis, and still does not disply the amount of exposed tooth rows seen in large specimens of the latter species (also with a 543 mm TL specimen from Surinam, that has 28/29 rows). A more comparably-sized specimen from Martinique (MNHN 7888, 400 mm TL) has 20/21 exposed rows. A 431 mm TL female specimen from Guyana (BMNH 1961.8.31.23) has 24/23 rows. A 490 mm TL female from Maranhão state (northern Brazil) has 26/25 rows, still less exposed tooth rows than 400 mm TL specimens from southeastern Brazil. Specimens of N. brasiliensis have in general five or six less vertical rows of exposed teeth than specimens of N. bancroftii (northern Brazil to North Carolina and the West Indies).

The dorsal color pattern is also different between N. bancroftii and N. brasiliensis. Specimens of the latter species typically do not present incomplete ocelli, formed of small spots outlining large ovoid or circular spaces over disc and tail regions (very few exceptions have

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been observed). The dorsal color pattern of N. brasiliensis consists typically of horizontally ovoid or circular ill-defined darker stripes over disc and tail, without isolated or partially fused small spots (smaller than eye-diameter). Smaller specimens also do not typically present the incomplete ocelli, but these are present in specimens of comparable size of N. bancroftii (fig. 24 of Bigelow and Schroeder, 1953 depicts this difference very well between specimens from Florida, St. Vincent [Lesser Antilles], Rio de Janeiro, and Santa Catarina [southern Brazil]). Specimens examined from close to the southern distribution of this species (Rio Grande do Sul state) are more greyish in background color, and may be devoid of conspicuous dorsal markings other than dull blotches over disc and tail. Many (perhaps most) preserved specimens have only antorbital blotches remaining, not including background coloration (e.g., lectotype of T. brasiliensis). The separation of both species is presently somewhat inadequate, but given their extreme geographical separation and the distinctions in tooth rows and coloration they are here considered two distinct species. Specimens from northeastern Brazil are being studied to discern to which species they belong, but preliminary results indicate they have fewer tooth rows than specimens from Rio de Janeiro, and are presently identified as N. bancroftii.

Specimens of 110 mm total length are free-swimming, without noticeable yolk-scars, and have already around 13/12 exposed tooth rows, with small, blunt cusps, but some specimens (e.g. type-series of T. ocellata Quoy and Gaimard, 1824) with relatively long and sharp cusps. Smaller specimens of about 72 mm total length generally have no external teeth, but spiracles are already papillated (some specimens of same size presented external teeth). Males mature sexually by about 250 mm total length, and presumably so do females.

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GEOGRAPHICAL DISTRIBUTION: Recognized previously as a very widespread species ranging from North Carolina to Argentina, N. brasiliensis is here restricted in distribution to occur only in the southwestern Atlantic, off the coast of southeastern Brazil (Espírito Santo state) and extending south to northern Argentina (Fig. 102). Its presence in northern Argentina is reported to be rare (specimens were not examined from Uruguay and Argentina). This is a shallow, in-shore species, collected in depths ranging from the intertidal to about 40 m.

MATERIAL EXAMINED: (216 specimens, 50 – 445 mm total length). **Brazil.** Espírito Santo: MZUSP (2 uncat.). Rio de Janeiro: ANSP 121547 (2); BMNH 1923.7.30.9; BMNH 1927.6.30.1-4 (2); DBAV-UERJ 1643; DBAV-UERJ 1644 (6); DBAV-UERJ 1571; DBAV-UERJ 702; DBAV-UERJ 703; DBAV-UERJ 792; DBAV-UERJ 873; DBAV-UERJ 1177 (2); ISH 1856-1968; MCZ 164 (2); MCZ 308; MCZ 309; MCZ 643 (6); MCZ 644 (2); MCZ 645; MCZ 655 (4); MCZ 49174; MNHN 1991-55; MNHN 1992-1288; MNHN 1992-1289; MNHN 7890 (5); MNRJ (Holotype of Narcine brachypleura Miranda Ribeiro, 1923), 321 mm total length adult male, Rio de Janeiro; MNRJ 760; MNRJ 567; MNRJ 550; MNRJ 553 (3); MNRJ 562; MNRJ 585; MNRJ 3598; MNRJ 15020; MNRJ 559; MZUSP 9921 (2); MZUSP (11; uncat.); ZMB 4577 (Lectotype of Torpedo brasiliensis von Olfers, 1831), Rio de Janeiro, Sello; ZMH 10429 (5). São Paulo: DBAV-UERJ 1176 (4); DBAV-UERJ 1657; MNRJ 561; MZUSP 3663 (4); MZUSP 1125; MZUSP 48201 (2); MZUSP 2097 (3); MZUSP 45104; MZUSP (67; uncat.); USNM 100880; ZMH 10428 (2); ZMH 10430. Santa Catarina: MCZ 232; MZUSP 13307. Rio Grande do Sul: MCP 963; MCP 3407; MCP 867; MCP 7343; MCP 7355; MCP 1435; MCP 1436; MCP 1524; MCP 2368; MCP 3381 – 3382 (2); MCP

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3382; MCP 3406; MCP 3429; MCP 3464; MCP 3490; MCP 4351 – 4353 (3); MCP 6599; MCZ 7578; MCP 7123; MZUSP 7433; MCP 7424; MCP 7582; MZUSP (5; uncat). Locality information not specified (only "Brasil"): BMNH (uncatalogued, stuffed spec.); MNHN 7516 (Lectotype of Torpedo ocellata Quoy and Gaimard, 1824), "Baie de La Table," South Africa (probably in error, see above), Uranie; MNHN 7891 (2; paralectotypes of Torpedo ocellata Quoy and Gaimard, 1824), "Baie de La Table," South Africa (probably in error, see above), Uranie; MNHN 7889; MNHN 8912 (3); MNHN 2898; MNHN 2899; MNHN 1984-24; MNHN 1984-49; MZUSP (uncat.); RMNH 4655; RMNH 16064; ZMB 2123; ZMB 4578; ZMB 32753.

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Narcine bancroftii (Griffith, 1834)

Figs. 18 – 23, Tables 8 – 9

Raja laevis Gronovius 1763: pl. 9, fig. 3 (descrption, illustration, not seen; declared unavailable by Opinion 89 of the ICZN, 1925: 27, cited in Bigelow and Schroeder, 1953: 112).

Torpedo bancroftii Griffith, in Cuvier, 1834: pl. 34 (original description, by indication on illustration by Dr. Bancroft; type-locality: unknown with certainty, but possibly Jamaica, see below).

Torpedo pictus Gray, 1854: 13 (original description based on manuscript of Gronovius, not illustrated; type-locality: "Antillas" [= Antilles]).

Narcine corallina Garman, 1881: 234 (original description, not illustrated; type-locality: Key West, Florida); Jordan, 1884: 105 (comparisons with N. umbrosa Jordan, 1884 sp. nov.); Bigelow and Schroeder, 1953: 122 (in synonymy of N. brasiliensis);

Narcine punctata Garman, 1881: 233 – 234 (original description, not illustrated; type-locality: Key West, Florida); Garman, 1913: 298 (in synonymy of Narcine brasiliensis bancrofti); Bigelow and Schroeder, 1953: 122 (in synonymy of N. brasiliensis).

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Narcine umbrosa Jordan, 1884: 105 – 106 (original description, not illustrated; type-locality: Key West, Florida); Bigelow and Schroeder, 1953: 122 (in synonymy of N. brasiliensis); Eschmeyer et al., 1998 (compilation).

Narcine brasiliensis bancrofti: Garman, 1913: 298 (synonymy, diagnosis).

Narcine brasiliensis corallina: Garman, 1913: 298 (synonymy, diagnosis).

Narcine brasiliensis: Bigelow and Schroeder, 1953: 121 – 123 (extensive synonymy with numerous references up to 1949, in part); Funicelli, 1975; Rudloe, 1989a; Rudloe, 1989b.

DIAGNOSIS: A dorsal coloration pattern composed of grey, brown or orange-brown background with strong antorbital patches, and numerous small spots that may outline horizontally elongate or circular ocelli over disc and base of tail regions, in combination with the possession of teeth usually in 21/22 – 24/25 exposed vertical rows in specimens over 340 mm total length, is unique for N. bancroftii, distinguishing it from all other species of Narcine. The presence of spiracles with warty, knob-like papillae on spiracular border further separates N. bancroftii from all other species of Narcine except N. brasiliensis and N. entemedor. The

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latter two species are distinguished from N. bancroftii on the basis of dorsal coloration and numbers of exposed vertical rows of teeth (see "Diagnosis" for N. brasiliensis and N. entemedor).

DESCRIPTION: Measurements and counts are given in Tables 8 and 9, respectively. Disc slightly variable, oval to rounded in outline, but generally slightly wider than long (means for disc width and length about equal; disc width ranges from 43.0 to 59.7 percent of total length, disc length ranges from 44.9 to 56.9 percent of total length). Greatest disc width at slightly before two-thirds of disc length, and at just under one-third of total length. Posterior disc margins slightly overlapping origin of pelvic fins. Pectoral axil with a slight notch in between disc and trunk (where pectorals are recurved). Snout rounded to broadly angular, but mostly angular, especially in larger adult specimens. Preocular snout length somewhat elongated, varying from 9.7 to 16.5 percent of total length, and occupying around one-fourth of disc length. Electric organs relatively long and wide, occupying between 19.8 to 29.2 percent of total length; electric organ width ranges from 7.2 to 14.1 percent of total length. Electric organs begin at about level of eyes on dorsal disc surface, and continue caudally to posterior one-fifth of disc. Gill-slits wide, more or less straight, but appearing faintly curved in some specimens. Gill-slits slightly directed anteriorly at mid-line, and situated progressively closer to mid-line from first to last gill-slit. Distance between last gill-slits inferior to distance between first and last gill-slits. Eyes relatively large and bulging in fresh or well-preserved specimens, and generally just larger than spiracles; eyes and spiracles adjacent. Spiracles circular to ovoid. Spiracles with thick, elevated borders containing wart-like papillae on entire spiracular margin.

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Papillae appear as closely-packed, roundish protuberances or knobs in adults, but in juvenile specimens they are isolated, more slender projections.

Nasal curtain much wider than long (nasal curtain width averaging 5.3 percent of total length, nasal curtain length averaging 2.3 percent of total length). Nasal curtain with more or less straight posterior margin, and without strong lateral lobes. Nasal curtain partially covering upper exposed tooth band. Pores of ventral snout region do not continue caudally beyond nostrils on nasal curtain. Nostrils generally small and circular, with small elevated border posteriorly. Prenasal snout length averaging slightly over one-tenth in disc length, but somewhat variable (ranging from 9.0 to 16.5 percent of total length). Mouth slightly wider than internarial width, but mouth corners do not project laterally beyond level of outer margin of nostrils. Tooth bands about equal in width. Both tooth bands with circular to sub-rectangular outlines, and occupying relatively large portion of mouth region. Tooth bands generally thicker than surrounding lips. Teeth generally in 17/17 – 21/22 vertical exposed tooth rows in pre-adult and adult specimens ranging from 225 to 400 mm total length (one very large specimen of 561 mm total length with 28/29 exposed rows; other large specimens of around 450 mm total length with 21/22 or 24/25 rows). Teeth in specimens smaller than, or close to, 200 mm in total length will have some four or five less exposed vertical rows of teeth in both upper and lower tooth bands. Generally more teeth in lower tooth band are present. Teeth with long, massive and sharp cups in larger adults (both in males and females), on both exposed and especially not exposed rows. Bases of teeth trapezoidal to sub-circular.

Pelvic fins wide and long (pelvic fin width ranging from 26.5 to 39.4 percent of total legth, pelvic fin length varying from 15.6 to 27.5 percent of total length). Pelvic fins originate

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from underneath posterior margins of disc and continue posteriorly to level of vertical through first dorsal fin origin. Pelvic fins with relatively large posterior free lobe at axils in females (free lobe is smaller in males where pelvics adjoin claspers). Lateral lobes of pelvic fins curved, not angular, and not fleshy and thick. Claspers relatively elongate, more or less straight from base to tip of clasper glans. In large adult males claspers project beyond distal tip of pelvics by as much as one-third of their total length, ending at vertical through posterior first dorsal fin base. Tail relatively wide at base (tail width averaging 21.3 percent of total length), and tapering significantly from base to tip of caudal fin in adult. Tail length less than disc width or length, measuring from cloaca 41.0 to 50.0 percent of total length ($x = 45.7$). Lateral tail folds originate on lateral aspect of tail at level of posterior two-thirds of first dorsal fin base, and project posteriorly to insert on lateral aspect of caudal peduncle. Dorsal fins slightly variable in shape and proportions. Second dorsal fin slightly larger than first, but dorsals more or less similar in height and length. First dorsal fin originates over posterior lobes of pelvic fins, or just posterior to pelvic axils. Dorsal fin height about one-tenth of total length. Dorsal fins with rounded to sub-acute apex, leaving slight free lobe posteriorly above base. Posterior margin of dorsals more or less straight or upright. First dorsal generally more upright, second dorsal more slanted. Caudal fin tall, fan-shaped, with posterior margin relatively straight. Caudal fin with sub-acute dorsal and ventral corners (more acute at dorsal apex). Ventral surface of caudal fin broadly rounded, and originating slightly more anteriorly in relation to dorsal lobe. Distance between dorsals about equal to distance between second dorsal and caudal fin.

Pores of lateral-line and ampullary systems generally similar to that of N. brasiliensis described above. On dorsal surface, pores of postorbital, supraorbital, infraorbital, and

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hyomandibular canals are present. Pores of posterior extension of lateral canal on lateral tail region appear slightly variable. Pores are situated in a more or less straight line just dorsal to lateral tail fold, but curve dorsally underneath both first and second dorsal fins in most specimens. Ventrally, scattered pores of ampullary system not occuring posterior to level of nostrils, as in N. brasiliensis.

Dorsal coloration conspicuous, but slightly variable. In preservative, background coloration ranging from brown to light brown, or grey to yellowish-brown. Specimens from Florida reportedly with an orange-brown background color (appearing more yellowish-brown in preservative). Dorsally, specimens present blotches and spots over most of disc and tail regions. Antorbital blotches are ususally present (absent in many large specimens from the northern coast of South America), and vary from covering most of preocular snout region to covering just major portions overlying antorbital cartilages. Spots forming incomplete ocelli are present over most dorsal disc and tail region. Spots are smaller than eye-diameter, and may be joined to form horizontally-elongated to circular, incomplete ocelli. These incomplete ocelli do not necessarily present darker background coloration, but may do so. Incomplete ocelli present over electric organs, lateral disc margins, base of tail and sides of tail, continuing over dorsal and caudal fins. Dark streaks are present at bases of dorsal and caudal fins, and continuing on fins, in some specimens. In larger specimens, generally only spots are present from incomplete ocelli, but some larger specimens (e.g. from Belize) with dark streaks and blotches persisting, not presenting pattern of incomplete ocelli. Specimens from the northern coast of South America with definite, small spots present from a relatively small size; in adults these spots appear unconnected to each other. Ventrally specimens are a uniform white or

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creamy white, but occasional dark grey or brown blotches and irregular spotting may occur at ventral pectoral axils, tail region, outlining posterior disc and pelvics, or on electric organs.

REMARKS: The earliest available name for this species is Torpedo bancroftii Griffith, 1834 (in Cuvier, 1834), which was published by indication, in an illustration of a specimen of Narcine executed by Dr. Bancroft, and is therefore available (ICZN, 1985: 33, Art. 12a, b). Griffith's account contains a single phrase concerning the new species, describing its coloration. The actual locality of the new species is not mentioned in the original description, but is presumably Jamaica, as Dr. Bancroft was known to have sent many specimens of fishes from Jamaica to collections in London (Caldwell, 1966). Jordan et al. (1930) listed Jamaica as the type-locality, but conclusive evidence is not available. An extensive search of the BMNH collection revealed no specimen that can be attributed to Bancroft, and therefore no type-specimen is considered extant. Bancroft's original plate is here reproduced as Fig. 18. The spelling of the specific epithet is retained here as originally published (as bancroftii), because emending it to bancrofti (e.g., Garman, 1913; Bigelow and Schroeder, 1953) is not required or justifiable (ICZN, 1985: 75, Art. 33d).

Torpedo pictus was described by Gray (1854) on the basis of a manuscript description by Gronovius. The manuscript was purchased by Gray in an auction (see Gray, op. cit., for details). Gronovius' manuscript was never published, and was accompanied by a small collection of fishes. Torpedo pictus Gray, 1854 lacks a type-specimen however, as the name was published solely on the basis of the description in Latin in Gronovius' manuscrpt. Wheeler (1958) lists the extant material in Gronovius' collection, and no specimens of Narcine are

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present (none were found in the BMNH collection either; also Wheeler, personal commun.). The original description clearly places the new species in Narcine primarily on the basis of snout shape, and along with coloration and locality information clearly allows it to be identified with N. bancroftii (Griffith, 1834).

Garman's (1881) description of N. punctata is rather brief, but he clearly describes the color pattern as "uniform olive brown, with the markings outlined by a series of small round spots" (1881: 234). The holotype of N. punctata is in very good condition, even though the spots described by Garman are mostly faded (Fig. 19). Garman described his species as a variety of N. brasiliensis (equal to "Var. 1" of Muller and Henle, 1841), but it is available at the specific level (ICZN, 1985: 87, Art. 45g). Narcine corallina Garman, 1881 was also described as a variety of N. brasiliensis, from two specimens (Fig. 20) taken at Key West, Florida. Both specimens are in relatively good condition. The larger specimen is here designated as lectotype (MCZ 44, 249 mm total length). Garman's account describes the coloration as distinctive, noting that the background coloration is orange or reddish. The majority of specimens examined from Florida have slightly distinctive background coloration in preservative (no fresh material or live coloration was examined), appearing light yellow or yellow-brown. Other characters provided by Garman (1881) to diagnose his new species vary greatly and inconsistently among specimens (truncate posterior borders of caudal and dorsal fins). This was noted by Garman himself who refrained from considering N. corallina as a new species because of intraspecific variation. Jordan's (1884) description of N. umbrosa is very similar to Garman's, as both species are based on material from Key West. The type specimens of both species are very similar (Figs. 20 and 21). CAS 18246 is chosen as lectotype of N. umbrosa as

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it is slightly better preserved than USNM 36940. Both Garman's and Jordan's nominal species are here synonymized with T. bancroftii Griffith, 1834. If the distinctions in background coloration eventually prove to be consistent once freshly preserved material and, more importantly, accounts of live coloration are available, then the validity of N. corallina Garman, 1881 should be reevaluated. The "truncate" and "sub-truncate" posterior margins of the dorsal fins, as described by Garman and Jordan respectively, are probably preservational or intraspecific variation. Proportional measurements and meristics of specimens from Florida fall within the range currently accepted for N. bancroftii, without any indication that a distinct species should be recognized from that area.

N. bancroftii, as here circumscribed, presents intraspecific variation in coloration and in proportional measurements, as does N. brasiliensis (see above). To a degree this is to be expected when a species is so widely distributed and large numbers of specimens are examined and measured. Presently, N. bancroftii is the only species of Narcine recognized from northeastern Brazil to North Carolina, encompassing the Gulf of Mexico, Caribbean Sea and the West Indies excluding the Bahamas (material from Bahamas was not available). Local variations in color, however, are frequent. However, these variations generally were not strong enough, or consistent enough, for the recognition of more than one species. Specimens from southern and western Florida, as discussed above, presented a slightly lighter background color in preservative due to an orange to reddish-orange background in live specimens (according to published reports), with deep-brown or reddish-brown antorbital blotches. However, in light of the absence of significant differences in other characters, and because fresh and live material

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was not examined, specimens from southern Florida are considered conspecific with those from throuout the range of N. bancroftii.

An even more striking example of intraspecific variation occurs for specimens from Guiana to northern Brazil. Numerous specimens from this region present a different color pattern, which is composed of numerous, small dark spots scattered more or less over entire dorsal disc and tail regions (Fig. 23), compared to the relatively fewer spots that ususally form incomplete circles and ocelli in typical specimens from farther north. The spots are the only remnants of dorsal coloration outside of background coloration in most very large specimens from this region (however, there are exceptions, see Fig. 23). The differences in coloration also extend to smaller specimens from this region. Specimens of about 110 mm total length typically have either more horizontally elongated rings and incomplete ocelli or more small dark spots compared to specimens of equal size from the Gulf of Mexico, West Indies or eastern United States. These differences are difficult to quantify, and more study of the dorsal coloration is needed. Specimens from Guiana to northern Brazil (Maranhão state) cannot presently be distinguished also on the basis of proportional measurements or meristics. These specimens are provisionally identified as N. bancroftii pending further work, which is in progress. There is no available nominal species for this form.

N. bancroftii is distinguished from N. brasiliensis on the basis of color pattern (specimens of all sizes of N. brasiliensis typically without ocelli formed of small spots, present in N. bancroftii), and number of exposed vertical rows of teeth (roughly five or six more rows in specimens of N. brasiliensis; discussed above under N. brasiliensis). Specimens from northeastern Brazil (Paraíba, Sergipe, and Bahia states) also have fewer exposed tooth rows

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than specimens from southeastern Brazil to northern Argentina (the range of N. brasiliensis), and are tentatively identified as N. bancroftii (but further comparisons are still being conducted).

There is abundant data concerning reproduction and life-history, electrogenic capacity, local distribution, stomach contents and other ecological aspects of N. bancroftii (identified as N. brasiliensis in the literature; see, e.g., references in Bigelow and Schroeder, 1953; more recent literature includes Funicelli, 1975; Rudloe, 1989a, 1989b), more so than in any other species of Narcine. My own observations indicate that sexual maturity for males occurs at about 250 mm total length, but may occur sometimes at a slightly larger (around 280 mm TL; specimens from northern Brazil) or smaller size (about 240 mm TL from North Carolina, 230 mm TL from Floida and Gulf of Mexico). Females probably achieve sexual maturity at similar dimensions. One female from Texas (350 mm TL) contained eight embryos of about 77 mm TL (mother was not examined). These embryos were late-term, close to free-swimming. Lateral tail folds and color pattern are similar to adults from same region (ocelli generally with more intense outlining in smaller specimens). It appears that both oviducts are synchronous in adult females, as numerous dissected females had embryos of similar size in both oviducts. A 479 mm TL female from Jamaica had six embryos in different stages of development, ranging from 45.5 to 96.9 mm TL (not determined in which, or both, oviducts embryos were present).

More data concerning reproduction was obtained from specimens from northern Brazil, in which abundant gravid females were available for dissection. A 470 mm TL female from Maranhão state contained no embryos, but presented very thick, non-transparent posterior portions of oviducts containing numerous villi leading almost to cloaca (embryos

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were aborted on board ship according to original field notes). Embryos were found in a 460 mm TL female from the same locality. This specimen had five embryos in the right oviduct (61 to 73 mm TL, two males and three females) and eight in the left (47 to 73 mm TL, one male and seven females). Both oviducts were very thin-walled, transparent and punctured very easily. The embryos occupied the majority of the oviductal space. Other specimens of this lot (USNM 216829; 32 specimens total) were aborted embryos, and smaller females (360 mm TL) also contained embryos. This lot was collected in May.

GEOGRAPHICAL DISTRIBUTION: This species, as here delimited, has a very wide-ranging distribution. The northern limit is North Carolina (specimens examined from Beaufort), extending south along the eastern coast of the United States, and bordering Florida and all of the continental U.S. This species occupies the Gulf of Mexico and the shallow portions of the eastern continental shelf of Central America, continuing along the northern border of South America in the Caribbean Sea, and extending as far as northeastern Brazil (specimens from Bahia state) in the western Atlantic. N. bancroftii is also present throughout the West Indies, from Cuba and Jamaica to the Lesser Antilles as far as Grenada (specimens have not been examined from Haiti to Antigua and Barbuda). Its presence in the Bahamas is still speculative, as no specimens were located from those islands (Fig. 102). As this species may be further subdivided in the future, its distributional limits will accordingly be more restricted. N. bancroftii is a shallow-water species, being captured in depths ranging from the intertidal to some 35 m.

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MATERIAL EXAMINED: (364 specimens, 45 to 615 mm total length): **Belize**: USNM 301384. **Brazil**: Amapá: FMNH 65830 (4); MCZ 40238 (2); MCZ 40392. Bahia: DBAV-UERJ 776 (5); DBAV-UERJ 1184 (2); MNHN 7892; MNRJ 564. Maranhão: MCZ 42949; USNM 222476 (5); USNM 216823 (2); USNM 216829 (32). Pará: BMNH 1850.4.8.13; USNM 156772; USNM 156817; USNM 222470; USNM 222475 (6). Paraíba: DBAV-UERJ 1563 (2); DBAV-UERJ 1564 (5). Sergipe: DBAV-UERJ 1128; DBAV-UERJ 1622. **Colombia**: ANSP 103930; MCZ 47448; MCZ 47449; MCZ 51817; USNM 222463; USNM 222496. **Cuba**: BMNH 1853.12.26.63 (2). **Dominica**: USNM 170232; USNM 222465 (2); USNM 222484. **French Guiana**: USNM 222472; USNM 222468 (5). **Grenada**: BMNH 1904.6.24.2-3 (2). **Guadeloupe**: MNHN 1338. **Guyana**: BMNH 1950.5.15.3; BMNH 1952.10.21.5; BMNH 1961.8.31.23; BMNH 1961.8.31.19-21 (3); BMNH (3; uncat.). **Jamaica**: ANSP 144667; BMNH 1848.1.12.1440-1442 (3 skins); BMNH 1897.7.1.31; BMNH 1897.7.1.32-38 (6); BMNH 1909.2.26.14-15 (2); FMNH 2803 (2); FMNH 2805; IRSNB 3762; USNM 32082; USNM 160376; USNM 187944; USNM 222469. **Martinique**: MNHN 6400; MNHN 7886; MNHN 7887; MNHN 7888 (2). **Mexico**: FMNH 59841 (2); MCZ 42451; USNM 37125; USNM 186409. **Panama**: USNM 81799. **St. Lucia**: USNM 41279. **St. Vincent**: MCZ 752 (Holotype of Narcine punctata Garman, 1913, 234 mm total length pre-adult female), Kingston. **Surinam**: ISH 251-1981 (2); MCZ 42950 (4); NSMT P4033; RMNH 21475; RMNH 21475; RMNH (uncat.); USNM 159203; USNM 186411; USNM 204066 (6); USNM 222464 (4); USNM 222485; ZMA 112.550; ZMA 109.540; ZMA 112.814; ZMB 4579; ZMB 4580. **United States**: Alabama: AMNH 84125; AMNH 98232. Florida: AMNH 2488 (3); AMNH 2489 (2); AMNH 16963; AMNH 19353 (3); AMNH

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19354 (8); AMNH 20803; AMNH 44037 (5); ANSP 16548; ANSP 69654 (2); BMNH 1903.6.13.49; CAS 18246 (Lectotype of Narcine umbrosa Jordan, 1884), Key West; FMNH 7066; MCZ 44 (2: lectotype of Narcine corallina Garman, 1881, 249 mm total length adult male; paralectotype of Narcine corallina Garman, 1881, 195 mm total length male), Key West; MCZ 1409; MCZ 36398 (9); MCZ 37143 (7); MCZ 39898; MCZ 39911 (4); MCZ 42475 (8); MCZ 51031; MCZ 51044; MCZ 51828; MCZ 59583; USNM 30178; USNM 36940 (Paralectotype of Narcine umbrosa Jordan, 1884), Key West; USNM 36993 (3); USNM 66986; USNM 66987 (14); USNM 116439; USNM 126936; USNM 155798; USNM 156725 (3); USNM 188098; USNM 222504; USNM 222471. Georgia: AMNH 73988; USNM 186427. Mississippi: AMNH 87211; FMNH 31784; USNM 158978 (4); USNM 186410 (2). North Carolina: AMNH 1776 (4); AMNH 1776 (5); AMNH 9054; BMNH 1913.12.8.2; MCZ 39807; USNM 70302; USNM 70303; USNM 70304; USNM 74285; USNM 74286; USNM 151968; USNM 152024; USNM 222486. South Carolina: AMNH 74329; AMNH 77069; MCZ 39687; USNM 222477; USNM 316629. Texas: AMNH 98244; ANSP 70605; FMNH 11189; FMNH 11190; FMNH 11191; FMNH 37814; FMNH 90094; MCZ 37988; MCZ 42422 (10); MCZ 42452 (2); MCZ 52290 (8); MCZ 147915 (5); USNM 121612; USNM 155649; USNM 156433. **Venezuela**: ANSP 120022; ANSP 120033 (4); ANSP 120145 (3); ANSP 120146; ANSP 120148; BMNH 1920.12.22.4; BMNH 1921.7.28.2; BMNH 1922.6.22.1; MCZ 51034; USNM 123093. Locality not specified: AMNH 211794 ("Gulf of Mexico").

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Narcine brevilabiata Bessednov, 1966

Figs. 24 – 27, Tables 10 –11

Narcine brevilabiata Bessednov, 1966: 81 (original description, illustrated; Gulf of Tonkin, Viet Nam); Bessednov, 1969: 111 – 112 (description, illustrated; Viet Nam); Carvalho et al., in press (accepted as valid, in identification key).

Narcine indica: ?Cantor, 1850: 1399 – 1400 (description; Malaysia); ?Suvatti, 1950: 184 (listed; Thailand); Monkolprasit, 1977: 3 (listed; Thailand); ?Suvatti, 1981: 8 (listed; Thailand); Monkolprasit, 1984: 146 – 147, fig. 79, pl. B-6 (description, in identification key, illustrated, photograph; Thailand); Monkolprasit, 1990: 391, pl. B, 6 (brief description, photograph; Thailand); Monkolprasit et al., 1997: 31 (listed, photograph [p. 14]; Thailand); Carvalho et al., in press (misidentification, distribution, illustrated).

Narcine lingula: Liu, 1932: 159 (misidentification; ?Tsingtao, China, Yellow Sea); Lindberg and Legeza, 1959: 156 – 157 (account compiled from Liu, 1932).

Narcine maculata: Chu, 1962: 89 – 90 (misidentification, illustrated; Gulf of Tonkin and South China Sea, various localities); Shen, 1964: 193 – 194 (brief description; Hong Kong); Chen and Chung, 1971: 5 (description; Taiwan); Institute of Oceanology-Academia Sinica, 1975: 20 (description, distribution, illustrated; China); ?Senta and Min, 1975: 1 (listed; Malaysia); Chu and Wen, 1982: 65 - 66 (illustration of lateral line and other

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sensory pore systems; China); Kyushin et al.,1982: 24 (brief description, photograph [p. 24]; South China Sea); ?Yu, 1988: 9 (listed; Taiwan); Institute of Oceanology-Academia Sinica, 1992: 17 (misidentification, description, illustrated; China); Chen and Joung, 1993: 79, pl. 11-4 (description, photograph [p. 621]; Taiwan); ?Shuyuan, 1993: 135 (listed; Taiwan).

Narcine timlei: Moshin and Ambak, 1996: 84 – 85, fig. 93, pl. 31 (misidentification, description, illustration, photograph; Malaysia).

DIAGNOSIS: A species of Narcine distinguished by the unique combination of a dorsal color pattern composed of numerous small dark brown spots (smaller than eye-diameter) over a brown background, with larger (diameter close to interocular distance) and fewer blackish-brown spots or blotches on dorsal disc, along with a preocular snout region with the same background color as dorsal disc with small spots present, and by possessing an upper tooth band much wider than lower tooth band (close to twice as wide). The tooth bands are of subequal width in all species of Narcine except N. tasmaniensis, N. sp. nov. B, N. sp. nov. C, and N. sp. nov. H, but only N. sp. nov. H has a dorsal color pattern with spots (coloration unifrom tan, brown or yellowish-brown in N. tasmaniensis, N. sp. nov. B and N. sp. nov. C, without spotting of any sort). N. brevilabiata can be distinguished from Narcine sp. nov. H by possessing relatively more numerous and smaller "small" spots (small spots of latter species subequal to eye-diameter and less numerous), and in having preocular snout region with the same (usually brown) background color as dorsal disc, generally with small spots present

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(preocular snout region of N. sp. nov. H with grey color, very distinct from brown background color of disc, and generally devoid of spots).

DESCRIPTION: Measurements and counts presented in Tables 10 and 11, respectively. Disc subcircular, generally wider than long (disc width is between 47.8 to 57.7 [x = 53.6] percent of total length, disc length is between 48.7 to 58.1 [x = 51.8] percent of total length). Disc widest slightly posterior to mid-disc length. Snout subacute, broad and relatively long (preocular snout length averaging 14.0 percent of total length); preocular snout length occupying close to one-third of disc length. Disc only slightly overlapping origin of pelvic fins posteriorly, and barely projecting forward just before contacting lateral aspect of trunk (leaving a slight notch in between disc and trunk). Electric organs relatively short, beginning dorsally just anterior to level of eyes on disc, and continuing caudally to between posterior one-fourth and one-fifth of disc (electric organ length averaging 24.7 percent of total length); electric organ width averages 11.0 percent of total length. Gill-slits beginning relatively posteriorly on disc, close to mid-disc and mid-electric organ regions, leaving a space close to two-thirds of distance between first and last gill openings between mouth and first gill-slit. Gill-slits slightly curved and situated progressively closer to mid-line from first to last gill-slit. Eyes and spiracles without gap in between. Eye length greater than spiracle length, but about equal to spiracle width. Spiracles elongated, wider than long, and situated at a slight angle in relation to eyes. Spiracles with slightly elevated borders, but these are somewhat flatenned in preserved specimens.

Nasal curtain wider than long, with more or less straight posterior margin but some specimens with slight median lobe present. Nasal curtain with slightly lobed lateral margins;

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median posterior lobe only barely covering upper exposed tooth band in well preserved specimens (nasal curtain slightly folded back in some specimens due to preservative). Sensory pores on nasal curtain continue posteriorly to just beyond level of nostrils. Nostrils relatively large and circular, with well developed and elevated margins posteriorly resembling a flap. Preoral snout length (x = 16.3) greater than prenasal snout length (x = 12.3), both being between about one-third and one-fourth of disc length; prenasal snout length about equal to preocular snout length. Mouth wider than distance between nostrils; mouth corners project laterally to just beyond level of outer margin of nostrils or to level of lateral margins of nasal curtain. Upper exposed tooth band clearly wider than lower exposed tooth band; both tooth bands triangular in outline, and both with teeth clustered close to mouth opening, leaving exposed portions of tooth bands without teeth (very few horizontal rows of teeth exposed). Upper tooth band slightly wider (at its greatest width) than long, but lower tooth band with greatest width (at mouth opening) about equal to length. Examined specimens from Viet Nam with greatly reduced lower tooth bands, devoid of exposed teeth. Exposed teeth small to moderately sized but not very numerous, in 13/7 – 14/10 vertical rows in adult or close to adult specimens from China, Malaysia and Thailand, and in 6/0 – 9/3 vertical rows in specimens from around 110 mm total length (China and Thailand). Specimens from Viet Nam with 9 – 14 rows exposed on upper tooth band (209 to 258 mm total length). Teeth with somewhat large cusps in larger specimens from China and Thailand; teeth with diamond-shaped bases, but bases are rounded posteriorly.

Pelvic fins poorly preserved in majority of specimens, but wider than long when measured together. Pelvic fin width averages 33.8 percent of total length, pelvic fin length

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averages 18.1 percent of total length. Pelvic fins with slightly more prominent lateral lobes anteriorly in specimens from Viet Nam, perhaps due to preservation (only one lot examined); other specimens with less prominent lateral lobes. Posterior margins of pelvic fins slightly concave in preserved Vietnamese specimens, otherwise more or less straight. Pelvic fins begin just underneath posterior aspect of disc and extend caudally to level of mid-base of first dorsal fin. Small free lobe present where pelvics adjoin tail posteriorly. Tail not greatly stout at base; tail length, as measured from cloaca, is less than disc length in all specimens. Lateral tail folds moderately well-developed, beginning on lateral aspect of tail at level of end of first dorsal fin base, and continuing caudally to insert on ventro-lateral portion of caudal peduncle. Dorsal fins large and subequal in height and length of base. First dorsal slightly taller than second, but second dorsal with faintly longer base. First dorsal fin with somewhat broader free lobe above base. Dorsals with different outlines. First dorsal fin more erect and more rounded at apex, second dorsal fin with more slanted anterior margin and slightly more pointed apex. First dorsal fin originates over posterior lobes of pelvic fins. Dorsals with slightly slanted posterior margins and moderate free lobe posteriorly (free lobe more developed in adult female from China). Caudal fin moderately tall (caudal fin height averaging 13.5 percent of total length), with slanted upper lobe anteriorly and oval apex (caudal fin prominent and relatively larger in adult female from China, CAS 114138). Posterior margin of caudal fin slightly inclined and with curved lower lobe. Dorsal and ventral lobes of caudal more or less same size, as measured from base of caudal fin, and beginning at about same level on caudal peduncle.

Pores of lateral-line and ampullary systems inconspicuous, difficult to observe. The dorsal coloration of the specimen prohibits clear observation of pores in all specimens except

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those from Viet Nam. Viet Nam specimens have clear series of pores of supraorbital, infraorbital and postorbital canals. These pores are located dorsally on snout and anterior disc regions, in straight semi-parallel rows over rostral ridges and between eyes and anterior disc margin. Pores of anterior branch of hyomandibular canal are clearly visible bordering electric organs anteriorly. On ventral surface, pores are present on snout region and outlining electric organs anteriorly and laterally. Pores on ventral snout area in more or less defined parallel antero-posterior rows, radiating from snout tip to nasal curtain region. Pores present lateral to nostrils and mouth, and two small groups of pores are present in between mouth and branchial openings.

Dorsal coloration distinctive, composed of large and very small dark brown spots over a light brown to tan background. The spots vary somewhat in size, but the large spots are just smaller than the distance between the eyes, while the smaller spots are smaller than eye diameter. The larger spots are fewer in number, and occur in specific areas: the largest spots over posterior two-thirds of electric organs, one on each side; two slightly smaller spots on disc antero-lateral to largest spots; a single spot over mid-disc; two spots posteriorly on disc, one on each side and close-together, just anterior to base of tail; two spots, one on each side, on disc lateral to eyes; and a pair of large spots on outer disc at about five-sixths of disc length. These spots may become faded in preservative, but faded remnants are present. These large spots or blotches are more or less circular, and may be formed by the fusion of the smaller spots. Specimens from Thailand, China, and Malaysia have relatively larger spots over posterior two-thirds of electric organs, and appear to lack the central spot posterior to interorbital space. Dark, undefined blotches are present on dorsal region of pelvic fins, and at

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base of dorsal and caudal fins. Smaller spots are more or less uniform throughout the dorsal surface, and are present within spiracles, bases of dorsal and caudal fins, and lobes of caudal fin. Dorsal fin lobes dark brown. Ventrally, coloration is a uniform pale white color, with darker, undefined grey or light brown undefined blotches on posterior pelvic and disc areas, occasionally on ventral electric organs as well. Light brown blotches are present on ventral tail region.

REMARKS: Specimens of this species have been misidentified in the literature prior to the original description of N. brevilabiata by Bessednov (1966). However, the earliest literature citation, that of Cantor (1850), is unclear as to the actual species involved, as Cantor could have been referring to Narcine sp. nov. H (described below), which is so far unrecorded from Malaysia (the locality of Cantor's fishes, but it probably occurs there), and is very similar to N. brevilabiata.

Narcine brevilabiata was described by Bessednov (1966) on the basis of a single specimen (265 mm total length male) collected in the Gulf of Tonkin, in 1960. This specimen was originally deposited in the Museum of the Pacific Research Institute of Fisheries and Oceanography (TINRO) in Vladivostok. When this institute was closed or relocated years ago, part of the collection of fishes, probably including the type specimen of N. brevilabiata (along with the type and only specimen of Narcine prodorsalis Bessednov, 1966) was discarded or destroyed (A. Neelov and D. Pitruk, personal communication). Some fishes from TINRO apparently were sent to the Institute of Marine Biology in Vladivostok and to the Zoological Institute of the Russian Academy of Sciences in St. Petersburg (ZISP). On my

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behalf, Drs. D. Pitruk and V. N. Dolganov of the Institute of Marine Biology in Vladivostok unsuccessfully searched their collections of fishes for the holotype of N. brevilabiata (Dr. Dolganov had moved specimens from TINRO to his institute). Dr. Neelov informed me that no skates or rays were sent to ZISP from TINRO as well, and there is presently no register of Bessednov's types having ever been re-located to ZISP. Therefore, the holotype of N. brevilabiata is considered lost.

Specimens examined from off Viet Nam (from vicinities of Nha Trang; CAS 98234) are from close to the type-locality of N. brevilabaiata (slightly north of Da Nang, in the southern Gulf of Tonkin). These specimens agree with the original description of N. brevilabiata in general diagnostic features, such as the arrangement of mouth, nostrils and tooth bands, eyes and spiracles, shape of dorsal and caudal fins, and also in coloration. They differ slightly in disc proportions and in the shape of the pelvic fins. The holotype of N. brevilabiata is depicted as having a disc proportionally not as broad, and pelvic fins that appear to have very concave posterior margins and laterally expanded anterior lobes. These characteristics, however, are typical of specimens that have undergone slight dessication as a result of preservation. Therefore, the examined specimens differ very little, if at all, from the now lost holotype of N. brevilabiata. The specimens from Viet Nam do appear to have pelvics with slightly concave posterior margins, but not nearly as concave as the depiction of the holotype. However, only one lot from Viet Nam was examined, and even though it contains six specimens, they were all subjected to the same preservation, and may all be slightly distorted in the same way. The pelvics in the examined Viet Nam specimens are not as intensely lobed antero-laterally as the sketch of the holotype of N. brevilabiata either. Specimens from Nha

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Trang also have a large, central spot on the disc, in bewteen the spots over the electric organs (posterior to interorbital space), that is not clearly depicted for the holotype of N. brevilabiata. The central spot is slightly faded in some specimens of CAS 98234, however, and may have been so in the holotype as well (the illustration of the holotype indicates that a faded spot may be present).

Some examined specimens (from Thailand and Guangdong Province of China) were slightly different than the Vietnamese specimens from close to the type locality of N. brevilabiata. These specimens do not have the large central spot on disc mentioned in the paragraph above, and have proportionally larger spots over electric organs (which are larger than any of the large spots typically present). These specimens differ in other ways as well from Vietnamese specimens: the lower tooth band is more clearly defined and proportionally wider in relation to the upper tooth band and contains exposed tooth rows (in Vietnamese specimens, lower tooth band is very slight and ill-defined, without exposed tooth rows); larger nostrils; mouth corners not projecting laterally to beyond level of inner nostril margin (mouth width is greater or subequal to distance between outer margin of nostrils in Vietnamese specimens); pelvics not as lobed anteriorly and not as concave at posterior margins; smaller size at maturity (a male from Gulf of Thailand has firm claspers at 230 mm total length, while a male from Viet Nam has flexible, but proportionally longer claspers at 257 mm total length, and same also applies to males of 234 and 224 mm total length from Viet Nam); shape of dorsals and caudal fins (greater free lobes in Thai and Chinese specimens); pores of dorsal sensory systems not as clearly defined.

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Some of the differences between specimens from Viet Nam and other localities can be inferred from accounts of other Thai specimens which are identified as Narcine indica (e.g. Monkolprasit, 1984, pl. B-6; Carvalho et al., in press), and lead to the conclusion that perhaps more than one species is present among specimens here called N. brevilabiata. However, not many specimens of this form (or forms) are available in collections, and freshly preserved material is needed from throughout its range to better understand color variations. Also, some of the differences, as mentioned, may be preservational (pelvic and dorsal fin shape). Therefore, these forms are lumped here under N. brevilabiata Bessednov, 1966, the oldest available name for them, until further work can be accomplished and more material procured.

The specimen from Sarawak (ZRC 679) has a higher number of pelvic radial elements (19, but two other specimens, one from China and one from Viet Nam, have 18), and a higher number of caudal vertebral centra (31, the second highest count is 28, then 26, both from China) which is reflected in the total number of vertebral centra (114, cf. to the second highest, 110).

Given the above discussion, usage of pelvic fin shape to separate N. brevilabiata from "N. indica" and N. maculata (= Narcine sp. nov. H here) by Carvalho et al. (in press) appears to have been misguided. Their key was based on few specimens then at hand, and with the examination of specimens from close to the type locality of N. brevilabiata, it became quite evident that Bessednov's specimen (holotype) was slightly distorted as a result of preservation. Their distinction of N. brevilabiata from the latter two species was also based on the presence of small spots on the caudal fin of N. brevilabiata. Having now examined more material, it is evident that small spots are also present on the caudal fin of their N. indica (not of Henle, 1834,

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which is synonymized with Raja timlei Bloch and Schneider, 1801 here). Their N. indica is presently considered conspecific with N. brevilabiata Bessednov, 1966 here, pending the examination of further material (detailed above). If proven distinct, then the species referred to as N. indica by Carvalho et al. (in press; and of other authors, see synonymy above) is new, as no available name exists for it.

Because there is potential confusion regarding the application of the nominal species N. brevilabiata Bessednov, 1966, as more than one species may be present in the region (from Gulf of Thailand to southwestern and eastern China) and these are very similar, and Bessednov's only specimen (now lost) was slightly distorted, it is considered necessary to designate a neotype. A 234 mm total length male (from CAS 98234) is from very close to the type-locality off Viet Nam, and closely agress with Bessednov's description (Fig. 24C, D). It is herein designated as the neotype of N. brevilabiata Bessednov, 1966. Another male specimen from the same lot is closer in size of the lost holotype (257 mm total length), but it's cranium has been dissected and removed from the specimen (but still present in the jar). The neotype is a pre-adult male. The holotype must also have been a pre-adult specimen, as the 257 mm total length male examined has flexible claspers.

N. brevilabiata is similar in the morphology of the mouth and tooth bands, and in general coloration and proportions to Narcine sp. nov. H from Myanmar and the Philippines. Distinctions between the two species are discussed in the "Remarks" section of Narcine sp. nov. H below.

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GEOGRAPHICAL DISTRIBUTION: N. brevilabiata, as here defined, occurs in relatively shallow (so far recorded from 41 to 70 m), off-shore continental shelf waters of the South China Sea, and has been reliably recorded from Viet Nam, Thailand, Malaysia and China. From China, confirmed records are from the island of Hainan, and Guangdong Province, including Hong Kong, and Taiwan (Fig. 104). Liu's (1932) report of this species mentions Tsing Tao (Qingdao) as a possible locality, albeit uncertain. It is highly possible that N. brevilabiata occurs that farther north into the East China and Yellow Seas, but specimens are needed to verify this. Liu (1932) mentions that the species is very rare "in the seas of North China."

MATERIAL EXAMINED: (16 specimens, 82 to 322 mm TL): **China**: CAS 40887; CAS 98233 (2); CAS 114138; FMNH 46990; USNM 26545; **Malaysia (Sarawak)**: ZRC 679; **Thailand**: CAS 98158; CAS 98160; **Viet Nam**: CAS 98234 (6).

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Narcine entemedor Jordan and Starks, 1895

Figs. 28 – 31, Tables 12 – 13

Narcine sp. indescr.: Jordan, 1885: 364 (listed, Panama).

Narcine entemedor Jordan and Starks, in Jordan, 1895: 387 – 388 (original description, not illustrated; La Paz [Baja California Sur] and Mazatlán [Sinaloa], Mexico); Jordan and Evermann, 1896: 2752 (repeat of Jordan and Starks, 1895); Gilbert and Starks, 1904: 15 (description; Panama); Osburn and Nichols, 1916: 144 (listed, Baja California Sur); Meek and Hildebrand, 1923: 74 (compilation; Panama); Breder, 1928: 5, fig. 2 (description; nothern and southern Gulf of California); Jordan et al., 1930: 27 (listed); Beebe and Tee-Van, 1941: 247 – 248, fig. 2 (description, distribution, compilation); Fowler, 1944: 479 (listed); Bohlke, 1953: 11 (listed in type-catalog); Castro-Aguirre, 1965: 211 – 212 (description, brief account, photograph [p. 212]); Castro-Aguirre et al., 1970: 118 (listed); Instituto Nacional de Pesca, 1976: 63, fig. 31 (in identification key, listed, photograph [p. 142]); Chirichigno, 1978: 13, 31 – 33, fig. 9 (brief account, proportional measurements, illustration; northern Peru); Thompson et al., 1979: 249 (name only); Bartels et al., 1983: 80 (listed; Costa Rica); Rodriguez-Romero et al., 1992: 89 (listed, Bahia Concepcion, east coast of Baja California Sur); Michael, 1993: 81 (brief account, photograph [p. 81]); Allen and Robertson, 1994: 32, pl. III, 9 (identification, brief account, photograph [p. 32]); Abitia-Cárdenas, 1994: 166 (listed, Bahia de La Paz, Baja California Sur); De La Cruz-Aguero et al., 1994: 22 (listed,

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west coast of Baja California Sur); Beltrán and Gaspar-Dillanes, 1995: 107 – 112 (identification, description, morphometrics, anterior rostrum illustrated); McEachran, 1995: 770, 771 (identification, distribution, illustration); De La Cruz-Aguero et al., 1996: 119 (listed, northern Baja California Sur); Eschmeyer et al., 1998 (compiled).

Narcine brasiliensis: Bigelow and Schroeder, 1953: 110 – 123 (considered N. entemedor Jordan and Starks a probable synonym of N. brasiliensis [von Olfers, 1831]; misidentification); Castro-Aguirre, 1978: 17 (misidentification, compilation); van der Heiden and Findley, 1988: 212 (misidentification, listed, Sinaloa); Torres-Orozco and Castro-Aguirre, 1992: 281 (misidentification, west coast of Baja California Sur); Bussing and López S., 1994: 32 – 33 (misidentified, listed, outline illustration); Castro-Aguirre and Pérez, 1996: 23 – 24 (misidentification, distribution).

DIAGNOSIS: The unique presence of four or five distinct circular ocelli over disc, more or less close to interocular distance in diameter (ocelli may become blotches or faded in very large specimens) and having preocular snout region uniform in color, devoid of conspicuous blotches and markings, distinguishes N. entemedor from all other species of Narcine. The presence of warty, knob-like papillae on spiracular border further separates N. entemedor (papillae absent in all species of Narcine except N. brasiliensis and N. bancroftii). From N. brasiliensis and N. bancroftii, N. entemedor is distinguished by its preocular snout region coloration and the ocelli on dorsal disc.

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DESCRIPTION: Measurements and counts are given in Tables 12 and 13, respectively. Disc oval, slightly longer than wide in specimens (disc width averages 49.5 percent of total length, disc length averages 48.7 percent of total length). Disc widest slightly before two-thirds of disc length. Disc overlapping origin of pelvic fins posteriorly only slightly (more obvious in fresh or well-preserved specimens), and projecting forward just before contacting lateral aspect of trunk (leaving a slight notch in between disc and trunk). Snout angular to rounded anteriorly, but mostly angular (snout strongly angular in some larger adult specimens). Preocular snout length moderately elongated, ranging from 10.7 to 14.4 percent of total length, and occupying around one-fourth of disc length. Electric organs dorsally begin just anterior to level of eyes on disc, and continue caudally to posterior one-fifth of disc (electric organ length ranges from 19.2 to 26.6 percent of total length); electric organ width occupies between 6.4 and 12.1 percent of total length. Gill-slits more or less straight, not semi-circular, and relatively close together. Gill-slits slightly directed anteriorly at mid-line, and situated progressively closer to mid-line from first to last gill-slit. Eyes and spiracles adjacent. Eyes bulging in fresh or well-preserved specimens, and generally just larger than spiracles. Spiracles more or less circular, not situated at a slight angle in relation to eyes. Spiracles with elevated borders, with papillae on entire spiracular margin. Papillae appear as isolated, pointed projections in smaller specimens, but in larger adults papillae are more robust, resembling closely-packed tubercles or knobs.

Nasal curtain relatively short and wide, with more or less straight posterior margin, and without lateral lobes. Posterior margin of nasal curtain rounded towards its center, bordered by slender fringes of skin. Nasal curtain partially covering upper exposed tooth band. Nasal curtain pores do not continue posteriorly beyond level of nostrils. Nostrils small and circular,

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with small elevated border posteriorly. Prenasal snout length just over one-tenth in disc length. Mouth slightly wider than internarial width, but mouth corners do not project laterally beyond level of outer margin of nostrils. Upper tooth band slightly wider than lower tooth band in most specimens; both tooth bands circular in outline. Teeth in 18/18 – 27/27 vertical exposed tooth rows in adult or pre-adult specimens close to or over than 300 mm in total length; specimens smaller than, or close to, 280 mm in TL will have some three or four less rows of teeth in both upper and lower tooth bands (the largest specimen measured [750 mm in TL] has 30/29 exposed rows). Many adult specimens with one or two more rows of exposed teeth in lower tooth band. Holotype with relatively less teeth (19/18). Teeth with long and pointed cups in larger adults (both in males and females), on exposed and especially not exposed rows; teeth with diamond-shaped to circular bases.

Pelvic fins wider than long when measured together; pelvic fin width ranges from 27.3 to 36.9 percent of total length, pelvic fin length ranges from 19.1 to 25.4 percent of total length. Pelvic fins begin just underneath posterior aspect of disc and extend caudally to level of mid-base of first dorsal fin. Pelvic fins connect at their posterior insertion to ventral aspect of tail leaving a moderately large free lobe in females (in males, free lobe is smaller where pelvics attach to claspers). Claspers elongate, not tapering significantly from base to tip of clasper glans. In adult males, claspers continue caudally to level of posterior first dorsal fin base, projecting beyond distal tip of pelvics by as much as one-third of their length. Tail length almost equal to disc length, averaging 46.9 percent of total length. Tail tapers significantly from base to tip of caudal fin in adult specimens (tail width measured at base averages more than 20 percent of total length). Lateral tail folds more prominent in smaller specimens where

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it is proportionally wider. Lateral tail folds begin on lateral aspect of tail at level of posterior two-thirds of first dorsal fin base, continuing caudally to insert on lateral aspect of caudal peduncle. Dorsal fins large; both dorsal fins similar in height and length. First dorsal fin originates over posterior lobes of pelvic fins. Dorsals with slight free lobe posteriorly where they inflect anteriorly to insert on tail; both dorsal fins sub-acute at apex appearing slightly pointed, and with more or less straight or upright posterior margins. First dorsal with more rounded anterior margin; second dorsal more slanted, with relatively straighter anterior margin. Caudal fin tall and fan-shaped, with relatively straight posterior margin, and acute at both dorsal and ventral corners, but more acute at dorsal apex. Ventral surface of caudal fin more rounded, dorsal surface straighter.

Pores of lateral-line and ampullary systems similar to that of N. brasiliensis, with pores running in a straight line from anterior disc margin to posterior to eyes, just mesial to eyes (pores of supraorbital canals). Pores of the infraorbital canals also very obvious, running in between eyes and spiracles and continuing anteriorly to disc margin. At mid-distance between eyes and anterior disc border, the infraorbital canal branches laterally into the hyomandibular canal, which loops around the electric organs on both sides of the disc. The pores associated with these canals are clearly visible especially in the holotype and in larger specimens. Pores on lateral tail region (posterior extension of lateral canal) run in a more or less straight line, just dorsal to lateral tail fold, from dorsal disc area (at junction with scapular segment) posteriorly towards caudal peduncle. Pores of lateral canal underneath second dorsal fin run closer to base of fin, arching dorsally in relation to lateral tail pores. Some specimens from varying localities have pores on lateral tail arching dorsally underneath both first and second dorsal fins.

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Ventrally, scattered pores of ampullary system not occuring posterior to level of nostrils. Pores on ventral snout area in semi-distinct rows running in more or less parallel lines from snout anterior border to nasal curtain. A small group of pores is present postero-lateral to each nostril.

Dorsal coloration slightly variable. In preservative, background coloration ranging from beige or tan (northern Baja California) and light olive-brown to dark purplish-brown in some specimens (in specimens from the Gulf of California to Colombia). Smaller specimens from the northern range of the species (Gulf of California) have very conspicuous ocelli on dorsal disc region (ocelli as yet unconfirmed in small specimens from more southern localities, in South America). These ocelli vary from four to five (more commonly four are present), and fade considerably in larger specimens. The ocelli are roughly 1.5 times the diameter of eyes, but may reach to 3 times eye diameter. The outer ring of the ocelli is lighter than the background surroundings, while the center of the ocelli is always darker than the background color (ocelli center is usually a dark or chocolate brown). The position of the ocelli do not vary much, with two ocelli present on posterior disc region more or less in same line of eyes and two slightly larger ocelli present over the posterior third of each electric organ. In some specimens a smaller ocellus is present posterior to eyes over mid-disc region. In larger specimens, ocelli are faded into blotches and eventually disappear. The larger ocelli present over electric organs generally are the most long-lasting, appearing as poorly defined dark blotches in larger specimens (see comments below under "Remarks" for more information concerning ocelli). Examined adult specimens from southern Mexico, Panama and Ecuador have a more uniform dark brown background coloration, slightly different from specimens

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from the type-locality and Gulf of California. A small ovoid dark brown blotch is present on tips of dorsal and caudal fins, and is more obvious on specimens that have ocelli. Some specimens with a vertical stripe of creamy white on posterior dorsal fins. Ventrally, specimens are a uniform creamy-white to yellowish-white in preservative, without distinct markings.

REMARKS: The original description of N. entemedor by Jordan and Starks (in Jordan,1895) mentions three specimens, two from Mazatlán (Sinaloa coast of Mexico) and one from La Paz (eastern coast of Baja California Sur). One of these specimens was deposited in the Stanford University (SU) collections (now in CAS), and the two remaining specimens were sent, according to the original registers of SU, to the British Museum of Natural History (London; the specimen from La Paz) and to the Natuurhistorisches Museum in Vienna. The London specimen is extant, but there is no information available regarding the Vienna specimen.

There is some question as to the composition of the type-series of N. entemedor. Jordan and Starks (in Jordan,1895, p. 388) indicate the "Type" as being "No. 1699, L. S. Jr. Univ. Mus.". Both the BMNH and CAS specimens have steel labels affixed to the disc region with this number (these are original SU markers; the number originally given to the specimens is 11699 and not 1699, according to the SU catalog; also Eschmeyer, 1998). However, as specimens were probably sent out as donations to other museums from Stanford before the publication of Jordan and Starks (in Jordan,1895, see p. 380), I interpret the designation of the "type" quoted above to refer exclusively to specimen 1699 (= 11699) deposited in the Stanford collection (holotype). This is further corroborated by the fact that Jordan and Starks clearly did not examine the BMNH specimen, or at least failed to take special notice of it, as they indicate

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in the original description (1895, p. 388) that the largest specimen of the species measured 20 inches (= 500 mm). The BMNH specimen is much larger, measuring 750 mm total length (= approx. 30 inches, being the largest specimen of Narcine that I have seen), a detail that would have been noticed by Jordan and Starks. The type locality is accordingly restricted to Mazatlán, Sinaloa (Mexico). Both Bohlke (1953) and Eschmeyer (1998) consider SU 11699 to be the holotype, but Eschmeyer is uncertain about the type-status of the BMNH specimen.

Jordan and Starks must have had more than one specimen at hand, or at least information concerning other specimens, as they mention that the "[l]ength of *largest* specimen ... [is] 20 inches" (p. 388, italics added), an indication that probably more than one specimen was examined. The specimen sent to Vienna, if found, would probably be the second specimen of Jordan and Starks (likely to also have been labelled 1699). However, I exclude it from the original type-series as well, contrary to the interpretation of others who have dealt with type-series of species published in Jordan (1895). Other authors have considered all specimens mentioned by Jordan and Starks in their new species descriptions (or by Jordan and other co-describers in Jordan, 1895) as constituting the type-series, in circumstances very similar to that of N. entemedor described above. For example, three specimens are mentioned in the original description of Urolophus rogersi Jordan and Starks, 1895 (= Urotrygon rogersi), but only one was isolated as "type". Subsequent authors (Paepke and Schmidt, 1988; Eschmeyer, 1998) have regarded all three specimens as part of the type-series. The reasons why I do not subscribe to this for N. entemedor is that Jordan and Starks clearly did not see one of the three original specimens mentioned (the BMNH specimen), and that in other species descriptions in Jordan (1895), "co-types" (= paratypes) were designated when type specimens other than the

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"special type" (= holotype) were created (e.g., in the description of the catfish Galeichthys gilberti Jordan and Williams, 1895, in Jordan, 1895, p. 395). Also, the term "types" (in the plural) was used when Jordan and his co-author designated more than one specimen in the type-series (e.g., Jordan and Starks, in Jordan, 1895, p. 428, in the description of Scomberomorus sierra), and only one catalog number was given (in the example above, as "Types, 1720, L. S. Jr. Univ. Mus.").

There is no doubt that the BMNH is the "third [specimen] procured by Mr. James A. Richardson in the harbor of La Paz" (1895, p. 388), as it conforms to label information of the specimen (erroneously labelled as "type" in the BMNH). James A. Richardson participated in the Hopkins expedition (Jordan and Starks, p. 379). Jordan and Starks mention the unique La Paz specimen only in passing, noting at the end of Jordan (1895) that the specimen collected by Richardson is badly decayed and was found on the beach.

The dorsal color pattern of N. entemedor is variable, with background coloration ranging from lighter to darker brown, olive-brown and purplish-brown. The ocelli are characteristic of smaller pre-adult specimens (to about 300 mm TL), but one adult male (USNM 165519) of 425 mm total length still clearly has all ocelli present. Ocelli have not been reported on smaller specimens from Costa Rica, Panama, Colombia, Ecuador and Peru, and are absent in almost all specimens examined from these areas (no specimens from Peru were available, and the reported specimens are adult; Chirichigno, 1978). However, one adult male of 430 mm total length from Colombia (USNM 222466) clearly has remnants of ocelli over electric organs, even though they are faded. Therefore ocelli are probably present in smaller

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specimens from throughout the range of the species. Breder (1928) accurately describes the ontogenetic variation in coloration from specimens in the Gulf of California.

A 211 mm total length juvenile male from Costa Rica clearly lacked any dorsal markings other than a light brown background color. This specimen has claspers that only reached to the posterior margins of pelvics (therefore reaching sexual maturity at a much larger size), and has small papillae on spiracular margins, but differs in overall color pattern from typical specimens of N. entemedor of similar size. Similarly, some specimens from Panama and southern Mexico have a uniform brown background coloration without conspicuous markings such as ocelli (specimens from USNM and ISH), although specimens of the same sizes from the Gulf of California present ocelli. These specimens also lack any sign of blotches on tips of dorsal and caudal fins (typical of ocellated specimens). These specimens are here identified as N. entemedor but further comparisons are needed. Small specimens (around 200 and 210 mm in total length) from Sinaloa, Mexico (Bahía Topolobampo) had only very faint remnants of ocelli, but larger specimens (369 and 334 mm TL) of the same lot presented the typical dark blotches over electric organs indicative that ocelli were once present. This indicates that preservation may be causing, at least partly, the variability observed in dorsal color pattern.

Narcine entemedor may enter brackish water (Castro-Aguirre, 1978; Castro-Aguirre and Lopez, 1996). The original description indicates that the holotype was collected in the estuary at Mazatlán. De La Cruz-Aguero et al. (1996) extend the northern range of the species to include Ojo de Liebre lagoon, at the border separating Baja California and Baja California Sur on the eastern coast of the peninsula. Their specimen is the largest recorded for the

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species, as well as for the entire genus (793 mm total length; N. entemedor is the largest species of the genus). Garman (1913) overlooked N. entemedor in his generic revision.

Chirichigno's (1978) extension of the range of this species to include the northern coastline of Peru (based on two specimens) has been overlooked by all authors who have published subsequent accounts on N. entemedor (e.g., Allen and Robertson, 1994; McEachran, 1995; Beltrán and Gaspar-Dillanes, 1995; Castro-Aguirre and Lopez, 1996). Chirichigno's (1978) identification is accepted here, even though specimens from Peru were not examined or located in collections, because Chirichigno's illustration of the ventral surface of one of her specimens does not depict the characteristic posterior projection of the nasal curtain of Discopyge tschudii (the most common narcinid off Peru). The description of the dorsal coloration provided also conforms to N. entemedor. Chirichigno (1978) used the identification keys of Beebe and Tee-Van (1941), which include Discopyge, and her measurements are comparable to those presented in Table 15.

Males are sexually mature between 342 and 372 mm in total length, and females are presumably mature at close to the same size. Allen and Robertson (1994) indicate that pups are free-swimming by 110 to 120 mm total length, and that females give birth to four to 15 pups. I could not confirm this information, or whether both uteri are functional and synchronous, as gravid females for dissection were not available.

GEOGRAPHICAL DISTRIBUTION: Widespread along the continental shelf of the sub-temperate and tropical eastern Pacific, from the Pacific coastline of Baja California Sur (Ojo de Liebre lagoon) and northern Gulf of California (Mexico) to Peru (bordering the Pacific margins

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of Mexico, Costa Rica, Panama, Ecuador and northern Peru) (Fig. 102), in waters ranging from less than one to reportedly 100 m in depth (Chirichigno, 1978). To my knowledge, N. entemedor has not been reported from Guatemala, El Salvador, and Nicaragua, but this is most probably a result of insufficient sampling. N. entemedor also occurs in the Revillagigedos islands (Socorro Island, Bahía Concepcíon; SIO 73-61).

MATERIAL EXAMINED: (41 specimens, 200 to 750 mm total length): **Ecuador**: FMNH 93205; ZMH 10412. **Colombia**: CAS 58354 (3); USNM 206986; USNM 206997; USNM 222466. **Costa Rica**: USNM 94615 (cf. N. entemedor). **Mexico**: AMNH 11798; AMNH 11800; AMNH 15694; AMNH 15695; BMNH 1895.5.27.340; CAS 3591; CAS 11699 (holotype), 421 mm TL adult female, Mazatlán, Sinaloa (Mexico); CAS 36588 (2); CAS (8, uncat.); ISH 263-1975 (5); SIO 73-61; SIO 47-53; USNM 165519; USNM 222505; YPM 1132; YPM 1142; YPM 1144. **Panama**: BMNH 1903.5.15.343; CAS 11899 (cf. N. entemedor); USNM 128385 (cf. N. entemedor).

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Narcine lingula Richardson, 1846

Figs. 32 – 37, Tables 14 – 15

Narcine lingula Richardson, 1846: 196 (original description, not illustrated, based on a figure by J. Reeves; type-locality: China);

Narcine prodorsalis Bessednov, 1966: 80 – 81 (original description, illustration of entire specimen, mouth region and gills; type-locality: Gulf of Tonkin, Viet Nam); Bessednov, 1969; Monkolprasilt, 1984; Monkolprasit, 1990; Monkolprasit et al., 1997; Eschmeyer et al., 1998 (compilation); Carvalho et al., in press (identification, brief description, distribution, in part). NEW SYNONYMY.

Narcine timlei: Bessednov, 1966; Bessednov, 1969; Monkolprasit, 1977; Monkolprasit, 1984; Monkolprasit, 1990; Carvalho et al., in press.

DIAGNOSIS: A species of Narcine distinguished from congeners by presenting the unique combination of a preocular snout length equal or subequal to preoral snout length, preocular snout length clearly and invariably greater than prenasal snout length, dorsal coloration with dark brown circular to ovoid spots greater than eye-diameter over brown background, nostrils relatively small, and mouth width equal or subequal to distance between outer margins of nostrils. In all other species of Narcine, the preocular snout length is subequal to prenasal snout length and clearly not as great as preoral snout length, except in N. maculata, and some

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specimens of N. timlei and N. sp. nov. F. However, dorsal coloration is uniform brown in N. timlei, and composed of white small spots or medium-sized ocelli over brown to purplish-brown background in N. sp. nov. F. N. maculata has large and prominent nostrils, and mouth width is not as great as distance between outer margins of nostrils.

DESCRIPTION: Measurements and counts presented in Tables 14 and 15, respectively. Disc large, subcircular in well-preserved specimens, slightly oval in less well-preserved material. Disc generally slightly wider than long (disc width varies between 43.1 to 56.9 [x = 51.1] percent of total length, disc length ranges from 42.6 to 52.9 [x = 48.9] percent of total length). Disc widest posterior at close to mid-disc length. Snout long, broad and circular, not acute; preocular snout length averages 12.9 percent of total length (ranging from 10.4 to 14.7 percent of total length), and occupying between one-third and one-fourth of disc length. Posterior disc margins overlap origin of pelvic fins, and leave a slight notch at axil, where disc connects to trunk. Electric organs originate anterior to, or at level of eyes dorsally on disc, continuing caudally to between posterior one-fourth to one-fifth of disc (electric organ length averaging 24.0 percent of total length); electric organ width averages 10.5 percent of total length. Gill-slits moderately wide, sub-circular, situated progressively closer to mid-line from first to last gill-slit; branchial basket length about equal to distance between last gill-slits. Eyes and spiracles adjacent. Eye length about equal to spiracle width. Eyes relatively far back on disc in relation to mouth, as preocular and preoral snout lengths are conspicuously more or less equal. Spiracles elongated to circular in some specimens, but generally wider than long and with elevated rims. Spiracles situated at a slight angle in relation to eyes in some specimens.

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Nasal curtain width much greater than nasal curtain length, with posterior aspect straight to slightly lobed mesially in some well-preserved specimens (the median lobe may cover a small portion of upper tooth band). Nasal curtain appearing relatively straight laterally in most specimens, but in fresh material a slight lateral lobe may be present. Sensory pores on nasal curtain continue posteriorly to just beyond level of nostrils. Nostrils round and moderate in size, with a small posterior flap present. The flap varies in size among specimens, being rather large in some individuals covering a large portion of nostril (flaps must be pulled back to ascertain siz e of nostrils). Preoral snout length (11.1 to 15.2 percent of total length, x = 13.1) greater than prenasal snout length (9.0 to 12.2 percent of total length, x = 10.8). Distance between outer margins of nostrils about equal to mouth width in most specimens, but some with slightly wider mouths than outer margins of nostrils. In some specimens, nostrils wider than mouth width, but nostrils are also relatively small. Upper tooth band about as wide as lower tooth band; both tooth bands generally circular in outline, varying in length (antero-posteriorly) from moderately slender to relatively long. Exposed teeth in 15/14 – 22/21 vertical rows in specimens of about 230 mm total length (just prior to sexual maturity) to largest specimens examined (496 mm total length). Tooth counts slightly variable, as one specimen from Taiwan (206 mm total length, male with small and soft clasper) has a tooth count of 11/12, while another specimen of same size and from same locality (pre-adult female) has a higher tooth count (16/15). Teeth with relatively large and sharp cusps in some specimens, but cusp size is slightly variable as well on exposed teeth, as some material had broad and more blunt cusps even though of comparable sizes. Long cusps are present on inner, not exposed,

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rows, and these overlap bases of teeth in row closer to mouth opening. Teeth closely set together, with relatively small bases that vary frm broad to more trapezoidal.

Pelvic fins variable in proportions and shape, as pelvics are highly affected by preservation. Pelvics wider than long when measured together; pelvic fin width is between 23.9 to 35.7 percent of total length (x = 30.8), pelvic fin length varies from 15.3 to 21.2 percent of total length (x = 18.6). Pelvic fins without fleshy, rounded lateral lobes. Pelvics angular laterally, with anterior margins long in relation to posterior margins in well preserved specimens, but pelvics not very elongated antero-posteriorly. Pelvic fins with slightly convex posterior lobes in well preserved material, otherwise more or less straight. Pelvics originate underneath underneath posterior margin of disc and extend caudally to insert on ventro-lateral tail at vertical through first dorsal fin origin. Small free lobe present where pelvics adjoin tail posteriorly. Claspers moderate in length, projecting to level of posterior tw-thirds of first dorsal fin base in adult males. Claspers in specimens of about 205 mm total length more or less equal in length to posterior lobe of pelvics. Tail moderately stout at base. Tail length slightly shorter than disc length as measured from cloaca. Lateral tail folds moderately to well developed, originating at level of posterior first dorsal fin base (on lateral tail region), continuing posteriorly to insert on ventro-lateral portion of caudal peduncle. Dorsal fins sub-equal in height and length and only moderately large, but second dorsal fin slightly taller and longer than first dorsal fin. Free lobe of dorsals above base of fin about equal in both dorsals, but may be larger in first dorsal in some specimens. First dorsal fin generally less slanted than second dorsal, and more pointed at apex in some specimens, but both dorsals with more or less rounded apex (some specimens with more oval apex, some with slightly pointed apex, but

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shape slightly influenced by preservation). Some specimens with more upright dorsal fins than others (e.g., from Madras, India). First dorsal fin originates over posterior tips of pelvic fins, slightly posterior to, or exactly above, pelvic fin insertion on trunk. In poorly preserved specimens first dorsal fin appears situated more posteriorly in relation to pelvics (pelvics are reduced in length). Dorsals with straight to slightly slanted posterior margins. Distance between second dorsal and caudal fin slightly greater than distance between dorsals. Caudal fin slightly variable in shape and proportions, but generally with slightly taller dorsal lobe in relation to ventral lobe. Caudal fin height variable, ranging from 7.8 to 12.0 percent of total length ($x = 9.7$). Caudal fin with slanted upper lobe and oval to rounded apex. Posterior margin of caudal fin slightly slanted to more or less upright or moderately rounded; curved lower margin of caudal fin. Ventral lobe originates slightly anteriorly on caudal peduncle.

Pores of lateral-line and ampullary systems not very conspicuous, not very visible without dissection. Pores of supraorbital, infraorbital and postorbital canals are present over dorsal snout region, running in more or less straight rows over rostral ridges and between eyes and anterior disc margin. Anterior branch of hyomandibular canal has pores bordering electric organs anteriorly (pores of dorsal disc region are relatively few in number). Pores of lateral canal (lateral tail region) generally arch dorsally beneath both dorsal fins. Pores on ventral surface present on snout region and outlining electric organs anteriorly and laterally (pores extend to posterior two-thirds of electric organs). Pores in more or less parallel, antero-posterior rows, radiating from snout tip to nasal curtain area, but not extending posteriorly behind level of nostrils on nasal curtain. Two groups of pores lateral to nostrils and mouth are

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present, extending anteriorly into ventral snout region. Two small and oblique rows of pores present posterior to mouth and before gill-slits on both sides.

Dorsal coloration composed of dark brown spots of varying shape and size over a lighter brown background. Pattern of spots markedly variable. In many specimens, pattern of spotting is complex, with spots oval to circular or semi crescent-shaped. Pattern of spotting alternates between larger blotches that are variously elongated, to smaller spots that may be fused forming partial reticulations over disc and tail regions (e.g., specimen from eastern India, Fig. 33). In specimens with this pattern, the smaller spots may be oval and as small as eye-diameter; larger spots may be irregularly-shaped and about as large as interocular distance. Spots are also present over tail, dorsal, caudal and pelvic fins in specimens of this pattern (spots on fins of varying diameter). Other specimens with fewer and larger spots that are more circular (e.g., from Taiwan; Fig. 34). In these specimens, spots are more uniformly-sized and distributed over disc and tail. Intermediate specimens present many spots conspicuous to the latter variety (fewer, larger spots) but with some spots fused into more elongate forms over lateral disc, base of tail and snout regions. Another specimen (from Madras, eastern India) have smaller (from about size of eye to twice eye-diameter), more clearly defined spots, that are also more numerous (Fig. 37). Specimens with this pattern may present spots that form elongated, curved markings over disc and tail that may also be darker than usual. Two specimens from Taiwan have smaller, more numerous spots over a reddish-brown background; these spots may also be elongated and fuse over disc and tail regions. Many specimens have spots slightly outlined in lighter shades, resembling weak ocelli, especially in smaller specimens. Ventrally specimens are uniform white to creamy in color. Large female from Taiwan

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(NTUM 04455) with smaller dorsal spots presenting ventral blotches at posterior disc, pelvic and tail regions.

REMARKS: Richardson (1846) based his description of N. lingula on an illustration executed for J. Reeves as part of a collection of illustrations representing the fishes of Canton (Guangzhou, China), where Reeves was based as an employee of the "India Company." Reeves had some 340 species of fishes illustrated from the region. Four sets of these illustrations were made, of which one was presented to J. Richardson of the British Museum of Natural History. Richardson's description of N. lingula is based solely on the plate of an electric ray referred to in Chinese as "Muh chu poo" and as "Wooden ladle handle ray" by Reeves (according to Richardson, 1846). Richardson does not mention any specimen in relation to his new species, and he explicitely refers to the illustration while describing it. I examined the original art-work for the "Muh chu poo" present in the Richardson set of Reeves' illustrations (deposited in the library of the BMNH in London), and it agrees very closely to the original description of N. lingula Richardson, 1846. Richardson also refers to a set of illustrations from "the late Dr. Wight in India" (1846: 196) which he accepts as also representing his new species, and bases his account of the ventral surface of N. lingula on the basis of these illustrations, as Reeves' figure depicts only the dorsal side. Richardson also gives the length of his new species as "length of the *figure* 13 inches" (1846: 196, italics added), implying that no specimens were available to him. The connection between the original depiction present in the Richardson copy of Reeves' illustrations, and the description of N. lingula, was previously reviewed by Whitehead (1970), who also concluded that N. lingula was

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described by indication only, based solely on the plate in Reeves' drawings of Chinese fishes. The illustration of N. lingula is here reproduced (Fig. 32) from a black and white reproduction (from Whitehead, 1970) of the original drawing, which is in color.

Eschmeyer et al. (1998) mistakenly accept two specimens (BMNH 1848.3.18.178-179) from China as syntypes of N. lingula, probably on the basis of label information which designate the specimens as types (= syntypes; however, the collection register does not do so). Both specimens are *not* types of N. lingula, and cannot be clearly identified with it. One specimen is an adult male of 215 mm total length easily identified as N. timlei (Bloch and Schneider, 1801; Fig. 61A, B), but the other specimen may be referrable to N. lingula. However, it is definetely not identified as the specimen from which Reeves' plate was based, which would be the holotype of the species described by Richardson. The original description and illustration of N. lingula is of a male specimen of 13 inches in length (approximately 330mm, which would make it an adult with calcified claspers), while the specimen in BMNH 1848.3.18.178-179 (that is not identified as N. timlei) is a female of 236 mm total length. The original description provides numerous diagnostic characters which are not present in the specimens accepted as syntypes of N. lingula by Eschmeyer et al. (1998). These include dorsal coloration (there are no spots and conspicuous markings diagnostic of N. lingula on the specimens, even under magnification, and Richardson describes coloration is detail) and proportional characters (Richardson indicates that disc width is equal to tail length as measured from the anus [sic], but disc width is greater than tail length in both specimens). Both specimens differ substantially from Reeves' illustration in proportions, shape and position of pelvic, dorsal and caudal fins, and very clearly in dorsal coloration, as both specimens are

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uniform in color dorsally. Even if they have deteriorated greatly in preservation, they could not have been similar to Reeves' illustration when Richardson would have examined them. There are no type specimens for N. lingula, a situation not uncommon for many species described by Richardson on the basis of illustrations provided by J. Reeves (see Whitehead, 1971 for an excellent history of Reeves' volumes of illustrations, and the subsequent species descriptions based on them).

Many specimens examined of N. lingula from Taiwan, China and India agree very closely with the illustration in Reeves' original set presented to Richardson, especially in coloration. Coloration, position of first dorsal fin in relation to pelvics, shape of caudal fin and disc, and configuration of eyes and spiracles in most specimens here identified as N. lingula are very similar to Reeves' plate. The original description is also corroborated by specimens in almost every character given. Perhaps the sole exception is size of dorsal fins, as Richardson states that the first dorsal is larger than the second, but this is contradicted by specimens examined. However, this difference is probably methodological, as Richardson's measure of dorsal fin size may have been related to the free lobe above the base, which may be greater for the first dorsal fin. The proportions given here for dorsal fin size relate to height (as measured from base to tip) and length of base, not length of free lobe above base.

This species, as noted in the description above, presents much variation in color pattern. Specimens representing extremes in color pattern are quite distinct from each other (e.g., Figs. 33 – 37), but many specimens bridge these differences. Some specimens from Taiwan have few, large spots, while others have many smaller spots and different intensities of background color, and even others present very distinctive patterns of alternating small and

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large spots, with elaborate shapes resulting from fusion of spots on disc. These distinctions could not be separated on the basis of geography or any other factor. N. lingula is presently considered, therefore, to be somewhat complex and variable in relation to its coloration.

It is on the basis of this variation in coloration that N. prodorsalis Bessednov, 1966 is provisionally considered a junior synonym of N. lingula. N. prodorsalis was described from a female specimen of 298 mm total length collected in 1960 from the Gulf of Tonkin, which is presently lost. The holotype and only specimen available to Bessednov was originally deposited in the Museum of the Pacific Research Institute of Fisheries and Oceanography (TINRO) in Vladivostok. As with the holotype of N. brevilabiata Bessednov, 1966, the holotype of N. prodorsalis was discarded (see discussion for N. brevilabiata above). The holotype is not present in the Institute of Marine Biology in Vladivostok (D. Pitruk, personal commun.) or the Zoological Institute in St. Petersburg (A. Neelov, personal commun.), institutions that received TINRO specimens before its closing. N. prodorsalis was distinguished from other species of Narcine on the basis of its dorsal coloration (also Monkolprasit, 1984, 1990), and compared by Bessednov (1966, 1969) to N. timlei (= N. lingula or N. maculata here).

Many specimens of N. lingula and N. maculata (see below) have numerous small spots dorsally, but this character alone seems insufficient to identify N. prodorsalis given the variation present in these species regarding coloration. One large female from Taiwan (376 mm total length; Fig. 36) resembles the color pattern described for N. prodorsalis. Its mouth and nasal curtain region is also similar to that described for the holotype by Bessednov, with small nostrils partially covered by posterior nasal flaps, and slender tooth bands that are not very

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broad. But this specimen is so close to other specimens of N. lingula from Taiwan that it cannot be considered as a separate species. More specimens with its coloration are needed to further comprehend its slight differences in mouth, nostrils and nasal curtain. One examined specimen from Singapore (also a large female, Fig. 44A), and identified as N. maculata, is similar in coloration to the description and illustration of N. prodorsalis, but it has very enlarged nostrils presently used to diagnose N. maculata (see next species account below), which contradicts Bessednov's description. It seems that relatively large male and female specimens may possess smaller, more clearly defined spots. The correlation of color pattern with size may be important, as Monkolprasit's (1984, 1990) identification of N. prodorsalis (the only other such identification in the literature outside of Carvalho et al., in press) was also based on a large specimen. I have never seen a small specimen of Indo-Pacific Narcine with numerous small dark spots as in the depiction of the holotype of N. prodorsalis. Small specimens of "spotted" Narcine that are newly free-swimming generally have proportionally larger spots.

N. prodorsalis may prove to be a valid species, but in the absence of the holotype and knowing how variable coloration can be in forms of Narcine with large dark brown spots over a brown background (N. lingula and N. maculata), N. prodorsalis Bessednov, 1966 is provisionally regarded as a junior synonym of N. lingula Richardson, 1846 until further material from Viet Nam (the type-locality of N. prodorsalis) of different sizes can be examined.

The separation of N. lingula from N. maculata (described below) is provisional and tentative at best (further discussed below under "Remarks" for N. maculata). Specimens of N. lingula seem to have more elongated spots that are laterally oriented, appearing as streaks over disc, surrounding electric organs, and running antero-posteriorly on pelvics, as in the original

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illustration of Reeves and examined specimens (Fig. 33). The separation between both species, as here defined, is based on dimensions of nostrils in relation to mouth (Fig. 33D and 42D), but this is provisional until further (and better-preserved) material is examined.

Small specimens are free-swimming by about 106 mm total length (specimen examined had faint yolk-scar present and no external teeth). Sexual maturity for males is determined to be from between 240 mm total length (specimen from Viet Nam) and 270 mm total length (specimen from Taiwan). Females achieve sexual maturity presumably at about 250 mm total length.

GEOGRAPHICAL DISTRIBUTION: This species is fairly widespread throughout the inshore, and mainly shallow northern Indian ocean, from western India, to the western Pacific and South and East China Seas reaching as far north as Shanghai and perhaps further north into the Yellow Sea (Fig. 105). Reports of this species from Japan (usually identified as N. timlei; Nakaya, 1986) are not common. Its presence in the Philippines has to be confirmed (specimens of this species from the Philippines were not available, but it has been recorded from there; Herre, 1953; Conlu, 1986). Records from Pakistan of a spotted Narcine are probably of this species (e.g., Bianchi, 1985).

MATERIAL EXAMINED: (40 specimens, 106 to 496 mm total length). **China**: ANSP 76544 (Hong Kong); BMNH 1848.3.18.178-179 (1 of 2 specimens, 236 mm total length female); BMNH 1884.2.26.52; CAS 9961 (2; Hong Kong); CAS 15846 (Taiwan); CAS 15918 (4; Taiwan); CAS 30991; CAS 34208 (Taiwan); CAS 49338; MCZ 45; NTUM 00006

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(Taiwan); NTUM 00023 (Taiwan); NTUM 01642 (Taiwan); NTUM 01648 (Taiwan); NTUM 04454 (Taiwan); NTUM 04455 (Taiwan); NTUM 05023 (Taiwan); USNM 192574 (3; Taiwan); ZMH 10431 (Shanghai). **India**: BMNH 1892.6.17.10; BMNH 1909.7.12.9; BMNH 1979.3.21.411; CAS 58353 (2); CAS 58357; CAS 141716 (2); MNHN 1339 (2); SMF 4589; ZMA 112.812. **Myanmar**: CAS 58361. **Thailand**: SIO 65-473. **Viet Nam**: CAS 33898.

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Narcine maculata (Shaw, 1804)

Figs. 38 – 44, Tables 16 – 17

Raja No. I: Russell, 1803: 1, pl. (description, illustration, not named, popular name: "Temeree"; Vizagapatnam, eastern India).

Raja No. II: Russell, 1803: 2, pl. (description, illustration, not named, popular name: "Nalla Temeree"; Vizagapatnam, eastern India).

Raja maculata Shaw, 1804: 316 (original description, not figured, based on the "Temeree" of Russell, 1803: 1; type-locality: Vizagapatnam, eastern India).

Raja bicolor Shaw, 1804: 316 (original description, not figured, based on the "Nalla Temeree" of Russell, 1803: 1; type-locality: Vizagapatnam, eastern India).

Narcine maculata Duméril, 1852: 55 –56 (original description, not figured; secondary homonym – preoccupied by Raja maculata Shaw, 1804; type-locality: Java, Indonesia).

Narcine firma Garman, 1913: 301 (original description, not illustrated; type-locality: off Colombo, Sri Lanka); Fowler, 1941: 335 (erroneously synonymized with N. brunnea Annandale, 1909); Bigelow and Schroeder, 1953 (synonym of N. brunnea, Annandale, 1909).

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Narcine timlei: Fowler, 1941: 334 – 335 (description compiled, distribution).

Narcine prodorsalis: Carvalho et al., in press (in part).

DIAGNOSIS: A species of Narcine distinguished by the following unique combination of characters: preocular snout length equal or subequal to preoral snout length, and invariably greater than prenasal snout length, dorsal coloration with circular and ovoid dark spots and blotches of varying diameter over brown background, nostrils distinctively large and circular, distance between outer margins of nostrils greater than mouth width. In all other species of Narcine, preocular snout length is less than preoral snout length, and subequal to prenasal snout length, except in N. lingula and in some specimens of N. timlei and N. sp. nov. F. Dorsal coloration is uniform brown in N. timlei, and composed of small white spots or medium-sized ocelli over brown to purplish-brown background in N. sp. nov. F. In N. lingula, the nostrils are small, and the mouth is generally wider than, or equal to, distance between outer margin of nostrils.

DESCRIPTION: Measurements and counts presented in Tables 16 and 17, respectively. Disc large and generally subcircular, about as wide as long (disc width is between 42.4 to 53.9 [x = 49.3] percent of total length, disc length ranges between 43.3 to 51.2 [x = 48.1] percent of total length). Disc widest posterior to mid-disc length. Disc shape slightly variable in preserved specimens, as some specimens with distorted, shrunken discs (affecting disc width; e.g., BMNH 1888.11.6.87-89), appearing more oval in outline. Snout circular, not angular or

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acute; snout very broad and relatively long (preocular snout length averaging 12.7 percent of total length); preocular snout length occupying between one-third and one-fourth of disc length. Disc overlaps origin of pelvic fins posteriorly, contacting lateral aspect of trunk leaving a slight notch at axil. Electric organs originate anterior to eyes dorsally on disc, and continue caudally to between posterior one-fifth of disc (electric organ length averaging 23.5 percent of total length); electric organ width averages 10.2 percent of total length. Gill-slits wide and sub-circular, situated progressively closer to mid-line from first to last gill-slit; large distance between gill-slits on either side. Eyes and spiracles adjacent. Eye length greater than spiracle length, but about equal to spiracle width. Eyes situated relatively posteriorly on disc, in relation to mouth. Spiracles elongated, wider than long and with slightly elevated borders. Spiracles situated at a slight angle in relation to eyes.

Nasal curtain much wider than long, with posterior margin generally folded back and shrunken in preserved specimens, but a slight median lobe may be originally present that partially covered upper tooth band. Nasal curtain with slightly lobed lateral margins in well-preserved specimens. Sensory pores on nasal curtain continue posteriorly to just beyond level of nostrils. Nostrils conspicuously large and circular, with well developed and elevated margins posteriorly resembling a flap. Preoral snout length (12.1 to 13.5 percent of total length, x = 13.0) greater than prenasal snout length (9.1 to 10.8 percent of total length, x = 10.2), but preoral snout distinctively more or less equal to preocular snout length (preocular snout length is greater than preoral snout length in some specimens). Distance between outer margins of nostrils conspicuously greater than mouth width; mouth corners project laterally to about mid-width of nostrils. Upper tooth band about as wide as lower tooth band; both tooth bands

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generally circular in outline (some specimens with broad lower tooth bands with more straight and angled lateral margins; e.g. holotype of N. firma). Exposed teeth in 16/15 – 22/21 vertical rows in most specimens (all presumably adult; one specimen of 302 mm total length from Singapore had only 13/12 exposed rows of teeth). Teeth with somewhat large cusps in most specimens (cusps long even on exposed teeth, long enough to clearly overlap bases of teeth in row closer to mouth opening). Teeth closely set in some specimens, with relatively small bases (size of bases varied slightly in specimens examined). Bases diamond-shaped, and posteriorly rounded to sub-acute.

Pelvic fins generally poorly preserved, but wider than long when measured together. Pelvic fin width ranges between 25.2 to 31.3 percent of total length (x = 29.5), pelvic fin length ranges from 13.1 to 19.8 percent of total length (x = 17.7). Pelvic fins without fleshy, rounded lateral lobes, and relatively long postero-lateral margins in well preserved specimens. Posterior margins of pelvic fins slightly convex in well preserved material, otherwise more or less straight. Pelvic fins begin just underneath posterior aspect of disc and extend caudally to level of first dorsal fin origin. Small free lobe present where pelvics adjoin tail posteriorly. Pelvics with very small free posterior lobe where they connect to claspers. Claspers relatively long, projecting beyond pelvics by about one-fourth of their length. Claspers in large males projecting posteriorly to close to, or just beyond, level of posterior base of first dorsal fin. Tail not very stout at base. Tail length, as measured from cloaca, is sub-equal to disc length, but does not vary as much as disc width or length. Lateral tail folds moderately to well developed, originating on lateral aspect of tail at level of posterior first dorsal fin base, and continuing caudally to insert on ventro-lateral portion of caudal peduncle. Dorsal fins moderately large

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and about sub-equal, but second dorsal fin slightly taller than first, and also with slightly longer base. Free lobe above base about equal in both dorsals. First dorsal fin more erect than second dorsal, but both dorsals generally rounded at apex (some specimens with more oval apex, perhaps due to preservation); second dorsal fin with relatively more slanted anterior margin (some specimens from eastern India with relatively more slanted dorsals). First dorsal fin originates over posterior tips of pelvic fins, slightly posterior to pelvic fin insertion on tail. Dorsals with more or less straight posterior margins. Distance between second dorsal and caudal fin greater than distance between dorsals. Caudal fin slightly variable in shape, but generally not very tall in relation to total length (caudal fin height ranging from 9.2 to 11.1 percent of total length, x =10.1). Caudal fin with slanted upper lobe anteriorly and oval to rounded apex. Posterior margin of caudal fin slightly slanted and more or less straight to moderately rounded, convex; lower margin of caudal markedly curved. Dorsal and ventral lobes of caudal more or less same size, as measured from base of caudal fin (dorsal lobe only slightly longer and taller); ventral lobe originates slightly anteriorly on caudal peduncle. Male specimen from Singapore and holotype of N. maculata Duméril, 1852 (Java) with slight notch on posterior margin of caudal (not preservational).

Pores of lateral-line and ampullary systems difficult to observe, not very conspicuous (dorsal coloration prohibits clear observation of pores without dissection). Dorsal pores of supraorbital, infraorbital and postorbital canals are present. These pores are located dorsally on snout and anterior disc regions, in more or less straight rows over rostral ridges and between eyes and anterior disc margin. Anterior branch of hyomandibular canal has pores bordering electric organs anteriorly. All pores of dorsal aspect of disc are relatively few in number. Pores

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of lateral canal, on lateral aspect of tail, are somewhat variable in distribution. In some specimens pores run in a straight line dorsal to lateral tail fold, while in others pores arch dorsally beneath both dorsal fins (specimens from Madras and Singapore). On ventral surface, pores are present on snout region and outlining electric organs anteriorly and laterally. Pores on ventral snout area in semi-defined parallel antero-posterior rows, radiating from snout tip to nasal curtain region, but not extending posteriorly behind level of nostrils on nasal curtain. Two rows of pores are present lateral to nostrils and mouth, continuing anteriorly to snout area.

Dorsal coloration slightly variable, but mostly composed of dark brown to blackish-brown spots over a light brown background. Spots are generally present covering dorsal, pelvic and caudal fins. Spots vary in both shape and size among specimens, but are generally circular to ovoid. Some spots are about equal to eye-diameter (occasionally smaller), while others are slightly larger (e.g., anterior to first dorsal fin on base of tail). Some spots may fuse into longer blotches. Specimens from Singapore differ from each other, and from most specimens, in number and size of spots: the female specimen (390 mm total length) is covered with numerous, relatively small spots of more or less equal size, evenly distributed throughout entire specimen including pelvic, dorsal and caudal fins, and anterior snout region; the male specimen (302 mm total length) has relatively larger and fewer spots on disc, pelvic and tail region, but with smaller spots covering dorsal and caudal fins. The female specimen from Singapore has a blackish blotch on right side of disc posterior to mid-disc region. Both Singapore specimens have a light brown background color. Some specimens from Madras

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also have relatively smaller spots (about size of spiracles), but not as numerous and small as the large female from Singapore. Ventrally specimens are white without conspicuous markings.

REMARKS: Raja maculata was described by Shaw (1804) for the "Temeree" of Russell (1803: 1), whose monograph on the fishes of the Coromandel coast is one of the first illustrated works on the fishes of eastern India. Russell (1803) provides a description and illustration (but not a specific name) of the fish locally known as "Temeree" (the description was repeated in part by Shaw, 1804). Russell's illustration depicts a species with a brown background and circular, dark brown spots larger than the eyes and spiracles. Shaw (1804) also named another fish described and illustrated by Russell (1803: 2, his "Nalla Temeree"). Raja bicolor Shaw, 1804 was coined for a species with white background dorsal color and black, smaller and more numerous spots. Both original illustrations of Russell (1803) are reproduced here as Figs. 38 and 39. Russell's original specimens were not deposited in an institution, and no type specimens exist for both nominal species. Shaw's (1804) nominal species are based exclusively on the illustrations of Russell (1803), and are available by indication (ICZN 1985: 35, Art. 12 b [7]).

The species here identified as Narcine maculata (Shaw, 1804) is distinguished from congeners, with the exception of N. lingula, by its dorsal color pattern (composed of large dark brown spots, generally larger than eye-diameter over a brown background), position of first dorsal fin (originating posterior to, or right above, pelvic fin insertion), proportional measurements of the dorsal fins (second dorsal slightly larger than first), and by having a distinctively enlarged preocular length relative to preoral length (both measurements about

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equal, whereas most other species of Narcine have a greater preoral length). N. maculata is distinguished from N. lingula by having conspicuously enlarged nostrils situated relatively farther apart (distance between outer margin of nostrils greater than mouth width; in N. lingula the nostrils are relatively smaller, and mouth corners may project laterally beyond outer margins of nostrils). The dorsal coloration and position of first dorsal fin in relation to the pelvics are present in both Russell's (1803) and Shaw's (1804) accounts, and are clearly depicted in the illustration of the "Temeree" in Russell (1803: 1). Russell (1803) also mentions that the nostrils are large in his Raja maculata, but his meaning of "large" is vague. Judging from the shape and dimensions of the pelvic fins and disc of the illustration provided by Russell, his specimen probably was somewhat shrunken. Examined specimens that have undergone slight distortion as a result of dessication are strikingly similar to the illustration of the "Temeree" of Russell (e.g., BMNH 1909.7.12.8 from Myanmar), displaying the same pelvic fin configuration, position and shape of dorsal fins, caudal fin shape and disc outline (cf. Figs. 38 and 42). In addition, the dorsal coloration in Russell's illustration is very similar to that of examined specimens from the east coast of India (e.g., specimens from Madras). These characters permit the binomen Raja maculata Shaw, 1804 to be applied to this species.

The separation between N. maculata and N. lingula is difficult. Numerous specimens examined from the western coast of India, both sides of the Bay of Bengal and Andaman Sea, Straits of Malacca, Gulf of Thailand, Indonesia, South China Sea and East China Sea, have not permitted a very clear separation into more than one species. Proportional measurements, meristics, coloration, dentition, and general morphology are very similar for both species. Even though minor distinctions may be present in one or more of these character complexes (e.g.,

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coloration, dentition), they never seemed consistent enough for the recognition of two separate species, as some of the differences appeared to be related to sex, size and preservation, or a combination of one or more of these constraints. The distinction in the configuration of the nostrils appeas to be independent of these constraints, and is presently the sole criterion adopted here for the recognition of the two species (Fig. 42D), but this is considered tentative until more evidence is examined. Freshly preserved material, photographs or accounts of live coloration, and more specimens from throughout their range, are required to corroborate the recognition of the two species. N. maculata (Shaw, 1804) and N. lingula Richardson, 1846 are the oldest available names for both forms (Raja bicolor Shaw, 1804 is discussed below; see also account on N. lingula above).

One paralectotype of Raja timlei Bloch and Schneider, 1801, is tentatively identified as N. maculata. ZMB 7588 is a stuffed adult female specimen of approximately 364 mm total length. Most of the specimen is badly distorted, and the (fake) eyes have been erroneously placed in the spiracles (common in stuffed specimens of Narcine). Some measurements and counts were possible to extract, but they are not very reliable (Tables 16 and 17). The coloration is very faded, but remnants of spots can be seen under magnification. The measurements taken indicate that the preoral length is smaller than preocular length, second dorsal is greater than first, and distance between second dorsal and caudal is greater than the distance between dorsal fins. First dorsal fin origin is posterior to pelvic insertion on trunk. The lectotype of Raja timlei, chosen on the basis of the best–preserved syntype (see account on N. timlei below), is not conspecific with N. maculata. The stuffed paralectotype of R. timlei is

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identified as N. maculata and not N. lingula on the basis of its apparently enlarged nostrils, but this may be related to the way in which the specimen was preserved.

Raja bicolor Shaw, 1804 is based on what appears to be a bleached specimen, as a white background coloration only occurs on specimens that are poorly preserved, having lost their original coloration (perhaps overexposed to direct sunlight) (Fig. 39). Specimens that have completely faded dorsal background coloration can still retain some remnants of dorsal spots, as these are naturally darker than the background color. There are no strictrly diagnostic characters provided for Raja bicolor other than the dorsal coloration. The illustration provided by Russell (1803: 2) appears to be of a specimen of N. maculata with slightly smaller spots, a common intraspecific variation in this character (Raja bicolor, however, appears to have better-preserved disc and pelvic fins compared to Raja maculata). Given that the only diagnostic features of Raja bicolor Shaw, 1804 are its (bleached) coloration and smaller spots, it is considered here a synonym of Raja maculata Shaw, 1804.

Narcine maculata Duméril, 1852 was based on a single specimen from Java (precise locality not specified). The holotype (Fig. 40) has lost most of its original coloration and is somewhat soft, but can still be identified with the species here called N. maculata (Shaw, 1804), on the basis of proportional measurements and meristics (see Tables 16 and 17 respectively), morphology of nostrils and mouth (distance between outer nostril margins is far greater than mouth width), and by its remaining color pattern (on disc, tail, pelvic and caudal fin regions). Duméril's (1852) name, however, is a secondary homonym of Raja maculata Shaw, 1804, and is therefore herein suppressed (ICZN 1985: 107, Art. 57c [i]). The holotype is similar to the male specimen from Singapore in possessing a caudal fin with a slight posterior

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notch (cf. Figs. 40 and 44). Both upper and lower tooth bands have very elongated cusps. McEachran and Séret (1986) erroneously synonymized this species with N. indica Henle, 1834 (= N. timlei [Bloch and Schneider, 1801] here).

Narcine firma was described by Garman (1913) on the basis of a single specimen from Colombo, Sri Lanka. The holotype is in relatively good condition apart from the dorsal coloration, which is all but gone (Fig. 41). Garman's description is extensive, but his specimen already lacked coloration when he received it. The holotype of N. firma has characters diagnostic of N. maculata, such as: configuration of the mouth, nostrils and nasal curtain region, with enlarged, circular, nostrils and tooth bands of more or less same width; mouth corners not projecting laterally beyond outer margins of nostrils; second dorsal fin larger than first and with a greater base; greater distance between second dorsal and caudal than between first and second dorsal fin; preocular length equal to preoral length; first dorsal fin originating posterior to pelvic fin insertion on tail. In addition, the holotype of N. firma has general proportions similar to those of N. maculata (disc width and length, electric organ length and width, clasper length, distance between snout and cloaca and cloaca and caudal fin, among many others; Table 16). Lateral tail fold, shape of dorsal, caudal, pelvic fins and disc, broad, rounded snout, number of exposed tooth rows, and other characters, all agree with examined specimens of N. maculata. The holotype of N. firma is bleached white dorsally and ventrally, but under magnification certain folded areas of the disc (e.g., where label is affixed to specimen on right disc side, underneath dorsal fins) revealed that the original coloration was composed of a brown background with small spots of darker brown, very similar to that described for the

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large female specimen from Singapore. N. firma Garman, 1913 is therefore here synonymized with R. maculata Shaw, 1804.

The large female specimen from Singapore (390 mm total length) differs substantially from any other specimen in relation to its color pattern, composed of numerous small brown spots. The male specimen from Singapore is smaller (302 mm total length) and has slightly larger spots. Both specimens are presumably from the same area (both procured from fish markets in Singapore), and illustrate well the type of variation that may be present in this species. Both specimens are very close in most features, differing slightly in meristics (Table 17), number of tooth rows and some proportional measurements (disc width and length, for example), but are presently considered conspecific. The pattern of smaller dorsal spotting may be related to size (see discussion above under "Remarks" for N. lingula).

Fowler (1941) erroneously synonymized N. firma with N. brunnea Annandale, 1909 (= N. timlei [Bloch and Schneider, 1801] here). Carvalho et al. (in press) used the nominal species N. timlei (Bloch and Schneider, 1801; in part) and Narcine prodorsalis Bessednov, 1966 (in part) for N. maculata. The similarities in color pattern led them to use Bessednov's nominal species for the specimens examined from Singapore. However, Carvalho et al. (in press) were limited to applying nominal species on the basis of the then current usage in the area (they followed Monkolprasit, 1984).

A 282 mm total length male from Orissa (eastern India) has firm claspers and is therefore sexually mature, but another male examined, a 302 mm total length specimen from Singapore, appears to have claspers not completely calcified (but relatively firm). Individuals of 125 mm total length are free-swimming. A 131 mm total length male (from Sabah) has

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14/12 exposed tooth rows, indicating that tooth row numbers do not increase greatly with age. This specimen has claspers that just reach posterior pelvic margins.

GEOGRAPHICAL DISTRIBUTION: This shallow, in-shore species is relatively widespread. Specimens have been examined from Sri Lanka (off Colombo), from western Bay of Bengal (Madras and Orissa coast, eastern India), Andaman Sea (off Rangoon, Myanmar), from Singapore and Sabah (Malaysia), from Java (Indonesia) and from southwestern China (Hong Kong) (Fig. 105). Specimens from Singapore are from a fish market, so their precise locality is not known, but is presumed to be from relatively close to Singapore.

MATERIAL EXAMINED: (24 specimens, 125 to 401 mm total length). **Cambodia**: MNHN 1988-465 (tentatively identified). **China**: CAS 13931. **India**: BMNH 1888.11.6.87-89 (3); CAS 41715; CAS 169800; ZMB 7588 (paralectotype of Raja timlei Bloch and Schneider, 1801), 364 mm total length adult female, Tranquebar, eastern India (tentatively identified). **Indonesia**: MNHN 1336 (holotype of Narcine maculata Duméril, 1852), 330 mm total length adult male, Java, ex-RMNH specimen (probably of Kuhl and van Hasselt); RMNH 2419 (stuffed); RMNH 2422 (stuffed); RMNH 4314. **Malaysia**: CAS 27722 (5; Sabah, Borneo). **Myanmar**: BMNH 1909.7.12.8. **Singapore**: ZRC 2101 (2). **Sri Lanka**: MCZ 75 (holotype of Narcine firma Garman, 1913), 401 mm total length adult male, Colombo, Sri Lanka, Capt. Putnam. **Viet Nam**: MNHN 7956; MNHN 8907. Specimen from unspecified locality: SMF 3928 (stuffed specimen; "Indian Ocean").

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Narcine rierai (Lloris and Rucabado, 1991)

Figs. 45 – 48, Tables 18 – 19

Heteronarce rierai Lloris and Rucabado, 1991: 327, figs. 1 – 3, tables 1 – 2 (original description, figured; type-locality: south of Beira, Mozambique, western Indian Ocean).

Narcine rierai: Compagno, 1995: vi, fig. 24a.1 (brief account, transferral to Narcine; Mozambique, close to type locality); Eschmeyer et al., 1998 (compilation).

DIAGNOSIS: A species of Narcine diagnosed by the unique presence of a nasal curtain that is longer than wide (nasal curtain length averaging 2.9 percent of total length, nasal curtain width averaging 2.4 percent of total length; nasal curtain is wider than long in all other species of Narcine).

DESCRIPTION: Measurements are given in Table 18 and counts in Table 19. Disc oval, slightly longer than wide and distinctively shovel-shaped; disc length is 37.0 to 42.4 percent of total length, disc width is 35.2 to 40.3 percent of total length. Disc fleshy and thick dorso-ventrally. Disc widest at its posterior third and barely overlapping pelvic fins. Disc directly attached to lateral aspect of trunk posteriorly (i.e., without inflecting anteriorly before contacting body, hence not forming a notch or groove between disc and body); margins of disc somewhat thick. Snout faintly acute to rounded anteriorly. Electric organs not clearly visible

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dorsally, beginning posterior to nostrils on sides of disc and extending to close to posterior one-fifth of disc. Five pairs of small, relatively close-together and faintly convex gill openings, extending from area posterior to first one-third of disc to just posterior to coracoid bar. Eyes and spiracles close together, without a significant gap between them. Eyes relatively large, slightly bulging and functional. Spiracles roughly as wide as long, with smooth borders, not fringed with papillae; spiracles crescent-shaped to circular, extending anteriorly to almost half of eye length.

Nasal curtain elongated, with small central projection posteriorly, and tapering slightly inward from nostrils to mouth. Nostrils fringed by small folds of integument (narial flaps) that may cover nostrils when distended (usually the narial flaps are folded back). Mouth small, just wider than distance between nostrils, and not very distensible. Upper and lower tooth bands exposed, and attached loosely to jaws through integument, easily detachable. Upper tooth band significantly wider than lower tooth band in specimens from Somalia, Tanzania, Mozambique (RUSI 48526) and in one paratype (IIPB 577/1986); tooth bands of more or less equal width in holotype and at least one paratype (IIPB 528/1986). Teeth in 15/9 – 16/15 vertical rows in the larger specimens (five specimens, 269 mm to 293 mm TL), and in fewer rows in the smaller (non-type) specimens examined. Individual teeth trapezoidal, closely set in quincunx, partially overlapping in some specimens, with a small medial cusp (particularly on inner, unexposed teeth) and wide base. The only male specimen examined in detail (ZMA 113.398) has more pronounced cusps than females, even though this specimen is smaller in total length compared to females examined.

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Pelvic fins wider than long (pelvic fin width ranging from 24.2 to 27.4 percent of total length [x = 25.8], pelvic fin length varies between 14.0 to 17.3 percent of total length [x = 15.2]). Pelvic fins beginning just anterior and ventral to disc termination. Pelvic fins with rounded, thick corners, projecting outward anteriorly so as to leave a slightly prominent lobe; no extensive free edge on pelvics where fins meet lateral aspect of tail posteriorly (pelvics adjoin tail throughout their length). Tail long and stout, sub-circular in cross section, wider than tall and not tapering significantly from base to caudal fin. Lateral tail folds not very distinct, barely noticeable, and very narrow, beginning as a thin keel at mid to end of first dorsal fin, continuing caudally close to ventral aspect of tail and terminating on ventral region of caudal peduncle. Dorsal fins well developed, widely spaced apart, and of almost equal height. First dorsal fin originates above posterior tip of pelvics. Posterior margins of dorsals not very rounded, connecting to tail leaving a small free edge posteriorly. Caudal fin low and long, with a slightly curved posterior margin. Dorsal lobe of caudal fin begins more anteriorly than ventral lobe.

Pores of lateral-line canal system not clearly visible (except on RUSI 48526). Pores widely spaced apart dorsally on outer disc margins, lateral to electric organs, few closely set pores on dorsal region of snout tip, and only scarce pores overlying rostral ridges of neurocranium, except close to eyes. Pores on tail not very numerous, extending posteriorly from disc in a more or less straight line at sides of tail, just dorsal to lateral tail folds, and extending posteriorly to terminate just after caudal peduncle, not continuing to mid caudal-fin. Pores of ampullary system numerous ventrally on nasal curtain, antorbital area and at mouth corners (again, more obvious on RUSI 48526).

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Dorsal coloration dark brown to reddish-brown, slightly darker over eyes, bases of dorsal fins, pectoral fin axils and over mid-disc region in some specimens. Holotype with distinctive darker streaks over mid- and outer-disc (Fig. 45). Ventral coloration a creamy white, except in RUSI 48526 which is slightly darker ventrally (perhaps related to preservation).

REMARKS: Lloris and Rucabado (1991) originally described this species in Heteronarce, and compared it to H. garmani Regan, 1921 (specimens of which were collected with the type series of N. rierai) and H. mollis (Lloyd, 1907), both from the western Indian Ocean. No comparisons with other species of Narcine were made in the original description (Narcine had not been reported from the western Indian Ocean at the time N. rierai was described). N. rierai is superficially similar to species of Heteronarce, and especially to H. garmani, its type species, in possessing an elongated tail and nasal curtain, and in coloration, both species being uniformly brown dorsally. However, N. rierai agrees with other species of Narcine not only in diagnostic characters of external morphology, but also on the basis of neurocranial and other skeletal features, from which it differs considerably from Heteronarce.

Although the nasal curtain of N. rierai is similar to Heteronarce in being elongated, it does not present the characteristic arrangement and number of nasal curtain ampullary pores of that genus (e.g., Fig. 4). Also, the nasal curtain of Heteronarce is substantially more fleshy (the general condition in narkids). The nostrils of N. rierai are not longitudinally elongated and do not run parallel to the nasal curtain as in narkids (Fig. 4). The tooth bands of N. rierai are exposed when the mouth is closed, which is typical of Narcine (and Discopyge), compared to

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Heteronarce which does not have exposed rows of teeth. The antorbital cartilages extend antero-laterally in N. rierai, as in narcinids. In narkids, including Heteronarce, the antorbitals extend in a more straight fashion anteriorly as small, stout cartilages, and there is no median posterior projection, which is present in N. rierai and other narcinids. The antorbitals of Heteronarce only branch out into more than one segment distally, near the disc margins, whereas in Narcine, including N. rierai, the antorbitals subdivide closer to the neurocranium. In Heteronarce the nasal capsules are farther apart compared to N. rierai and other species of Narcine – the ethmoidal region of the neurocranium has a different configuration altogether in these two genera. The scapular region of the shoulder girdle is conspicuously shaped in Heteronarce, forming close to a 45 degree angle with the suprascapula, while in N. rierai the scapula and suprascapula are more or less in-line horizontally, which is more typical of Narcine.

N. rierai superficially resembles N. tasmaniensis, Narcine sp. nov. B and Narcine sp. nov. C from the coast of Australia in dorsal coloration and in possessing an elongated tail region compared to disc length. However, N. rierai is easily distinguished from N. tasmaniensis by having the spiracles and eyes closer together (separated by a small gap in N. tasmaniensis), and is distinct from all three species by having a much longer joint nasal curtain (wider than long in all three Australian species), as well as by rostral and antorbital cartilage morphology.

The holotype (IIPB 82/1987) has 11 tooth rows on the upper tooth band and 13 rows on the lower. These counts were taken from the photograph of the holotype (Fig. 46), and differ from the number of tooth rows given in the original description. Lloris and Rucabado (1991) report 10 rows on the lower jaw, but it is not clear if this refers to the holotype (an adult male, reported to be 257 mm TL) or to all type specimens. Their illustration of teeth of the

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lower tooth plate shows 11 rows for the holotype (their fig. 3b), but it is not clear if non-exposed rows are included. No direct information is published concerning the number of upper tooth rows of the holotype in the original description. Lloris and Rucabado (1991: 329) report that cusps are present only in males, but females also have cusps, however not as pronounced.

Two female apparently mid-term embryos (73.2 and 72.6 mm TL) were found in one specimen (RUSI 48526, 272 mm TL). Both were greatly coiled and present in the right uterus, and were still attached to yolk-sacs that were smaller than the specimens themselves (but of a substantial size, close to 10 mm in diameter). No indications of any nutrient-supplying structures other than an external yolk-sac were evident (e.g., trophonemata, uterine placenta). Both uteri were also devoid of spatulate villi reported for "N. indica" by Prashad (1920). N. rierai definitely has a yolk-sac (aplacental) viviparous (ovoviviparous) reproductive mode, which is widespread in torpediniforms (Breder and Rosen, 1966; Wourms, 1977; Compagno, 1990).

Both uteri are extremely thin-walled and fragile, the left uterus more so than the right one. The left uterus of RUSI 48526 contained two yolk-masses that are smaller than the yolk-sacs of the embryos taken from the right uterus. This may be an indication that both uteri are functional in N. rierai. Both embryos resemble adults in external features, bearing the diagnostic morphology of the joint nasal curtain, an elongated tail, shovel-shaped disc and small nasal flaps enveloping nostrils. The spiracles were well concealed behind the eyes, although fully opened, and the external gill filaments had already been resorbed. The disc is fully formed, not presenting an antero-lateral notch typical of embryonic specimens of Narcine of earlier stages (Prashad, 1920) or of near-term embryos of Torpedo (Bigelow and Schroeder,

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1953). Both embryos have a light brown dorsal coloration. The embryos were not dissected to verify if whether an internal yolk-sac is present.

The embryos present in the 272 mm TL female indicate that all paratypes are adult females, the transition from juvenile to adult for females occuring at around 265 mm TL. The male specimen examined (235 mm TL, from Tanzania) has claspers projecting beyond the posterior border of the pelvic fins, although not as much as in the holotype. The claspers of this male specimen are not very rigid, suggesting that it is still a juvenile, albeit probably close to maturity. No information is published regarding the sexual maturity of the holotype, but it is here considered an adult on the basis of its TL and elongated claspers in comparison to the Tanzania specimen examined.

N. rierai is known from 18 specimens (including the two embryos) from distant localities in the western Indian Ocean, along the east African continental slope (see below). Although widely distributed in the western Indian Ocean (spanning some 35° of latitude), the specimens are similar in diagnostic characters, not showing significant variation in coloration, dentition and proportions, including among specimens from both geographical extremes (Somalia and Mozambique). One specimen examined (RUSI 48526), however, presents minor differences in sensory ampullary pore number and distribution, as well as in ventral coloration. RUSI 48526 has well defined and easy to distinguish sensory pores in apparently greater quantity, and is slightly darker ventrally (perhaps due to preservation). All other specimens examined have well concealed sensory pores that are difficult to discern even under magnification. The specimens also differ faintly in the distribution of lateral line pores along the dorsal surface of disc (lateral to electric organs), and in ampullary pores on ventral snout area.

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RUSI 48526 also has fewer exposed teeth (nine rows) on the lower tooth band (which is proportionally less wide) than specimens of similar size from Mozambique (paratypes, with 12-15 lower tooth band rows). Precise locality data is lacking for this specimen, but it is probably from Mozambique, although there is a small chance it is from South Africa (P. Heemstra and A. Bentley, personal commun.). However, these differences are considered here to be minor and not species-specific. More specimens from Somalia and especially from the southern range of this species are needed to further determine the taxonomic value of these features.

GEOGRAPHICAL DISTRIBUTION: Originally described from just south of Beira, Mozambique, this species is now known from five localities throughout the western Indian Ocean (one specimen [RUSI 48526] has no locality information, as mentioned above) (Fig. 104). Compagno (1995) reported additional specimens from close to the type locality. Subsequent discovery of specimens in the collections of Amsterdam (ZMA) (from Tanzania, off Dar es Salaam), and Hamburg (ISH) (from off central Somalia), considerably extend the range of this species. Narcine rierai has been captured in waters ranging from roughly 169 m to 500 m in depth. However, it is probably restricted to depths of around 169 m to just over 300 m, as the continental shelf and slope are very narrow off Tanzania and Somalia where N. rierai has been captured.

MATERIAL EXAMINED: (12 specimens, 213 to 296 mm TL): **Mozambique**: IIPB 82/1987 (holotype; radiograph and photographs only), adult male, originally reported to be 257 mm TL, 21°10'S, 035°37'E, 169 – 188 m, caught by demersal shrimp trawler, 11.xi.1982; IIPB

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527/1986 (paratype), 269 mm TL adult female, caught with holotype; IIPB 528/1986 (paratype), 293 mm TL adult female, caught with holotype; IIPB 577/1986 (paratype), 288 mm TL adult female, 21°17'S, 035°37'E; IIPB 578/1986 (paratype), 281 mm TL adult female, caught with IIPB 577/1986 (as is paratype IIPB 579/1986, female, reported to be 296 mm TL in original description, but not examined here), 184 – 188 m, caught by same trawler as rest of type series (data for type series follows Lloris and Rucabado, 1991); RUSI 48526, 272 mm TL gravid female (carrying two near-term embryos in right uterus), no specific locality data associated with this specimen, probably from Mozambique (P. Heemstra and A. Bentley, personal communication; perhaps from South Africa). **Somalia**: ISH 255-1975, 223 mm TL pre-adult (?) female, 06°12' S, 049°18' E, 255 m, FFS Dr. F. Nansen (FAO project, Kenya), 26. ii. 1975. **Tanzania**: ZMA 113.398 (2), 213 mm TL pre-adult male, 235 mm TL adult female, off Dar es Salaam, in waters 300 m to 500 m deep, 26 – 28. vi. 1974; ZMMU 14835, adult male approx. 260 mm TL, Pemba Channel region, 5°46'S, 39°11'E, 6. i. 1976 (photographs only, specimen not examined; photos courtesy of P. Last).

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Narcine tasmaniensis Richardson, 1841

Figs. 49 – 52, Tables 20 – 21

Narcine tasmaniensis Richardson, 1840: 29 (name only, not available).

Narcine tasmaniensis Richardson, 1841: 22 (original description; Port Author, Tasmania); Richardson, 1849: 178 –183, pl. XI, figs. 2a, 2b (detailed description, illustrated); Gray, 1851: 102 (listed); Bleeker, 1855: 3, 19 (listed; Tasmania); Duméril, 1865: 504, 517 (in identification key, description); Gunther, 1870: 452 (brief account); Macleay, 1881: 310 (brief account); Engelhardt, 1913; Garman, 1913: 297, 301 – 302 (in identification key, compilation); McCulloch, 1919: 11, pl. iii, fig. 34a (brief account, illustration compiled); McCulloch, 1927: 11, pl. iii, fig. 34a (repeat of McCulloch, 1919); Fowler, 1941: 337 (compilation); Bigelow and Schroeder, 1953: 111 (in identification key, accepted as valid); Stead, 1963: 145 – 146 (brief account); McKay, 1966: 73, 77 (accepted as valid, comparisons); Edgar et al., 1982: 24, fig. 9 (brief account, photograph); Last et al., 1983: 146–147 (identification, brief account,illustration compiled); Hutchins and Swainston, 1986: 26 – 27 (brief account, illustrated); May and Maxwell, 1986: 136 (identification, illustration compiled); Grant, 1987: 40 (brief account, photograph); Paxton et al., 1989: 61 (compilation); Kuiter, 1993: 15 (brief account, photograph); Michael, 1993: 81 (compilation, photograph); Last, 1994: 155 – 156 (brief account, photograph); Last and Stevens, 1994: 374, 378, pl. 66 (identification, description, distribution, illustrated); Edgar, 1997: 397 (brief

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account, photograph); Eschmeyer, 1998: 2182 (listed); Eschmeyer et al., 1998: 1653 (compilation).

Narcinops tasmaniensis: Whitley, 1940: 160, 164 – 165, figs. (placement into new monotypic genus Narcinops); Bigelow and Schroeder, 1953: 107 (placed in synonymy of Narcine tasmaniensis).

DIAGNOSIS: A species of Narcine diagnosed by the unique combination of: tail length, as measured from cloaca, greater than disc length and width (averaging 53.3 percent of total length, vs. an average of 43.4 for disc width and 41.6 for disc length), uniform dark brown dorsal coloration, wider than long nasal curtain, flap-like lateral taild fold, and preocular snout length averaging 7.8 percent of total length. All other species of Narcine have tail length subequal to, or not as great as, disc width and length, except N. rierai, N. westraliensis, N. sp. nov. A, N. sp. nov. B and N. sp. nov. C. N. tasmaniensis is distinguished from N. rierai by having a wider than long nasal curtain (distinctively longer than wide in N. rierai). N. tasmaniensis is separated from N. westraliensis and N. sp. nov. A by having a uniform brown dorsal coloration (dorsal coloration composed of horizontal stripes in N. westraliensis and large spots surrounded by smaller spots in N. sp. nov. A). N. tasmaniensis is distinguished from N. sp. nov. B and N. sp. nov. C by having a darker dorsal color (usually a dark or chocolate brown, compared to light brown, tan or yellowish-brown in N. sp. nov. B or N. sp. nov. C), more developed and flap-like lateral taild fold (tail fold reduced to a slight ridge in both N. sp.

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nov. B and N. sp. nov. C), slightly greater disc width (averaging 43.4 percent of total length in N. tasmaniensis, vs. 40.3 in N. sp. nov. B and 38.4 in N. sp. nov. C), and preocular snout length not as great (averaging 7.8 percent of total length in N. tasmaniensis, vs. 10.1 in N. sp. nov. B and 9.7 in N. sp. nov. C).

DESCRIPTION: Measurements and counts are presented in Tables 20 and 21, respectively. Disc distinctively shovel-shaped, generally only slightly wider than long (disc width is 32.7 to 51.8 percent of total length, disc length is 34.5 to 46.8 percent of total length). Disc widest at posterior one-third to one-fourth of its length in adults, and at around one-sixth in juveniles. Disc overlapping origin of pelvics very little at its posterior aspect, not leaving prominent free lobe posteriorly. Snout rounded to slightly angular in some specimens, even sub-acute with a blunt tip in others. Disc angular antero-laterally at about level of eyes, and rounded posteriorly at level of greatest width. Snout region relatively short. Preocular snout length averaging less than one-tenth of total length, and about one-fourth in disc length; preocular snout length about equal to prenasal snout length. Preoral snout length only about one-tenth of total length. Electric organs not clearly outlined dorsally, more conspicuous in juveniles. Electric organ begin just anterior to level of eyes dorsally and continue posteriorly to between four-fifths and five-sixths of disc length; ventrally electric organs commence just posterior to level of nostrils. Electric organs length is between 17.5 to 23.7 percent of total length, and electric organ width is between 5.3 and 10.4 percent of total length. Gill slits semi-circular, small and arranged in a slight curve from first to last gill slit. Distance between last gill slits and branchial basket length about equal. Spiracles separated from eyes by a small gap in juveniles and adults, but gap is

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more obvious in juveniles; spiracles without strongly elevated rims. Spiracle length and width about equal. Spiracles with well-rounded posterior margins and not curving anteriorly to a large extent at outer margins, remaining more or less perpendicular to eyes. Eyes slightly bulging, longer than spiracles and sometimes slightly darker than background disc color.

Nasal curtain wider than long, and slightly trilobed in some well-preserved specimens, but barely projecting laterally posterior to nostrils (other specimens with nasal curtains that have more staright posterior margins). Small central lobe of nasal curtain sometimes projects over upper exposed tooth band when lobe is well preserved. Nostrils very circular with slightly elevated rims. Mouth slightly wider than distance between nostrils in general. Mouth projects slightly forward at corners in some specimens. Upper tooth band wider than lower tooth band; upper and lower tooth bands fairly circular in outline, but some specimens with triangular lower tooth bands that are much narrower than the upper tooth band (holotype). Teeth in 10/7 – 20/16 exposed vertical rows in pre-adults and adults (ranging from 215 to 450 mm total length, but a typical adult of 300 mm in total length may have 16/10 rows). Teeth with trapezoidal, slightly wider than long bases, and long cusps especially on inner rows; more exposed teeth with worn down cusps, but occasionally long cusps on exposed teeth as well. Teeth set in quincunx arrangement.

Pelvic fins wider than long when pelvics are measured together. Pelvic fins broadest anteriorly, with much longer posterior lobes compared to anterior lobes (averaging 15.3 and 9.2 percent of total length, respectively). Pelvic fins leave a small free lobe posteriorly. Pelvics extend posteriorly from just underneath disc to just posterior to underneath origin of first dorsal fin on tail. Pelvics with a faintly concave posterior lobe and slightly rounded lateral

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corners. In large males claspers protude to underneath posterior one-third of base of first dorsal fin (about one-fifth of their total length beyond tips of pelvics). Tail relatively long, occupying from 49.4 to 57.0 percent of total length as measured from cloaca. Tail not very broad at base (averaging 17.4 percent of total length), sub-circular in cross section. Tail more or less straight from base to second dorsal fin, but tapering more intensely from second dorsal to caudal fin. Lateral tail folds ranging from prominent, well developed flaps to low ridges in some specimens that are appear dried. In well-preserved specimens, lateral tail fold begin underneath level of mid-first dorsal fin base, and extend caudally to insert on lateral aspect of caudal peduncle close to its ventral margin. Rounded to faintly sub-acute dorsal fins at apex, with sloping anterior and curved posterior margins, and small free lobes posteriorly. Second dorsal sometimes with a more straight posterior margin than first dorsal (which appears more rounded), but dorsal fins generally very similar in proportions and outline. Distance between second dorsal and caudal fins is usually slightly greater than distance between dorsal fins. Caudal fin height about 10 percent of total length; apex sub-angular to slightly rounded. Caudal fin moderately long, approximately 13 to 14 percent of total length, with relatively straight to rounded posterior margin. Height of caudal fin, as measured with both upper and lower lobes together, is slightly greater than height of dorsal fins on average. Lower lobe of caudal fin begins just anterior to level of origin of upper caudal fin lobe in larger specimens.

Sensory pores of lateral-line and ampullary systems difficult to locate and identify on dorsal and ventral surfaces, except on ventral snout region. Ampullary pores on ventral snout area situated in semi-parallel rows, from anterior margin of snout to nasal curtain. Rows generally not very straight antero-posteriorly, and varying somewhat in orientation, but with

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two predominant rows reaching level of nostrils. Small triangular to crescent-shaped group of pores anterior to each nostril generally present. Few pores on nasal curtain continue posterior to level of anterior margins of nostrils. Isolated pores present posterior to nostrils, lateral to nasal curtain. Pores on lateral tail region situated just dorsal to lateral tail fold, sometimes curving dorsally ventral to second dorsal fin or between dorsals, but running close to lateral tail fold posteriorly to caudal peduncle. Few scattered pores outline electric organs both dorsally and ventrally.

Specimens with a uniform color dorsally. Dorsal coloration dark brown to blackish brown, but occasionally lighter brown. Areas of lighter intensity dorsally over pelvic fin margins, anterior region of pelvic fins, anterior snout area and posteriorly over disc and lateral tail base regions. Dorsal and caudal fins lighter to semi-transparent in freshly collected specimens. Dorsal surface of clasper also slightly darker than disc in some specimens. In preserved specimens, dorsal coloration may be slightly lighter, similar to Narcine sp. nov. C. Ventrally specimens are a pale white to cream color, sometimes with scattered dark brown blotches on posterior disc, base of tail and pelvic fin regions, as well as ventrally on pectoral axils.

REMARKS: Richardson's (1840) first mention of Narcine tasmaniensis ("Narcine Tasmaniensis") was as name only, without any descriptive text or indication, and is therefore a *nomen nudum*, lacking official nomenclatural status (ICZN, 1985: 33, Art. 12 a, b). The specific name must therefore date from the first subsequent valid account, which is Richardson (1841). Richardson (1849) later provided a much more comprehensive description and the first

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illustration of N. tasmaniensis, including anatomical comparisons with species described in Henle (1834). The holotype (BMNH 1848.3.18.6) is in relatively good condition, even though the specimen was previously dissected on its right dorsal surface, presumably to reveal the electric organ. The skin is rather loose, and a ventral slit is present running antero-postreriorly in between the gill arches. However, diagnostic characters of the species are clearly present.

Whitley (1940) erected the new genus Narcinops for N. tasmaniensis on the basis of differences with the type-species of Narcine, N. brasiliensis. These included neurocranial proportions (a wider neurocranium at orbital region in N. tasmaniensis) and configuration (lack of small cartilage between rostrum and antorbital cartilages, and presence of a transverse foramen in rostrum of N. tasmaniensis), "margin of nasal valves" and "form of body." Narcinops was placed in the synonymy of Narcine by Bigelow nd Schroeder (1953) as these differences apply at the species level, a decision followed herein.

Narcine tasmaniensis is similar in proportions and external appearance to both Narcine sp. nov. B (primarily from Western Australia) and Narcine sp. nov. C (from Queensland) (both species are described below). These three species have minor differences in disc width and length (as proportions of total length, cf. Tables 20 to Tables 30 and 32), coloration (N. tasmaniensis is generally darker than the other two species), lateral tail fold (appearing as a laterally expanded flap in N. tasmaniensis while in both Narcine sp. nov B and C lateral tail fold is only a slight ridge) and in snout length (snout is proportionally not as long in N. tasmaniensis as in the other two species; Tables 20, 30, 32). All three species are disjunct in distribution as far as is known, and N. tasmaniensis is the only species of the three to reach inshore shallow

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waters (primarily off Tasmania, but off Victoria as well). These three species may form a monophyletic group.

Males and females appear to reach sexual maturity at around 250 mm in total length. Mature females had large egg masses in both uteri, suggesting uteri to be synchronous. In a 420 mm total length female, five mid-term embryos were found, two in the left uterus and three in the right uterus. All embryos were around 45.5 mm total length, attached to yolk masses of close to 30 mm in diameter. The embryos at this length presented: distinguishable claspers in males; neurocrania incompletely encasing brains; spiracles completely open and adjacent to eyes, no gap is present; spiral valves already formed; livers visible through semi-transparent and very delicate skin; very long external respiratory filaments attached to gills; general lack of intense pigmentation; ampullary pores on ventral snout visible; nostrils closed but small, slit-like mouth is open; no teeth present on barely noticeable exposed tooth bands; first dorsal fin is clearly posterior to pelvics; general proportions of disc and tail region already present. Embryos are born at around 80 mm in total length; pups of 73 mm in total length still contained small yolk-masses of 14 mm in diameter and few external gill filaments attached to gills.

There is some variation in dorsal color pattern in this species. Few specimens are lighter in color, being a light brown very close to the color of Narcine sp. nov. C. It is difficult to establish how much of this variation is preservational. Photographs of small live specimens indicate that they may have undefined brown blotches over mid and posterior disc regions, but these probably fade by maturity. Male specimens appear to have slightly more elongated cusps on both external and internal tooth rows compared to females of about same size. Narcine

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tasmaniensis reaches a larger size than the other Australian species of Narcine, as far as is known.

GEOGRAPHICAL DISTRIBUTION: Narcine tasmaniensis is abundantly distributed throughout the continental shelf and slope of New South Wales (from 20 to 567 m), inshore Tasmania (from 4 to 104 m) and off the coast of Victoria (10 to 135 m) (Fig. 106). It appears to be very common in the Bass Strait and off the northern and eastern coast of Tasmania. However, according to my records, it is yet to be captured from the western coast of Tasmania, even though it probably does occur there. Seven specimens from the northwestern Tasmanian coast was examined (NMV A 1412, from W – NW of West Point). This species also occurs on the contiental slope of Southern Australia (one locality, 370 to 400 m), and on the contiental shelf of Western Australia (one locality, 147 to 179 m). More collecting is needed to further substantiate its presence in the Great Australian Bight. So far as is known, N. tasmaniensis inhabits deeper waters on the relatively narrow continental slope of New South Wales compared to its bathymetric distribution off Tasmania, where it is very common close to shore (also Last and Stevens, 1994).

MATERIAL EXAMINED: (122 specimens, 45.5 to 482 mm in TL): **New South Wales**: AMS IA. 1952, 314 mm TL adult male, NE of Green Cape, 37°04'S, 150°09'E, 70.2 – 82.8 m, 1984; AMS IA. 2968 (3), 73 to 94 mm TL juvenile females, off Port Hacking, 34°04'S, 151°11'E, 72 – 90 m, A. Ward; AMS IB. 4330, 116 mm TL juvenile, NE of Broken Bay, 33°S, 151°E, 246.6 m, 19. vi. 1959; AMS IB. 4751, 257 mm TL pre-adult male, Bermagui,

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36°25'S, 150°04'E, J. Campbell, 1960; AMS IB. 4752, 225 mm TL pre-adult female, off Bermagui, 36°25'S, 150°04'E, J. Campbell, 1960; AMS IB. 8267, 265 mm TL pre-adult or adult female, off Wollongong, 34°S, 151°E, 234 m, B. Goldman, 30. vi. 1968; AMS I. 15975-012, 252 mm TL pre-adult or adult female, SE of Newcastle, 33°11'S, 152°23'E, 567 m, FV Kepala, 29. iv. 1971; AMS I. 15990-004, 235 mm TL pre-adult female, NE of Batemans Bay, 35°33'S, 150°43'E, 421 m, 8. vi. 1971; AMS I. 16574-001 (3), 101 to 110 mm TL juvenile males, 110 mm TL juvenile female, off Sydney, 33°S, 152°E, 274 m, FRV Kepala, viii. 1972; AMS 17178-035, 351 mm TL adult male, off Sydney harbor, 33°50'S, 151°16'E, 20 m, J. Paxton; AMS I. 19091-005 (4), 147 to 285 mm TL pre-adult to adult females, NE of North Solitary Island, 29°55'S, 153°40'E, 360 m, FRV Kepala, 10. x. 1975; CSIRO CA 117, 241 mm TL pre-adult male, E – NE os Sydney, 33°33'S, 151°57'E, 305 m, RFV Courageous, Sta. 318, 1977; CSIRO CA 118, 117 mm TL juvenile male, same data as CA 117; CSIRO CA 119, 105 mm TL juvenile male, same data as CA 117; CSIRO H 949 (2), 331 to 360 mm TL adult males, E of Sydney, 33°38'S, 151°38' E, 128 m, 1985; CSIRO CA 3187, 203 mm TL pre-adult female, E of Sydney, 33°44'S, 151°49'E, 348 – 350 m, 1982; CSIRO CA 3201, 201 mm TL pre-adult male, E of Sydney, 33°42'S, 151°51'E, 296 – 300 m, 1982; CSIRO CA 3202, 201 mm TL pre-adult male, data as in CA 3201; CSIRO CA 3203, 226 mm TL pre-adult female, data as in CA 3201; NMV A 13075 (3), 102 to 122 mm TL juvenile males, 114 mm TL juvenile female, E – SE of Bermagui, 36°27'S, 150°18.2'E, 215 – 220 m; MCZ 38599, 362 mm TL adult female, J. K. Howard, 1954 (no further data). **South Australia**: NMV A 2165, 199 mm TL pre-adult male, SW of Beachport, 37°51'S, 139°48'E to 37°45'S,

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139°39'E, 370 – 400 m. **Tasmania**: AMS IA. 4102, 215 mm TL pre-adult male, D'Entrecasteaux Channel, 43°15'S, 147°16'E, 9 m, x. 1929; AMS I. 13001, 249 mm TL adult male, Wineglass Bay, 42°10'S, 148°18'E; AMS I. 14803, 210 mm TL pre-adult female, Bellerive beach, 42°52'S, 147°22'E; AMS 9981, 259 mm TL pre-adult female, E coast of Flinders Island, Bass Strait, 40°01'S, 148°02'E, FRV Endeavor; AMS 9982, 220 mm TL pre-adult female, same data as AMS 9981; AMS I. 17549-011 (3), 261 mm TL adult female, 78 to 81 mm TL juvenile males, Oyster Cove, 43°07'S, 147°15'E, 4 m, W. Ivantsoff, 1. xii. 1972; AMS I. 20749-004 (3), 90 to 215 mm TL pre-adult females, Partridge Island, D'Entrecasteaux Channel, 43°23'S, 147°06'E, 20 m, 23. v. 1970; AMS I. 21304-006, 223 mm TL pre-adult male, E of Hippolytes Island, 43°09'S, 148°06'E, 103 m, FRV Challenger, 9. x. 1979; BMNH 1848.3.18.6 (holotype), 276 mm TL adult female, Port Arthur, J. Richardson; BMNH 1875.11.12.28-30 (3), 305 mm TL adult female, 2 female newly born juveniles, Presley Morton Allport, vi. 1874 (no further data); CSIRO H 857-03, 291 mm TL pre-adult to adult female, off Eddystone Point, 41°34'S, 148°34'E, 1986; CSIRO H 940-02, 216 mm TL pre-adult female, E of Eddystone Point, 41°05'S, 148°24'E, 1986; CSIRO T 1051 (2), 201 mm TL pre-adult male, 202 mm TL pre-adult female, Kingston Beach, 42°59'E, 147°19'E; CSIRO T 1070, 216 mm TL pre-adult female, no further data; CSIRO T 1246, 68 mm TL late-term male embryo, no further data; CSIRO T 1289 (3), 70 to 75 mm TL late-term female embryos, 81 mm TL juvenile male, Nutgrove Beach, 42°55'S, 147°21'E; CSIRO T 1679-04, 136 mm TL juvenile female, off Triabunna, 42°30'S, 147°E, 1981; CSIRO T 1743, 76 mm TL female embryo, Taroona, 42°57'S, 147°21'E; CSIRO H 2502-01, 88 mm TL juvenile male, "Channel

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area, Isthmus Bay," 12 m, 1990; CSIRO uncat. ("T.F.D.A"), 330 mm TL adult female, Frederick Henry Bay, 10 m, 7. viii. 1981; NMV A 1210, 311 mm TL adult female, SE of Cape Adansan, Three Hummock Island, central Bass Strait, 40°31.1'S, 145°04'E, 29 m; NMV A 1299, 294 mm TL adult male, E of Cape Rochon, Three Hummock Island, central Bass Strait, 40°22.2'S, 145°17'E, 40 m; NMV A 1326 (2), 275 to 306 mm TL pre-adult and adult males, NE of Stanley, central Bass Strait, 40°48.8'S, 145°22'E, 22 m; NMV A 1340 (4), 325 to 386 mm TL adult females, 301 mm TL pre-adult male, off Cape Rochon, Three Hummock Island, central Bass Strait, 40°23.8'S, 145°32'E, 66 m; NMV A 1344 (5), 220 to 321 mm TL pre-adult and adult males, N of North Point, central Bass Strait, 40°40.3'S, 145°15'E, 33 m; NMV A 1412 (7), 197 mm TL juvenile male, 420 mm TL adult female (with 5 early-term embryos of about 45.5 mm TL each), W – NW of West Point, western Bass Strait, 40°48.31'S, 144°17.06'E to 40°49.71'S, 144°14.38'E, 100 – 104 m; NMV A 1556 (2),213 mm TL pre-adult female, 220 mm TL pre-adult male, N – NE of Eddystone Point, eastern Bass Strait, 40°43.79'S, 148°32.68'E to 40°43.82'S, 148°34.41'E, 54.9 – 58.6 m; NMV uncat. (3), 226 to 245 mm TL pre-adult females, 254 mm TL pre-adult male, E coast of Flinders Island, eastern Bass Strait,, "Commonwealth Fisheries Dep. Trawler Endeavor," 16. vi. 1909; NMV uncat., 215 mm TL pre-adult male, D'Entrecasteaux Channel, "CSIRO boat," 15. i. 1949; NMV uncat. (3), 200 to 300 mm TL pre-adult to adult males, Bass Strait, "Marine Studies Group – Cruise 8," acc. no. 79.1, iii. 1970; NMV uncat. (2), 100 to 166 mm TL pre-adult females, Great Taylor Bay, 20 m, 14. ii. 1968; QM I. 10484, 76 mm TL newly born or late-term embryonic male, Simpson's Bay entrance, Bruny Island, 10.5 m (35 feet), N. Coleman, 15. ii. 1972; QM I. 30348, 106 mm TL juvenile male, Great Bay, Bruny Island, 43°12'S, 147°22'E,

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T. Walker, 20. ii. 1975. **Victoria**: CSIRO CA 18, 261 mm TL pre-adult to adult female, S of Cape Co, Bass Strait, 38°15'S, 148°45'E, 130 m, 1976; CSIRO H 3528 (2), 251 mm TL pre-adult female, 274 mm TL adult male, S of Gabo Island, 37°46'S, 149°55'E, 120 m, A. Graham, 1993; NMV A 1492, 166 mm TL pre-adult female, SW of Cape Otway, western Bass Strait, 39°01'S, 143°22.1'E, 84 m; NMV A 1603, 275 mm TL pre-adult male, SE of Point Hicks, eastern Bass Strait, 37°57.85'S, 149°30.5'E to 37°4.3'S, 149°34.52'E, 131 – 135 m; NMV A 1606 (4), 185 mm TL pre-adult male, 305 to 361 mm TL adult females, SE of Point Hicks, eastern Bass Strait, 38°7.82'S, 149°16.6'E to 38°1.95'S, 149°11.08'E, 117 – 148 m; NMV A 1625, 305 mm TL adult female, SW of Cape Liptrap, central Bass Strtait, 39°6.83'S, 144°49.64'E to 39°5.86'S, 144°45.87'E, 65 – 67 m; NMV A 2195, 265 mm TL, S – SE of Cape Woolamai, Philip Island, Bass Strait, 38°37'S, 145°24'E, 46 m; NMV A 2342, 215 mm TL pre-adult female, W of Leonard Point, 39°01.7'S, 146°15.8'E, 50 m; NMV A 3754, 291 mm TL pre-adult female, S of Lake Tyres Entrance, eastern Bass Strait, 38°12'S, 148°06'E, 56 m; NMV uncat. (2), 203 to 255 mm TL pre-adult females, W side of Port Philip Bay, 10 – 20 m, "Cruise 30, sta. 72 & 73," acc. no. 79.1, 7. xii. 1972; NMV uncat. (2), 195 mm TL pre-adult male, 143 mm TL pre-adult female, S – SW of Lakes Entrance, Bass Strait, 28.8 – 36 m (16 to 20 fathoms), A.D. Butcher, 17. iii. 1948; NMV uncat. (3), 110 to 266 mm TL pre-adult males, 121 mm TL pre-adult female, same locality as previous lot, 27. iv. 1948; NMV uncat., 131 mm TL pre-adult female, Bass Strait, "(F & W cat. No. 2064)," acc. no. 79.1, I. W. Brown, 1970. **Western Australia**: NMV A 98778 (4), 41 to 74 mm TL embryonic males, 73 to 74 mm TL embryonic females, apparently from specimen NMV A 11290 listed

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below; NMV A 11289 (2), 444 mm TL adult female (with 73 mm TL female late-term embryo), S – SW of Middini Beach, Great Australian Bight, 33°13'S, 127°02'E to 33°14.4'S, 126°51'E, 147 – 179 m; NMV A 11290, 482 mm TL adult female, same data as NMV A 11289.

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Narcine timlei (Bloch and Schneider, 1801)

Figs. 53 – 64, Tables 22 – 23

Raja timlei Bloch and Schneider, 1801: 359 (original description, not illustrated; type-locality: off Tranquebar, Coromandel coast, southeastern India).

Narcine indica Henle, 1834: 35, pl. II, figs. 2, 2a (original description, comparisons, illustrated; type-locality: off Tranquebar, Coromandel coast, southeastern India). NEW SYNONYMY.

Narcine microphthalma Valenciennes, 1852: 56 (original description, not illustrated; type-locality: off Malabar coast, western India).

Narcine macrura Valenciennes, 1852: 57 (original description, not illustrated; type-locality: "mer des Indes" [Indian Ocean]).

Narcine brunnea Annandale, 1909: 45, pl. iiia, fig.2 (original description, illustration of teeth and mouth; type-locality: Orissa and Arrakan coasts, Bay of Bengal, India); Menon and Yazdani, 1963: 98 (listed, type-catalog); NEW SYNONYMY.

DIAGNOSIS: A species of Narcine distinguished from congeners by the unique combination of: dorsal coloration uniform light brown to greyish- or purplish-brown (without distinct

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markings such as stripes, spots, blotches or ocelli) eyes smaller than spiracle length and width, nasal curtain wider than long, and small size at sexual maturity. The dorsal coloration is varioulsy spotted, ocellated, horizontally striped, or with other distinctive markings in addition to background color in all other species of Narcine, except in N. rierai, N. tasmaniensis, N. sp. nov. B and N. sp. nov. C. N. timlei is distinguished from N. rierai by having a wider than long nasal curtain (nasal curtain longer than wide in N. rierai). N timlei is distinguished from N. tasmaniensis, N. sp. nov. B and N. sp. nov. C by having eyes smaller than spiracle length and width (eye length averages 2.1 percent of total length, spiracle length and width averages 2.4 and 2.3 percent of total length in N. timlei, vs. 3.6, 2.3 and 2.6, repectively in N. tasmaniensis, 3.3, 2.2 and 2.4 in N. sp. nov. B, and 3.4, 2.2 and 2.3 in N. sp. nov. C). Also, males of N. timlei achieve sexual maturity at around 135 mm total length (presumably females achieve maturity at close to same size), much smaller than in any other species of Narcine as far as known (males of other species are mature at least over 175 mm total length).

DESCRIPTION: Measurements and counts are presented in Tables 22 and 23, respectively. Disc slightly variable in shape, but almost always (in preserved specimens) wider than long (disc width is between 40.2 to 60.6 [x = 50.7] percent of total length, disc length ranges from 39.0 to 59.8 [x = 47.0] percent of total length). Disc ranges from subcircular to slightly oval to subtrapezoidal in preserved specimens, but disc shape (especially disc width) is greatly affected by preservation (see below). Disc in holotypes of N. indica and N. microphthalma angled at lateral margins (at greatest disc width); disc appears more rounded in type-series of N. brunnea, but when distended disc shape becomes trapezoidal. Syntype of N. timlei (designated lectotype

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below) with more rounded disc laterally, but specimen highly affected by preservation (when disc is laterally outstretched actual sub-trapezoidal shape becomes evident). Disc widest close to its mid-length (usually just posterior to mid-disc length). Snout broadly rounded, but angled laterally in some specimens. Preocular snout length averaging 12.9 percent of total length, and occupying between one-third and one-fourth of disc length. Disc overlapping origin of pelvic fins posteriorly only slightly, with only moderate free lobe posteriorly. Gill-slits beginning at close to mid-disc length, just anterior to mid-length of electric organs. Gill-openings more or less straight, not very broad; moderate gap present between gill-slits (branchial basket length averaging 10.4 percent of total length). Gill-slits situated progressively closer to mid-line from first to last gill-slit. Eyes relatively small; eye length slightly variable in preserved specimens (eye length smaller or about equal to spiracle length). Eyes and spiracles adjacent. Spiracles very rounded, but may be at slight angle in relation to eyes in preserved specimens in which spiracular borders are flatenned. Elevated borders of spiracles generally well developed. Electric organs moderately developed, beginning dorsally at about level of eyes on disc, and continuing caudally to posterior one-fifth of disc. Electric organ length averaging 23.1 percent of total length; electric organ width averages only 8.8 percent of total length.

Nasal curtain relatively short and much wider than long (close to three times wider), with more or less straight posterior margin except at center, where median, subtriangular lobe is present in well presereved specimens. Lateral margins of nasal curtain with rounded to broadly triangular corners posterior to nostrils. Laterally, nasal curtain lobes projecting to level of outer aspect of nostrils. Exposed upper tooth band partially covered by triangular median lobe of nasal curtain in well preserved specimens. Sensory pores on nasal curtain very

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numerous, continuing posteriorly to just beyond level of nostrils. Nostrils relatively large and circular, with small elevated rims posteriorly. Preoral snout length (x = 14.1) greater than prenasal snout length (x = 10.7), both being slightly greater than one-fourth to one-fifth of disc length, respectively Prenasal snout length less than preocular snout length. Mouth slightly wider than distance between nostrils (mouth corners project laterally to about level of outer margin of nostrils). Exposed tooth bands about equal in width, but upper tooth band slightly wider. Tooth bands relatively wide, occupying about one-half of mouth width, and short antero-posteriorly. Both tooth bands broadly rounded in outline. Exposed teeth very small, numerous and closely packed, in 15/15 – 25/24 vertical rows in adult or close to adult specimens, from about 135 mm total length (typically with 22/20 rows in specimens of 200 mm total length); 9/5 rows in specimen not quite 50 mm total length (from Sumatra); a 99 mm total length specimen from Pakistan has 15/15 exposed tooth rows. Teeth with somewhat large, broad, posteriorly angled, diamond-shaped bases and very small, blunt cusps close to mouth opening (larger cusps typically present on inner, non-exposed rows).

Pelvic fins relatively wide, much wider than long when measured together. Pelvic fin width averages 33.3 percent of total length (ranging from 28.9 to 40.4 percent); pelvic fin length averages 18.9 percent of total length (ranging from 15.9 to 22.0 percent). Pelvic fins without prominent lateral lobes antero-laterally. Posterior margins of pelvic fins relatively straight, not concave in well-preserved specimens. Posterior lobe of pelvics greater than anterior lobe, but subequal in poorly preserved specimens (such as holotype of N. indica). Pelvic fins begin just underneath posterior aspect of disc and extend caudally to level of anterior base of first dorsal fin. Only a very small free lobe present where pelvics adjoin tail

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posteriorly. Tail moderately stout at base; tail length, as measured from cloaca, is just less than disc length in many specimens. Lateral tail folds not resembling expanded flaps, beginning on lateral aspect of tail at posterior half of first dorsal fin base, and continuing caudally to insert on ventro-lateral to lateral portion of caudal peduncle. Dorsal fins relatively small, and subequal in height and length of base. Second dorsal slightly taller than first in some specimens (such as lectotype of Raja timlei and one paralectotype of N. brunnea), and second dorsal with faintly longer base, but ranges very similar for both dorsal fins. Dorsals with slightly different outlines. First dorsals varying slightly in shape, from broad and rounded at apex with a relatively extended free lobe above base, to generally less broad and faintly more acute at apex. First dorsal fin more erect and rounded at apex compared to second dorsal, which has a more slanted anterior margin and slightly more pointed apex with a smaller free lobe above base. Dorsals with posterior margins upright, not slanted, and slightly convex in some specimens. First dorsal fin originates just posterior to pelvic fin insertion on lateral aspect of tail, over posterior free lobes of pelvic fins. Caudal fin moderately developed (caudal fin height averaging only 10.2 percent of total length), with slanted upper lobe and subacute to rounded oval apex. In some specimens (e.g., from Myanmar) upper lobe is lower and less inclined, while in others upper lobe is taller and more inclined. Posterior margin of caudal fin generally rounded, but varying from broadly convex to more or less straight. Lower lobe of caudal markedly curved to angular posteriorly. Dorsal lobe of caudal generally greater than lower lobe, as measured from base of caudal fin; ventral lobe begins slightly more anteriorly than dorsal lobe.

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Pores of lateral-line and ampullary systems numerous. On dorsal surface, clear series of pores are present of supraorbital and infraorbital canals (located dorsally on snout and anterior disc regions, in straight semi-parallel rows over rostral ridges and between eyes and anterior disc margin). Scattered pores of hyomandibular canal, outlining electric organs dorsally, are present anteriorly and laterally. Lateral line pores on tail run dorsal to lateral tail fold, arching dorsally in bewteen first and second drosal fins. On ventral surface, numerous pores are present on snout region, evenly closely packed from snout tip to nasal curtain region. Groups of pores are present lateral to nostrils and mouth, and a small row of pores radiating obliquely outward posterior to mouth and anterior to branchial clefts is also sometimes present. The large number of closely packed pores on ventral snout region, reaching posteriorly to level of nostrils, is characteristic of the species and easy to observe.

Dorsal coloration very distinctive, composed of a more or less uniform light brown to tan coloration in preservative, and devoid of defined or conspicuous blotches, spots and reticulations of any kind. The uniform dorsal coloration may vary in intensity and somewhat in color, as some specimens from India (Kerala coast) and Myanmar (all in CAS) were darker. These specimens presented a greyish or purplish brown to dark brown dorsal color, with posterior margins of dorsal fins, lateral tail region and posterior pelvic borders whitish. Other specimens, including the lectotype of N. timlei, are a lighter brown, but have obviously faded in preservative. Posterior borders of the disc and pelvic fins is slightly lighter in some specimens. Ventral coloration is a uniform creamy white to white.

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REMARKS: Raja timlei was the first species of Narcine to be described. Bloch and Schneider (1801) described this species on the basis of three specimens from off the coast of Tranquebar, south of Pondicherry (Coromandel coast), southeastern India. All three specimens are extant, two of which are in relatively good condition (Figs. 53 and 54). One of these specimens subsequently became the holotype of Narcine indica Henle, 1834 (Fig. 54). The original type-series of R. timlei, however, is composite, being composed of two species. Two specimens are preserved in alcohol (including the holotype of N. indica), and one is a stuffed specimen, very distorted and lacking much of its skeleton (tentatively identified as N. maculata, see above). The two alcoholic specimens are conspecific, and are illustrated in Henle (1834, pl. II; Figs. 53 and 54 here).

Specimen ZMB 4581 is here designated lectotype of Raja timlei Bloch and Schneider, 1801 (Fig. 53). The lectotype is an adult male, although relatively small at 154 mm total length, and is partially dried, displaying a slightly shrunken disc and pelvic fins. This specimen is conspecific with the holotype of Narcine indica Henle, 1834, which is therefore synonymized with it. The holotype of N. indica (ZMB 4582, and not 5482 as in Paepke and Schmidt, 1988 and Eschmeyer et al., 1998), now a paralectotype of R. timlei, is also an adult male and also relatively small at 166 mm total length. The disc of ZMB 4581 was originally more trapezoidal in shape, presently appearing rounded to oval.

The holotype of N. indica shares many features with typical N. timlei and with the lectotype of Raja timlei. Both type specimens (ZMB 4582 and ZMB 4581, respectively), as mentioned above, are adult males (or very close to adult) even though quite small. No other species of Narcine matures at such a small length (males are mature at around 140 mm total

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length). Both type specimens are from the same locality, and have similar general proportions (Table 22), positions of fins, configuration of nostrils, nasal curtain, tooth bands, teeth, sensory pores, meristics (Table 23), among other features. The shape of the disc is different, but this is almost certainly preservational as the disc in the lectotype of R. timlei is noticeably shrunken laterally, and disc shape is slightly variable in examined specimens of this species from throughout its range (specimens of N. timlei appear to be very affected by shrinkage in preservative – perhaps due to its small size, as in Narke dipterygia Bloch and Schneider, 1801 – which greatly influences disc shape). Both specimens have pelvic fins that are slightly shrunken, exposing the clasper more than is normal, and contributing to the large gap between disc and pelvic fins. The holotype of N. indica is almost completely bleached, but under magnification certain regions (e.g., under dorsal fins) indicate that it probably was unifrom brown dorsally, as is the lectotype of Raja timlei. The skin is very loose and flaccid in the holotype of N. indica, accounting for the flatenned appearance of the spiracular rim. The minor differences among the holotype of N. indica and the lectotype of R. timlei appear either to be preservational or considered here to be intra-specific.

The holotypes of N. microphthalma Valenciennes, 1852 (MNHN 1342; Fig. 56) and N. macrura Valenciennes, 1852 (MNHN 2095; Fig. 55) are here unequivocally identified as conspecific with the lectotype of R. timlei Bloch and Schneider, 1801 (ZMB 4581), and are therefore also junior synonyms. The holotype of N. microphthalma is in better condition than that of N. macrura, which is highly deteriorted. MNHN 2095 lacks pelvic fins, has damaged dorsal and ventral disc surfaces (especially ventral side), and the mouth and nostril regions are disfigured. Nevertheless, the configuration of its eyes and spiracles, position and shape of

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dorsal and caudal fins, extent of lateral tail fold and dorsal coloration lacking any spots (being composed of a uniform brown color, as observed under the microscope), allows N. macrura to be identified with Raja timlei. Proportional measurements are also very close to those of typical N. timlei (Table 22), and the radiograph of the holotype (Table 23) indicates that it is close in available meristic featrures. The holotype of N. microphthalma agrees in proportional measurements, position of fins, arrangement of tooth bands, extent of clasper, coloration and in meristics with specimens of N. timlei including the lectotype of Raja timlei. It is particularly similar to the holotype of N. indica Henle, 1834, displaying the same sub-trapezoidal disc shape. The coloration is faded, but under magnification it is clear that it was a uniform brown devoid of spots.

Narcine brunnea was described by Annandale (1909) from the Bay of Bengal (at least from the Orissa and Aracan coasts), on the basis of seven specimens. Two of these were sent to the British Museum (Natural History) in London, one was sent to Amsterdam (ZMA) and four apparently remained in the Zoological Survey of India in Calcutta. Annandale (1909), however, did not specify a type-series, which was delimited here on the basis of museum catalog information, original label information and the type-catalog of the Indian Museum published by Menon and Yazdani (1963). The specimens of the Indian Museum were not examined, and it is not known if they are still extant. Annandale also did not specify a type-locality, but the Golden Crown, the steamer that collected Annandale's material, sampled primarily off the Orissa coast, eastern India (Bay of Bengal). Locality information is not very specific for any of the three syntypes examined (labelled as "Orissa coast" [BMNH 1909.7.12.10], "Arrakan coast" [BMNH 1909.7.12.11] and "Bay of Bengal" [ZMA

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112.827]). All three specimens have original Indian Museum steel labels still attached, and are fairly well preserved. They agree with the type specimens of R. timlei in proportional measurements (Table 22), meristics (Table 23), dentition, coloration, mouth, nasal curtain, and tooth band morphology, and sensory pore distribution.

ZMA 112.827 (ex-Indian Museum specimen 2345/1) is here chosen as lectotype of N. brunnea Annandale, 1909, as it is the best preserved specimen of the three syntypes examined. It is an adult male, 182 mm total length (its original label reads "type, SS Golden Crown 1908"). BMNH 1909.7.12.10 and 1909.7.12.11 are therefore paralectotypes, as are all four Indian Museum syntypes (if extant). Both BMNH specimens have elongated claspers and are adult (1909.7.12.11, 225 mm total length) or almost adult (1909.7.12.10, 135 mm total length). The 225 mm total length male had its mouth removed, perhaps by Annandale (1909) for his study of the mouth and teeth of this species.

Little information is available for the paralectotypes deposited in the Indian Museum. Menon and Yazdani (1963) provide catalog numbers and locality data for the four paralectotypes: F 2349/1 and F 2350/1, collected by the Golden Crown from the Aracan [sic] coast; F 11577 and F11578, "Sand heads, Hooghly; R. M. Daley Coll." (apparently from the Hugli river mouth). No information exits regarding state of preservation, sex and size of these paralectotypes.

Numerous authors have misidentified this species (see synonymy above). Although the very common application of the nominal species N. brunnea Annandale, 1909 is consistent with its type-series, it is clearly a junior synonym of Raja timlei Bloch and Schneider, 1801. The latter nominal species was applied very erroneously and inconsistently by past authors, and has

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been used for a form of Narcine with spots and greater size at maturity, among many other differences from the lectotype of R. timlei. The usage in the literature of this nominal species is also inconsistent with the poorly preserved and stuffed paralectotype of R. timlei that is still extant (ZMB 7588). This specimen (364 mm total length female, presumably adult) differs greatly from typical N. timlei, and is very distorted and damaged. On this basis it could not be chosen as lectotype of R. timlei and is tentatively identified as N. maculata (Shaw, 1804; see section on this species above). The application N. indica in the literature is even more inconsistent. Many recent authors have applied this nominal species to forms that have upper tooth bands much broader than lower tooth bands (e.g., Monkolprasit, 1984, 1990; Carvalho et al., in press). An examination of the original description of N. indica would have clearly demonstrated that its holotype has tooth bands of equal width with numerous teeth, a very clear and straightforward character that distinguishes it from species of unequal tooth bands. Carvalho et al. (in press) were constrained to use nominal species as currently applied in the region of coverage at the time of composition, although they note the general misapplication of nominal species in the area.

Annandale (1909) reported on some intraspecific variation within N. brunnea (= N. timlei). He noted that disc shape and eye size are particularly variable, and not dependent on size, "coloration" or sex. This agrees with my observations of specimens from throughout the range of the species (differences are not locality-dependent). However, there appears to be slight variation in shape of dorsal fins as well, as some specimens have dorsal fins with proportionally greater free lobes above the base, and a more rounded apex. These differences, however, are considered intraspecific and preservational (both eye length and disc shape,

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especially disc width, are greatly affected by preservation). The difference in dorsal fin morphology was not consistent enough to warrant specific separation (this difference is more noticeable in some specimens from Bombay, but from other areas as well). Annandale, with great foresight, noted that "it was not possible to separate Henle's Narcine indica from N. timlei, Bloch and Schneider, on the ... [basis] ... of the shape of the disc" (1909: 45) – a character originally used by Henle (1834) to distinguish both species. If further examination of material, including freshly captured specimens, corroborate that there is a clear distinction regarding disc shape, eye size and dorsal fin morphology such that specific separation is warranted, then both nominal species N. indica and N. microphthalma would be available for this distinct species (N. indica would have priority). Presently, however, only a single species warrants recognition.

N. timlei is the smallest species of Narcine. Maturity for males is estimated at around 140 mm total length (perhaps at 135 mm total length). Sexual maturity for females is less known, but is presumably around the same size (specimens were not dissected to discern sexual maturity). Annandale (1909) reported that specimens as small as 55 mm total length were already free-swimming as they lacked that yolk-sac rudiments.

GEOGRAPHICAL DISTRIBUTION: This abundant species is relatively widespread from Pakistan in the west to at least the western Sunda shelf region in the east (extending as far as southwestern China), bordering the Indian subcontinent and southeast Asia (Fig. 104). It is apparently more rare farther northwest of the Gulf of Thailand, in the South China Sea (only one specimen examined from China, presumably southwestern China). This species is not

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reported at all for the South China Sea and southwestern China. N. timlei is a shallow water, in-shore species.

MATERIAL EXAMINED: (65 specimens, 49.8 to 237 mm total length): **China**: BMNH 1848.3.18.178 – 179 (1 of 2 specimens, 215 mm total length adult male). **India**: AMS I. 49; BMNH 1909.7.12.10 (paralectotype of Narcine brunnea Annandale, 1909); BMNH 1909.7.12.11 (paralectotype of Narcine brunnea Annandale, 1909); BMNH 1889.2.1.4189 – 4193 (4 of 6 specimens, 105 to 133 mm total length females); BMNH 1979.3.21.407; BMNH 1979.3.21.409 – 410 (2); CAS 41712 (2); CAS 41714 (2); CAS 41713; CAS 58355; CAS 58360 (11); IRSNB 25244; MNHN1340; MNHN 1342 (holotype of Narcine microphthalma Valenciennes, 1852); MNHN 1799; MNHN 7893 (4); RMNH 8578; ZMA 112.827 (lectotype of Narcine brunnea Annandale, 1909); ZMB 4581 (lectotype of Raja timlei Bloch and Schneider, 1801); ZMB 4582 (paralectotype of Raja timlei Bloch and Schneider, 1801, holotype of Narcine indica Henle, 1834). **Indonesia**: BMNH 1983.1.7.1 – 3 (3); RMNH 26905 (Sumatra); ZMH 10432 (Sumatra). **Malaysia**: FMNH 47257 (Selangor). **Myanmar**: CAS 58356; CAS 98159. **Pakistan**: USNM 199666; USNM 222474; ZMH 4466. **Singapore**: CAS 130983 (4; Ketam Island). **Sri Lanka**: BMNH 1883.5.24.49; CAS 58400; USNM 222478; USNM 222479 (2). **Thailand**: SMF 22219. Specimens currently without locality data: BMNH 1852.9.13.181; MNHN 2095 (holotype of Narcine macrura Valenciennes, 1852; "mer des Indes," probably India); RMNH 7429; SMF 3927 ("Indian Ocean").

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Narcine vermiculatus Breder, 1928

Figs. 65 – 67, Tables 24 – 25

Narcine vermiculatus Breder, 1928: 6, figs. 3 and 4 (original description, illustrated, photograph; 1.5 miles west of San Benito, Mexico); Beebe and Tee-Van, 1941: 248 – 249, fig. 3, pl. I, fig. 1 (diagnosis, description, distribution, comparisons, illustration compiled, photograph; La Libertad, El Salvador); Hildebrand, 1948: 3 (cf. to Narcine schmitti, described as new); Bigelow and Schroeder, 1953: 110, 111 (accepted as valid, in identification key); Castro-Aguirre, 1965: 213 – 214 (description, photograph [p. 213]); Instituto Nacional de Pesca, 1976: 63, fig. 32 (in identification key, listed, photograph compiled [p. 145]); López S. and Bussing, 1982: 8 (listed, Costa Rica); van der Heiden and Findley, 1988: 212 (listed; Sinaloa); Moore and Boardman, 1991: 27 (type-catalog); Bussing and López S., 1994: 32 – 33 (listed, ouline illustration; Costa Rica); Castro-Aguirre and Pérez, 1996: 23 (accepted as valid, in identification key, distribution); McEachran, 1995: 770, 771 (identification, distribution, illustration compiled); Eschmeyer et al., 1998 (compilation); Eschmeyer, 1998 (listed in a classification).

Narcine sp.: Hiyama, 1937: 21, pl. 54, fig. B (description, illustrated).

Narcine schmitti Hildebrand, 1948: 1 – 3, fig. 1 (original description, illustrated; "White Friars Island, off the mouth of the Gulf of California"); Bigelow and Schroeder, 1953: 111

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(accepted as valid, in identification key); Castro-Aguirre, 1965: 185 (in identification key only); Castro-Aguirre and Pérez, 1996: 24 (accepted as valid, in identification key); Eschmeyer et al., 1998 (compilation); Eschmeyer, 1998 (listed in a classification). NEW SYNONYMY.

DIAGNOSIS: A species of Narcine distinguished from all congeners by its unique dorsal color pattern composed of irregular white horizontal stripes and reticulations over a reddish-brown background.

DESCRIPTION: Measurements and counts are presented in Tables 24 and 25, respectively. Disc rounded to oval, slightly longer than wide for most specimens (means for disc length and width are very similar, at 47.5 and 48.4 percent of total length, respectively). Disc is widest portion of body, fairly wider than pelvic fins (pelvics averaging only 30.3 percent of total length). Disc slightly overlaps origin of pelvic fins posteriorly. Disc leaves very small free lobe posteriorly at point where it contacts side of trunk. Disc is widest at just posterior to its mid-length. Snout region rounded anteriorly, not acute. Preocular snout region ranging from 11.9 to 15.3 precent of total length and roughly one-third in disc length. Electric organs occupy in length from 18.4 to 28.2 percent of total length, beginning just anterior to level of eyes dorsally and at level of nostrils ventrally. Electric organs continue posteriorly to beyond level of last gill-slit ventrally. Electric organ width also somewhat variable, being between 6.6 and 11.7 percent of total length. Outline of electric organs more clear in ventral view. Gill-slits rather small, not strongly semi-circular and faintly directed anteriorly from outer to inner margins.

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Gill-slits situated progressively closer to mid-line from anteriormost to posteriomost gill-slit. Distance between last gill-slits smaller than branchial basket length on average. Spiracles and eyes adjacent, without any space in between. Spiracles with relatively well-developed rims, reaching anteriorly to posterior one-third of eye length at outer sides of eyes. Spiracles oval, just slightly longer than wide on average. Eyes relatively small, not longer than spiracles.

Nasal curtain wider than long, nasal curtain width reaching 4.8 to 6.4 percent of total length and nasal curtain length reaching only 1.6 to 2.8 percent of total length. Nasal curtain with moderately developed central lobe posteriorly. Nostrils small and circular, with slightly elevated posterior rims. Prenasal snout length just inferior to preocular snout length. Mouth on average slightly wider than distance between nostrils. Upper tooth band slightly wider than lower tooth band. Both upper and lower tooth bands circular in outline, but lower tooth band appears more angular at corners than upper tooth band. Teeth in 14/13 – 19/20 exposed rows in specimens 185 mm total length or larger; a 107 mm total length female has 13/12 exposed tooth rows. Teeth with single, long and sharp cusp generally only on inner (not exposed) rows. Crowns with wider-than-long, diamond-shaped bases, with cusps occupying about one-half of crown-base in width. Some adult specimens with slightly wider bases in lateral rows. Teeth set in quincunx arrangement.

Pelvic fins wider than long, with relatively long posterior lobes. Posterior lobes of pelvics more or less straight. Lateral corners of pelvics blunt. Posterior lobe of pelvics contact claspers or lateral aspect of trunk (in females) leaving only a very small free lobe. Pelvics extend from underneath posterior disc region to underneath level of mid-first dorsal fin base; developed clapers extend posteriorly to first dorsal fin base end. Claspers in mature males

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relatively thin, not projecting greatly beyond pelvic fins. Tail only moderately long as measured from cloaca, and shorter than snout to cloaca length (cloaca to caudal fin length ranges from 42.9 to 47.1 percent of total length, snout to cloaca ranges from 47.9 to 52.5 percent of total length). Tail length shorter on average to both disc width and length. Tail width at base moderately broad and variable, ranging from 15.0 to 24.6 percent of total length, and sub-circular in cross section. Lateral tail fold not greatly prominent, extending from in between first and second dorsal fin bases to lateral aspect of caudal peduncle. Second dorsal fin slightly taller than first dorsal fin (second dorsal ranging from 8.4 to 10.0 percent of total length, cf. to 7.3 to 9.0 percent for first dorsal). Dorsal fin bases almost equal. First dorsal fin more rounded at apex than second dorsal; second dorsal is generally wider at mid-fin height. Both dorsal fins leave slight free lobe posteriorly. Caudal fin somewhat tall, angular at apex, relatively not elongated, and with more or less straight posterior margin. Length of dorsal and ventral lobes of caudal about equal, but dorsal lobe slightly taller. Distance between second dorsal and caudal fins generally slightly greater than distance between dorsal fins.

Dorsally, sensory pores are visible in straight, antero-posterior rows on snout region, in between eyes and lateral to eyes. Pores also visible outlining external aspect of electric organs and over base of tail region. Pores on lateral aspect of tail running dorsal to lateral tail fold, arching dorsally underneath second dorsal fin, and terminating on lateral aspect of caudal base. Pores on dorsal surface sometimes darkly pigmented. Ventrally, sensory pores are scattered on snout region in abundance, extending posteriorly to level of nostrils. Pores on ventral surface also oulining electric organs and extending to pelvic fin level on ventral disc. Pores on ventral snout area in more or less parallel antero-posterior rows.

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Dorsal background coloration slighty variable, ranging from light to dark brown or purplish-brown in preserved specimens. Numerous creamy white vermiculations and irregular spots and blotches dorsally, from snout to caudal fin. Over dorsal snout region, markings appear faded, not as defined. On lateral and mid-disc region, curved vermiculations (horizontally elongated blotches) predominate, forming irregular reticulated pattern. Some blotches appear connected forming longer streaks of creamy white running across disc. Streaks sometimes alternate with more defined spots over base of tail region. Number of streaks or vermiculations may vary, from many (appearing as a thin reticulated pattern) to few. Below and/or anterior to dorsal fins and over caudal fin there are blotches and streaks in all specimens, giving the appearance of well-defined stripes laterally on tail. Ventrally specimens are more uniform creamy white in coloration, sometimes appearing darker laterally on disc and pelvic fins.

REMARKS: The holotype of Narcine schmitti agrees with N. vermiculatus in proportional measurements (Table 31), meristics (Table 32), and in external morphology, and is therefore synonymized with it. The holotype of N. schmitti is slightly dried, and becomes hard with brittle dorsal and caudal fins if left out of preservative. The coloration has faded to a pale yellowish-tan, and this is clearly due to preservation, as remnants of the conspicuous markings and vermiculations diagnostic of N. vermiculatus can be seen upon close inspection. Some authors have accepted N. schmitti as a valid species, but without examination of the holotype (e.g., Bigelow and Schroeder, 1953; Bussing and López S., 1994). Hildebrand's (1948)

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description, however, provides obvious indications that his species may be a synonym of N. vermiculatus, as the only characters given to distinguish both species are the slightly smaller spiracles and dorsal coloration of N. schmitti (he did not examine specimens of N. vermiculatus). N. schmitti was described in 1948, but the holotype was collected in 1934, therefore Hildebrand did not see the specimen when it had its original coloration. The holotype of N. vermiculatus (YPM 1142) is in good condition, presenting no signs of distortion due to preservation. Presently, its coloration is not as intense as depicted by Breder (1928), however, having faded slightly.

Hiyama's (1937) brief account was based on two specimens (without precise locality), one of which is clearly of N. vermiculatus as it is very well illustrated. The other specimen is probably of N. entemedor, as it is described as being two feet in length, well over the largest recorded length of N. vermiculatus, and in possessing a "much angular snout" (p. 21), which is prevalent among specimens of N. entemedor (N. vermiculatus has a more rounded snout).

Males appear to reach sexual maturity at about 190 mm in total length, but definitely by 200 mm. Specimens of around 54 mm in total length are free swimming, with very faint yolk-scars (if present) and with few external teeth already visible. The smallest specimens examined (54 mm or slightly larger) already disply the typical color pattern of the species, with vermiculations present on the outer dorsal disc margins and before dorsal and caudal fins. Data concerning sexual maturity is scant for females, but they must achieve reproductive potential before 200 mm in total length.

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Specimens of N. vermiculatus from both distributional extremes are uniform in coloration and in proportions. The greatest observed variation regarding coloration was observed among specimens from the same locality (FMNH 63711, from above San Benito, off the Chiapas coast of Mexico). The variation concerns the size and amount of vermiculations present, as one specimen (adult male, 196 mm in total length) has very thin vermiculations, contrasting with the blotches, ocelli and streaks present in the other 14 specimens of the lot.

Narcine vermiculatus is similar to Narcine sp. nov. F from Colombia in general morphology and size (see "Remarks" section of Narcine sp. nov. F below for characters distinguishing both species). It is easily separated from N. entemedor by proportional measurements of disc and tail regions, coloration and size.

GEOGRAPHICAL DISTRIBUTION: Narcine vermiculatus has a relatively wide distribution, ranging from the mid-Gulf of California to Costa Rica (Fig. 102), on the continental platform, in waters at least 7.2 to 48.4 m deep.

MATERIAL EXAMINED: (31 specimens, data available on request): **El Salvador**: CAS 57001 (1); **Guatemala**: ZMH 10410 (1); **Mexico**: CAS 3426 (1); CAS 4395 (1); CAS 4396 (1); CAS 4447 (1); CAS 4765 (1); CAS 49094 (2); CAS 54014 (1); FMNH 62372 (1); FMNH 63711 (15); MNHN 1894-24; USNM 94044 (holotype of Narcine schmitti), 212 mm TL adult male, "White Friars Island, off mouth of the Gulf of California," 5 to 10 fathoms, Mr. Waldo L. Shmitt, 3. iii. 1934; USNM 101857 (1); USNM 181305 (1); YPM 1143 (holotype of

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Narcine vermiculatus), 204 mm TL adult male, 14°40.20'N, 92°40.30'W, R/V Pawnee, otter trawl, 9. iv. 1926.

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Narcine westraliensis McKay, 1966

Figs. 68 – 71, Tables 25 – 27

Narcine westraliensis McKay, 1966: 73 (original description, comparisons, illustrated; type-locality: Shark Bay, Western Australia); Allen, 1985: 2504 (listed); May and Maxwell, 1986: 136 (brief comparison); Allen and Swainston, 1988: 26 (in part, brief account, illustration); Paxton et al., 1989: 61 (in part, compilation); Hutchins and Smith, 1991: 5 (listed in type catalog); Last and Stevens, 1994: 374, 379, pl. 67 (identification, brief description, distribution, illustrated); Allen, 1997: 46 (brief account, illustration); Eschmeyer et al., 1998: 1789 (compilation); Eschmeyer, 1998: 2182 (listed in a classification).

DIAGNOSIS: A species of Narcine distinguished from all congeners by its unique dorsal color pattern composed predominantly of brown or dark brown horizontal stripes of varying thickness across disc (posterior to eyes) and dorsally on tail, over a light brown or tan background.

DESCRIPTION: Measurements and counts are presented in Tables 26 and 27, respectively. Disc oval to subcircular, slightly wider than long, and widest at mid-disc region. Disc length 29.5 to 45.1 percent of total length (x = 39.4), disc width goes 35.3 to 46.0 in total length (x = 41.1). Disc slightly overlaps origin of pelvic fins posteriorly; disc not projecting anteriorly to form notch where it meets tail region, therefore not leaving a small posterior free lobe. Snout

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circular anteriorly, not acute. Preocular snout region not particularly elongated, 6.7 to 10.0 percent of total length, and occupying normally between one-fifth and one-sixth of disc length. Electric organs not greatly visible in dorsal view, beginning lateral to mid-length of eyes anteriorly and continuing to close to posterior one-fifth or one-sixth of disc length; electric organs varying in width from 4.4 to 10.0 percent of total length. Gill slits semi-circular, small and relatively close-together, curving slightly towards mid-line from first to last gill-slit. Eyes and spiracles close together, spiracles usually without strongly elevated rims. Eyes just slightly longer than spiracles. Spiracles circular posteriorly, with relatively straight anterior margin.

Nasal curtain relatively long, covering upper tooth band entirely or almost entirely. Nasal curtain with semi-circular posterior margin, and projecting laterally at its posterior aspect so as to be wider than distance between nostrils. Nasal curtain pores continue posteriorly on nasal curtain to around its mid-length, close to level of nostrils. Nostrils small and very circular, with slightly elevated lateral margins. Prenasal snout length just shorter generally than preocular snout length. Mouth wider than internarial distance (5.4 to 8.3 percent of TL vs. 3.2 to 4.7 percent of TL, respectively). Upper tooth band slightly wider than lower tooth band, both circular in outline and wider than long. Teeth in 11/9 – 20/16 exposed vertical rows in adults and pre-adults. Teeth with longer cusps only on inner-rows, near mouth opening; teeth closely set together. Cusps small and triangular on outer rows, usually worn-down. Longer cusps slightly overlap bases of teeth in next horizontal row. Crowns diamond-shaped, with rounded or blunt posterior margins, and about as wide as long.

Pelvic fins wider than long, with posterior lobes longer than anterior lobes; pelvic fins broadest anteriorly. Pelvic fins begin underneath posterior aspect of disc, and insert on tail

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posteriorly directly underneath insertion of first dorsal fin. Pelvic fins posteriorly with a small free lobe. Claspers relatively thin, projecting beyond pelvics in mature specimens to about one-fifth of their total length as measured from cloaca (projection is greater in dried specimens). In holotype, claspers project to level of posterior one-third of first dorsal fin. Claspers not connected to inner margin of pelvics throughout entire length. Tail long, much longer than disc length, occupying from 41.2 to 56.6 percent of total length. Tail broad at base (14.2 to 23.1 percent of total length), tapering to caudal fin, and sub-circular in cross-section (tail wider than tall). Lateral tail folds relatively prominent, especially in smaller specimens, beginning ventral to mid-length of first dorsal fin and inserting on ventro-lateral aspect of caudal peduncle. Lateral tail folds not as visible in dried or distorted specimens, appearing absent at first glance. Dorsal fins only moderately developed, both dorsals about equal in height and length. First dorsal fin originates at level of posterior base of pelvics, over small free lobe of posterior pelvic fin. Dorsals leaving small free lobe posteriorly, only sub-acute at apex, with sloping anterior lobes and slightly convex posterior margins. Distance between dorsals and distance between second dorsal and caudal fins about equal. Caudal fin low and relatively long, with upper lobe only gradually increasing in height posteriorly towards apex. Lower lobe slightly longer than upper lobe, and upper lobe slightly taller than lower lobe. Both lobes of caudal fin originate at more or less same level of caudal peduncle. Caudal fin posteriorly only moderately curved, with continuous margin between upper and lower lobes (some adult males with more straight posterior margin).

Pores and canals of lateral line system very difficult to discern on dorsal surface, even under magnification. Lateral canal (flanking both sides of tail region) with pores situated from

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each other in a more or less straight line, and at a distance roughly equal to one and one-half length of eyes. On holotype and other specimens, anti-penultimate pore of lateral canal is situated above canal, not below it as are other pores of lateral canal. Pores of ampullary system scattered on dorsal and ventral surfaces. On ventral snout region, pores of ampullary system are numerous on and around nasal curtain. Nasal curtain with pores posterior to level of nostrils. Scattered pores (ampullary and lateral-line?) outlining anterior portions of electric organs.

Coloration very distinctive, and slightly variable on dorsal surface. Coloration in preserved specimens composed of a light tan background color, with horizontal darker brown stripes of varying thickness across disc and tail, extending posterior to caudal fin region. Snout region uniformly light brown or yellowish, without horizontal stripes. Horizontal stripes may be slightly broken on disc to form blotches laterally around mid-disc region. Generally a strong horizontal stripe across each dorsal fin and lateral on tail beneath dorsal fins. Base of caudal fin with prominent dark stripe, and posterior aspect of caudal fin with either stripes or blotches (blotches may be broken-up stripes). Region posterior to spiracles may have a posteriorly curved stripe outlining blotches over mid-disc region. In some specimens, stripes vary in thickness, alternating a thin stripe with a thicker stripe from post-spiracular disc area posterior to tail region. Stripes also over pelvic fins. Distal tips of dorsal clasper area may have brown spot, more noticeable in fresh specimens. In late-term embryos, three or four large brown spots dominate dorsal disc region. Ventrally, specimens are all creamy white to a faded yellow, depending on preservation. Fresh specimens white and slightly transparent underneath.

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REMARKS: The dorsal color pattern of N. westraliensis easily distinguishes it from other species of Narcine. The only species that can be confused with N. westraliensis is Narcine sp. nov. A (see below), from the Gulf of Carpentaria and lower Arafura Sea region. Both species are similar in dimensions, nasal curtain morphology, among other aspects. However, the nasal curtain is relatively longer compared to its width in N. westraliensis. Also, the undescribed Carpentaria species has a distinctive pattern predominantly composed of dark brown blotches and spots on the dorsal surface, unlike N. westraliensis which has predominantly horizontal stripes, although some blotches connected to horizontal stripes occur on some specimens, including the holotype. These species also appear to be geographically isolated, as neither has been collected from the continental shelf of northern Western Australia northeast of Dampier Land (lower Timor Sea region), even though both occur at similar depths (usually as deep as 60 or 70 m, up to 100 m exceptionally). Both species have been previously confused in the literature (Gloerfelt-Tarp and Kailola, 1984; Sainsbury et al., 1985; Allen and Swainston, 1988; Paxton et al., 1989).

McKay's (1966) original description is based on abundant material collected in 1960 and 1962 from Shark Bay (Western Australia), and is very comprehensive, providing details of development, reproduction, morphometrics and even behavioral notes based on aquarium observations. According to McKay, his aquarium specimens (four adults) remained covered by sand during most of the day, with only eyes and spiracles protruding (very much like stingrays), and were more active during dusk and early morning hours. McKay observed that the gut contents of nine adults trawled in Shark Bay contained annelid worms. McKay also compared his new species to other species of Narcine that he recognized as valid, as well as to species of

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Heteronarce which he (erroneously) considered a junior synonym of Narcine. The type-series, composed of 44 specimens, is in very good condition.

Narcine westraliensis does not appear to overlap in distribution with Narcine sp. nov. B, also from Western Australia, as both species occupy different depth ranges. N. westraliensis occurs on the continental shelf, in more shallow waters (up to 100 m), while Narcine sp. nov. B appears restricted to the continental slope are in depths greater than 170 m. These two species are easily distinguished from each other in dorsal coloration pattern, many proportional differences (including disc, snout, tail, and nasal curtain), dentition, sensory pore pattern, nasal curtain morphology, and meristics.

Female specimens of N. westraliensis mature at around 170 to 180 mm in total length, as observed in females carrying embryos (see also McKay, 1966), and males are considered adult from about 175 to 195 mm in total length. McKay (op. cit.) reports that gravid females were collected throughout the year, but that breeding occurs from May to November (peaking during September and October -- his data are from specimens collected in Shark Bay). He also reports that females may carry one to eight embryos, and that both embryos of early and late stages may be present in one given female. The greateset number of embryos that I was able to find was three in one female (various specimens), but I confirm his observation that different-stage embryos can be present in one female. Fully-developed embryos were found in both uteri of one gravid female, confirming that both uteri are functional and synchronous. Embryos were found predominantly with the tail directed toward the cloaca, but in one female a late-term embryo was facing the cloaca. All late-term embryos had their discs folded over the ventrally located yolk-masses, and were positioned in the same dorso-ventral aspect as their

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mothers. Yolk-masses attached to fully-developed pups (more or less 50 mm in TL) were around 1 cm across. The uterine walls and oviduct of gravid specimens are very thin, off-white, and the embryos or egg-masses situated inside can easily be seen through the semi-transparent walls. The uterus is devoid of villi in this species (see also McKay, 1966).

A dissected female of 237 mm in total length had nine visible rings comprising the intestinal valve. The liver of this same specimen is predominantly composed of a long and slender right lobe, and a shorter and wider left lobe which tapers posteriorly.

GEOGRAPHICAL DISTRIBUTION: Restricted to the continental shelf of Western Australia (Fig. 106), in depths ranging from one to 100 m, but the great majority of specimens were collected at a depth ranging from 10 to 65 m. This species appears to be locally abundant in Shark Bay and off Ningaloo Reef (Western Australia), as implied by the great quantity of specimens in the collections of the Western Australian Museum in Perth (some lots contain many specimens). Commonly collected as by-catch by prawn trawls in Shark Bay. Specimens from Shark Bay and Ningaloo Reef have been collected from more shallow waters compared to specimens from the northern-most extension of the species (off-shore of Dampier Archipelago and Port Hedland, south of the Rowley Shoals).

MATERIAL EXAMINED: (84 specimens, 35 – 272 mm TL): **Western Australia**: AMS 15585-001 (2), 177 mm TL pre-adult female and 151 mm TL pre-adult male, Shark Bay, 26°S, 114°E, R.J. McKay, viii. 1965; AMS 33312-023 (2), 201 mm TL adult female with 51 mm TL pup (aborted?), 40 km S of Carnarvon, 25°34'S, 14.6 -- 18.3 m, N. Coleman, 3. vi.

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1972; CSIRO C 2515, 252 mm TL adult female, Shark Bay, 1953; CSIRO H 1074-01, 232 mm TL adult female, off Cape Preston, 19°52.7'-- 54.8'S, 116°15.2' -- 14.8'E, 64 m, FRV Soela sta. 787/95, silty sand bottom, 4. x. 1987; CSIRO H 1038-02, 176 mm TL pre-adult female, off Port Hedland, 19°33.4'-- 33.9'S, 117°54.2'-- 52.7'E, 62 -- 64m, FRV Soela sta. 787/50, 29. ix. 1987; CSIRO H 1038-01, 211 mm TL adult female, same data as H 1038-02; CSIRO CA 2274, 210 mm TL adult male, E of Barrow Island, 20°39'S, 116°00'E, 28 m, FRV Soela sta. 179/4, 2. xii. 1979; CSIRO CA 1309, 232 mm TL adult female, Port Hedland Beach, 20°18'S, 118°35'N, 1980; CSIRO CA 4220, 225 mm TL adult female, NW of Port Hedland, 19°34.2'-- 32.7'S, 117°57.4'-- 58'E, 60 -- 65 m, FRV Soela sta. 582/63, 5. x. 1982; CSIRO CA 4221, 241 mm TL adult male, same data as CA 4220; CSIRO uncat., 144 mm TL immature male, 19°44' -- 46'S, 116°02'E, 100m, R/V Soela sta. 14, 2. xii. 1979; CSIRO uncat., adult or pre-adult male, no further locality data, photograph of freshly captured specimen only; NTM S. 10959-031 (4), 226, 196 and 195 mm TL adult females, 61.4 mm TL male pup (stuck in cloaca of 195 mm TL adult female), N of Port Hedland, 19°01'S, 119°25'E, 80 m, RV Tung Mao, 18. iv. 1983; NTM S. 11672-006 (2), 183 mm TL adult male, 158 mm TL pre-adult female, S of Rowley Shoals, 19°02'S, 118°30'E, 82 -- 86m, "NT Observers" team, 2. vi. 1985; NTM S. 11673-011 (2), 212 mm TL adult female, 207 m TL adult male, S of Rowley Shoals, 19°12'S, 118°41'E, 76 -- 80 m, "NT Observers" team, 1. vi. 85; NTM S. 11671--004, 203 MM TL adult female, S of Rowley Shoals, 19°03'S, 118°24'E, 82 -- 88m, "NT Observers" team, 2. vi. 85; NTM S. 10980--003, 134 mm TL immature female, NW of Monte Bello Island, 19°54'S, 115°39'E, 98 m, L. Bullard, 18. ix. 1982; QM

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I.10220, 209 mm TL adult female, Shark Bay, 30 miles S of Carnarvon, 25°16'S, 113°40'E, N. Coleman, 3. vi. 1972; WAM P 6963.001 (holotype), 211 mm TL adult male, Shark Bay, 8 miles NW of Cape Peron, 25°30'S, 113°30'E, 16.3 -- 18.1 m (9 -- 10 fathoms), R. J. McKay, 5. x. 1960; WAM P 5027.001 (paratype), 201 mm TL adult female, Shark Bay (locality for *all paratypes* and non-types, unless otherwise noted, are listed as "Shark Bay, WA, 25°21'S, 113°44'E" in WAM collection print-out, but this may represent only a "generalized" locality for Shark Bay and not the actual collection coordinates for paratypes and non-types, even though they all came from Shark Bay; G. Allen, personal commun.), R/V Peron (along with *all paratypes*, listed below), vi. 1960; WAM P 6946.001 (paratype), 214 mm TL adult male, vi. 1960; WAM P 6947.001 (paratype), 175 mm TL pre-adult or adult male, vi. 1960; WAM P 6948.001 (paratype), 215 mm TL adult female, vi. 1960; WAM P 6949.001 (female), 192 adult female, vi. 1960; WAM P 6950.001 (paratype), 270 mm TL adult female, vi. 1960; WAM P 6951.001 (paratype), 204 mm TL adult male, vi. 1960; WAM P 6952.001 (paratype), 189 mm TL pre-adult or adult female, vi. 1960; WAM P 6953.001 (paratype), 181 mm TL pre-adult or adult female, vi. 1960; WAM P 6954.001 (paratype), 187 mm TL pre-adult or adult male, vi. 1960; WAM P 6955.001 (paratype), 173 mm TL pre-adult male, vi. 1960; WAM P 6956,001 (paratype), 188 adult male, vi. 1960; WAM P 6957.001 (paratype), 180 mm TL pre-adult or adult male, vi. 1960; WAM P 6958.001 (paratype), 198 mm TL adult male, vi. 1960; WAM P 6959.001 (paratype), 202 mm TL adult male, vi. 1960; WAM P 6960.001 (paratype), 106 immature female, vi. 1960; WAM P 6961.001 (paratype), 183 pre-adult or adult male, vi. 1960; WAM P 6962.001 (paratype), 203 mm TL adult male, vi. 1960; WAM P 6064.001 (paratype), 210 mm TL adult female; WAM P 6965.001 (paratype), 159

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pre-adult female; WAM P 6966.001 (paratype), 196 mm TL adult male; WAM P 6967.001 (paratype), 183 mm TL pre-adult or adult male; WAM P 6968.001 (paratype), 192 mm TL adult female; WAM P 6969.001 (paratype), 157 pre-adult male; WAM P 6970.001 (paratype), 202 mm TL adult male; WAM P 6971.001 (paratype), 212 mm TL adult male; WAM P 6972.001 (paratype), 178 mm TL pre-adult male; WAM P 6973.001 (paratype), 116 mm TL immature male; WAM P 6974.001 (paratype), 197 mm TL adult female; WAM P 6975.001 (paratype), 187 mm TL adult male; WAM P 6996.001 (paratype), 187 mm TL pre-adult or adult female, vi. 1960; WAM P 6997.001 (paratype), 200 mm TL adult male, vi. 1960; WAM P 6998.001 (paratype), 191 mm TL adult female, vi. 1960; WAM P 6999.001 (paratype), 187 mm TL pre-adult female, vi. 1960; WAM P 7003.001 (paratype), 195 adult female, vi. 1960; WAM P 7004.001 (paratype), 188 pre-adult or adult female, vi. 1960; WAM P 7005.001 (paratype), 192 mm TL adult male, vi. 1960; WAM P 7009.001 (paratype), 198 adult female, vi. 1960; WAM P 7016.001 (paratype), 223 mm TL adult female with three pups in uteri (50.3 mm TL male, 51.8 mm TL female, 54.1 mm TL female) , 9. xii. 1962; WAM P 7018.001 (paratype), 237 mm TL female with three pups (all about 35 -- 40 mm TL), 9. xii. 1962; WAM P 7031.001 (paratype), 220 mm TL adult female, 9. xii. 1962; WAM P 7033.001 (paratype), 195 mm TL adult female, 9. xii. 1962; WAM P 7035.001 (paratype), 192 mm TL adult male, 9. xii. 1962; WAM P 5002.001, 272 mm TL adult female; WAM P 14801.001 (4), 266 mm TL adult female, 195 mm TL pre-adult or adult male, 154 mm TL adolescent female, 80 mm TL newly born female, Block Island, Shark Bay, A. McKenzie, viii. 1965; WAM P 23424.001, 163 mm TL pre-adult female, Exmouth Gulf, Learmonth, WA, P. Berrett-Lennard, vi. 1973; WAM P 23837.001, 200 mm TL adult male, Exmouth Gulf, R. Rowe, viii. 1973; WAM P

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29334.011 (2), 246 mm TL adult female, 119 mm TL juvenile male, 22°20'S, 113°51'E, Ningaloo Marine Park, 0.1 -- 1.0 m, G. R. Allen, 14. iv. 1987; (121 specimens examined but not measured): **Western Australia**: WAM 5003.001; WAM 5004.001; WAM 5005.001; WAM 5006.001; WAM 5007.001; WAM 5008.001; WAM 5009.001; WAM 5010.001; WAM 5012.001; WAM 5013.001; WAM 5014.001; WAM 5015.001; WAM 5016.001; WAM 5017.001; WAM 5018.001; WAM 5019.001; WAM 5020.001; WAM 5021.001; WAM 5022.001; WAM 5023.001; WAM 5024.001; WAM 5025.001; WAM 5026.001; WAM 5028.001; WAM 5029.001; WAM 5838.001; WAM 6976.001; WAM 6977.001; WAM 6978.001; WAM 6979.001; WAM 6980.001; WAM 6981.001; WAM 6982.001; WAM 6983.001; WAM 6984.001; WAM 6985.001; WAM 6986.001; WAM 6987.001; WAM 6988.001; WAM 6989.001; WAM 6990.001; WAM 6991.001; WAM 6992.001; WAM 6993.001; WAM 7000.001; WAM 7001.001; WAM 7002.001; WAM 7006.001; WAM 7010.001; WAM 7011.001; WAM 7012.001; WAM 7017.001; WAM 7019.001; WAM 7020.001; WAM 7021.001; WAM 7022.001; WAM 7023.001; WAM 7024.001; WAM 7025.001; WAM 7026.001; WAM 7027.001; WAM 7028.001; WAM 7029.001; WAM 7030.001; WAM 7032.001; WAM 7034.001; WAM 7720.001; WAM 7721.001; WAM 7722.001; WAM 7723.001; WAM 7724.001; WAM 7725.001; WAM 7726.001; WAM 7727.001; WAM 7728.001; WAM 7729.001; WAM 7730.001; WAM 7731.001; WAM 7732.001; WAM 7733.001; WAM 7734.001; WAM 7797.001; WAM 7798.001; WAM 7799.001; WAM 7800.001; WAM 7801.001; WAM 7802.001; WAM 7803.001; WAM 7804.001; WAM 7807.001; WAM 7808.001; WAM 7809.001; WAM 7810.001; WAM 7848.001; WAM 7849.001; WAM 7850.001; WAM 7851.001; WAM 7852.001;

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WAM 7853.001; WAM 7854.001; WAM 7855.001; WAM 7856.001; WAM 7857.001; WAM 7858.001; WAM 7859.001; WAM 9079.001; WAM 9080.001; WAM 9081.001; WAM 9082.001; WAM 9083.001; WAM 9084.001; WAM 9085.001; WAM 9086.001; WAM 9087.001; WAM 9088.001; WAM 9092.001 (adult female and three embryos); WAM 9143.001; WAM 9144.001.

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Narcine sp. nov. A

Figs. 72 – 76, Tables 28 – 29

Narcine westraliensis: Gloerfelt-Tarp and Kailola, 1984: 36 (misidentification, photograph); Sainsbury et al., 1985: 44, 330 (misidentification, brief description, listed, photograph); Allen and Swainston, 1988: 26 (in part, misidentification, illustration); Paxton et al., 1989: 61 (in part, misidentification);

Narcine sp. A: Last and Stevens, 1994: 375 (identification, description, distribution, illustrated); Carvalho et. al., in press (identification, brief description, distribution, illustrated).

Narcine sp.: Allen, 1997: 46 (brief account, illustration).

DIAGNOSIS: A species of Narcine distinguished from all other congeners by its unique dorsal color pattern, composed of dark brown, large and medium-sized spots (generally larger than interocular distance) that appear variously fused and elongated, surrounded by a network of smaller spots (smaller than eye-diameter) on most of dorsal surface including tail region.

DESCRIPTION: Measurements and counts are presented in Tables 28 and 29, respectively. Disc generally oval, slightly longer than wide on average (disc length is 36.5 to 44.0 percent of total length, disc width is 30.4 to 42.8 percent of total length). In well-preserved or fresh

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specimens disc slightly overlaps origin of pelvic fins posteriorly, but in most preserved specimens disc ends posteriorly at level of origin of pelvic fins. Disc connects directly to side of trunk, not leaving any distinguishable free lobe. Snout region circular anteriorly, not acute; preocular snout reaching 7.5 to 11.6 percent of total length. Precocular snout region about one-fourth to one-fifth of disc length. Electric organs not heavily outlined in dorsal and ventral views (more conspicuous in ventral view), beginning dorsally at level of anterior margins of eyes, and ventrally at level of nostrils. Electric organs continue posteriorly on disc to between four-fifths and five-sixths of disc length. Electric organs much longer than wide, electric organ length occupying from 12.9 to 24.8 percent of total length, electric organ width goes from 5.4 to 10.2 percent in total length. Gill slits semi-circular and very small, and relatively close together; gill-slits situated closer to mid-line progressively from first gill-slit to last gill-slit. Distance between last gill-slits and length of branchial basket almost equal. Spiracles begin adjacent to posterior aspect of eyes; spiracles without strongly elevated rims. Eyes just slightly longer than spiracles on average; spiracles about as wide as long. Spiracles very circular posteriorly.

Nasal curtain relatively long in well-preserved or fresh specimens, covering the upper tooth band almost entirely. Nasal curtain with circular posterior margin that is wider than area between nostrils. Ampullary pores on nasal curtain continue posteriorly to level of posterior margin of nostrils, which is close to nasal curtain mid-length. Nostrils small, circular and with slightly elevated borders. Prenasal snout length just inferior to preocular snout length. Mouth wider than internarial distance (6.0 to 8.1 percent of TL vs. 1.8 to 4.1 percent of TL, respectively). Upper tooth band slightly wider than lower tooth band, both fairly circular in

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outline with exposed portions wider than long, however lower tooth band may be sub-triangular in some specimens. Teeth in 12/9 – 17/18 exposed vertical rows in adults and pre-adults (one specimen had an unusual count of 13/18, accounting for the high extreme of lower tooth rows, which would otherwise be 14). Teeth with small cusps generally, especially on exposed rows; teeth on inner-most rows with slightly more extended cusps; adult males with longer cusps than adult females of similar size. Crowns small, diamond-shaped, wider than long, closely set in quincunx arrangement.

Pelvic fins not very prominent, wider than long, with posterior lobes longer than anterior lobes. Posteriorly pelvic fin has a very small free lobe. Pelvics extend from level of posterior insertion of pectoral fins to underneath level of origin of first dorsal fin on tail. Pelvics not greatly rounded or blunt at lateral corners. Claspers relatively thin, attached to pelvics without leaving a significant free lobe. Claspers in mature males project posteriorly beyond pelvic fins to about one-fifth of their total length as measured from cloaca, reaching to level of mid first dorsal fin base. Tail long, longer than disc length, and distinctively occupying from 49.5 to 58.4 percent of total length as measured from cloaca. Tail relatively broad at base (compared to disc width, tail is 14.1 to 22.0 percent of TL vs. 36.5 to 44.0 percent of TL), sub-circular in cross-section. Lateral tail fold not as prominent as observed in N. westraliensis, beginning just posterior to first dorsal fin base and extending caudally to insert on lower aspect of lateral caudal peduncle. Lateral tail fold commences as a slight ridge, barely noticeable, and is more difficult to observe in dried and distorted specimens. Dorsal fins about equal in height and length of base, first dorsal appearing only slightly taller, second dorsal slightly more slanted. Dorsal fins relatively rounded at apex in most specimens, sub-acute in larger adults.

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Dorsals with rounded to more or less straight posterior margins, and with small free lobe posteriorly (sometimes more pronounced on second dorsal fin). First dorsal fin originates dorsally on tail at level of small free lobe of pelvic fins or dorsal to posterior pelvic fin base. Distance between dorsals about equal to distance between second dorsal and caudal fin (means of 6.8 and 6.9 percent of total length, respectively). Caudal fin generally low, not reaching one-half of dorsal fin height (applying to both upper and lower lobes of caudal fin when measured separately). Caudal fin long, with rounded, continuous posterior margin; lower caudal fin lobe beginning anterior to upper caudal fin lobe in some larger specimens.

As in N. westraliensis, pores and canals of lateral-line system difficult to distinguish on dorsal surface. Pores on lateral aspect of tail few, not closely packed and continue posteriorly just dorsal to lateral tail fold. Ampullary pores numerous on ventral snout area, continuing on nasal curtain posteriorly to just beyond nostrils. One pair of ampullary pores present posterior to mouth, one on each side situated mesially in relation to first gill slits. Scattered pores outlining anterior one-third of electric organs on ventral surface.

Coloration very distinctive (even on preserved specimens), composed on dorsal surface of large and small dark brown spots over a background color that is usually creamy white, but may be light brown in specimens from the Timor Sea or from greater depths (see below). Spots vary in diameter, from roughly just larger than an ampullary pore to close to five to six times length of eye. Spots generally circular, but may also be irregular in shape, or even fused to other spots of same size appearing oval and elongated on disc longitudinally and across base of tail (CSIRO H 773-01). Smaller spots appear to outline larger spots on disc and base of tail region. Eyes and spiracles generally surrounded by numerous very small spots, which can also

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be present on disc margins outlining disc area. On dorsal disc region, there is generally one to three medium-sized spots (about equivalent to two or three eye-sizes) on snout region, a medium-sized spot in between eyes (only faintly visible on some specimens), two brown crescent-shaped markings posterior to spiracles, two large spots posterior to level of spiracles and crescent-shaped markings with a slightly smaller spot in between, one row of four medium- to large-sized spots across posterior one-fourth of disc, and medium-sized spots outlining disc. These spots are surrounded by numerous smaller spots which may be irregular in shape and may connect with each other, appearing to form a reticulated network over dorsal disc area. Large spots are present anteriorly on dorsal fins, covering portions of the fin bases and continuing underneath dorsal fins laterally on tail region (resembling elongated stripes). Large spot on lateral tail region in between dorsal fins. Large spot also on anterior caudal fin and sometimes present apically as well. Large spots on dorsal and caudal fins also with smaller peripheral spots. Dorsal pelvics also with medium-sized spots. Continuous horizontal stripes are lacking in this species except occasionally at base of tail (these are clearly the result of fusion of two larger spots, as may occur over mid-disc region; cf. N. westraliensis which has continuous, strong horizontal stripes that are not due to fused spots). Ventrally specimens are creamy white, even those that have light brown dorsal background color (see below). Larger specimens, males and females, may present few small spots or blotches ventrally posterior to pelvic fins on tail region, continuing caudally to level of second dorsal fin. Some specimens from the Timor Sea and from greater depths of the Arafura Sea display a dorsal color pattern composed of fewer and less defined medium to large spots, darker background color, and lack of smaller spots surrounding larger spots forming reticulated patterns (if present, then not as

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defined). Some of these specimens have very few large spots that may be present only marginally on disc (other specimens from Timor and Arafura Seas may have similar patterns to those described above for "typical" Narcine sp. nov. A, just with a darker background color; see below under "Remarks" for more details).

REMARKS: This highly colorful, undescribed species is similar to N. westraliensis in many proportional and external characters. Both species are readily separated by color pattern, and are, as far as known, disjunct geographically. Narcine sp. nov. A has a pattern of three medium-sized spots on dorsal snout region, whereas N. westraliensis has a uniformly colored dorsal snout region devoid of markings. Even though the spots covering Narcine sp. nov. A may be fused on occasion, these do not form the typical pattern of horizontal stripes characteristic of N. westraliensis. N. westraliensis may present blotches outlining horizontal stripes on the dorsal disc region, but these never appear to be the result of fused, well-defined large spots as seen on Narcine sp. nov. A. Also, Narcine sp. nov. A has a slightly more oval disc, with disc length being just greater than disc width in general (disc width ranges from 30.4 to 42.8 percent of TL, x = 36.9; disc length rages from 36.5 to 44.0 percent of TL, x = 40.2), compared to N. westraliensis, which has a disc width slightly greateror equal to disc length (disc width goes 35.3 to 46.0 percent in TL, x = 41.1; disc length goes 20.5 to 45.1 percent in TL, x = 39.4). However, as disc width seems to be affected by poor-preservation or shrinkage in Narcine sp. nov. A, caution must be used in using this character to separate it from N. westraliensis. The lateral tail fold appears more prominent in N. westraliensis.

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The variation observed in the color pattern of Narcine sp. nov. A is not necessarily depth-, locality- or size-related, although some correlation might occur. Specimens from the Gulf of Carpentaria, the eastern-most limit of this species, are uniform in dorsal color pattern, presenting the typical highly marked array of spots of various sizes over a creamy background color. Most specimens from the Gulf are from similar depths, spanning some seven degrees of latitude in between extremes. However, specimens from more western localities show more variation in color pattern. NTM 12269-003, for example, from the Arafura Sea north of Goulburn Island (NT) and collected in waters 80 m deep, displays the typical color pattern of Narcine sp. nov. A (great contrast between spots and background color). Specimens NTM 12924-001 and NTM 13576-008 were collected from the same area (differing in less than one degree of latitude and longitude from NTM 12269-003), but have more drab dorsal coloration, with a darker background color and fewer, less-defined spots. The latter specimens are from slightly deeper waters (from 96 to 105 m), and are much larger. Another specimen from the same locality (NTM 13347-002, 123 mm TL), however, is closer in size to NTM 12269-003 (155 mm TL), but also has fewer less-defined spots over a darker background color. The specimens from the Timor Sea are also slightly heterogeneous in color pattern, as NTM 13329-001 shows more spotting dorsally compared to NTM 13400-001 which is more uniform. NTM 13329-001 is more similar to Carpentaria specimens, but with darker dorsal background coloration and spots slightly less-defined. All these specimens are presently considered to belong to one species, from the Timor Sea to the Gulf of Carpentaria.

Narcine sp. nov. A may co-occur with specimens from the northeastern-most distribution of Narcine sp. nov. B (see below), north of Melville Island (NT) and south of

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Tanimbar Island (Indonesia). Specimens of Narcine sp. nov. B have been collected so far in slightly deeper waters (178 m is the shallowest record to date of Narcine sp. nov. B). Both species are easily distinguished by dorsal color pattern (uniformly light tan in Narcine sp. nov. B), nasal curtain proportions (nasal curtain much wider than long in Narcine sp. nov. B, and relatively much longer in Narcine sp. nov. A), nasal curtain sensory pore pattern (many more pores in Narcine sp. nov. A), disc shape (oval in Narcine sp. nov. A and shovel-shaped in Narcine sp. nov. B) and in general proportions.

Males appear to mature at about 180 mm in total length, but because many of the specimens are slightly shrunken, which renders the claspers more firmness, sizes at maturity may be slightly greater. Females probably mature are similar sizes to males. Two dissected females of about 240 mm in total length contained eggs of about the same dimensions in both uteri, suggesting both to be functional and probably synchronous. Four to eggs were found in each uteri. Less than ten intestinal rings are present in each of these females.

GEOGRAPHICAL DISTRIBUTION: This recently discovered species is known from the continental shelf region of the Timor and Arafura Seas, but primarily from the Gulf of Carpentaria (off Western Australia, Northern Territory and northwestern Queensland, Australia) (Fig. 106). It extends from 126°59'E to 140°57'E, varying little in latitude in the Timor and Arafura Seas, and reaching south in the Gulf of Carpentaria to just north of Wellesley Island. This species has been collected so far in waters ranging from 48 to 132 m deep.

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MATERIAL EXAMINED: (29 specimens, 115 to 241 mm TL): **Queensland**: AMS I 15557-015, 204 mm TL adult female, Gulf of Carpentaria, 12°37'S, 140°57'E, 61.2 m (34 fathoms), I. Munro, 29. iv. 1964; CSIRO H 1115-01, 212 mm TL adult male, Arafura Sea/Gulf of Carpentaria, 10°38'S, 139°46'E, 53 m, FRV Kulasi, Sta. 2 (Shot 1), P. Kailola, 6. xi. 1987; CSIRO H 1116-01, 194 mm TL adult female, Arafura Sea/Gulf of Carpentaria, 10°36'S, 140°01'E, 54 m, FRV Kulasi, Sta. 3/4 (Shot 6), P. Kailola, 5. xi. 1987; CSIRO CA 2273, 194 mm TL adult male, Arafura Sea/Gulf of Carpentaria, SW of Prince of Wales Is., 10°44'S, 139°55'E, 58 m, FRV Soela, S02/81/28, prawn trawl, 13. vi. 1981; CSIRO 3646-02 (2), 186 mm TL pre-adult male, 169 mm TL pre-adult or adult female, Gulf of Carpentaria, 12°58'S, 139°10'E, 56 m, G. Yearsley, 1. xi. 1993; QM I 11150, 194 mm TL adult male, Gulf of Carpentaria, 16°58'S, 140°57'E, MV Laakanuki, Sta. 26; QM I 23187 (2), 241 and 240 mm TL adult females, Gulf of Carpentaria, 16°S, 140°E, , "Q. F. S.," 19. x. 1983; QM I 25766, 197 mm TL adult male, Gulf of Carpentaria, 10°37.3'S, 140°08'E, 52 m, P. Kailola, 5. xi. 1987; QM I 27854, 237 mm TL adult female, Gulf of Carpentaria, 14° 30.2'S, 139° 42'E, 59 m, CSIRO cruise no. S50390, Sta. 75, J. Johnson, 7. xii. 1990; QM I 27918, 155 mm TL juvenile female, Gulf of Carpentaria, 11° 59.5'S, 139° 41.8'E, 57 m, J. Johnson, 8. xii. 1990; QM I 28005, 223 mm TL adult female, Gulf of Carpentaria, 13° 30.9'S, 137° 32.1'E, 48 m, CSIRO cruise Sta. 99, J. Johnson, 12. xii. 1990. **Northern Territory**: CSIRO H 773-01, 166 mm TL pre-adult or adult male, Arafura Sea, N of Cape Wessel, Wessel Is. Group, 9°48'S, 136°57'E, 80 m, R/V Chin Wei 1, 28. iii. 1987; CSIRO C 4079, 220 mm TL adult male, Arafura Sea/Gulf of Carpentaria, 13°S, 137°E, 1963; NTM 11680-012, 161 mm TL juvenile

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male, Arafura Sea, N of Cape Wessel, 10°30'S, 136°21'E, 56 -- 57 m, Sta. WH 85-4, W. Houston, 9. iii. 85; NTM 12262-003, 177 mm TL sub-adult or adult male, Arafura Sea, NE of Goulburn Is., 10°20'S, 134°29'E, 59 m, NT Fisheries Obs., Sta. BAG 8706A; NTM 12264-003, 184 mm TL pre-adult or adult male, Arafura Sea, NE of Goulburn Is., 10°21'S, 134°24'E, 59 m, NT Fisheries Observers, Sta. BAG 8706C, 12. vi. 1987; NTM 12269-003, 115 mm TL juvenile male, Arafura Sea, N of Goulburn Is., 10°19'S, 133°30'E, 80 m, NT Fisheries Observers, Sta. BAG 8706H, 20. vi. 1987; NTM 12924-001 (2), 214 mm TL adult male, 123 mm TL juvenile male, Arafura Sea, 9°43'S, 133°25'E, 105 m, Sta. RW 90-25, R. Williams, 14. xi. 1990; NTM 12983-002, 170 mm TL pre-adult male, Arafura Sea, 10°18'S, 132°50'E, 68 m, Sta. HL 90-55, H. Larson, 1. xi. 1990; NTM 13347-002, 123 mm TL juvenile male, Arafura Sea, 9°39'S, 133°19'E, 115 m, 14. xi. 1990; NTM 13576-008 (2), 228 and 215 mm TL adult females, Arafura Sea, 9°46.2'S, 133°44.5'E, Sta. RW 92-64, R. Williams, 19. x. 1992. **Western Australia**: AMS 21634-002, approx. 200 mm TL adult female, Timor Sea, 11°42'S, 127°29'E, 132 m, R/V Courageous, J. Paxton, 2. vi. 1979; NTM 13329-001 (2), 178 and 173 mm TL pre-adult males, Timor Sea, 12°47'S, 128°16'E, 99 m, NT Fisheries Observers, Shot 199, 7. xii. 1990; NTM 13400-001, 204 mm TL adult female, Timor Sea, 12°05'S, 126°59'E, 87 m, NT Fisheries, Shot 173.

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Narcine sp. nov. B

Figs. 77 – 81, Tables 30 – 31

Narcine sp. 1: Gloerfelt-Tarp and Kailola, 1984: 36 (listed).

Narcine sp.: Sainsbury et al., 1985: 44, 330 (brief comparison, listed).

Narcine sp. B: Last and Stevens, 1994: 376 (identification, desciption, distribution, illustrated); Williams et al., 1996: 144 (listed); Carvalho et al., in press (identification, brief description, distribution, illustrated).

DIAGNOSIS: A species of Narcine diagnosed by the following unique combination of characters: tail length as measured from cloaca much longer than disc width and length (averaging 53.7 percent of total length, vs. averages of 40.3 for disc width and 42.1 for disc length), wider than long nasal curtain, a uniform yellowish-brown to light brown dorsal color pattern without any spotting or other markings, ridge-like lateral tail fold, preocular snout length averaging 10.1 percent of total length. All other species of Narcine have tail length less than or subequal to disc width and length, except N. rierai, N. tasmaniensis, N. westraliensis, N. sp. nov. A and N. sp. nov. C. From N. rierai, N. sp. nov. B is distinguished by having a wider than long nasal curtain (nasal curtain conspicuously longer than wide in N. rierai). From N. westraliensis and N. sp. nov. A, N. sp. nov. B is distinguished by having a uniform yellowish-brown to light brown dorsal color pattern without any spotting or other markings

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(N. westraliensis has horizontally elongated stripes over disc and tail, N. sp. nov. A has large spots surrounded by smaller spots over disc and tail). From N. tasmaniensis, N. sp. nov. B is distinguished by having a low, ridge-like lateral tail fold (resembling a broader flap in N. tasmaniensis), relatively more slender disc (disc width averaging 40.3 percent of total length, vs. 43.4 in N. tasmaniensis), greater preocular snout length (averaging 10.1 percent of total length, vs. 7.8 in N. tasmaniensis) and by a lighter dorsal coloration (usually a dark chocoloate brown in N. tasmaniensis). From N. sp. nov. C, N. sp nov. B is distinguished by having a relatively wider and longer disc (averaging 40.3 and 42.1 percent of total length, respectively, vs. 38.4 and 40.2 in N. sp. nov. C), and by generally having a yellowish-brown background (extending into preocular snout region) compared to a light brown background (preocular snout region sometimes lighter) in N. sp. nov. C.

DESCRIPTION: Measurements and counts are presented in Tables 30 and 31, respectively. Disc slightly oval, generally longer than wide (disc length is 38.2 to 48.6 percent of total length, disc width is 34.1 to 45.2 percent of total length), and distinctively shovel-shaped. Disc widest at posterior one-fourth of its length in adults, and at around one-sixth in juveniles. Disc just barely overlaps origin of pelvics at its posterior aspect; disc does not leave free lobe posteriorly. Slightly rounded snout and apex regions. Preocular snout length averaging about one-tenth of total length, and about one-third in disc length. Electric organs not clearly outlined dorsally, more conspicuous in juveniles. Electric organs begin just anterior to level of eyes dorsally and continue posteriorly to about five-sixths of disc length; ventrally electric organs begin just posterior to level of nostrils. Electric organs length is between 16.7 to 24.0 percent of total

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length, and electric organ width is between 5.0 and 9.4 percent of total length. Gill slits semi-circular, small and positioned in more or less a striaght line from first to last gill slit. Distance between last gill slits and branchial basket length about equal. Spiracles separated from eyes by a small gap in juveniles, but gap is reduced in adults; spiracles without strongly elevated rims. Spiracle length and width about equal; spiracles with well-rounded posterior margins. Eyes longer than spiracles and darker than background disc color. Eyes slightly bulging.

Nasal curtain wider than long, with small central posterior lobe generally present in well-preserved specimens. Nasal curtain projects slightly laterally posterior to nostrils, giving nasal curtain a faint trilobed appearance. Nostrils very circular with slightly elevated rims. Prenasal snout length proportional to preocular snout length, in relation to total length (averaging close to 10 percent of total length). Mouth generally only slightly wider than distance between nostrils. Upper tooth band wider than lower tooth band; upper tooth band fairly circular in outline, lower tooth band more acute in outline appearing sub-triangular in some specimens. Teeth in 11/8 – 20/15 exposed vertical rows in pre-adults and adults (a typical adult of more than 300 mm in total length may have 19/15 rows). Teeth trapezoidal with long cusps especially on inner rows; more exposed teeth with worn-down cusps. Teeth set in quincunx arrangement, with diamond-shaped bases that are slightly wider than long.

Pelvic fins wider (when measured together) than long, with longer posterior lobes compared to anterior lobes. Pelvic fins leave a small free lobe posteriorly. Pelvics extend caudally from just underneath disc anteriorly to underneath origin of first dorsal fin on tail. Pelvics slightly rounded laterally, with fleshy lateral corners. In males claspers protude to underneath base of first dorsal fin. Claspers in malture males project to about one-fifth of their

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total length beyond tips of pelvics, reaching close to one-half of first dorsal fin base length. Tail long, occupying from 50.0 to 57.1 percent of total length as measured from cloaca. Tail not very broad at base (x = 16.5 percent of total length), sub-circular in cross section. Tail does not taper greatly from base to second dorsal fin, but appears to taper more from second dorsal to caudal fin. Lateral tail folds not very prominent, difficult to discern in some specimens, appearing as a slight ridge only. Lateral tail fold beginning underneath level of first dorsal fin base, from origin to mid-base level, in well-preserved specimens, inserting on lateral aspect of caudal peduncle close to its ventral margin. Dorsal fins slightly rounded to sub-acute at apex, with sloping anterior and curved posterior margins. Dorsal fins insert on tail leaving a small free lobe posteriorly. Dorsal fins very similar in proportions and outline. Distance between second dorsal and caudal fins is greater generally than distance between dorsal fins. Caudal fin low and moderately long (reaching to approximately 13 to 14 percent of total length), with relatively straight posterior margin. Height of caudal fin, as measured with both upper and lower lobes together, is about equal to height of dorsal fins. Lower lobe of caudal fin begins just anterior to level of origin of upper caudal fin lobe in larger specimens.

As in all Australian species, pores of lateral-line and ampullary systems very difficult to observe and identify on dorsal and ventral surfaces. Few pores on lateral tail region, situated just dorsal to lateral tail fold. Very few scattered pores outlining electric organs both dorsally and ventrally. Ampullary pores on ventral snout region in two more or less straight antero-posterior rows, with last pores of each line situated slightly more laterally. These pores do not continue posterior to level of anterior margins of nostrils. Two small group of pores anterior to each nostril on ventral snout area.

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Dorsal coloration light tan to beige or pale yellow. Specimens with a very uniform color dorsally, with areas of lighter intensity over pelvic fin margins, anterior region of pelvic fins, anterior snout area and at lateral tail base regions. Dorsal and caudal fins semi-transparent posteriorly. In preserved specimens, dorsal coloration may seem even lighter, but always a yellowish beige or tan. Ventrally specimens are a pale white to cream color, without any distinct markings.

REMARKS: This species was first reported by Gloerfelt-Tarp and Kailola (1984) in a survey of trawled fishes of Indonesia and northwestern Australia. It was listed as "Narcine sp. 1," and has been suspected of being new for more than a decade, but only recently was it characterized in any detail (Last and Stevens, 1994). It is very similar to Narcine sp. nov. C from off the Queensland coast (see "Remarks" section of Narcine sp. nov. C below for characters distinguishing both species).

A 234 mm total length male is close to being sexually mature, and maturity for males appears to be at around 250 mm total length. A few examined male specimens larger than 265 mm total length appeared to have "soft" claspers, but very close to sexual maturity if not already mature (one 297 mm total length specimen with relatively soft claspers as well). A 331 mm total length female was found to have two late-term embryos present, one in each uterus, as well as one large egg-mass in the right uterus (egg-masses found in both uteri in other large females with late-term pups). The embryos measured 72 and 77 mm in total length (male and female, respectively), both with yolk-sacs and stalks still attached. Uteri are extremely thin-walled and transparent, without any nutrition-supplying function.

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GEOGRAPHICAL DISTRIBUTION: This recently discovered species has a wide distribution, occurring in the Arafura Sea (eastern Indonesia, south of Tanimbar Island; also off the Northern Territory, Australia) and extending southwest along the continental slope of Australia as far south as the Houtman Abrolhos, off Geraldton, Western Australia (Fig. 106). Narcine sp. nov. B has been found in depths ranging from 178 to 333 m.

MATERIAL EXAMINED: (57 specimens measured, 135 – 365 mm TL): **Western Australia**: AMS I 22821-007 (5), 204 mm TL juvenile male and 227 to 255 mm TL pre-adult females, 18°16'S, 118°12'E, 320 m, FRV Soela, J. Paxton, 10. iv. 1982; AMS I 31174-010, 234 mm TL pre-adult male, Shark Bay, 26° 42.3'- 42.1'S, 112° 38.4' - 38.5'E, 285 m, FRV Sourveyor, 30. I. 1991; CSIRO CA 327, 198 mm TL pre-adult female; CSIRO CA 330, 360 mm TL adult female, "Northwest Shelf, WA", FRV Courageous, v. 1978; CSIRO CA 347, 245 mm TL pre-adult male; CSIRO H 1035 (3), 330 – 331 mm TL adult females, 272 mm TL adult male, N of Dampier archipelago,19°08'S, 116°54'E, 196 -198 m, FRV Soela, S06-86-84, 24. X. 1986; CSIRO H 1036 (3), 312 to 325 mm TL pre-adult and adult females, N of Cape Lambert, 19°06'S, 117°08'E, 178 - 183 m, FRV Soela, S07-87-129, 12. x. 1987; CSIRO CA 1486, 206 mm TL pre-adult male; CSIRO H 2547-10, 321 mm TL adult female, W of North West Cape, 21°37'S, 113°59'E, 209 – 215 m, FRV Southern Surveyor, SS 0191/7, 24. i. 1991; CSIRO H 2597 (2), 302 mm TL adult male, 365 mm TL adult female, W of Green Head, 29°59'S, 114°28'E, 265 m, FRV Southern Surveyor, SS 0191/63, 8. ii. 1991; CSIRO CA 2812, 298 mm TL adult female, N of Forestier Island, 18°10'S, 118°20'E, 300 m, FRV Soela, sta. 2/82/36, 10. iv. 1982; CSIRO CA 2813, 258 mm TL pre-adult female, same

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data as CSIRO CA 2812; CSIRO CA 2873, 315 mm TL adult female, N of Forestier Island, 18°31'S, 118°09"E, 200 m, FRV Soela, sta. 2/82/14, 2. iv. 1982; CSIRO H 3054-03, 361 mm TL adult female, N of Carnarvon, 24°40'S, 113°43'E, 225 m, 28.ix. 1990; CSIRO H 3222-06, 315 mm TL adult female, N of Dampier archipelago, 19°12'S, 116°25'N, 190 m, SS 2/90/136, 11. x. 1990; CSIRO H 4031-81, 117 mm TL pre-adult male, N of Cape Lambert, 18°57'S, 117°14'E; CSIRO H 4070 (4), 162 to 256 mm TL pre-adult males, 244 mm TL pre-adult female, NW of Port Hedland, 18°12'S, 118°14"E, 269 m, SS 8/95/123; CSIRO CA 4361, 216 mm TL pre-adult female, N of Port Hedland, 18°11'S, 118°16'E, 304 m, FRV Soela, S 01/84/29, 2. ii. 1984; CSIRO CA 4367, 261 mm TL pre-adult male, SE of Mermaid Reef, 17°18'S, 120°09'E, 304 m, FRV Soela, S 0184/39, 4. ii. 1984; NMV A 1798 (2), 270 mm TL adult or pre-adult male, 305 mm TL adult female, SW of Shark Bay, 27°07'S - 27°01'S, 112°48'E - 112°49'E, 238 – 248 m, RV Hai Kong, 3. iii. 1981; NMV A 9656, 254 mm TL pre-adult or adult male, 85 km SW of Geraldton, 29°15'S, 113°56'E, 320 – 325 m; NTM S 12641-021, 297 mm TL adult male, NW of Lynher Bank, 14°50'S, 121°35'E, 275 – 280 m, J. Baillie, 15. xii. 1989; NTM S 14266-006, 202 mm TL pre-adult female, NW of Houtman Abrolhos, 28°15.9'S, 113°19.5'E, 240 – 333 m, P. Alderslade, 11. Vii, 1987. **Northern Territory**: NTM S 13065-002 (4), 275 mm TL adult male, 246 – 262 mm TL pre-adult to adult females, N of Bathurst Island, 09°49'S, 130°15'E, 260 m, FV Invincible, D. Evans, 12. xii, 1990; NTM S 13147-013 (4), 272 – 285 mm TL pre-adult to adult males, 312 – 321 mm TL adult females, 09°37'S, 130°26'E, 255 m, FV Invincible, D. Evans, 9. xii. 1990; NTM S 13578-009, 311 mm TL adult female, 08°55.3'S, 133°41.1'E, 179 – 187 m, RW 92-66, R.

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Williams, 20. x.1992; NTM S 13579-004, 250 mm TL pre-adult female, 09°01'S, 133°19.7'E, 193 – 195 m, RW 92-67, R. Williams, 20. x. 1992; NTM S 13580-039 (4), 241 – 267 mm TL pre-adult males, 325 – 328 mm TL adult females, 09°04.7'S, 133°04.7'E, 179 – 205 m, RW 92-68, R. Williams, 20. x. 1992. **Indonesia**: MNHN 1996-1556 (3), 115 to 190 mm TL juvenile males, 302 mm TL adult female, off Tanimbar Island, 9°01'S, 132°42'E, 246 - 253 m, Karubar expedition, sta. CP62, 1. xi. 1991; MNHN 1996-1557 (4), 144 to 162 mm TL pre-adult females, 145 mm TL pre-adult male, off Tanimbar Island, 9°26'S, 131°13'E, 225 m, Karubar expedition, sta. CP86, 4. xi. 1991. (4 specimens examined but not measured): **Western Australia**: CSIRO H 1035 (2 late-term embryos extracted from uteri of 331 mm TL female, each approximately 75 mm in TL; data for specimens specified above); CSIRO H 3054 (2 late-term embryos; data specified above).

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Narcine sp. nov. C

Figs. 82 – 84, Tables 32 – 33

Narcine sp. C: Last and Stevens, 1994: 377 (identification, description, distribution, illustrated); Carvalho et al., in press (identification, brief description, distribution, illustrated).

DIAGNOSIS: A species of Narcine distinguished by the following unique combination of characters: tail length as measured from cloaca much longer than disc width or length (tail length averaging 54.1 percent of total length, vs. 38.4 and 40.2 for disc width and length, respectively), a wider than long nasal curtain, dorsal coloration a uniform light brown devoid of any spotting or markings, and a ridge-like lateral tail fold. Tail length is smaller than or subequal to disc width and length in other species of Narcine, except N. rierai, N. tasmaniensis, N. westraliensis, N. sp. nov. A and N. sp. nov. B. N. sp. nov. C is distinguished from N. rierai by having a wider than long nasal curtain (longer than wide in N. rierai). N. sp. nov. C is distinguished from N. westraliensis and N. sp. nov. A by having a uniform light brown dorsal coloration devoid of any spotting or markings of any sort (horizontal stripes are present in N. westraliensis, and few large spots and numerous smaller spots are present in N. sp. nov. A). N. sp. nov. C is separated from N. tasmaniensis by having a slender, ridge-like lateral tail fold (flap-like lateral tail fold in N. tasmaniensis), uniform light brown or tan dorsal color pattern (dark chocolate brown in N. tasmaniensis), more slender disc (disc width averages 38.4 percent of total length, vs. 43.4 in N. tasmaniensis). N. sp. nov. C is distinguished from N. sp. nov. B

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by its slightly different dorsal color (generally light brown, compared to yellowish-brown in N. sp. nov. B), and by disc proportions (disc more slender and not as long, see "Diagnosis" for N. sp. nov. B above).

DESCRIPTION: Measurements and counts are presented in Tables 32 and 33, respectively. Disc faintly oval, generally longer than wide (disc length is 35.6 to 44.9 percent of total length, disc width is 28.6 to 43.7 percent of total length), and characteristically shovel-shaped. Disc widest at posterior one-third to one-fourth of its length in adults, and at around one-sixth in juveniles. Posterior aspect of disc overlaps origin of pelvics only slightly; disc does not leave pronounced free lobe posteriorly at apex. Snout slightly rounded to faintly acute; pectoral fin (disc) apex region rounded. Preocular snout length averages about one-tenth of total length, and about one-fourth in disc length. Electric organs not very visible dorsally (more pronounced in juveniles); electric organs begin just anterior to level of eyes dorsally and reach posteriorly to about five-sixths of disc length. Ventrally, electric organs begin just posterior to level of nostrils. Electric organs length is between 14.3 and 23.5 percent of total length; electric organ width is between 5.1 and 9.4 percent of total length. Gill slits small, semi-circular, and positioned in more or less a straight line from first to last gill slit. Distance between last gill slits and branchial basket length about equal. Spiracles without strongly elevated rims and separated from eyes by a small gap in juveniles (gap is less conspicuous in adults). Spiracle length and width almost equal; spiracles with rounded posterior margins. Eyes slightly pronounced (bulging) and darkern than background disc color. Eye length greater than spiracle length.

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Nasal curtain distinctly wider than long, sometimes with small central posterior lobe present in well-preserved specimens. Nasal curtain wider than distance between nostrils. Circular nostrils have slightly elevated rims. In average, prenasal snout length proportional to preocular snout length in relation to total length (prenasal snout length has greater range, but both averaging 9.7 percent of total length). Mouth generally wider than distance between nostrils. Upper tooth band wider than lower tooth band; upper tooth band fairly circular in outline, lower tooth band circular to sub-triangular in some specimens. Mouth projects anteriorly at corners in some specimens. Teeth in 9/5 – 16/12 exposed vertical rows in pre-adults and adults (few specimens have 16 exposed upper tooth rows; an adult of some 280 mm in total length may typically have 12/9 rows). Teeth trapezoidal, some specimens without very pronounced cusps even in adults (longer cusps only on inner rows), other adults with well-developed and sharp cusps; more exposed teeth with worn-down, blunt cusps (exceptionally, some adult males with well-developed exposed cusps). Teeth set in quincunx arrangement, with wider-than-long diamond-shaped bases.

Pelvic fins close to twice as wide as long, with longer posterior lobes compared to anterior lobes. Pelvic fins leave a small free lobe posteriorly. Posterior lobes of pelvic fins appear slightly concave in preserved specimens. Pelvics originate anteriorly from underneath disc, extending caudally to just anterior to level of first dorsal fin origin on tail. In males, claspers protrude posteriorly to underneath mid-length of base of first dorsal fin. Claspers in malture males project to about one-fifth of their total length beyond tips of pelvics. Tail relatively long, occupying from 50.5 to 56.6 percent of total length as measured from cloaca. Tail relatively thin at base, but varying from juvenile to adult (12.7 to 20.0 percent of total

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length; adults with proportionally wider tails), sub-circular in cross section. Tail more or less straight, not tapering greatly from base to second dorsal fin, or from second dorsal to caudal fin. Lateral tail folds not prominent, generally difficult to discern, appearing as a slight ridge only. Origin of lateral tail fold on lateral aspect of tail at level of posterior one-third of first dorsal fin base, in well-preserved specimens, inserting on lateral aspect of caudal peduncle close to its ventral margin. Dorsal fins semi-transparent in some specimens, slightly rounded to sub-acute at apex, with sloping anterior and curved to relatively straight posterior margins. Dorsal fins insert on tail so as to leave a small free lobe posteriorly. Both first and second dorsal fins very similar in proportions and outline, but second dorsal may be more inclined than first dorsal fin in some specimens. Distance between second dorsal and caudal fins is almost equivalent to distance between dorsal fins (both averaging 9.1 percent of total length). Caudal fin low and moderately long (averaging roughly 12 to 13 percent of total length), with relatively straight posterior margin. Combined height of both upper and lower lobes of caudal fin about equal to height of first and second dorsal fins. Upper and lower lobes of caudal fin begin at about same level on caudal peduncle.

Pores of ampullary and lateral-line systems very difficult to observe and identify on both dorsal and ventral surfaces. Few scattered pores on lateral tail region, situated dorsal to lateral tail fold, but precise pattern difficult to discern. Very few scattered pores outlining electric organs both dorsally and ventrally. Ampullary pores on ventral snout area are situated in semi-parallel rows, from snout anterior margin to region of nostrils. Ampullary pores anterior to nasal curtain situated in two well-defined, more or less parallel and central antero-posterior rows. Posterior three or four pairs of ampullary pores from both rows radiate

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outward from mid-line just above level of nostrils in many adults. Pores do not continue posteriorly from level of anterior margins of nostrils onto nasal curtain. Small group of pores in either semi-straight or crescent-shaped pattern anterior to each nostril.

Dorsal coloration generally a uniform light brown, sometimes with a streak of slightly darker brown on dorsal tail surface. Freshly collected specimens present a faint pinkish hue on edges of disc and ventrally on snout region and pelvic fins. Snout sometimes semi-transparent in freshly captured specimens, and generally more tan, lighter than rest of dorsal background color. Dorsal clasper surfaces light tan or off-white, with dorsal clasper glans area sometimes with shades of brown. Dorsal and caudal fins semi-transparent (more obvious in fresh material). Specimens ventrally are a uniform pale white to cream color, without any distinct markings.

REMARKS: This newly discovered species is very similar to Narcine sp. nov. B from the continental slope of Western Australia and Northern Territory. Both species are comparable in morphometric proportions and external and internal morphology. The Queensland species has a darker dorsal color, and presents a slightly more acute and less rounded snout in most specimens. Characters that may further differentiate these two species include the distance between the first and second dorsal fins (in Narcine sp. nov. C, the average distance is 9.1 percent of total length compared to an average of 7.7 percent of total length in Narcine sp. nov. B), disc width (in Narcine sp. nov. C, the average is 38.4 percent of total length, in Narcine sp. nov. B average disc width is 40.3 percent of total length), and disc length (in Narcine sp. nov. C the average is 40.2 percent of total length, compared to 42.1 percent of total length in Narcine sp. nov. B). Narcine sp. nov. C has relatively fewer rows of exposed teeth on upper

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and lower jaws compared to Narcine sp. nov. B (Narcine sp. nov. C has 9/5 – 16/12 exposed rows [typically with 12/9 exposed rows in adults], compared to 11/8 – 20/15 exposed rows in Narcine sp. nov. B [typically with 19/15 rows in adults]). As both species are completely separated geographically, it is best presently to consider them as separate species given the morphological differences above, even though these are not great. This was also the conclusion of Last and Stevens (1994).

Males are unequivocally sexually mature at 245 to 260 mm total length, but some specimens of close to 210 mm total length have rigid claspers. Clasper rigidity, however, may be an artifact of preservation as dried specimens will appear to have claspers that are more firm. Some males that may be sexually mature at just over 200 mm total length did appear to be slightly dehydrated. But as one female specimen of 190 mm total length had a close-to-term embryo protruding from its cloaca, then it is possible that male sexual maturity occurs close to 210 mm total length for at least some specimens. As other males were undoubtedly not sexually mature at 235 and 240 mm total length, then size at maturity may vary from specimen to specimen and/or in relation to some as yet unknown parameter. Claspers begin to project beyond pelvic fins at about 160 mm total length.

The embryo of the 190 mm total length female was a male specimen of 84 mm in total length, and occupied the right uterus. Its disc was partially coiled, flexing ventrally. No yolk-mass was evident, and the embryo protruded from the cloaca tail first. Another female of 310 mm total length contained a late-term embryo of about 80 mm total length in its right uterus, but with its head directed towards cloaca. Its disc was wrapped around the ventral yolk-mass

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(measuring 22 mm in diameter), with the tail and pelvic fins curled and folded, respectively. The left uterus contained two large, partially connected, egg masses.

More specimens of Narcine sp. nov. C have been captured compared to the two other new species of Narcine from Australia. Many specimens have been collected together, suggesting more dense populations compared to, for example, Narcine sp. nov. B.

GEOGRAPHICAL DISTRIBUTION: Restricted to the off-shore Queensland coast, this species has been collected in two principal areas: east of Dunk Island, and further south off Swain and Suamarez Reefs (Fig. 106). Narcine sp. nov. C occurs in waters ranging from 140 to 540 m deep. This species has not yet been captured in between these two distributional extremes, but is believed to occur in relative abundance there.

MATERIAL EXAMINED: (103 specimens, 75 to 347 mm in TL): **Queensland**: AMS I. 20968-009 (6), 85 to 242 mm TL juvenile to pre-adult males, 100 to 195 mm TL juvenile to pre-adult females, E of Hinchinbrook Island, 18°03'S, 147°10'E, 357 m, 27. iii. 1979; AMS I. 25804-013 (6), 217 mm TL pre-adult to adult male, 174 to 227 mm TL pre-adult females, N of Townsville, 17°59'S, 147°03'E, 260 m, FRV Soela, 9. vi. 1986; AMS I. 25808-012 (6),199 mm TL pre-adult female, 79 to 200 mm TL juvenile to pre-adult males, N of Townsville, 17°59'S, 147°06'E, 306 m, FRV Soela, 11. i. 1986; AMS I. 25837-009 (2), 208 mm TL pre-adult or adult male, 190 mm TL adult female, N of Townsville, 17°55'S, 146°53'E, 142 m, 20. i. 1986; CSIRO H 718-24, 123 mm TL juvenile female, 22°52'S, 152°42'E; CSIRO H 719 (11), 254 to 313 mm TL adult males, 280 to 347 mm TL adult females, S of Suamarez Reef,

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Capricorn Channel, 22°56.7'S, 153°00.8'E to 22°53.3'S, 152°59.3'E, 325 – 338 m, FRV Soela, S06-85-12, P. Last, 18. xi. 1985; CSIRO H 1217 (5), 116 to 150 mm TL pre-adult males, 131 to 157 mm TL pre-adult females, S of Swain reef, Capricorn Channel, 22°52'S, 152°42'E, 225 – 282 m, FRV Soela, S06-85-13, 19. xi. 1985; CSIRO uncat., 257 mm TL pre-adult male, FRV Soela, S06-85-4; CSIRO uncat., 305 mm TL adult female, FRV Soela, S-85-05; CSIRO uncat., 184 mm TL pre-adult male, FRV Soela, S06-85-10; CSIRO uncat. (2), 255 to 266 mm TL pre-adult to adult males, FRV Soela, S06-85-11; CSIRO uncat., 217 mm TL pre-adult femlae, FRV Soela, S06-85-44; NMV A 4389 (4), 191 to 200 mm TL pre-adult females, 216 to 217 mm TL pre-adult males, E of Dunk Island,18°0.1'S, 147°3.4'E to 17°56.9'S, 147°0.1'E, 264 m; NMV A. 4390 (3), 222 to 262 mm TL pre-adult females, E of Dunk Island, 17°59.1'S, 147°3.4'E to 17°57'S, 147°1'E, 260 m; NMV A. 4391 (15), 135 to 234 mm TL pre-adult females, 154 to 220 mm TL pre-adult males, E of Dunk Island, 17°59'S, 147°5.7'E to 17°57.7'S, 147°3.5'E, 302 – 308 m, FRV Soela, S01-86-15; NTM S. 11750-003, E of Dunk Island, 17°57'S, 147°01'E; NTM S. 11751-011 (4), 212 to 225 mm TL pre-adult females, E of Dunk Island, 18°00'S, 147°03'E, 264 m, H. Larson, 10. i. 1986; NTM S. 11754-005 (3), 175 mm TL pre-adult male, 120 to 172 mm TL pre-adult females, E of Dunk Island, 17°58'S, 147°04'E; NTM S. 11756-010 (3), 107 to 280 mm TL pre-adult (to adult?) females, E of Dunk Island, 17°57'S, 147°04'E, 298 – 300 m, H. Larson, 11. i. 1986; NTM S. 12723-011, 232 mm TL pre-adult female, E of Dunk Island, 17°53'S, 146°51'E, 140 – 142 m, H. Larson, 20. i. 1986; QM I. 15812 (6 of 12 specimens), 117 to 220 mm TL pre-adult females, 155 to 161 mm TL pre-adult males, E of Hinchinbrook Island, 18°03'S, 147°10'E,

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320 - 360 m, 27. ii. 1979; QM I. 18540, 305 mm TL adult female, 22°54'S, 152°12'E to 22°59'S, 152°12'E, 342 – 360 m, 3. x. 1980; QM I. 18761, 304 mm TL adult female, 23°11'S, 153°00'E to 23°01'S, 152°55'E; QM I. 18972, 250 mm TL pre-adult or adult male, 21°30'S, 152°56'E to 21°41'S, 152°54'E; QM I. 19272, 295 mm TL adult female, 23°11'S, 153°00'E to 23°01'S, 152°55'E, 20. ix. 1980; QM I. 20002, 221 mm TL pre-adult female, 23°30'S, 153°04'E to 23°18'S, 153°00'E, 540 m, 20. ix. 1980; QM I. 20009, 213 mm TL pre-adult male, S of Swain Reefs, 22°51.7'S, 152°45.7'E, 261 m, 3. x. 1980; QM I. 20904, 154 mm TL pre-adult female, E of Capricorn Group, 23°15'S, 153°18'E, 425 m, FV Southern Intruder, 6. ix. 1983; QM I. 21622 (3), 80 to 310 mm TL embryonic and adult females, E of Capricorn Group, 23°07'S, 153°24'E, 400 m, FV Southern Intruder, 6. ix. 1983;QM I. 21629, approx. 220 mm TL pre-adult female, off Swain Reefs, 22°00'S, 153°00'E, 200 – 500 m, FV Southern Intruder, viii. 1983; QM I. 22095, 257 mm TL pre-adult or adult male, off Swain Reefs, 22°02'S, 153°10'E, 210 m, FV Southern Intruder, 30. viii. 1983; QM I. 23095, 230 mm TL pre-adult or adult male, Off Swain Reefs, 20°49.9'S, 151°52.8'E, 288 m, 20. ix. 1986; QM I. 23426 (2), 186 to 217 mm TL pre-adult males, off Capricorn Group, 23°22'S, 152°45'E, 310 – 350 m, FV Southern Intruder, 30. xi. 1983; QM I. 24143, 159 mm TL pre-adult female, 17°55'S, 147°01'E, 295 – 309 m, M. Pichon, A. Birtles, P. Arnold, 16. v. 1986. (6 specimens not measured): **Queensland**: QM I. 15812 (6), collection data specified above (all specimens previously dissected).

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Narcine sp. nov. D

Figs. 85 – 87, Tables 34 – 35

Narcine indica: Norman, 1939: 12 (misidentification; Gulf of Aden); Baranes and Randall, 1989: 99 (listed in material examined).

Narcine maculata: Fowler, 1956: 49 (listed, based on Norman, 1939).

Narcine sp.: Debelius, 1993: 32 (photograph, brief notes; Oman); Randall, 1996: 41 (photograph, partial diagnosis; Oman).

DIAGNOSIS: A species of Narcine distinguished from congeners by the unique combination of: first dorsal fin greater than second in both height and length of base, upper and lower tooth bands roughly equal in width and broadly circular in profile, dorsal coloration with reticulated light brown to reddish-brown network with white or creamy-white oval and circular spots and brain-shaped blotches of variable sizes, with white spots on dorsal fins, 64 to 68 precaudal vertebral centra, 109 to 119 total vertebral centra, and branchial basket length greater than distance between last gill openings. The dorsal fins are equal, subequal or second dorsal fin is greater than first in all other species of Narcine except N. brevilabiata, N. sp. nov. E, N. sp. nov. H and N. sp. nov. I. The upper tooth band is clearly wider than lower tooth band, and with subtriangular profiles, in N. brevilabiata and N. sp. nov. H. Dorsal coloration with small, dark brown spots scattered over disc and tail, and present in spiracles, in N. sp. nov. I. N. sp.

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nov. D can be distinguished from N. sp. nov. E by having slightly less precaudal vertebral centra (64 to 68, only one specimen with 68, vs. 68 to 71, and only two of seven specimens have below 70 in N. sp. nov. E), less total vertebral centra (N. sp. nov. D with 109 to 119, vs. N. sp. nov. E with 119 to 127), in disc width and length (disc not as wide or long, averaging 44.9 and 43.8, respectively, vs. 48.0 and 47.5, in N. sp. nov. E), and by presenting a greater branchial basket length relative to distance between last gill openings (branchial basket length subequal to distance between last gill clefts in N. sp. nov. E).

DESCRIPTION: Measurements and counts are presented in Tables 34 and 35, respectively. Disc distinctively sub-trapezoidal, slightly wider than long. Disc length 40.5 to 46.7 percent of total length, disc width 41.9 to 47.7 percent of total length. Disc widest at just posterior to its mid-length, slightly overlapping origin of pelvic fins posteriorly. Snout sub-acute, anterior margins of disc extending posteriorly from snout at abrupt angle anterior to eyes. Preocular snout area only moderate, not very elongated, 7.5 to 9.7 percent of total length, and occupying only approximately one-fifth of disc length. Disc angled laterally at point of greatest width, and inflecting anteriorly at posterior tip, leaving a small free lobe. Electric organs beginning from level of nostrils ventrally, extending to close to posterior one-fourth of disc; electric organs relatively wide, their width being 7.8 to 9.2 percent of total length. Gill slits situated relatively far apart, lateral to level of mouth and nostrils; gill-slits relatively wide, sequentially situated closer to mid-line from first to fifth and last gill slit. Eyes and spiracles close together. Eyes conspicuously large and bulging, eye length 3.1 to 3.7 percent of total length. Spiracles large, generally wider (2.9 to 4.0 percent of total length) than eyes, circular and with slightly elevated

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rims. Spiracles conspicuously curving anteriorly as antero-lateral border inflects mesially to form a semi-closed off anterior border. Spiracles distinctively not continuing anterior to eyes on either side.

Nasal curtain short and wide, continuing posteriorly in a straight fashion to level of upper exposed tooth band. Nasal curtain pores restricted to upper-most area, between nostrils. Nostrils circular, narial flaps low and more elevated on posterior nostril margins. Mouth about as wide as distance between nostrils, and not very distensible. Upper and lower tooth bands of about equal width and circular in profile, exposed and easily dettached from jaws. Teeth in 22/20 – 27/30 exposed vertical rows. Teeth diagnostically shaped, with a wide crown, a more prominent central cusp, and blunt anterior projections lateral to the central cusp more noticeable on inner-most rows. Central cusp more prominent in inner, non-exposed tooth rows, reaching a length that approximates length of labial (i.e., non-cuspidate) region of crown. Long central cusps in both males and females examined. Teeth on exposed and outer-most inner rows blunt, without prominent cusp and lateral cusplets due to wearing. In 291 mm TL adult male from Gulf of Aden (BMNH 1939.5.24.15), teeth on outer rows very worn down, and longer central cusp and lateral cusplets only present in very inner rows. Teeth with relatively wide bases, wider than length of non-cuspidate crown region. Teeth in 112 mm TL female late-term embryo extracted from CAS 66838 has no exposed teeth, but non-exposed teeth are generally without cusps, although a lingually protruding "platform" is present, and is an obvious precursor of the central cusp and lateral cusplets.

Pelvic fins commencing from underneath disc, anterior to termination of disc. Pelvic fins close to twice as wide as long, contacting tail region posteriorly as to leave a small free

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edge (i.e., inflecting anteriorly at posterior-most point before contacting tail). Pelvics not connected ventrally at posterior margins. In a live specimen (Debelius, 1993: 32) pelvics extend caudally as far as posterior margin of first dorsal fin; in preserved specimens pelvic fins terminate anterior to posterior margin of first dorsal fin. Tail as measured from cloaca longer than disc length, and 48.9 to 53.8 percent of total length. Tail base relatively stout, sub-circular in cross section being wider than tall. Lateral tail folds well-developed, extending as prominent flaps from level of posterior termination of first dorsal fin to caudal peduncle, inserting on caudal peduncle at its ventral-most lateral aspect. Dorsal fins tall and prominent, much taller than long, originating from close to mid-pelvic length (on less well-preserved specimens, first dorsal fin origin is more posteriorly situated, but still clearly over pelvic fins). First dorsal fin taller than second dorsal fin in adult female (CAS 66838), and to a lesser extent in males (and embryos). Anterior margin of dorsals sloping posteriorly from base to tip; posterior margins of dorsals relatively straight, contacting tail region so as to leave a posterior free lobe. Free lobe of first dorsal fin greater than free lobe of second dorsal fin. Distance between dorsals and between second dorsal and caudal almost equal. Caudal fin tall, slightly fan-shaped with somewhat pointed upper corner. Upper lobe taller than lower lobe, and upper lobe sloping posteriorly at close to a 45 degree angle. Upper lobe of caudal longer than lower lobe. Upper and lower lobes of caudal fin originating on tail at same level. Caudal fin of largest male examined (350 mm TL) very pointed at dorsal tip.

Pores of lateral-line canal system faintly visible, extending posteriorly on lateral aspects of tail in a more or less straight line dorsal to lateral tail-folds, terminating posterior to caudal peduncle. Ampullary pores on ventral snout area radiating in parallel rows in a somewhat

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straight line from anterior region of nasal curtain to closeer to snout tip. Scattered pores countering electric organs laterally, widely spaced apart, on both dorsal and ventral surfaces. Isolated pores around eyes.

Dorsal coloration (in live specimens and to a lesser degree in preserved specimens) composed of a reticulated light brown to reddish-brown pattern, of varying intensity, interspaced with white to yellowish-white, oval and circular spots and brain-shaped blotches of variable sizes throughout. Reticulations occurring as more intense blotches laterally and anteriorly on disc, over pectoral axils, over mid-disc, dorsally on pelvic fins, and over preocular snout region. Pelvics with small whitish spots more concentrated over posterior region. Dorsal and caudal fins with whitish spots over a darker brown background, background color of fins varying in intensity from dark reddish-brown to light brown. Bases of dorsal fins with reticulated pattern apparent. Embryos with large, dark spots over mid-disc, antero-laterally and laterally on disc, and pectoral axils; background coloration of embryos a light brown to yellowish-brown color. Ventrally adults and embryos are white to yellowish-white, with dark posterior borders to pectoral and pelvic fins. Dark grey to brown blotches on antero-lateral margins of disc also present, which are continuous with antero-lateral dorsal blotches. Grey and brown small, irregular blotches also present ventrally on tail, extending from tail origin to caudal fin. In preserved specimens, coloration variable from light brown to dark reddish-brown dorsally, with reticulations less obviously demarked than in live specimens. Two male specimens examined (BMNH 1939.5.24.15 and TCWC 8863.01) have strong dark brown blotches on dorsal disc periphery, antero-lateral snout area and anterior to rostrum, as well as on bases of dorsal fins. Adult female examined (CAS 66838) has a very dark and more

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uniform dorsal coloration, which is clearly similar to photographs of live specimens but with apparently less reticulations. In preserved specimens, posterior half of dorsal fins white to creamy white, contrasting intensely with anterior half of fins (not so in photograph of live specimen; Randall, 1993).

REMARKS: The first report of a specimen of this species (misidentified), is by Norman (1939), collected by the John Murray Expedition of 1933 – 1934. His account is also the first on Narcine from the northwestern and western Indian Ocean, but he fails to give precise locality information for the specimen other than "Gulf of Aden." Reports of the Murray Expedition compiled subsequently confirm the locality as being from off northern Somalia (S. Davidson, personal commun.). This species is very distinctive and easily identified, and therefore it is surprising that a specimen has lain misidentified in the Natural History Museum in London for such a long time. This species is morphologically closer to Narcine sp. nov. E (see below) than to any other species of Narcine, being very similar in external appearance and in skeletal features as well (see acount of Narcine sp. nov. E for further details).

The adult female specimen from Oman (CAS 66838; Fig. 85) contained three late-term embryos extracted supposedly from the right uterus (the specimen was dissected prior to my examination of it). The left uterus contained substantial egg masses, apparently composed of compacted eggs, an indication that both uteri are functional but perhaps not synchronously. The right uterus was removed, but the left uterus is thin-walled, transparent and quite fragile. Nine intestinal rings are present. The embryos extracted are similar to adults in coloration and

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external morphology, presenting the characteristic spiracular rims and large eyes. Males are sexually mature at least by 240 mm total length, but possibly at smaller sizes.

GEOGRAPHICAL DISTRIBUTION: This newly discovered species is restricted to the northern Arabian Sea and adjacencies: five specimens from Oman (one adult male and one adult female with three late-term embryos) and two specimens from Somalia (Gulf of Aden), collected from localities very proximal to each other (Fig. 103). The specimens from Oman were collected from a small area in the Gulf of Oman, near the capital city of Muscat. The first collected specimen is from the Gulf of Aden (off the northern Somalian coast). The distribution of this species is probably greater than presently known, but is believed not to extend as far south as Madagascar and into the Mozambique channel, where Narcine sp. nov. E occurs.

MATERIAL EXAMINED: (7 specimens, 105 to 350 mm TL): **Oman**: CAS 58368, 240 mm TL adult male, Gulf of Oman, off Muscat, 23°33'N, 058°48'E, 106 – 152 m, International Indian Ocean Exp., R/V Anton Bruun, cruise 4B, sta. 269B, 03. xii. 1963; CAS 66838 (4), 325 mm TL adult female, 105 – 112 mm TL late-term female embryos, 109 mm TL late-term male embryo, Gulf of Oman, North Point, Al Fahal Island, 21 m (70 ft.), J.K.L. Mee, 31. viii. 1988. **Somalia**: BMNH 1939.5.24.15, 291 mm TL adult male, Gulf of Aden, 11° 57'12"N, 050°35'0"E to 11°56'42"N, 050°39'12"E, otter trawl, 37 – 91 m, John Murray Expedition, 12. x. 1933; TCWC 8863.01, 350 mm TL adult male, Gulf of Aden, 11°53'18"N, 050°58'0"E, 33 – 37 m, G. Small, 12. i. 1987.

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Narcine sp. nov. E

Figs. 89 – 90, Tables 36 – 37

Narcine sp. B: Baranes and Randall, 1989: 98, 99 (listed, brief comparison; Madagascar).

Narcine sp.: Compagno, 1995: vi-vii, fig. 24a.2 (brief diagnosis, outline illustration; Mozambique).

DIAGNOSIS: A species of Narcine distinguished from congeners by the unique combination of: first dorsal fin taller and with longer base than second dorsal fin, upper and lower tooth bands equal in width and broadly circular in outline, dorsal coloration composed of a light brown to yellowish-brown background with darker brown to reddish-brown blotches forming faint, irregular reticulations, 68 to 71 precaudal vertebrae, 119 to 127 total vertebrae, and branchial basket length subequal to distance between last gill openings. The dorsal fins are equal, subequal or second dorsal is greater than first in other species of Narcine except N. brevilabiata, N. sp. nov. D, N. sp. nov. H and N sp. nov. I. The upper tooth band is clearly wider than the lower tooth band, and subtriangular in outline, in N. brevilabiata and N. sp. nov. H. N. sp. nov. I has numerous small dark brown spots over most of disc and tail regions, and inside spiracles. N. sp. nov. E can be distinguished from N. sp. nov D by having higher number of precaudal vertebrae (68 to 71 vs. 64 to 68, respectively), higher number of total vertebrae (119 to 127 vs. 109 to 119, respectively), by possessing a relatively wider and longer disc (disc width and length averaging, respectively, 48.0 and 47.5 in N. sp. nov. E, vs. 44.9 and 43.8 in

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N. sp. nov. D), and by presenting a branchial basket length subequal to distance between last gill openings (distance between first and last gill openings greater than distance between last gill openings in N. sp. nov. D).

DESCRIPTION: Measurements and counts are summarized in Tables 36 and 37, respectively. Disc about as wide as long, sub-trapezoidal in outline, similar to Narcine sp. nov. D. Disc length 43.5 to 50.9 percent of total length, disc width 40.4 to 54.9 percent of total length. Disc widest posterior to its mid-length, but close to mid-length, and overlapping origin of pelvic fins posteriorly. Snout sub-acute, preocular snout area not greatly elongated at 8.7 to 11.4 percent of total length, and only extending close to one-fifth in disc length. Anterior border of snout diagnostically very oval. Disc inflecting anteriorly prior to contacting tail region at its posterior margins, leaving small free edge. Electric organs relatively wide, occupying 7.9 to 11.7 percent of total length, beginning posterior to level of nostrils and extending to between one-fourth and one-fifth of disc length. Outline of electric organs visible dorsally. Gill slits wide, largest gill slit close to width of lower tooth band, and first three gill slits situated lateral to level of mouth and nostrils. Gills slits relatively close together, branchial basket length only 7.7 to 9.2 percent of total length. Eyes and spiracles adjacent. Eyes conspicuously large (as in Narcine sp. nov. D), eye length 3.3 to 4.7 percent of total length. Spiracles large (mean length and width is 3.2 percent of total length), rounded to slightly oblique, with elevated rims all around, even on anterior borders. Spiracles with well defined anterior borders, not continuing anteriorly beyond posterior-most aspect of eyes.

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Nasal curtain short and wide, covering upper tooth band entirely in well preserved specimens, reaching only to level of upper tooth band in others not as well preserved. Nasal curtain projects posteriorly in a straight line towards mouth corners. Posterior margin of nasal curtain straight across, with slight bulging process in middle. Sensory pores not reaching posterior to level of nostrils. Nostrils circular, with elevated narial flaps only on posterior nostril margins. Mouth corners more or less on same level as nostrils, mouth not very distensible. Lips rounded on outer margins. Upper and lower tooth bands of equal width, semi-circular in outline, with rounded anterior (on upper tooth band) and posterior (on lower tooth band) margins. Tooth bands easily detached from underlying integument. Teeth in 14/11 – 24/23 exposed vertical rows (including juveniles and adolscent specimens; adult female examined with 24/21 rows, adolescent [almost adult] male with 23/23 rows). Teeth with lateral cusplets or projections (as in Narcine sp. nov. D) and a more pronounced central cusp (more pronounced on inner rows); crown wide. Both males and females with long central cusp. Exposed teeth with blunt or completely worn down cusps. Teeth in smallest specimen examined (juvenile male, 135 mm TL) already with noticeable central cusp in inner rows.

Pelvic fins begin from underneath disc anteriorly. Pelvic fins much wider than long (pelvic fin width 26.5 to 35.8 percent of total length, pelvic fin length only 13.2 to 21.4 percent of total length). Pelvics with slight free edge posteriorly, contacting tail after inflecting anteriorly. Pelvics not connected ventrally at posterior margin. Pelvics do not extend caudally posterior to posterior margin of first dorsal fin in adolescent specimens. Tail longer between cloaca and caudal fin tip (47.7 to 50.6 percent of total length) than between snout and cloaca (43.5 to 47.1 percent of total length). Tail base stout, wider than tall, sub-circular in cross

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section. Lateral tail folds well developed, beginning at level ventral to posterior tip of first dorsal fin base, extending caudally to insert ventro-laterally on caudal peduncle. Origin of first dorsal fin at mid-length of pelvic fin. Dorsal fins tall and broad, well developed antero-posteriorly, especially first dorsal fin. First dorsal fin much taller and broader than second dorsal fin, very rounded at apex, with a great free lobe posteriorly where it meets tail. Second dorsal fin just more than one-half as broad as first dorsal fin, more oval at apex, and a smaller free lobe posteriorly. Distance between dorsals more or less equal to distance between second dorsal fin and caudal fin. Caudal fin with well developed dorsal and ventral lobes of relatively similar proportions, but slightly different shape. Dorsal lobe with sloping anterior margin up to approximately its mid-length, where it becomes more level and straight; caudal fin tip rounded to oval. Ventral lobe very tall, with rounded ventral tip. Dorsal and ventral lobes originating at same level on caudal peduncle. Claspers of males (all adolescent) not reaching posteriorly far beyond pelvic fins.

Pores and canals of lateral-line system not easy to discern. Lateral-line system composed of supraorbital, postorbital, hyomandibular, scapular, and lateral canals; infraorbital and supratemporal canals not visible and perhaps absent. Canals with few branches that are not elongate. Ampullary pores faintly visible externally, radiating in more or less parallel rows from nasal curtain to snout, with distance between rows increasing closer to snout.

Dorsal coloration similar to Narcine sp. nov. D. In preserved specimens (primarily MNHN 1996-1553; Fig. 89), dorsal aspect composed of a light brown to yellowish-brown background coloration, with darker brown to reddish-brown blotches and faint, irregular reticulations. Larger dark brown blotches on snout tip and lateral to eyes on disc margins, and

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at posterior and lateral disc regions. Antero-dorsal region of first dorsal fin very dark greyish-brown; anterior portion of second dorsal fin and upper lobe of caudal fin brown. Large brown stripe at caudal peduncle, and more irregular stripes on tail underneath both dorsal fins (these stripes are more or less continuous with the anterior portions of the dorsal fins). Pelvics with dark postero-lateral margins dorsally in some specimens. In a freshly captured specimen from Mozambique, coloration is very similar to well preserved specimens (e.g., MNHN 1996-1553). In large adult female (MNHN 1996-1555; Fig. 90), coloration more uniform dorsally, with less markings although remnants of blotching is still noticeable. Ventral coloration a uniform creamy white. Most preserved specimens have lost their coloration, retaining a faint yellowish tone, with scattered spots of darker color over disc (remnants of the blotches and reticulations).

REMARKS: This species is very similar to Narcine sp. nov. D from the Gulf of Oman and Gulf of Aden. The most distinguishing characteristic separating these two species is shape and size of the first dorsal fin: in Narcine sp. nov. E, the first dorsal fin is much broader, with a greater free posterior lobe, and is more rounded at apex. Certain proportional differences, although not failproof, further help to separate both species: disc length (Narcine sp. nov. E: 43.5 to 50.9 percent of TL, x = 47.5; Narcine sp. nov. D: 40.5 to 46.7 percent of TL, x = 43.8), preocular snout length (Narcine sp. nov. E: 8.7 to 11.4 percent of TL, x = 10.2; Narcine sp. nov. D: 7.5 to 9.7 percent of TL, x = 8.7), preoral snout length (Narcine sp. nov. E: 12.3 to 15.6 percent of TL, x = 14.2; Narcine sp. nov. D: 11.9 to 13.1 percent of TL, x = 12.7), prenasal snout length (Narcine sp. nov. E: 9.0 to 11.6 percent of TL, x = 10.7; Narcine sp. nov. D: 8.1 to 10.0 percent of TL, x = 9.1), interspiracular distance (Narcine sp. nov. E: 5.2 to 6.0

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percent of TL, x = 5.6; Narcine sp. nov. D: 4.5 to 5.4 percent of TL, x = 4.8). Narcine sp. nov. E also has slightly more precaudal vertebral centra (68 to 71; only two of seven specimens had below 70) than Narcine sp. nov. D (64 to 68; only one specimen with 68), which is also reflected in total amount of vertebral centra (Narcine sp. nov. E: 119 to 127; Narcine sp. nov. D: 109 to 119).

Males of Narcine sp. nov. D achieve sexual maturity at a smaller size than those of Narcine sp. nov. E. Specimen CAS 58368 from Oman (Narcine sp. nov. D) has firm claspers at 240 mm TL (clasper length: 31.2 mm), while MNHN 1996-1554 from Madagascar (Narcine sp. nov. E) has claspers relatively much less firm at 266 mm TL (clasper length: 34.1 mm). Another adult male from the Gulf of Aden (Narcine sp. nov. D) has claspers of 31.1 mm and is 291 mm in TL. Size at sexual maturity is not precisely known for females.

Presently, it is advisable to separate Narcine sp. nov. D and Narcine sp. nov. E based on the characters discussed above, as both species are also geographically separate and there is no great overlapping in proportional differences mentioned or in other features used here to diagnose both species. If, however, further collecting reveals that both species are not as geographically separated as presently believed, and that intermediate specimens bridge the morphological differences discussed, then both distributional extremes are best considered conspecific.

The specimen from Mozambique shows slight differences from Madagascar specimens. Its second dorsal fin is very close in both size and extent of the free posterior lobe to the first dorsal fin, and there is also apparently a small posterior projection of the joint nasal curtain at its mid-width. The specimen from Mozambique is a female, perhaps adolescent, and differs in

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these respects also from the adult female from Madagascar examined (MNHN 1996-1555), which has a larger first dorsal fin than second, and no projections of the joint nasal curtain. More specimens from Mozambique are needed to further evaluate these differences.

GEOGRAPHICAL DISTRIBUTION: Known from eight specimens only, this species has been captured from the northwest and southwest coasts of Madagascar and from the western Mozambique channel off the coast of Mozambique (Fig. 103), in depths ranging from 69 to 175 m. At least two localities in Madagascar are known, and one specimen supposedly from Madagascar lacks precise locality information (MNHN 1996-1553). The species is probably distributed along the continental slope region throughout the Mozambique channel.

MATERIAL EXAMINED: (8 specimens, 135 to 356 mm TL): **Madagascar**: MNHN 1996-1549, 135 mm TL juvenile male, northwest Madagascar, 23°12'S, 043°22'E, 150 m, field no. 777, 31. iii. 1969; MNHN 1996-1550, 151 mm TL juvenile male, northwest Madagascar, 23°12'S, 043°32'E, 150 m, field no. 776, 31. iii. 1969; MNHN 1996-1551, 151 mm TL juvenile female, same locality data and date as MNHN 1996-1550, field no. 778; MNHN 1996-1552, 232 mm TL adolescent female, same locality data and date as MNHN 1996-1550, field no. 779; MNHN 1996-1553, 257 mm TL, pre-adult male (almost adult), precise locality data not available, label reads "1634 FAO 60 73122, Torpedinidae CR 18"; MNHN 1996-1554, 266 mm TL pre-adult male (almost adult), off western Madagsacar, 15°21'S, 46°12.5'E, 150 m, R/V Vauban, sta. CH 52, field no. F 325, 8. ix. 1972; MNHN 1996-1555, 356 mm TL adult female, western Madagascar, 15°20'S, 46°11.5'E, 170 – 175 m, R/V Vauban, sta. CH

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130, field no. F 516, 19. i. 1975. **Mozambique**: SAM, uncatalogued, 216 mm TL adolescent female, R/V Algoa, sta. COO 830-014-027-2022, 69 m, 18°30'S, 37°15'E (photographs only, specimen not examined; photos and information courtesy of L. J. V. Compagno).

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Narcine sp. nov. F

Figs. 91 – 93, Tables 38 – 39

DIAGNOSIS: A species of Narcine distinguished by its unique dorsal coloration composed of numerous small white to creamy-white spots or ocelli, over a brown to reddish-brown background.

DESCRIPTION: Measurements and counts are presented in Tables 38 and 39, respectively. Disc rounded, about as wide as long on average (mean disc width is 52.0 percent of total length, mean disc length is 53.4 percent of total length). Disc width is somewhat more varible than disc length. Disc is widest portion of body, being much wider than pelvic fins (pelvic fin width averages only 33.5 percent of total length). Disc overlaps origin of pelvic fins posteriorly only slightly; disc with very small free lobe posteriorly where it contacts sides of trunk. Greatest width of disc posterior to its mid-length, but somewhat variable. Snout region rounded anteriorly. Preocular snout ranging from 12.7 to 15.7 precent of total length and roughly one-third in disc length. Electric organ length from 22.8 to 29.2 percent of total length, beginning just anterior to level of eyes dorsally and at level of nostrils ventrally. Electric organs continue posteriorly to beyond level of last gill-slit ventrally. Electric organ width between 9.8 and 12.1 percent of total length. Electric organs difficult to discern in dorsal view, but more clear in ventral view. Gill-slits small, only slightly curved and in more or less straight line from first to last gill slit. Distance between last gill-slits smaller than branchial basket length on average. Spiracles and eyes adjacent, without any space in between. Spiracles with

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somewhat developed rims. Spiracles circular to oval, just slightly longer than wide on average. Eyes relatively small, about as long as spiracles on average.

Nasal curtain wider than long, nasal curtain width reaching 5.0 to 6.6 percent of total length and nasal curtain length reaching only 1.0 to 2.4 percent of total length. Nasal curtain with more or less straight margin posteriorly, but faintly developed central lobe is present. Nostrils small and circular; distance between nostrils slightly greater than nasal curtain width at posterior margin. Prenasal snout length inferior to preocular snout length on average. Mouth on average about as wide as distance between nostrils. Upper and lower tooth bands about equal in width. Upper and lower tooth bands circular in outline. Teeth in 12/8 – 16/12 exposed rows in specimens about 175 mm total length or larger, but a 146 mm total length female has 11/13 exposed teeth rows. Teeth relatively small, set in quincunx arrangement. Teeth with single, sharp cusps, even on small specimens (e.g., 146 mm total length specimen); inner rows with very sharp teeth. Crowns wider-than-long at bases; bases sub-circular.

Pelvic fins wider than long, with relatively long posterior lobes. Posterior lobes of pelvics more or less straight, not concave. Posterior lobe of pelvics contact claspers or lateral aspect of trunk (in females) leaving only a very small free lobe posteriorly. Lateral corners of pelvics blunt, not acute. Pelvics generally extend from underneath posterior disc region to underneath beginning first dorsal fin base. Clapers of larger males extend posteriorly to close first dorsal fin base end. Claspers in mature males not projecting greatly beyond pelvic fins. Tail only relatively short as measured from cloaca, and shorter than snout to cloaca length (cloaca to caudal fin length ranges from 39.7 to 47.0 percent of total length, snout to cloaca length ranges from 50.0 to 54.8 percent of total length). Tail length much shorter to both disc

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width and length. Tail sub-circular in cross section; its width at base moderately broad and somewhat variable, ranging from 15.4 to 21.6 percent of total length. Lateral tail fold not greatly prominent, extending as a thin keel in a staight line laterally on tail from level of mid- to posterior first dorsal fin base to lateral aspect of caudal peduncle. Dorsal fins sub-equal in height; second dorsal fin only slightly taller than first dorsal fin (second dorsal ranging from 7.5 to 9.9 percent of total length, cf. to 6.8 to 9.3 percent for first dorsal). Dorsal fin bases also almost equal. Both dorsals similar in outline, and both leaving slight free lobe posteriorly. Caudal fin with angular apex, relatively tall and not elongated, and with more or less straight posterior margin. Length of dorsal and ventral lobes of caudal about equal, but dorsal lobe slightly taller than ventral lobe. Distance between second dorsal and caudal fins slightly greater generally than distance between dorsal fins.

Sensory pores difficult to observe dorsally and ventrally. Sensory pores few, scattered on ventral snout area and oulining electric organs both dorsally and ventrally. Few sensory pores dorsally in more or less straight rows on snout region. Pores on lateral aspect of tail running dorsal to lateral tail fold, apparently in a straight line and terminating on lateral aspect of caudal base. Even dorsal to lateral tail fold pores are very scattered and not numerous. Pores on ventral snout area in more or less parallel antero-posterior rows, not extending posteriorly much beyond level of nostrils.

Dorsal background coloration composed of a light brown to dark brown or purplish-brown background, with white to creamy-white spots or ocelli (in larger specimens) covering most of disc region (generally posterior to eyes), and extending posteriorly over tail. Dorsal and caudal fins also with spots. Spots and ocelli generally not fused into irregularly shaped

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blotches, especially in smaller specimens where spots are clearly separated from each other. Spots may be very round in shape, but may also appear slightly oval, varying in definition from sharply defined to appearing somewhat out of focus. Spots may be present in between eyes, especially in smaller specimens, or anterior to eyes over dorsal snout region. Smaller specimens with spots ranging in size from small (about equivalent to diameter of eyes and spiracles) to slightly larger (about twice size of eyes). Larger specimens with more variable coloration, with ocelli closely or loosely packed together. Ocelli composed of central white to creamy-white spot, surrounded by ring of darker brown. Dorsal coloration restricted to only background coloration in some larger specimens, but remnants of ocelli can be seen, and spots remain present on dorsal and caudal fins. Ventrally specimens are a uniform creamy-white, but some larger adults may have the posterior disc and pelvic fins outlined in light brown.

REMARKS: This newly discovered species is very similar to Narcine vermiculatus, which occurs farther north, along the continental shelf of Central America (reaching as far south as Costa Rica, as far as is known). Narcine sp. nov. F has only been collected from four different but very proximal localities, all from the coast of Colombia. It is here considered a separate species, distinct from N. vermiculatus, on the basis of its dorsal color pattern, composed of white to creamy-white spots which may become ocelli in larger specimens. The spots almost never appear fused into larger blotches and vermiculations, as in N. vermiculatus, and are generally smaller than the blotches in the latter species. The spots in Narcine sp. nov. F are present even on newly born individuals. Newly born specimens of N. vermiculatus, however, clearly display the typical blotches and vermiculations characteristic of its species. The spots

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may be lost however, as larger specimens of Narcine sp. nov. F have more uniform dorsal coloration without clearly defined spots. However, these specimens differ from typical adults of N. vermiculatus in having lateral tail folds that begin underneath first dorsal fin base (either at its mid-length or slightly farther posteriorly), and not in between dorsal fins. Other differences between the two species are: disc proportions (disc is generally more rounded in Narcine sp. nov. F, with a greater disc length, averaging 53.4 percent of total length, while N. vermiculatus has a disc length averaging 48.4 of total length), and origin of first dorsal fin on tail (first dorsal fin originates further posteriorly in Narcine sp. nov. F compared to N. vermiculatus, averaging 68.0 percent of total length while for N. vermiculatus the average snout to first dorsal fin length averages 64.1 percent of total length). Presently, it is best to recognize this species as distinct from N. vermiculatus, as its known distribution is disjunct from that of N. vermiculatus. Both species share numerous features, however, suggesting that they are probably monophyletic.

One dissected female of 277 mm in total length had a large egg mass in the right uterus, while a female of 200 mm contained two small but late-term pups in the left uterus. Both embryos are female, just slightly over 50 mm in total length, and the smallest one still has remnants of a yolk-stalk. No external gill-filaments or external teeth are present, but few internal teeth with small cusps can be observed. Both specimens were probably very close to birth. One small male of 127 mm in total length still displayed a fading yolk-scar and claspers that did not project beyond the distal tips of pelvic fins. Males probably mature at around 180 mm in total length, as a 174 mm male has claspers almost completely firm.

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GEOGRAPHICAL DISTRIBUTION: This undescribed species is known from four localities on the continental shelf of Colombia, off the coasts of Buenaventura and Cabo Manglares (south of Tumaco) (Fig. 102), in depths ranging from 5 to 18 m.

MATERIAL EXAMINED: (15 specimens): **Colombia**: USNM 222198 (5 specimens); USNM 222199 (6); USNM 222200 (1); USNM 222498 (1); USNM 222500 (1); USNM 235519 (1).

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Narcine sp. nov. G

Figs. 94 – 95, Table 40

Narcine indica: Gloerfelt-Tarp and Kailola, 1984: 36 (brief account, misidentification, outline illustration of N. indica [= N. timlei] compiled from Day, 1875).

DIAGNOSIS: A species of Narcine diagnosed by its unique dorsal color pattern, composed of a network of numerous small (about eye-sized) brownish, ovoid spots and fewer larger dark brown blotches, interspersed with creamy-white, slender reticulations over a light brown to tan background color. N. brevilabiata, N. sp. nov. H and N. sp. nov. I also possess smaller more numerous spots with fewer, larger spots or blotches, but without a white reticulated background pattern. Additionally, N. sp. nov. G has tooth bands of subequal with and broadly circular in outline (both N. brevilabiata and N. sp. nov. H have subtriangular tooth bands, with upper tooth bands clearly wider than lower tooth bands), and dorsal fins subequal in height and length of base (first dorsal fin conspicuously taller and longer at base than second dorsal fin in N. sp. nov. I).

DESCRIPTION: Measurements and counts presented in Table 40. Disc with somewhat circular outline, wider than long (disc width is 51.3 percent of total length, disc length is 47.1 percent of total length). Disc tapers slightly as of level of eyes, anterior to level of greatest disc width. Disc widest slightly posterior to mid-disc length. Snout rounded and broad, relatively long (preocular snout length 11.5 percent of total length); preocular snout length occupying

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around one-fourth of disc length. Disc overlapping origin of pelvic fins posteriorly only slightly, and barely projecting forward just before contacting lateral aspect of trunk (leaving a slight notch in between disc and trunk). Electric organs dorsally begin just at level of eyes on disc, and continue caudally to posterior one-fifth of disc (electric organ length 22.9 percent of total length); electric organ width is 9.3 percent of total length. Gill-slits relatively close together and wide. Gill-slits straight, not semi-circular, and slightly directed anteriorly at mid-line. Gill-slits situated progressively closer to mid-line from first to last gill-slit. Eyes and spiracles without gap in between. Eye length and spiracle width about equal. Spiracles elongated, wider than long, and situated at a slight angle in relation to eyes. Spiracles with elevated borders, but these are slightly flatenned in preserved specimen.

Nasal curtain short and wide, with more or less straight posterior margin, lacking significant median posterior projection. Lateral margins of nasal curtain straight, without lateral lobes. Nasal curtain only partially covering upper exposed tooth band, but nasal curtain slightly pulled anteriorly due to preservative. Nasal curtain pores continue posteriorly to just beyond level of nostrils. Nostrils small and circular, with very small and inconspicuous elevated border posteriorly, not resembling a developed flap. Prenasal snout length just over one-tenth in total length, about equal to preocular snout length. Mouth wider than internarial width, and mouth corners project laterally to just beyond level of outer margin of nostrils. Upper exposed tooth band slightly wider than lower exposed tooth band; both tooth bands circular in outline, much wider than long. Teeth very small and numerous, in 26/21 vertical exposed rows. Teeth with small cusps even on inner, non-exposed tooth rows; teeth with diamond-shaped bases, but bases are rounded posteriorly.

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Pelvic fins relatively long and wide, but wider than long when measured together. Pelvic fin width is 37.4 percent of total length, pelvic fin length is 20.2 percent of total length. Pelvic fins conspicuously wide anteriorly, with prominent, greatly curved, lateral lobes. Lateral aspect of pelvic fins slightly concave in preserved specimen. Pelvic fins begin just underneath posterior aspect of disc and extend caudally to level of mid-base of first dorsal fin. Pelvic fins connect at their posterior insertion to ventral aspect of tail leaving a small free lobe. Tail stout, it's length almost equal to disc length, being 47.4 percent of total length as measured from cloaca. Tail tapers significantly from base to tip of caudal fin (tail width measured at base more than 20 percent of total length). Lateral tail folds are prominent flaps, beginning conspicuously on lateral aspect of tail at level in between first and second dorsal fin base, and continuing caudally to insert on ventro-lateral portion of caudal peduncle. Dorsal fins large and about equal in height and length of base, but differently shaped. First dorsal fin more erect and more rounded at apex, second dorsal fin with more slanted anterior margin and more pointed apex. First dorsal fin originates over posterior lobes of pelvic fins. First dorsal fin also broader at it's mid-height compared to second dorsal fin. Dorsals leave slight free lobe posteriorly as they inflect anteriorly to insert on tail; dorsals with more or less straight or upright posterior margins. Caudal fin tall and prominent. Upper lobe moderately slanted, with rounded but elongated apex. Posterior margin of caudal fin relatively straight but with curved lower lobe. Dorsal lobe of caudal slightly greater than ventral lobe. Dorsal and ventral lobes of caudal fin begin at same level on caudal peduncle.

Pores of lateral-line and ampullary systems difficult to observe, as pores are not high-lighted with darker pigments and ventral coloration is very light. The dorsal coloration of the

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specimen prohibits clear observation of the pores, but few and scattered pores are visible over lateral tail fold (posterior extension of lateral canal), running parallel to it, and continuing caudally to end on lateral aspect of caudal fin base. Ventrally, many pores are present on snout region, evenly distributed and closely packed. Pores continue to just posterior to level of posterior margin of nostrils on nasal curtain. Pores present lateral to nostrils and mouth. Two small groups of pores are present posterior to mouth and close to branchial openings. Pores are also present outlining, on ventral surface, anterior and lateral aspects of electric organs.

Dorsal coloration highly distinctive, composed of a network of small and large dark brown to lighter brown spots and reticulations over a light brown to tan background color. The spots vary greatly in size, ranging from darker blotches larger in diameter than the length of dorsal fin bases, to smaller, lighter spots and blotches that may fuse into a complex reticulated network. The smaller spots, when in isolation, may also range in size from smaller to greater than the diameter of eyes, but never appear to achieve the size of the larger blotches. The larger blotches are fewer in number, and situated directly posterior to eyes, on mid-line of disc posterior to eyes, on central and lateral disc areas at mid-disc, and at bases of tail. Some of these blotches are circular, others are laterally elongated and oval, while others appear to be the result of fused smaller spots. Dark, undefined blotches and streaks are present on dorsal region of pelvic fins, and over apex of dorsal and caudal fins. Pelvic and caudal fins outlined in creamy white. Ventrally, coloration is a uniform pale white color, with darker, undefined grey bands on posterior pelvic and disc areas. Also, light brown blotches are present on ventral tail region.

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REMARKS: Although known from a single specimen, this species is distinct from all other known species of Narcine in possessing a reticulated and spotted (large blotches and small spots) dorsal coloration and tooth bands similarly shaped and of sub-equal width, as evidenced by the relatively (and proportionally) high tooth count. All other species of Narcine with a dorsal coloration composed of few large spots and numerous small spots have very narrow lower tooth bands, much narrower than the upper tooth band, with the exception of Narcine sp. nov. I (from Oman, Sri Lanka and Myanmar). Narcine sp. nov. G can be separated from the latter species on the basis of pelvic, dorsal and caudal fin configuration, meristics, and coloration (Narcine sp. nov. I does not display the reticulated pattern of Narcine sp. nov. G). The first dorsal fin of Narcine sp. nov. I is distinctively larger than the second (both dorsals are about equal in size in Narcine sp. nov. G). The pelvics of Narcine sp. nov. G are laterally lobed anteriorly with rounded corners, very different from the pelvics of Narcine sp. nov. I, which are relatively not as long and without prominent lateral lobes (see discussion under Narcine sp. nov. I below for further separation of both species). In addition to having the lower tooth band much narrower than the upper tooth band, other species of Narcine with large and small spots also do not display the reticulated network present in Narcine sp. nov. G.

The only known specimen is female and presumably sexually mature.

GEOGRAPHICAL DISTRIBUTION: Known from a single specimen collected during the Jetindofish Survey (Gloerfelt-Tarp and Kailola, 1984), from the continental shelf in between the Indonesian islands of Bali and Lombok (Fig. 105), in depths of about 60m.

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MATERIAL EXAMINED: (1 specimen): **Indonesia**: BMNH 1984.4.11.12, 306 mm total length adult female, Indonesia (between Bali and Lombok), 8° 37'S, 115° 59'E, 60 – 63 m, Jetindofish trawling survey of S. Indonesia, 19. viii. 1980.

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Narcine sp. nov. H

Figs. 96 – 99, Tables 41 – 42

Narcine maculata: ?Cantor, 1850: 1399 – 1400 (description; Malaysia); ?Suvatti, 1950: 184 (listed; Thailand); Bessednov, 1966: 78, 79, figs. 1, 2 (description, illustrated; Gulf of Tonkin, Viet Nam); Bessednov, 1969: 108 – 109, figs. 99, 100 (description , illustrated; Gulf of Tonkin, Viet Nam); ?Suvatti, 1981: 8 (listed; Thailand); Monkolprasit, 1984: 147 – 148, fig. 80 (in identification key, description, illustrated; Thailand); Monkolprasit, 1990: 391 – 392, pl. B, fig. 7 (in identification key, description, photograph; Thailand); Monkolprasit et al., 1997: 31 (listed; Thailand); Carvalho et al., in press (identification, distribution, illustrated).

DIAGNOSIS: A species of Narcine distinguished by the following unique combination of characters: upper tooth band much wider than lower tooth band and both tooth bands subtriangular in shape, dorsal coloration composed of relatively numerous, dark brown spots (about equal to eye-diameter or slightly larger) over a light brown to tan background, with larger and fewer brown spots or blotches on dorsal disc (larger spots close to dorsal fin base in diameter), and preocular snout region dusky grey to grey-brown and devoid of spots. Tooth bands broadly subcircular in shape and of subequal width in all species of Narcine except N. brevilabiata, N. tasmaniensis, N. sp. nov. B and N. sp. nov. C. Dorsal coloration unifrom tan, brown or yellowish-brown in N. tasmaniensis, N. sp. nov. B and N. sp. nov. C, without spotting of any sort. N. sp. nov. H can be separated from N. brevilabiata by presenting fewer

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and larger "small" spots (small spots of latter species smaller than eye-diameter and more numerous), and in having preocular snout region dusky grey to grey-brown and generally devoid of spots (in N. brevilabiata, preocular snout with same brown background color as dorsal disc, generally with small spots present).

DESCRIPTION: Measurements and counts presented in Tables 41 and 42, respectively. Disc subcircular, about as wide as long (disc width is between 46.0 to 56.3 [x = 52.6] percent of total length, disc length is between 45.4 to 56.5 [x = 51.2] percent of total length). Disc widest posterior to mid-disc length. Snout subacute or oval, broad and relatively long (preocular snout length averages 13.3 percent of total length). Preocular snout length is slightly less than one-third of disc length. Disc just barely overlapping origin of pelvic fins posteriorly, and projecting forward only slightly before contacting lateral aspect of trunk (leaving a slight notch in between disc and trunk in well preserved specimens). Electric organs originate dorsally at more or less level of eyes on disc, and continuing caudally to about posterior one-fifth of disc (electric organ length is in average 25.2 percent of total length); electric organ width is in average 11.6 percent of total length. First gill-slit positioned relatively posteriorly on disc, at about mid-disc (and mid-electric organ) region. The gap between mouth and first gill-slit is about two-thirds of distance between first and last gill openings. Gill-slits close together, but distance between first and last gill-slit is greater than distance between last pair of gill openings. Gill-slits more or less straight (not really crescent-shaped), situated progressively closer to mid-line from first to last gill-slit. Eyes and spiracles without gap in between. Gill-slits in specimens from Myanmar with small, fringed, posterior projections at mid-length. Eye length

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generally greater than spiracle length, but about equal to spiracle width. Spiracles elongated, wider than long, and situated at a slight angle in relation to eyes (spiracles from Myanmar specimens slightly greater in width). Spiracles with slightly elevated borders, but these are somewhat flatenned in most preserved specimens.

Nasal curtain short and wide, more than twice as wide as long. Posterior margin of nasal curtain slightly upturned at corners, with more or less straight central posterior margin, lacking median posterior projection in well preserved specimens. Lateral margins of nasal curtain straight, without lateral lobes. Nasal curtain only partially covering upper exposed tooth band, but nasal curtain slightly shrunken and folded back due to preservative in most specimens. Nasal curtain pores continue posteriorly to about mid-nostril level. Nostrils relatively large, circular, and with conspicuous elevated borders posteriorly, resembling a developed flap. Prenasal snout length averaging just over one-tenth in total length, less than preocular snout length. Mouth wider than internarial width. Mouth corners do not project laterally to beyond level of outer margin of nostrils. Upper exposed tooth band slightly wider than lower exposed tooth band. Tooth bands very triangular in outline, and lower tooth band containing very few exposed rows of teeth. Large areas surrounding teeth of both upper and lower tooth bands devoid of teeth (teeth seem to be confined to central tooth band region). Usually only a single vertical row of teeth exposed in lateral-most rows on upper and lower tooth bands. Teeth very small, with samll cusps in 10/6 – 11/8 vertical exposed rows in specimens from Myanmar, and in 10/6 – 17/11 exposed vertical rows in specimens from the Philippines (pre-adult males and females, some close to being sexually mature). Teeth with wide and posteriorly rounded bases, with a single, worn and not very prominent cusp.

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Pelvic fins somewhat distorted in most specimens as a result of preservation. Pelvics appear to be about twice as wide as long (width measured including both fins), with silghtly longer posterior lobes in relation to anterior lobes. Pelvic fin width averages 34.3 percent of total length, pelvic fin length averages 17.7 percent of total length. Pelvic fins not appearing to have very prominent lateral lobes anteriorly. Pelvic fins begin just underneath posterior margins of disc and extend caudally to level of mid-base of first dorsal fin. Pelvic fins connect at their posterior insertion to ventral aspect of tail leaving a very small free lobe in females; in males, a very small free lobe is present at insertion on clasper. Tail moderately stout at base, and not as long as disc length as measured from cloaca (averaging 45.9 percent of total length). Lateral tail folds are prominent flaps in well preserved specimens, beginning on lateral aspect of tail from in between first and second dorsal fin base, and continuing caudally to insert on ventro-lateral portion of caudal peduncle. Dorsal fins relatively large and about equal in height and length of base. Both dorsals very similar in shape, but second dorsal slightly more slanted than first dorsal fin. Dorsals rounded at apex, and generally broad antero-posteriorly (especially in specimens from the Philippines). Dorsals leave slight free lobe posteriorly as they inflect anteriorly to insert on tail; dorsals with somewhat curved posterior margins. First dorsal fin originates over posterior lobes of pelvic fins. Caudal fin relatively prominent, with sloping upper lobe and highly curved lower lobe. Upper lobe generally with rounded apex. Posterior margin of caudal fin slightly rounded. Dorsal lobe of caudal slightly greater than ventral lobe. Dorsal and ventral lobes of caudal fin begin at more or less same level on caudal peduncle. Distance between dorsal fins and distance between dorsal and caudal fins about equal.

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Pores of lateral-line and ampullary systems not clearly visible, especially on dorsal surface (dorsal coloration prohibits clear observation of the pores), but few and scattered pores are visible over lateral tail fold. These pores (posterior extension of lateral canal) continue posteriorly from disc at about two-thirds height of tail, to close to beginning of second dorsal fin base, where they project ventrally to close to lateral tail fold, and continue parallel to it all the way to caudal fin base. Ventrally, many pores are present on snout region, evenly distributed and closely packed in antero-posterior rows. Nasal curtain pores are present to just posterior to level of posterior margin of nostrils. Small clusters of pores present lateral to nostrils and mouth. Two small groups of pores are present posterior to mouth and close to branchial openings. Pores are also present outlining, on ventral surface, anterior and lateral aspects of electric organs.

Dorsal coloration conspicuous and slightly variable, composed of small and large dark brown to lighter brown spots over a light brown to tan or yellowish-tan background, with a generally grey-brown dorsal snout region. The large spots are isolated, about equal in diameter to distance between eyes, and invariably occur in restricted areas of disc: over posterior one-third of electric organ (paired, and generally the largest spots), mesial to insertion of pectoral fin on lateral aspect of tail (also paired), posterior to interspiracular region (single), laterally on disc at level of greatest disc width (paired) and on disc lateral to posterior extent of electric organs (paired). Occasionally, large spots are present on dorsal snout region as well. Large spots may also occur at base of first and second dorsal fins, and anterior to first dorsal fin on tail. These large spots may vary slightly in size, but are generally easily separated from the smaller spots that are more numerous and cover most of dorsal disc and tail regions. The

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smaller spots may frequently be slightly oval and elongated, and may fuse to form longer, pear-shaped blotches. These spots are more or less equal to the diameter of eyes, and may be oriented laterally or antero-posteriorly on disc and tail. Specimens from Myanmar appear to have fewer, larger and more circular spots, that may rival the larger spots (observed in male specimen from Myanmar). The largest specimen from Myanmar (a female of 336 mm total length) has spots apparently quite faded and less-defined, without clear remnants of larger spots persisting. Dorsal areas of pelvic fins, posterior disc regions, and dorsal and caudal fins are grey to brown in specimens from the Philippines. Specimens from the Philippines have more numerous spots generally. Ventrally, coloration is a uniform pale white color, with darker, undefined grey to dark brown bands and blotches on posterior pelvic and disc areas. Also, light brown blotches are present on ventral tail region. Some specimens from the Philippines are heavily pigmented underneath. Specimens from Myanmar are more uniformly colored ventrally, without large areas with dark blotches.

REMARKS: This species is considered distinct from N. brevilabiata, with which it shares various similarities. Both species possess a dorsal color pattern of few large spots with many smaller spots distributed over disc and tail regions, and both species have tooth bands of different widths, the upper tooth band being broader than the lower tooth band, which contains few exposed rows of teeth. However, the "smaller" spots of Narcnie sp. nov. H are larger and less numerous than the smaller spots of N. brevilabiata. Also, specimens of Narcine sp. nov. H have dorsal snout regions (approximately from level of eyes forward), mostly devoid of any spotting, and of an opaque grey color that is different than the dorsal disc background color

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(the dorsal snout area of N. brevilabiata is similar to the brown dorsal disc background color, and small spots are generally present). Proportional measurements between the two species are similar, but some differences are worth noting (all values are percent of total length; values for N. brevilabiata in parentheses): nasal curtain width ranges between 4.9 and 6.1 percent, averaging 5.5 (vs. 5.6 to 7.9 percent, averaging 6.3); posterior lobe of pelvic fin ranges between 11.7 and 19.4 percent, averaging 15.2 (vs. 13.4 to 20.2 percent, averaging 17.0); length of the dorsal lobe of caudal fin ranges between 13.2 and 19.6 percent, averaging 16.6 (vs. 14.0 to 16.8 percent, averaging 15.1); length of ventral lobe of caudal fin ranges between 13.4 to 18.8 percent, averaging 15.5 (vs. 13.1 to 16.6 percent, averaging 14.8); height of dorsal lobe of caudal fin ranges between 4.1 to 7.1 percent, averaging 5.2 (vs. 5.0 to 7.0 percent, averaging 6.0); height of ventral lobe of caudal fin ranges between 3.4 to 6.2 percent, averaging 4.8 (vs. 5.0 to 7.1 percent, averaging 6.0); height of caudal fin ranges from 10.0 to 15.3 percent, averaging 11.7 (vs. 12.3 to 15.9 percent, averaging 13.5); snout to cloaca distance ranging from 44.7 to 54.8 percent, averaging 50.2 (vs. 49.6 to 53.0 percent, averaging 51.0); snout to first dorsal fin distance ranging between 51.8 to 62.5 percent, averaging 57.7 (vs. 57.8 to 60.3 percent, averaging 59.1).

The proportional differences related to the pelvic fin are, at least in part, influenced by preservation, but the shape and dimensions of the caudal fin appear to be significant. All measurements related to the caudal fin showed some degree of proportional difference. The caudal fin appears to be relatively longer but not as tall in Narcine sp. nov. H compared to N. brevilabiata. In addition, Narcine sp. nov. H and N. brevilabiata differ in mesopterygial morphology. The mesopterygium of Narcine sp nov. H is slender and relatively long, reaching

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to close to mid-length of most basal propterygial segment (closest to pectoral girdle). In N. brevilabiata, the mesopterygium is characteristically short and club-shaped, being noticeably more broad at distal end (farthest from pectotal girdle). The mesopterygium in N. brevilabaiata extends to about one-third of length of basal propterygial segment. The difference in mesopterygial morphology is clear in all specimens radiographed.

Specimens of Narcine sp. nov. H have nostrils and tooth bands similar to some specimens of N. brevilabiata from Thailand and China (referred to as N. indica by Carvalho et al., in press). These specimens differed from typical N. brevilabiata in having larger nostrils and mouths that did not extend beyond level of outer margins of nostrils, as well as having more defined and proportionally larger lower tooth bands with exposed rows of teeth (see discussion under N. brevilabiata above). Presently, Narcine sp. nov. H is considred a separate and valid species, even though it shares features of its lower tooth band and nostrils with some specimens identified as N. brevilabiata.

Specimens from Myanmar have more ventral caudal radial elements (and therefore more total caudal radials) than specimens from the Philippines (30 – 32 ventral caudal radials and 51 – 52 total caudal radials cf. to 25 – 28 and 47 – 48, respectively). Other differences between specimens from Myanmar and the Philippines are mentioned above in the description, but these are presently not considered species-specific. More specimens from the Andaman Sea are needed for further comparisons.

Males from the Philippines appear to be sexually mature at around 230 mm total length, but the rigidity of the claspers may be slightly enhanced as specimens are faintly dessicated. A 275 mm total length male from Myanmar was definetely an adult. Presumably,

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females achieve sexual maturity at close to the same size. A 103 mm total length specimen was free swimming but had an abnominal scar remnant between the fifth gill-slits. The teeth of this specimen are already exposed in one horizontal row on lower tooth band, and in two horizontal rows on upper tooth band.

GEOGRAPHICAL DISTRIBUTION: Known from two major localities only, off the coast of Myanmar in the Andaman Sea, west and southeast of the Irrawady deltas, and from the Philippines (from more than one locality; Fig. 104). This in-shore, continental shelf species has been captured from depths of 34 to 90 m.

MATERIAL EXAMINED: (13 specimens, 103 to 336 mm total length): **Myanmar**: CAS 58358 (2); CAS 58359. **Philippines**: USNM 137884; USNM 263394; USNM 263398; USNM 263399; USNM 263400 (2);USNM 263401; USNM 263402 (2); USNM 263403.

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Narcine sp. nov. I

Figs. 100 – 101, Tables 43 – 44

DIAGNOSIS: A species of Narcine distinguished from congeners by the unique combination of: first dorsal fin clearly taller, and with longer base, than second dorsal fin, upper and lower tooth bands subequal in width and broadly circular in shape, and dorsal coloration composed of numerous small brown spots, about equal to or smaller than eye-diameter, over disc and tail regions (and inside spiracles), with fainter large spots on dorsal disc area. The dorsal fins are either equal, subequal or second dorsal fin is larger than first in all species of Narcine except N. brevilabiata, N. sp. nov. D, N sp. nov. E and N. sp. nov. H. The upper tooth band is clearly broader than the lower tooth band, and tooth bands are subtriangular in shape in N. brevilabiata and N. sp. nov. H. Both N. sp. nov. D and N. sp nov. E do not possess small dark brown spots on dorsal disc and tail regions.

DESCRIPTION: Measurements and counts presented in Tables 43 and 44 respectively. Disc with sub-circular outline, broadly wide in well-preserved specimens. Disc width ranges between 52.2 to 58.4 percent of total length (x = 54.8), and disc length varies between 47.0 to 54.2 percent of total length (x = 50.4). Disc continues posteriorly from snout region in a more or less straight fashion, until mid-disc area, where it is slightly angled laterally. Disc is highly curved in outline posterior to mid-disc area. Disc widest slightly posterior to mid-disc length. Snout rounded and broad, relatively long (preocular snout length averaging 12.1 percent of total length); preocular snout length occupying around one-fourth of disc length. Disc slightly

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overlapping origin of pelvic fins posteriorly; faint notch is present in between disc and trunk. Electric organs on dorsal surface begin just anterior to level of eyes on disc, and continue caudally to posterior one-fifth to one-sixth of disc (electric organ length averaging 22.8 percent of total length); electric organ width averaging 10.5 percent of total length. Gill-slits relatively close together and wide. Gill-slits slightly undulated, with small median lobe projection posteriorly, relatively wide, and only barely directed anteriorly at mid-line. Gill-slits situated progressively closer to mid-line from first to last gill-slit. Eyes and spiracles adjacent. Eye length in between spiracle length and width. Spiracles broad and long, very prominent and sub-circular to oval (spiracle width greater than length). Spiracles with elevated borders, but these are slightly flattened in preserved specimens. Interocular distance greater than interspiracular distance.

Nasal curtain width much greater than length, with more or less straight posterior margin (nasal curtains were weakly upturned and distorted in some specimens; a slight median posterior projection is present in BPBM 21418). Lateral margins of nasal curtain relatively straight, without lateral lobes. Nasal curtain not covering upper exposed tooth band in preserved specimens. Pores on nasal curtain continue posteriorly to just beyond level of nostrils only in one specimen (CAS 98157), otherwise nasal curtain broadly devoid of sensory pores. Nostrils relatively small and circular, with very small and inconspicuous elevated border posteriorly. Prenasal snout length varying from 7.1 to 12.0 percent of total length ($x = 9.8$), less than preocular snout length. Preoral snout length between one-third and one-fourth of disc length. Mouth wider than internarial width, and mouth corners project laterally to just beyond, or at, level of outer margin of nostrils. Tooth bands semi-circular in outline and broad, much

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wider than long and relatively small in length, not projecting beyond level of lips antero-posteriorly. Upper exposed tooth band slightly wider than lower exposed tooth band. Tooth bands smaller in length and less exposed in specimen from Myanmar (tooth bands with small portion devoid of teeth in this specimen, and lower tooth band partially concealed by skin, but this may be preservational). Teeth relatively small and numerous, in 20/19 – 20 vertical exposed rows in specimens from Oman and Sri Lanka (tooth bands, especially lower tooth band, slightly distorted in latter specimen), and in 16/13 in specimen from Myanmar. Teeth more tightly packed in lower tooth band. Exposed teeth with small, highly worn, broad cusps in specimens from Oman and Sri Lanka; slightly longer and sharper cusps are present in exposed tooth rows in specimen from Myanmar. Both Oman and Sri Lanka specimens have teeth with small cusplets adjacent to main cusp (unconfirmed in Myanmar specimen; cusplets in Sri Lanka specimen only visible in teeth that are intact as many teeth are damaged). Teeth with diamond-shaped bases, somewhat rounded posteriorly.

Pelvic fins moderately broad, about twice as wide as long when measured together. Pelvic fin width averages 35.6 percent of total length, pelvic fin length averages 18.1 percent of total length. Pelvic fins with anterior margin (x = 12.4) long relative to posterior margin (x = 17.2; posterior lobe of pelvic normally much longer compared to anterior lobe in congeners). Lateral aspect of pelvic fins straight, not concave in preserved specimens (pelvics distorted in CAS 58398). Pelvics begin ventral to posterior lobes of disc and extend caudally to level of posterior two-thirds of first dorsal fin base. Free posterior lobe of pelvics is relatively well developed. Tail moderately stout at base, but relatively short compared to disc length or width; tail length averages 47.3 percent of total length as measured from cloaca. Lateral tail folds are

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prominent, appearing as wide flaps and originating on lateral aspect of tail at level in between first and second dorsal fin base, continuing caudally to insert on ventro-lateral portion of caudal peduncle. Dorsal fins large. First dorsal fin conspicuously larger than second in both height and length of base. First dorsal fin more erect and more rounded at apex, second dorsal fin with more slanted anterior margin and more pointed apex; both dorsals with somewhat straight and upright posterior margins. First dorsal fin with greater free lobe above base. First dorsal fin originates anterior to level of pelvic fin connection to tail. Caudal fin tall and prominent, with moderately slanted dorsal lobe. Apex of dorsal lobe rounded. Posterior margin of caudal fin relatively slanted but with broad, curved lower lobe. Ventral lobe of caudal slightly greater than dorsal lobe in both Oman and Sri Lanka specimens, but dorsal lobe just greater than ventral lobe in specimen from Myanmar. Dorsal lobe of caudal fin begins just anterior to ventral lobe on caudal peduncle.

Sensory pores of lateral-line and ampullary systems not obvious dorsally (dorsal coloration hampers observation of pores). Few pores are present running more or less parallel to lateral tail fold (posterior extension of lateral canal), just dorsal to it. These pores continue caudally to end on lateral aspect of caudal fin base. Ventrally, pores are present on snout region, evenly distributed in rows running from upper nasal curtain area to snout anterior margins. Pores continue to about level of anterior margin of nostrils on nasal curtain, but in specimen from Myanmar pores extend to posterior margin of nostrils. Small clusters of pores are present lateral to nostrils and mouth, continuing laterally to outer disc region anterior to electric organs (more or less at level of antorbitals). Pores outlining anterior and lateral aspects of electric organs are present ventrally.

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Dorsal coloration in specimen from Oman (best preserved representative; BPBM 21418) with few, large brown spots or blotches, and many small darker spots covering disc, tail, and areas of fins (pelvic, dorsal and caudal fins), over a light brown or tan background. Large blotches are present in photograph of freshly captured specimen from Oman (Fig. 100), but only remnants of larger spots are presently visible in specimen (Fig. 101A and 101B). Larger blotches are located over outer disc area at close to mid-disc (at greatest disc width), over electric organs, at base of tail and faintly underneath dorsal fin base (more visible under first dorsal fin). Larger spots or blotches vary in size from just larger than spiracles to greater than interorbital distance. Snout region dusky grey from more or less level of spiracles forward, contrasting with background color of rest of dorsal surface. Small spots vary from eye-size to smaller than eye-diameter, and cover entire surface of specimens, including inside of spiracles. Small spots may fuse or appear oval; large spots vary in shape from fairly circular to undefined blotches. Spots on dorsal and caudal fiins clearly defined. Larger blotches appear to be defined by connected or closely packed smaller spots. This color pattern is present in CAS 58398 but more faded and difficult to observe. Ventrally, both Oman and Sri Lanka specimens are white, with posterior margins of disc and pelvic fins grey. Mid-tail region with slight light brown markings. Myanmar specimen slightly distinct in coloration (although presenting the same general patterns described for Oman and Sri Lanka specimens; coloration of the Myanmar specimen is further described below).

REMARKS: This species is relatively poorly known, as only six specimens are available of which three are late-term pups. It is distinct from almost all species of Narcine in the

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combination of having rounded upper and lower tooth bands of sub-equal width and dorsal coloration composed of few large blotches with numerous small, dark spots that are scattered over entire disc, tail and fins. All other species of Narcine with a color pattern of few, large spots and numerous small spots have tooth bands of unequal width, with lower tooth band very small compared to upper tooth band (tooth bands are also more triangular in these species). This combination of characters is also present in Narcine sp. nov. G from Indonesia, but both species can be distinguished by the following: dorsal coloration (Narcine sp. nov. G has a complex network of spots and reticulations [compare Figs. 94 and 100], and dorsal and caudal fins with very dark anterior portions, while Narcine sp. nov. I has dorsal and caudal fins with numerous small spots); proportions of fins (first dorsal fin clearly greater than second in Narcine sp. nov. I, dorsals of Narcine sp. nov. G sub-equal, but second dorsal is actually slightly larger than first); pelvic fins (pelvics proportionally longer in Narcine sp. nov. G, with greater posterior margins and broad, rounded lateral lobes, while pelvics of Narcine sp. nov. I are without broad and curved lateral lobes); preocular snout length greater than prenasal snout length in Narcine sp. nov. I (sub-equal in Narcine sp. nov. G); distance between first gill-slits greater in Narcine sp. nov. I (but this may be slightly influenced by preservational distortion of disc); number of second dorsal fin radial elements (10 in Narcine sp. nov. I, cf. to 6 in Narcine sp. nov. G even though the latter has a greater second dorsal fin); number of vertebrae (Narcine sp. nov. I has greater counts of trunk, precaudal, and caudal centra). These distinctions are based on few specimens (only four adult specimens of both species are available), and not all are very significant given the variation observed in other species of Narcine (e.g., number of vertebral centra, distance between first gill-slits, shape of pelvics

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which is greatly influenced by preservation). However, the differences in color pattern and proportions of dorsal fins are considered significant and strong enough to identify two distinct species.

The examined specimen from Myanmar is slightly distinct from the specimens from Oman and Sri Lanka in number of tooth rows (fewer in Myanmar specimen), in having tooth bands with small portions devoid of teeth (tooth bands entirely covered by teeth in Oman and Sri Lanka specimens), in caudal fin proportions (upper lobe of caudal slightly greater than lower lobe, while in specimens from Oman and Sri Lanka lower lobe is slightly greater), and in coloration. The Myanmar specimen has a darker dorsal background color, but the same general pattern of small, numerous spots and larger, fewer and more undefined spots is evident even though more difficult to discern given the darker background. Ventrally, the Myanmar specimen is more marked in indistinct grey blotches on the disc region. The configuration of the eyes and spiracles, position, shape and dimensions of dorsal fins (first dorsal beginning over pelvics), extent of lateral tail fold, and general proportions and coloration, permit this specimen to be presently identified with those from Oman and Sri Lanka. More material is needed to corroborate this assignment.

The late-term embryos examined (WAM 25996-004) are from the adult female from Oman, and agree with it in all proportional dimensions, position of fins, lateral tail fold and shape of gill-slits. The color pattern for the embryos is slightly distinctive, as the size of the spots are not as clearly demarked: the larger spots are only slightly larger than the smaller spots, which are fewer in number compared to the adult specimen. The spots are more uniform in size in late-term embryos. Few teeth are exposed in the embryos (107 – 113 mm

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total length males), and the claspers fail to reach tip of pelvic fins. One pup (107 mm total length) had remnants of the yolk stalk and sac still present, but size of free-swimming individuals must be close to 107 mm total length. Sexual maturity is unknown for males (no adult males were available).

GEOGRAPHICAL DISTRIBUTION: Known from the Gulf of Oman and both sides of the Bay of Bengal (Fig. 104), this poorly known, in-shore species has been captured in depths of at least 27 m (Fig. 104).

MATERIAL EXAMINED: (6 specimens, 107 – 360 mm total length): **Myanmar**: CAS 98157. **Oman**: BPBM 21148; WAM 25996-004 (3 late-term pups from BPBM 21148). **Sri Lanka**: CAS 58398.

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COMMENTS ON SPECIES LIMITS AND RELATIONSHIPS

Twenty species of Recent Narcine are recognized, of which 11 are previously described (out of 26 nominal species) and nine are described as new. This revision is based on a large number of examined specimens of all species, including almost all extant type-specimens. Of the 26 nominal species applicable to Recent Narcine, five species are based on illustrations or manuscript descriptions of other authors – cases in which no specimens could be associated with the nominal species (Raja maculata Shaw, 1804, Raja bicolor Shaw, 1804, Torpedo bancroftii Griffith, 1834, Narcine lingula, Richardson, 1846, and Torpedo pictus Gray, 1854). The specimens on which the illustrations or manuscript descriptions of these five nominal species were based are not extant. Two additional species have no type-specimens as their holotypes are lost and believed to have been discarded (N. brevilabiata and N. prodorsalis, see section on these species in species accounts for details). A neotype was deemed necessary for N. brevilabiata, as this is a valid species that may potentially be confused with Narcine sp. nov. H (see above). All other species of Narcine have extant type-specimens, and all of these were examined with the exception of some secondary types (however, primary types and other secondary types were examined for those species) and one extant holotype (of Heteronarce rierai Lioris and Rucabado, 1991, but photographs and a radiograph were examined of the holotype). With few exceptions, specimens from the full range of the species were examined. Much of the existing confusion in the literature in relation to the application of certain nominal species is clarified (e.g., the correct identification of Raja timlei and Narcine indica). However, some "fine-tuning" is still considered necessary in relation to some of the species (e.g., the

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separation of N. lingula and N. maculata, the limits of N. sp. nov. B and N. sp. nov. C, and how these are related to N. tasmaniensis, and the separation of N. sp. nov. D and N. sp. nov. E).

Some species appear to be more-closely related to each other, forming species-groups. This is the case for N. bancroftii, N. brasiliensis and N. entemedor, all of which present papillated spiracles (unique for this group within Narcine) and greatly-expanded and branched antorbital cartilages. Within this complex, N. bancroftii and N. brasiliensis appear to be sister-groups, sharing the presence of strong antorbital blotches. All three species are very similar in both external and internal morphology. N. vermiculatus and N. sp. nov. F are also very similar to each other in external and internal morphology, and differ primarily on the basis of their coloration, putatively forming another species-pair. Similarly, N. tasmaniensis, N. sp. nov. B and N. sp. nov. C form a species-group, all being very similar in external and internal morphology, and with very conspicuous, slender antorbital cartilages. N. westraliensis and N. sp. nov. A appear to be sister-groups as well, both generally similar in proportions, and in external and internal structure. N. rierai may be the sister-group to the Australian species, all sharing an elongated tail compared to disc width and disc length, and possessing shovel-shaped discs. Other species-groups within Narcine are N. brevilabiata and N. sp. nov. H (similar in coloration, with unequally broad and triangular tooth bands; whether the unequal tooth bands are independently derived for the group composed of N. tasmaniensis, N. sp. nov. B and N. sp. nov. C remains to be seen), N. lingula and N. maculata (sharing putatively derived similarities in coloration), and N. sp. nov. D and N. sp. nov. E (similar in coloration and

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antorbital cartilage morphology). The phylogenetic relationships among the species of Narcine is currently being studied, along with their historical biogeography.

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FOSSIL TORPEDINIFORMES

Fossilized remains of electric rays are not abundant in comparison to other batoids and include for the most part isolated teeth (Cappetta, 1987). The earliest fossils presently ascribed to the Torpediniformes date from the Early Paleocene (isolated teeth from Europe and north and west Africa; Cappetta, 1987: 160; Cappetta et al., 1993: 604). The only more or less "complete" fossil was described by Jaekel (1894) from the Eocene (Ypresian) of Monte Bolca, northeastern Italy. This fossil taxon (described and subsequently referred to as Narcine molini Jaekel, 1894) was known from a single specimen (in part and counter-part), but is further described below on the basis of additional, newly discovered material. Jaekel's (1894) species, however, cannot presently be assigned to Narcine or any other Recent electric ray genus.

The extinct genus Eotorpedo White, 1934 was erected for isolated teeth from the Tertiary that superficially resemble those of Recent Torpedo. Eotorpedo reportedly differs from Recent Torpedo in the configuration of the crown-base and the size of the cusp. The teeth of Eotorpedo jaekeli, the type-species (White, 1934), are shown as having a ventrally curved, tetra-lobed, crown base, with a very elongated (up to 1 cm high), sigmoidally curved cusp. The crown-base is anteriorly indented to form two distinct, down-curved anterior lobes. The roots of the type-species are not illustrated in the original descriptions of E. jaekeli and are probably not preserved. Presently, four species of Eotorpedo have been described (Cappetta, 1987, Cappetta 1988). Eotorpedo jaekeli White, 1934 (type-species), from the Late Paleocene of Gada, Nigeria, also occurs in the Thanetian (Late Paleocene) of Niger (Cappetta, 1987). E. hilgendorfi (Jaekel, 1904), the first species to be described (originally in Torpedo), is more

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widespread, being recorded from the Early Tertiary of Cameroon (Balangi on Mundo), Thanetian of Niger (Cappetta, 1972) and Morocco (Arambourg, 1952), Paleocene of Cabinda, Angola (Dartevelle and Casier, 1943), and in the Ypresian (Early Eocene) of Tunisia (Arambourg, 1952). E. nolfi Herman, 1974 is known only from the type-locality, Forest-les-Bruxelles (Belgium), in Ypresian (Early Eocene) strata (Herman, 1974; Cappetta, 1987). E. zennaroi Cappetta, 1988 is recorded from the Danian (Early Paleocene) of Morocco.

It is yet to be demonstrated if these other species of Eotorpedo have the same distinguishing features used to separate the type-species, Eotorpedo jaekeli, from Torpedo. If not, then these species should not be placed in Eotorpedo, and their generic affinity would remain unknown. The validity of Eotorpedo itself is questionable, as not enough is known concerning variation in tooth structure among Recent electric rays. Also, an isolated (fossilized) tooth can be assigned to the Torpediniformes only if there are defining characters in electric ray teeth (i.e., synapomorphies) that are also present in the fossil. However, this mentality is not common among researchers of fossilized elasmobranch remains. Therefore, the countless hundreds of nominal elasmobranch taxa based on isolated remains must eventually be re-evaluated to determine their validity, a practice that has recently been applied to ammiid fishes quite successfully (Grande and Bemis, 1998).

Reported fossilized teeth from the Langhian (middle Miocene) of Europe (Rhone valley and southern France) have been assigned to Torpedo, without being identified to species (Cappetta, 1987, 1988). Fossilized isolated teeth referred to Narcine have been collected in Europe and Africa (Ypresian and Lutetian), but details concerning their shape and structure are

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not available (Cappetta, 1987, 1988). Their generic assignments, therefore, are not very reliable, and no fossils can be assigned to Narcine with much assurance.

"Narcine" molini Jaekel, 1894

Figs. 107 – 110

Narcine molini Jaekel, 1894: 111, pl. III (original description, illustration); Eastman, 1904: 27 (listed, name only); Stanghellini, 1979: cover photograph, 38 (name only, species name mispelled "moloni"); Blot, 1980: 344 (listed, name only); Cappetta, 1987: 161-162, fig. 138L (brief description, outline illustration); Cappetta et al., 1993: 604 (compilation).

TYPE-SPECIMENS: UP 26275 and UP 26276 (part and counter-part).

STRATIGRAPHIC LOCALITY, HORIZON AND PALEOECOLOGY: All specimens of "Narcine" molini come from the Monte Postale fossil beds, located approximately two kilometers northeast of the village of Bolca (which is about 25 km north-northeast of Verona, Italy). Monte Postale is one of the sites bearing fossil fishes of the famous Monte Bolca locality (the other well-studied locality is the "Pesciara" or Cerato quarry, located almost adjacently; referred to also as "Pesciara Cerato"). No fossils of electric rays have been extracted from the Pesciara quarry which has been the richest source of fossil fishes, including

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many other batoids (presently, the quarry is virtually exausted). The age of these fossil fish beds is Eocene, and the stage is usually given as either topmost Ypresian (e.g., Blot. 1980; Cappetta et al., 1993) or lowermost Lutetian (e.g., Patterson, 1993), some 50 to 52 million years before present. The Bolca environment is considered to have been a tropical coral reef atoll with relatively shallow, warm waters and a diverse fauna and flora (Sorbini, 1972, 1983).

DESCRIPTION: Specimens of electric rays examined from Monte Bolca vary greatly in size, from about 50 mm in total length to close to 915 mm TL (holotype of Narcine molini) or more. The following description is based largely on the type-specimen, as it was studied in more detail, and because not all specimens of electric rays examined from Monte Bolca can presently be assigned to the same species. The larger specimens UP 26275 + UP 26276 (part and counter-part), MCSN 135576 and MCSN 91128 + MCSN 91129 (part and counter-part) appear to be of the same species, while the two much smaller specimens appear distinct from the larger specimens but are morphologically uniform and represent the same taxon. The description given here is of the larger specimens which are assigned to Narcine molini Jaekel, 1894.

The holotype is exposed in ventral view, and is to some extent crushed with little three-dimensionality remaining. Prismatic calcification is present over most skeletal components that were preserved, including the neurocranium (excluding portions of the antorbital cartilages), synarcual cartilage, jaws, scapulo-coracoid, puboischiadic bar, and pectoral basal elements. The holotype (both part and counter-part) is preserved almost in its entirety, from mid-region

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of rostral fontanelle in the anterior neurocranium to distal tip of caudal fin. UP 26276 has more anatomical structures preserved.

Disc oval in outline and slightly wider than long, with anterior disc region more acute. Disc length a little more than one-third in total length; tail region very long and perhaps very thin as well (difficult to discern from fossils as only area of vertebral column is preserved).

The rostrum is wider anteriorly close to posterior margin of rostral fontanelle in holotype, but in other specimens rostrum is more straight laterally, not tapering from rostral fontanelle to nasal capsules. Precerebral fontanelle not visible in ventral view. Rostral fontanelle with circular posterior border, indicating that rostral fontanelle was probably similar to Recent narcinids in configuration. Small extension is present lateral to rostral fontanelle very similar to fibrous bridge that connects lateral rostral cartilages to antero-lateral aspect on neurocranium in Recent narcinids. This is an indication that perhaps lateral rostral cartilages were present but not preserved. Antorbital cartilages preserved as Y-shaped cartilages that are thick but not very elongated. Antorbitals articulate with lateral aspect of nasal capsules. No foramina visible on antorbitals. Postero-median projection of antorbitals missing in all specimens, and was probably absent originally, as posterior projection is preserved in smaller species (see below). Antorbitals not contacting propterygium of pectoral fin in any specimen studied. Antorbitals lacking distal filiform processes, but probably due to lack of preservation as these extensions are hialine and fibrous and without superficial calcification in Recent electric rays. Nasal capsules crushed underneath jaws, not clearly visible.

Jaws not very stout proportionally compared to much smaller Recent narcinids. Jaws wider than rostrum, reaching in width to about distance between both antorbitals at level where

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antorbitals bifurcate. No clear indications of labial cartilages are present, but in UP 26276 there is a small sub-triangular outline on right side of lower jaw that may represent a labial cartilage (if this is true, then labial cartilages are similar to those of Recent narcinids, but as labial cartilages are hialine without intense prismatic calcification, it is probable that they are not preserved). Numerous teeth present mesially on jaws. Teeth worn and very small, mostly disarticulated from tooth band, but single more or less sharp cusp is visible on some teeth.

Gill arches preserved in outline, not many gill-arch structures discernable. Width of gill arches less than width of jaws, similar in proportions to Recent torpediniforms. In most specimens just fragmented pieces of ceratobranchials and basibranchial copula remaining, covered with prismatic calcification. In MCSN 135576 more of the ventral gill arch structure is present, with clearly separated ceratobranchials. Just posterior to jaws are the slender and elongated hyomandibulae, positioned as in Recent narcinids and covered with prismatic calcification. Basibranchial fragmented in MCSN 135576 and no hypobranchial structures clearly visible. Fifth ceratobranchial seems to contact scapular process of shoulder girdle on right side of MCSN 135576 (as in Recent torpediniforms). If this is the case, then ventral pseudohyal is preserved in this specimen (on both sides) as six ventral gill arch elements are clearly preserved posterior to hyomandibulae. Synarcual cartilage not well-preserved, somewhat crushed, without leaving distinct outline; prismatic calcification from synarcual scattered over gill arches. Synarcual cartilage continues posteriorly past level of suprascapula, as in Recent torpediniforms.

Scapulo-coracoid greatly arched posteriorly, with only propterygium and metapterygium preserved or originally present. Propterygium apparently segmented as in

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Recent narcinids. Some 36 total pectoral rays present in holotype. Radial elements segmented into about three segments of more or less equal length. Radials bifid distally at anterior pectoral fin, close to antorbitals. Metapterygium long, continuing to posterior tip of pectoral fin. No sign of mesopterygium, but this is perhaps due to preservation as mesopterygium can be very inconspicuous and not heavily calcified in Recent torpediniforms.

Puboischiadic bar thin and wide, with prominent pre-pelvic processes clearly preserved. Pre-pelvic processes extend anteriorly to level of articulation between pectoral basals and shoulder girdle. Basipterygium long, with some 23 radials on holotype. Radials bifurcating distally, no true indication that first radial element is enlarged as in Recent narcinids. Obturator foramina and iliac processes not preserved, but probably present originally.

Vertebral column with individual calcified vertebrae noticeable anteriorly as of shoulder girdle area. Some 153 total vertebral centra present, divided into 34 centra from shoulder girdle to pelvic girdle and 119 centra from pelvic girdle to posterior tip of caudal fin. Hemal processes visible along most of vertebral column. About ten elongated ribs present at region of pelvic girdle as in Recent narcinids (number of ribs difficult to estimate from holotype). It is difficult to discern if dorsal fins are present. On the holotype there are two areas along the vertebral column posterior to pelvic fins that may be remnants of dorsal fins. The anteriormost is just posterior to pelvics, and the the posteriormost is located about halfway between possible first dorsal fin and caudal fin. However, these vestiges lack internal skeletal support. Further examination is needed to determine if "Narcine" molini had dorsal fins. The caudal fin is low and relatively short. Over 20 radials can be counted dorsally and ventrally in the caudal fin of

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MCSN 135576, and elongated hemal elements are visible anterior to the caudal fin of the holotype, as in Recent narcinids.

REMARKS: The general configuration of the neurocranium, antorbital cartilages, scapulo-coracoid, puboischiadic bar, caudal fin and other features of the skeleton, along with the space that accomodated the electric organs (between the basal pectoral cartilages and central axis of the trunk), indicate that these fossils are unquestionably of electric rays. Their assignment to the Narcinidae is based on the acute angle of the anterior disc region (anterior disc region straight in Torpedinidae and Hypnidae), general morphology of the rostrum, jaws and hyomandibulae (different in Narkidae, Torpedinidae and Hypnidae), the presence of tooth bands (lacking in Torpedinidae and Hypnidae), and presence of rostral fontanelle (lacking in non-narcinid torpediniforms).

Jaekel's (1894) description mentions the presence of a single dorsal fin located mid-distance between pelvic and caudal fins. This is not clear from the holotype which is the specimen (UP 26276) that Jaekel provides an outline for along with a photograph (1894, plate III). In the outline he clearly illustrates the dorsal fin supporting cartilages, however this could not be corroborated by examining his specimen. Nor is there any real sign of a dorsal fin in the counter-part (UP 26275) or in MCSN 135576. The other specimens examined (MCSN 91128 and MCSN 91129) have some small, parallel and short elements present posterior to pelvic fins, but these may be only preserved hemal arches. I prefer to consider the dorsal fin as not being present until further examination of all five specimens is made.

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MATERIAL EXAMINED: (3 specimens, 2 in part and counter-part): MCSN 91128 and MCSN 91129 (part and counter-part); MCSN 135576; UP 26275 and UP 26276 (holotype, in part and counter-part).

Narcinidae indet.

Fig. 111

STRATIGRAPHIC LOCALITY, HORIZON AND PALEOECOLOGY: Same as for Narcine molini above.

DESCRIPTION: Both specimens of this newly discovered species are small, measuring 98 mm TL (MCSN 135581) and approximately 50 mm TL (MB uncat.). Both are only partially preserved (MCSN 135581 is missing the tail as from pelvic fin region, and MB uncat. is missing the distal tip of tail), and slightly disarticulated. Details concerning disc proportions are difficult to discern as fossils are not preserved in original shape but appear with pectoral basal elements displaced outwards. One specimen is dorsally preserved (MCSN 135581) and one is ventrally exposed (MB uncat.).

Neurocranium with preserved posterior region of circular rostral fontanelle. Precerebral fontanelle partially preserved as well, and is rectangular and longer than wide. Antorbital cartilages with median posterior projection, as in Recent narcinids. Antorbitals

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bifurcate further lateral to posterior median projection, but distal portions of antorbitals missing.

Jaws and hyomandibulae stout. Jaws with rounded lateral corners. Teeth present on one specimen (MB uncat.), very small and without apparent cusps. Hyomandibulae thicker where they articulate with otic region of neurocranium, as in Recent narcinids. Four epibranchials visible in gill arch region. Synarcual better preserved than in "Narcine" molini, but lateral stays are not detectable. Synarcual projecting posteriorly past level of suprascapula.

Propterygium has at least five segments (MB uncat.). Mesopterygium elongated and oriented forward, running parallel and adjacent to propterygium. Metapterygium short and slightly curved, projecting posteriorly. All pectoral basals articulating with radials. Scapulo-coracoid with large, triangular anterior fontanelle very similar to Recent narcinids. Scapular process (visible in MB uncat.) stout and sub-triangular, similar to that of Discopyge, with very straight and short suprascapula (not possible to confirm if suprascapula was fused).

Disarticulated ribs present at level of pelvic girdle (not possible to know how many ribs were originally present). Pelvic girdle with elongated pre-pelvic processes as in Recent narcinoids, however distal tips of pre-pelvic processes are not preserved. At least one pair of obturator foramina is present on lateral portion of puboischiadic bar. First radial element enlarged as in Recent narcinids. Some 20 radials articulating with basipterygium; radials divided into two segments. No sign of dorsal fins (in MB uncat., that has more of the tail region preserved). Hemal processes very small, except for those anterior to pelvic girdle, which seem slightly more elongated (but this may be due to the orientation in which the vertebral column is preserved).

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REMARKS: Both specimens of this undescribed species are here reported for the first time. They undoubtedly represent fossils of electric rays, possessing typical neurocranial, antorbital, pelvic girdle and pectoral girdle morphology of a narcinid. There is also a clearly demarked area between the propterygium and gill-arch region that was occupied by electric organs in both specimens.

Both specimens appear to be of the same species, but are distinct from "Narcine" molini in antorbital morphology: both specimens have clear posterior processes on the antorbitals mesial to level where antorbitals bifurcate (posterior processes lacking in "Narcine" molini). These specimens are considered a new species, and are perhaps related to Discopyge tschudii as specimen MB uncat. has scapular processes shaped similar to those of D. tschudii. Further comparisons are needed.

MATERIAL EXAMINED: (2 specimens): MCSN 135581; MB uncatalogued.

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PART II

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INTRODUCTION

The classic "Interrelationships of Fishes" volume (Greenwood et al., 1973) contained an influential paper by L. J. V. Compagno (1973) that presented what quickly became a widely adopted classification scheme for Recent elasmobranchs (sharks, skates and rays). Compagno's paper contains a wealth of anatomical information and served as a landmark for the understanding of elasmobranch phylogeny, even though strict diagnoses of the major groups was maintained on a phenetic basis. Compagno (1977) attempted to rectify this problem by presenting what he considered diagnostic characters for his major groups. The recognized 12 orders of Recent elasmobranchs were grouped into four superorders as in 1973 (Fig. 112A): the Galeomorphii, Squalomorphii, Squatinomorphii and Batoidea. Again, the relationships among the superorders were left unresolved. Compagno's (1973, 1977) orders were widely accepted by many researchers and are now entrenched (e.g., Compagno, 1984; Springer and Gold, 1989; Eschmeyer, 1990; Pratt et al., 1990) even though some groups, e.g., the Squaliformes, seem to lack defining features.

The "orbitostylic" hypothesis of Maisey (1980) was the first attempt to relate at least some of Compagno's superorders. The Squatinomorphii (containing the angel-shark Squatina) was considered the sister-group to the Squalomorphii (which included the Hexanchiformes, or six- and seven-gilled sharks, and Pristiophoriformes, the sawsharks). The relationships of batoids (comprising all the rays and skates) and galeomorphs were left unresolved. Maisey (1984a) again adopted this three-fold division of Recent elasmobranchs ("orbitostylic" sharks, galeomorphs and batoids), without further elaborating on their phylogenetic placement.

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The first hypothesis to relate all of Compagno's superorders was that of Shirai (1992c). Shirai defended a sister-group relationship between Pristiophoriformes and batoids, which together form the sister-group to Squatina. This hypothesis became known as the "hypnosqualean hypothesis," and this taxon was formalized as the superorder Hypnosqualea by Carvalho and Maisey (1996). The "squaloid" sharks (dogfish sharks; Squaliformes of Compagno, 1973, 1977, 1984; Squaloidea of Bigelow and Schroeder, 1948) were considered by Shirai to be paraphyletic, forming successive sister-groups to hypnosqualeans. Hexanchiform sharks were also deemed paraphyletic with hexanchoids related more closely to all other squaleans than to Chlamydoselachus (Shirai, 1992c; Fig. 112B).

It has been noted that perhaps one of the most significant advances in the "cladistic revolution" is the concept of paraphyly (G. Nelson, 1989a, b; Farris, 1991). From this perspective, recent contributions in the systematics of elasmobranchs may best be understood by reviewing those papers in which taxa long recognized have succumbed under the scrutiny of phylogenetic analyses and parsimony algorithms. Shirai's (1992a, c) papers concerning the higher-level phylogeny of Compagno's (1973, 1977) superorders are a case in point. In those papers, Shirai has argued extensively that the recognition of a monophyletic Hexanchiformes and Squaliformes (as traditionally perceived, e.g., Compagno, 1984) is unsubstantiated by character evidence. To further investigate these claims, I analyzed a matrix containing 67 morphological features which includes characters incongruent with some of Shirai's components. My analysis reports on the paraphyly of two of Shirai's own higher-level clades (his unnamed hexanchoids + ("squaloids" + hypnosqualeans), and unnamed Squalidae + Hypnosqualea), and supports the monophyly of six- and seven-gilled sharks (Hexanchiformes)

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as well as a slightly modified Squaliformes. The classification presented here is closer to a compromise between Compagno's and Shirai's conclusions and stems from the inclusion of characters not considered by Shirai, as well as differences in the interpretation and coding of many features.

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METHODOLOGY

The phylogenetic analysis presented below is based in part on characters described by previous authors, including Regan (1906), Garman (1913), White (1937), Holmgren (1940, 1941, 1942), Compagno (1973, 1977, 1988) and Maisey (1984a, b, 1985, 1986a, 1986b). Many of these characters were compiled and summarized by Shirai (1992c), whose analysis included new characters and a data matrix. Specimens examined to substantiate these characters are listed in Table 45.

Shirai (1992c) presented a detailed and rigorous phylogenetic analysis of many Recent elasmobranch taxa, representing all higher-level groups. The matrix presented in Table 47, which is the matrix adopted in this paper, is based in part on the matrix presented by Shirai (op. cit.). Because the interrelationships of skates and rays is not further considered here (for reviews see Nishida, 1990; McEachran et al., 1996; Shirai, 1996; Lovejoy, 1996) all ray and skate (batoid) groups are represented as a single terminal (Batoidea). Justifications for the coding of characters are discussed in the character section.

The single outgroup used represents a hypothetical ancestor created based on the phylogenies of Schaeffer and Williams (1977), Schaeffer (1981), Maisey (1984a, 1984b, 1986b, 1989a), G. C. Young (1982) and Gaudin (1991). These authors have advanced a well corroborated hypothesis (summarized in Fig. 113A) establishing a sequence of fossil taxa that form successive sister-groups to Recent sharks and rays, facilitating outgroup comparison (Shirai, 1992c; Carvalho and Maisey, 1996). Although there is disagreement as to the placement of certain fossil taxa (primarily the Paleozoic Cladoselache and symmoriids, cf.

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Zangerl, 1981; Lund, 1985), this does not affect the optimization of the characters discussed below.

A list of characters present in the matrix (Table 47) is detailed in Table 46, which contains information on the different states of each character. All 16 multi-state characters were analyzed as non-additive (unordered). Autapomorphies present in the tree have homoplastic distributions – no single entries were included in the matrix (Carpenter, 1988; cf. Yeates, 1992), except when the autapomorphy represents part of a multi-state series or is coded as present in one taxon and as a "?" in another. Many taxa presented below have numerous defining characters, but only those with potential for grouping (synapomorphy) are included.

Parsimony analysis was undertaken using version 1.5 of Hennig86 (Farris, 1988). Although there is much homoplasy required by the resulting tree, an exact tree construction procedure was implemented (ie* algorithm). The resulting single most-parsimonious tree is summarized in Fig. 113B (ordinal level relationships) and shown in detail in Fig. 114. Tree diagnostics and optimizations were performed using the Dos Equis function of Hennig86 and the program Clados ver. 1.1 (Nixon, 1992). The results obtained with Hennig86 were confirmed using PAUP ver. 3.1.1 (Swofford, 1993), which produced the same number of equally most parsimonious trees and of the same length. When conflict in optimization occurred, characters were placed at the most basal node possible, favoring reversals over independent gains. This was done to maximize initial putative homology propositions and to give characters a greater generality (for a review see de Pinna, 1991). Alternative optimizations are discussed below under the appropriate character, and were diagnosed with

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the aid of MacClade ver. 3.01 (Maddison and Maddison, 1992), Clados ver. 1.1 (Nixon, 1992), and by hand.

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RECENT ELASMOBRANCHS

Recent elasmobranchs are monophyletic (as defined below) and are divided into two large monophyletic groups, the Galeomorphii and Squalea. Recent elasmobranchs are not the equivalent of Neoselachii (Fig. 114), which is a more inclusive taxon. Neoselachian monophyly is discussed in Compagno (1973, 1977), Schaeffer and Williams (1977), Reif (1977), Schaeffer (1981), Maisey (1984a, 1984b, 1986b, 1994), Thies and Reif (1985), Cappetta (1987) and Gaudin (1991), and references cited therein. The definition of Neoselachii (Euselachii of Moy-Thomas, 1939; Reif, 1977; Euselachiformes of Maisey, 1975) varies, and may be restricted to Recent elasmobranchs (which includes only fossil taxa that are phylogenetically placed well within Recent groups, e.g., numerous Cenozoic forms known from isolated teeth; Maisey, 1986b) or may include fossil taxa that fall just outside of Recent groups (e.g., Palaeospinax, Synechodus?, Acronemus?, Sphenodus?, anacoracids), which is the usage here (Compagno, 1988). Maisey (1986b) mentions only two characters that unite Recent forms to the exclusion of Palaeospinax, and both characters are unavailable in fossils (both biochemical; but see Maisey, 1984b). Therefore, it is quite apparent that discussions concerning the monophyly and higher-level interrelationships of living elasmobranchs should not be based solely on living forms, but must take the above fossil taxa into consideration (more on this issue below).

Parsimony analysis resulted in a single most-parsimonious tree (L = 132 steps, ci = 0.67, Ri = 0.80), which is depicted in Fig. 114. This is the tree adopted for the character section below. My results conflict with those of Shirai (1992c), but agree in some fundamental aspects (cf. Fig. 112B). Characters that are discussed here are numbered as in Table 46. The

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terms "component," "node," and "clade" are used interchangeably and refer to a particular monophyletic group. Complete diagnoses of all nodes are provided in the figure legend of Fig. 114. The consistency index (ci) for each character is given in brackets following the character number. Recent elasmobranchs are defined by four characters, all of which are reversed at lower levels in the phylogeny:

Extrabranchial cartilages on hyomandibula (epihyal) only (character 19) [ci = 0.66]. This character is unknown in immediate outgroups (perhaps due to preservational reasons), and because it is only present in galeomorphs and hexanchoids it can be considered a synapomorphy at this level. The alternative view is to consider the plesiomorphic condition for Recent taxa the absence of extrabranchial cartilages on the hyomandibula (the state in Chlamydoselachus, rajoids and myliobatidoids), in which case this feature would characterize galeomorphs and hexanchoids independently.

Adductor mandibulae superficialis present (character 28) [0.5]. This character has an interesting distribution, occurring in Heterodontus and squaleans except Chlamydoselachus, torpedinoid and myliobatidoid rays. It illustrates that characters presently included in the matrix shared by Heterodontus and squaleans can be considered synapomorphies of Recent elasmobranchs, and therefore loss of any such character would define galeomorphs minus Heterodontus (= Galeoidea).

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Right and left coracoids fused (character 37) [0.5]. This character is reversed to the primitive condition for hexanchiforms. Gaudin (1991) considers the single coracoid a defining feature of a monophyletic group including Hybodus, Palaeospinax and Recent elasmobranchs, but there is very little or no support for this. There is nothing in the available descriptions of the Lower Jurassic Palaeospinax to suggest that a single coracoid element was present (Dean, 1909; Schaeffer, 1967; Maisey, 1977; Cappetta, 1987), nor in the specimen examined (the type species, P. priscus AMNH VP7085). Maisey (1989a) reconstructs the Upper Pennsylvanian hybodont Hamiltonichthys with separate coracoid bars, and his descriptions of more "modern" hybodonts do not lead to the impression that they differ from Hamiltonichthys in this respect (Maisey, 1982, 1986c, 1987, personal commun.). The Cretaceous Synechodus has unfused coracoids, which lends support for its placement as a primitive neoselachian along with Palaeospinax, and not a basal galeomorph as advocated by Maisey (1985), although there is evidence for its galeomorph affinities as well (Maisey, op. cit.). The Carboniferous symmoriid Denaea is credited with possibly showing a single coracoid unit, but again on weak grounds (Zangerl, 1981), and it is more reasonable to assume that it lacked this character. Recent chimaeroids also have a fused coracoid (Didier, 1995), but this is homoplastic as basal euselachians have unfused coracoids. Compagno (1973) regarded the single coracoid as a character of living forms only, and this is the usage here, which contradicts the interpretation of Shirai (1992c) and Carvalho and Maisey (1996) – papers that did not support a monophyletic Hexanchiformes, a prerequisite for this optimization. The discovery of a single, ventrally-fused shoulder girdle in Palaeospinax would not require extra steps in this character for the phylogeny adopted.

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Teeth with "aprons" (character 59) [0.33]. This character can alternatively be considered a synapomorphy of Galeomorphii (lost in "higher" galeoids) and of non-hexanchiform squaleans independently.

Galeomorphii

The monophyly of this supraordinal clade is highly corroborated. It is defended by seven characters (Fig. 113B and node **a** of Fig. 114), two devoid of homoplasy. The findings of the present analysis (and that of Shirai, 1992c) support a two-fold division within the Galeomorphii, the superorders Heterodontea and Galeoidea (cf. Compagno, 1973, 1977, 1988). Shirai's (1992c) characterization of this group differs from that given below in that he considers the pharyngobranchial blade to be primitive at this level. His optimization of the insertion of suborbitalis muscle (character 27) is also different. Of Compagno's (1988: 382) five synapomorphies of galeomorph sharks, only "shortened otic capsules" is considered below (character 13, although stated differently).

Closed lateral line canal (character 2) [0.33]. The lateral sensory canal is open in Recent elasmobranchs only in Chlamydoselachus (Allis, 1923; AMNH specimens), Notorynchus (Daniel, 1934) and Echinorhinus (Garrick, 1960). Daniel (1934) credits "hexanchoids" as possessing an open lateral line canal, but this was contradicted by the specimens examined for this paper. The condition in Heptranchias is coded here as in Shirai (1992c; confirmed on an

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adult male uncatalogued AMNH specimen). Recent chimaeroids (Didier, 1995) and fossil outgroups (e.g., hybodonts, particularly Egertonodus basanus, Maisey, 1983; many Paleozoic taxa, Zangerl, 1981; cf. Lund, 1985) present the open condition as well, which is why the apomorphic expression is hypothesized as a defining feature here. Other neoselachians such as Palaeospinax may present the closed condition, which would then alter the optimization presently adopted, but data for this is lacking (unless Palaeospinax is erroneously considered a galeomorph, as did Glickman, 1967; Cappetta, 1987; Cappetta et al., 1993). A minimum of three steps are required.

Ethmoidal region of neurocranium downcurved (character 4) [0.5]. Shirai's (1992c: 20) characterization of this feature is slightly different although it implies the same attribute. This character is stated here as in Maisey (1985: 18, character 16). The downcurved ethmoidal area is present only in Heterodontus and orectolobiforms (and secondarily in some rajiforms, according to Maisey, 1985: 7), but can be optimally interpreted as a galeomorph character. Compagno's (1988: 382) "sliding articulation in specialized ethmopalatine grooves on the cranium" used in support of a Heterodontus + Orectolobiformes clade corresponds to the downward curvature between the ethmoidal and orbital areas. This character exemplifies that any character previously used to support a monophyletic Heterodontus + Orectolobiformes can be optimized as a defining feature of Galeomorphii, due to the placement of orectolobiforms as the sister-group to "higher" galeomorphs on the phylogeny of Figs. 113B and 114 (other characters also behaved in this fashion).

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The Mesozoic taxa Synechodus dubrisiensis and Sphenodus nitidus (= S. macer?) also have this feature (Maisey, 1985). If these taxa are regarded as basal neoselachians, the ethmoidal downcurvature must then be primitive at this level, with the loss of such a condition also characterizing squaleans (as well as lamniforms + carcharhiniforms). Because the phylogenetic position of Synechodus, and especially Sphenodus, are still unresolved beyond recognizing their neoselachian affinities, this character is interpreted as a galeomorph synapomorphy (Maisey, 1985).

Hyomandibular fossa located anteriorly in the otic region (character 13) [1.0]. This character corresponds to Compagno's (1988: 382) "shortened otic capsules," and is used here following Maisey (1985: 18, character 18). Paleozoic sharks (e.g., Xenacanthus, Tamiobatis) and Mesozoic hybodonts present the hyomandibular facet located far from the post-orbital processes, as do squalean elasmobranchs (Maisey, 1985). The condition in galeomorphs, wherein the hyomandibular fossa abutts the orbit, is therefore derived (also in Synechodus: Maisey, 1985).

Suborbitalis muscle originating on upper preorbital wall (character 26) [0.8]. This character is present only in Heterodontus, parascylliids and orectolobids (Shirai, 1992c), but due to their position on the tree it can be considered a galeomorph synapomorphy. Hemiscylliidae and Rhincodontidae possess this muscle (= levator labii superioris or preorbitalis of other authors) originating on the supraorbital surface, while all remaining galeomorphs show the suborbitalis arising from the posterior aspect of the nasal capsule. Orectolobiforms were scored with the

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same state as in Heterodontus (i.e., state 4), however, because this is believed to be the primitive condition within the order (Compagno, 1988; note that the phylogeny of Dingerkus [1986] implies a different coding). The outgroup condition is unknown, and the discovery of this character in a related neoselachian, albeit highly improbable, may change this interpretation.

The origin of the suborbitalis from either the upper preorbital wall (state 4) or from the ectethmoid process (state 3) can be interpreted as a defining feature of Recent elasmobranchs, as the placement of either of these conditions at the base of the tree (ingroup node) requires no extra steps. The state present in basal squaleans (state 3) is not considered diagnostic for all extant elasmobranchs, however, because it is only present in taxa endowed with an ectethmoid process (which is absent, so far as known, from Palaeospinax and other fossil neoselachians). State 3 is left as a squalean synapomorphy (transformed again for Squaloidea + Hypnosqualea, see below). State 4 was also not considered a synapomorphy of Recent elasmobranchs (which would imply two independent transformations, with state 4 at the root of the tree: $4 \rightarrow 2$ [within galeomorphs] and $4 \rightarrow 3 \rightarrow 0 \rightarrow 1$ [within squaleans]). The placement of this character state as a galeomorph feature is maintained because those taxa with it show corresponding modifications in neurocranial architecture (Maisey, 1985) not present in stem-group neoselachians. Although Maisey (1985: 11) noted similarities in the ethmo-orbital regions of Synechodus, Heterodontus and orectolobiforms, he concluded that they do not support the presence of a suborbitalis originating from the upper preorbital surface in Synechodus, because its postorbital articulation presents constraints for suction feeding.

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Suborbitalis muscle inserting directly on mandibula anterior to adductor mandibulae (character 27) [0.5]. As described by Shirai (1992c: 64), this derived condition occurs only in Heterodontus and basal orectolobiforms (coding for these taxa follows the same reasoning of character 26 above). Homoplasy is required as "higher galeoids" show the plesiomorphic condition that is also present in squaleans.

Nasoral groove present (character 55) [0.5]. Compiled from Compagno (1988: 382), this character has the same distribution as character 4 above (and, within galeomorphs, of characters 26 and 27). Squatina also has, independently, the derived state of this character (Maisey, 1984a).

Pharyngobranchial blade present (character 67) [1.0]. The pharyngobranchials of many Recent elasmobranchs present ventro-lateral projections of varying degree, originating from the proximal terminus (site of articulation with epibranchials). The pharyngobranchial blade is one such projection in which the arcualis dorsalis and interpharyngobranchialis muscles originate. Shirai (1992a, c) regards the loss of this feature as a squalean synapomorphy, in the belief that fossil euselachians also possess the pharyngobranchial blade. However, Carvalho and Maisey (1996) argue that there is only evidence for the presence of this character in galeomorphs, and this is the interpretation followed here. Because the proximal terminus of the pharyngobranchial may present various projections (e.g., double headed articulations, the "joint for pharyngobranchial and succeeding epibranchial" of Shirai, 1992a, c), this character needs confirmation from the dissection of additional taxa, as knowledge of the dorsal gill arch

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musculature is necessary in discerning the correct structure. Heterodontus francisci clearly presents the pharyngobranchial blade (AMNH 96795), as does Heterodontus zebra (Shirai, 1992c). Carvalho and Maisey (1996) present data concerning the shape of the pharyngobranchial in other galeomorph and squalean taxa.

Comments – The monophyly and interrelationships of galeomorphs is discussed at length by Compagno (1973, 1977, 1988), who also reviews the earlier literature. The definition given above for this group differs from that of Compagno (1988). The pseudosiphon could not presently be evaluated in light of the cluttered terminology surrounding mixopterygial components, but its distribution solely within galeomorphs, as advocated by Compagno (1988), is possible. The "rostrum not trough-shaped, possibly reduced" (another galeomorph character of Compagno, 1988) is coded differently here, where a rostrum representing a trabecular outgrowth (presumably of the trabecula communis) is primitive for neoselachians in general. The tripodal rostrum of carcharhiniforms and lamniforms (possibly all formed as further extensions and chondrification of the lamina orbitonasalis) is therefore derived (see below). A rostrum that is not "trough-shaped" is present in many squalean taxa (e.g., Dalatias, Squaliolus, Centroscymnus, AMNH specimens; Isistius, Zameus, Shirai, 1992c). In summary, within galeomorphs there appears to be two conditions that are derived: the tripodal rostrum and the secondary loss of the rostrum (Heterodontus). The rostral process of orectolobiforms is primitive in that it is formed as a projection from the trabecula (although the specific shape formed may be derived; Dingerkus, 1986). The "loss of the lateral commissure" also mentioned by Compagno (1988) occurs outside of galeomorphs as well, although it is retained

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(secondarily?) by some squaleans (Squatina, basal rajiforms, some "squaloids"; Holmgren, 1941; Maisey, 1984a, 1984b; Shirai, 1992c). The lateral commissure was not included here because its precise distribution is unclear. Compagno's (1988) "reduced post-orbital processes" is probably primitive at this level, as basal squaleans also have post-orbital processes reduced compared to hybodonts and Paleozoic xenacanths. This character may not be distinct from the reduced lateral commissure.

One character not included, but which has been used with much weight by previous authors, are the patterns formed by secondary calcifications of the vertebral centra. These patterns are difficult to interpret phylogenetically in Recent sharks. The monograph of Hasse (1879 – 1885) has influenced many later workers who have used secondary calcification patterns in their classifications (most notably White, 1937). Coding this character proved extremely difficult as generalizations regarding the specific patterns of calcification formed are met with many exceptions. Furthermore, there seems to be a correlation between habitus and the specific pattern formed, even if tenuous (Applegate, 1967; Compagno, 1988; Maisey, personal commun.). Squaleans generally do not have secondary calcification patterns comparable to most galeomorphs, which may present calcifications formed either as "solid" intermedialia or radii that originate from the outer zone cartilage of the centrum (Compagno, 1988). This is what has been termed "radial asterospondylic," even though Hasse's terminology has fallen out of use by many authors. Some squaleans show conspicuous patterns, such as Squatina (the "squatinoid" type of Applegate, 1967) which is similar to the vertebral centra of Cetorhinus (Compagno, 1988; AMNH 57264). It seems that the patterns derived from secondary calcifications (those stemming from the intermedialia) may potentially

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define carcharhinoids or subgroups therein (e.g., the "Maltese cross" type), or even galeomorphs, but these are difficult to delimit with any precision. This has been the attitude of some recent reviewers (Applegate, 1967; Compagno, 1977, 1988; cf. Maisey, 1984a), and is reluctantly followed here. Shirai (1992c) correctly codes terminal squalean taxa (squatinoids, pristiophoroids and rajiforms) with derived conditions, but only as different autapomorphies, therefore crediting this character with no potential for grouping at this level.

SUPERORDER HETERODONTOIDEA: HETERODONTIFORMES (node **b** of Fig. 114). – This order contains the sole genus Heterodontus. Along with its many autapomorphies, Heterodontus is characterized by the following (homoplastic) features:

Absence of rostral cartilages (character 1) [1.0]. Also shared with stingrays, but the condition in myliobatidoids is distinct, however, due to the presence of the anterior section of the rostral cartilage at least in the juvenile of some forms (Miyake et al., 1992, as "rostral appendix"; McEachran et al., 1996; McEachran, personal commun.). Certain skate taxa also lack a distinct rostrum (e.g., Pavoraja, Pseudoraja; McEachran et al., 1996; McEachran, personal commun.). This character is complex and attempts to code it over a wide selection of taxa, as is the case here, may become increasingly difficult as more specializations are described (Miyake et al., 1992). A distinct rostral process is not present in Heterodontus (Daniel, 1934; Compagno, 1977; AMNH 96795; Fig. 115).

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Circumnarial grooves and folds present (character 57) [1.0]. Present in orectolobids and hemiscylliids as well, but orectolobiforms were coded with a "?." More homoplasy is required in a more inclusive matrix.

Heterodontus plesiomorphically retains a dorsal fin endoskeleton composed of a basal cartilage and finspine (Compagno, 1977), an adductor mandibulae superficialis muscle, and an unfused condition of the posteriormost dorsal gill arch elements ("gill pickaxe:" Daniel, 1934, further discussed below).

SUPERORDER GALEOIDEA: ORECTOLOBIFORMES + LAMNIFORMES + CARCHARHINIFORMES (node **c** of Fig. 114). – Six features characterize this component (two without homoplasy, Fig. 114). Shirai (1992c) interprets differently both the "gill pick-ax" and the adductor mandibulae superficialis muscle, here used as galeoid characters. This node is not present in Compagno (1988).

Separate foramen for superficial ophthalmic nerve (character 7) [1.0]. Described in detail by Goodrich (1986), Holmgren (1940, 1941) and more recently by Maisey (1985) and Compagno (1988). Although not included in my analysis, the absence of a prefacial commissure (separating the hyomandibular foramen from the prootic foramen or orbital fissure) in orectolobiforms and carcharhiniforms (Compagno, 1988) is correlated with this character.

Complete fusion of posterior dorsal gill arch elements ("gill pick-ax") (character 24) [0.5]. The fusion of pharyngobranchial 5 to epibranchial 5, which in turn fuse to pharyngobranchial 4,

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forming a wishbone shaped structure, was used as an elasmobranch synapomorphy by previous authors (Daniel, 1934). This fusion, termed "gill pick-ax" by Shirai (1992b, c), is incomplete in Chlamydoselachus (Allis, 1923), hexanchoids (Shirai, 1992c), Heterodontus (Daniel, 1934) and, according to Shirai (1992c), in Trigonognathus, Narcine and Plesiobatis. Shirai (1992c) chose to exclude this character, on the basis that outgroup information is lacking or ambiguous. Some of the taxa listed above have these elements contacting each other, and partial fusion to some degree does occur, forming what seems to be different patterns. In Heptranchias the last two pharyngobranchials appear to be fused together, and these articulate with, or contact, the last epibranchial. In Chlamydoselachus the last pharyngobranchial and epibranchial seem to be united, and these contact the penultimate pharyngobranchial (Allis, 1923). According to Shirai (1992c), the condition in Hexanchus seems similar to that of Heptranchias, although these sharks have a different number of gill arches. Heterodontus parallels Chlamydoselachus in that the fusion (of whatever extent) is between the last pharyngobranchial and epibranchial, which in turn contacts pharyngobranchial 4 (Daniel, 1934). Hamdy (1961) provides ontogenetic evidence that for various rajiform species the fusion between the last pharyngobranchial and epibranchial takes place before the addition (fusion) of the penultimate pharyngobranchial. This sequence was observed in embryos of Sphyrna lewini (AMNH 12464) by Dingerkus (unpubl.). If this is a generalized occurrence, then it is plausible to hypothesize that the condition in hexanchoids is secondary to that of, e.g., Chlamydoselachus, and would represent an additional character of hexanchoids. Fossil euselachian taxa have poorly preserved dorsal gill arch elements (Zangerl, 1981; Maisey, 1982, 1989b). However, pharyngobranchial cartilages are preserved in the only known hybodont specimen from Solnhofen (Egertonodus

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fraasi, Brown, 1900; Maisey, 1986c), and in Permian xenacanths from Germany (Fritsch, 1889, 1895; Jaekel 1895, 1906; Koken, 1889) (also known from a few other taxa). Not much anatomical detail of these structures is available in these specimens, but it is possible to confirm that the posterior pharyngobranchials were not fused into a larger structure. Many Recent chimaeriforms, however, have the last three pharyngobranchials and last two epibranchials fused into a robust plate (Didier, 1995; AMNH specimens). There is evidence that this fusion also occurs in fossil holocephalans and paraselachians (E. Grogan and R. Lund, personal commun.). Two steps are required for this character.

Adductor mandibulae superficialis absent (character 28) [0.5]. This character shows considerable homoplasy as Chlamydoselachus, torpedinoid and myliobatidoid rays also lack the adductor mandibulae superficialis (Shirai, 1992c).

Elongated ventral marginal cartilage of clasper (character 43) [1.0]. White (1937) used this character in support of her "Galea" (= Galeoidea), but Compagno (1977, 1988) has given it little importance, noting that it may not be universally distributed within galeoids (Parascyllium has relatively short marginals: Compagno, 1977) and that elongated marginals also occur in rays. The basal rajiform condition is coded here as not having elongated marginals, however, and this feature is therefore free of homoplasy.

Dorsal fin endoskeleton composed of radial elements only (character 49) [0.4]. Among Recent taxa, this condition occurs in Chlamydoselachus. Many Paleozoic elasmobranchs, such

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as the symmoriids (e.g., Cobelodus, Symmorium, Denaea), have a dorsal fin with only endoskeletal radials (Zangerl, 1981), but galeoids have developed them independently, as the condition in more closely related euselachians is a basal cartilage with a fin-spine.

Anal fin endoskeleton composed of radials only (character 51) [0.5]. The anal fin is absent from the majority of Paleozoic elasmobranchs (Zangerl, 1981), being present most notably in xenacanthids (sometimes as a conspicuous "double-anal" fin). Some ctenacanthids (e.g., Goodrichthys) are reconstructed with an anal fin composed solely of radials, but this is to some extent questionable. Even so, the state in galeoids, which is also intriguingly the same as in Chlamydoselachus, is independent, as other Mesozoic euselachians have an anal fin with basal cartilages and radials.

ORECTOLOBIFORMES (node **d** of Fig. 114). – This order has been divided into as many as eight families (Compagno, 1973). Both Dingerkus (1986) and Compagno (1988) present phylogenies for this order and discuss characters unique to it. Orectolobiforms have a levator palatoquadrati not separated from the spiracularis muscle (character 30; ci = 0.5), which is also present in rajiforms.

LAMNIFORMES + CARCHARHINIFORMES. – This node (**e** of Fig. 114) contains the "higher" galeoids of previous authors. Six characters group lamniforms with carcharhiniforms, almost all showing some degree of homoplasy. These include ethmoidal region of neurocranium not downcurved (character 4, ci = 0.5), suborbitalis originating on posterior

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aspect of nasal capsule (character 26, 0.8), suborbitalis inserting on adductor mandibulae and/or dermal tissues around mouth corner (character 27, 0.5), loss of nasoral groove (character 55, 0.5), jaw teeth without aprons (character 59, 0.33) and tripodal rostrum (character 1, 1.0). Characters 4, 26, 27 and 55 are all mentioned above under Galeomorphii, character 59 under Recent Elasmobranchs.

LAMNIFORMES (node **f** of Fig. 114). – Characters defining this order can be found in Compagno (1973, 1977, 1984, 1990) and Cappetta (1987). The relationships within lamniforms were most recently analyzed by Compagno (1990), but there is evidence supporting a node that contradicts his results. The node (Alopias + ((Mitsukurina + Pseudocarcharias) + (Carcharias + Odontaspis)) is defended by the presence of lateral rostral fenestrae, dental bullae and a rostral apex. These characters and some others that define groups within this node are still under scrutiny and it would be premature to include them here (along with other features, they are part of an ongoing project; Gomes et al., unpubl.). Lamniforms are characterized by one feature that was coded as a "?" in orectolobiformms (intestinal valve of "ring" type; character 64, ci = 1.0].

CARCHARHINIFORMES. – Compagno (1988) reviews many aspects of the biology and phylogeny of this order, and provides a taxonomic revision as well. No further characters defining carcharhiniforms were discovered in this analysis.

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Squalea

This supraordinal taxon was presented by Shirai (1992c), and clusters three of Compagno's (1973, 1977) superorders – the Squalomorphii, Squatinomorphii and Batoidea. Maisey's "orbitostylic" group was identical to the Squalea excluding the Rajiformes. Other authors have defended a higher-level group similar in composition, but at least one component was always excluded from their classifications (e.g., hexanchiforms; Goodrich, 1986; Glickman, 1967). Shirai's (1992c) analysis provided the necessary evidence of a monophyletic Squalomorphii + Squatinomorphii + Batoidea. The Squalea (node **g** of Fig. 114) is composed of four superorders, the Notidanoidea, Echinorhinoidea, Squaloidea and Hypnosqualea, and is defended by nine characters.

Ectethmoid process present (character 8) [0.75]. Considerable confusion exists regarding what is termed the "ectethmoid" process. Posteriorly directed projections from the post-nasal wall area are a common feature in many elasmobranch groups. There is more than one "type" of projection, however, and terminology must be coherently applied to correctly interpret their phylogenetic significance (Carvalho and Maisey, 1996). The ectethmoid process proper is defined as the ventrally projecting process originating on the posterior aspect of the nasal capsule and lying beneath the orbitonasal canal (which connects the nasal and orbital venous sinuses transmitting the orbitonasal vein). As such, it is restricted in distribution, occurring in Chlamydoselachus, hexanchoids, and Echinorhinus. Centroscymnus has an "ectethmoid" process similar to Echinorhinus, projecting from the posterior wall of the nasal capsule, but

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less pronounced (AMNH specimens; Compagno, 1973). The "antorbital" cartilage of rajiforms and the unchondrified equivalent of pristiophorids has been considered the putative homolog of the ectethmoid process (Holmgren, 1941; Shirai, 1992c; Carvalho and Maisey, 1996). These structures are therefore regarded here in the same multi-state series. The "membranous antorbital cartilage" of squaliforms (as here defined), referred to by Holmgren (1941), would further fill in the gap between the above taxa, but this structure has not been confirmed or properly described. Many elasmobranch taxa possess a dorsal posterior projection which overlies the orbitonasal canal, and this structure is interpreted as the preorbital process (Compagno, 1977). This process is widespread among many Palaeozoic and Mesozoic taxa and has been regarded as a synapomorphy at a higher level (Maisey, 1984b, 1986b, as "ectethmoid" process). The ethmopalatine process of Egertonodus basanus lies ventral to the preorbital process, but is very distinct from the ectethmoid process of Recent taxa and does not bear the same topographic relationship to the orbitonasal canal (Maisey, 1983). Four steps are minimally required by the tree, one of which is autapomorphic (for rajiforms).

Orbital articulation present (character 9) [0.5]. This character is used here as outlined by Maisey (1980) and followed by Shirai (1992a, c) and Carvalho and Maisey (1996; cf. Compagno, 1988).

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Suborbital shelf absent (character 10) [0.5]. Usage follows Carvalho and Maisey (1996), who argue that the suborbital shelf of galeomorphs does not transform into the basitrabecular process of squaleans (see below), but is instead lost at this node.

Basitrabecular process present (character 11) [0.5]. This character was interpreted by Shirai (1992c; Carvalho and Maisey, 1996) to be a separate feature from the suborbital shelf on the basis of its topographic relationships (to the subotic shelf and neighboring structures) and development (Holmgren, 1941).

Suborbitalis muscle originating on ectethmoid process (character 26) [0.8]. This character is strongly correlated with the presence of the ectethmoid process, and has an almost identical distribution (this muscle originates from the suborbital surface in hypnosqualeans). See discussion under Galeomorphii above.

Arcualis dorsalis originating from two muscle slips (character 32) [0.33]. This muscle originates on the pharyngobranchials (with one or two heads of origin) and inserts on the epibranchials. This character shows considerable incongruence, requiring three steps: lost in Chlamydoselachus and batoids (in electric rays the arcualis dorsalis originates from two muscle slips, and in Trigonognathus the primitive condition is again present, thus requiring two extra steps, but these taxa are not scored here; Shirai, 1992c).

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Notochordal constriction reduced (character 44) [0.5]. The notochord is constricted by its expanding sheath early in development (Goodrich, 1986). The sheath expands and chondrifies between the membrana elastica externa and interna due to the invasion of matrix-depositing cells at the bases of the dorsal and ventral arcualia (the membranae become ruptured and eventually disappear into the "chordal" centra, in contrast to the "perichordal" centra of actinopterygians and tetrapods, according to Goodrich, 1986). The designation "primary calcification" was used by Shirai (1992c) to distinguish this process from the "secondary" calcifications that later originate from the intermedialia (Shirai's terms reflect Maisey's [1985: 17] characters 7 and 8 respectively).

According to Goodrich (1986), Chlamydoselachus maintains an unconstricted notochord in the trunk region. This is in contrast to the plesiomorphic condition seen in the vast majority of extant elasmobranchs (along with Palaeospinax and Synechodus; Maisey, 1977, 1984a, 1984b, 1985), in which the notochord is constricted along the entire vertebral column (except intervertebrally in some taxa). Hexanchoids, Echinorhinus and certain squaliform sharks show the more extreme condition of having an unconstricted notochord along practically the entire column (Shirai, 1992c). However, the degree to which this is different from the partial constriction in Chlamydoselachus is difficult to determine. Moreover, partial constriction of the notochord has been reported in Heptranchias and possibly Hexanchus as well (Regan, 1906; Schaeffer, 1967; Compagno, 1977). These taxa were therefore coded equally here. A reversal to the plesiomorphic state further defines Squaloidea + Hypnosqualea, even though some isolated squaliform taxa lack notochordal constriction as well (e.g., some

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Somniosus species, Aculeola; Ridewood, 1921; Shirai, 1992c), requiring further homoplasy in a generic-level matrix.

Complete hemal arches in precaudal tail region (character 47) [0.5]. A "complete" hemal arch is one in which the basiventral processes unite ventrally at the mid-line. The interpretation of this character heavily depends on the condition of fossil outgroups, but little information is available. Zangerl (1981) mentions "hemal arches" in the tail peduncle of some Paleozoic forms of which adequate skeletons are available, noting that they are "paired, fairly delicate rods that tend to fuse distally; near the base of the tail fin they usually are considerably enhanced ..." (p. 27). The questions to be answered are if whether the hemal elements form true arches, and where along the vertebral column do the arches begin (if in the beginning of the precaudal tail region, above the anal fin, etc.). Hemal elements from the caudal origin are known from some xenacanths (primarily Orthacanthus; Maisey, personal commun.), ctenacanths, Tristychius (Dick, 1978), Onychoselache (Dick and Maisey, 1980), and possibly symmoriids, among others. Precaudal hemal elements, however, are more scarce. More importantly, the condition of these elements in forms closer to Recent elasmobranchs is also poorly known. The oldest "complete" hybodontoid, Hamiltonichthys (Maisey, 1989a), has been restored with precaudal hemal arches similar to those of chimaeroids (Patterson, 1965), galeomorphs and Chlamydoselachus, i.e., true arches form only as of the anal fin region, and not from the second dorsal fin. This is believed to be the case for other hybodontoids as well (the Triassic Lissodus cassangensis; Maisey, 1990, personal commun.). The Jurassic Palaeospinax might have been similar, although no basiventral processes are apparent in the

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specimen examined (AMNH VP7085) or from Dean's (1909) account (which is based on the same specimen of P. priscus). The lack of good preservation in the precaudal region of many of the taxa above might be an indication that the basiventral processes were not very developed or calcified, and possibly not forming arches at all. Accordingly, the formation of true hemal arches in the precaudal tail region of squaleans is considered derived.

Dorsal fin endoskeleton composed of basal cartilage without a finspine (character 49) [0.4]. The plesiomorphic condition of this character is found in Recent as well as a great number of fossil groups (Maisey, 1982). Although homoplastic (5 steps are required for the tree adopted here), the loss of a finspine characterizes squaleans, with a reversal to the primitive state occurring for Squaliformes. A reversal to the squalean condition occurs for higher squaliforms (Somniosidae + Dalatiidae).

Comments – The definition of Squalea provided above differs from that of Shirai (1992c). Shirai (1992c) regarded the loss of the pharyngobranchial blade as a squalean synapomorphy, here considered to be a galeomorph feature. One character derived for hexanchiforms was also considered a squalean character (absence of pectoral propterygial radials) because he did not recognize a monophyletic Hexanchiformes (a discussion of this character follows). Shirai's (1992c) "nasal capsules separated from each other by a wide internasal space" was discredited by Carvalho and Maisey (1996) who found much variation in taxa examined, at least in relation to how this character is presently defined, and it is accordingly not incorporated here.

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SUPERORDER NOTIDANOIDEA: HEXANCHIFORMES. – This node (**h** of Fig. 114) is not present in the classification of Shirai (1992c), and is characterized by seven features:

Post-orbital articulation present but without complete articular facet ("non-suspensory post-orbital processes") (character 12) [1.0]. This character is best described as "post-orbital processes and upper jaws connected by loose connective tissue, but the upper jaws are relatively mobile and the post-orbital articulations readily disarticulate when the jaws drop" (Compagno, 1977: 308). This feature occurs in Chlamydoselachus, Pseudocarcharias and Aculeola among Recent taxa (Maisey, 1980; Shirai, 1992c), but it is equally parsimonious to consider it a hexanchiform synapomorphy. The articulation in Pseudocarcharias is not adequately described (Compagno, 1973, 1977), and may differ from that of Chlamydoselachus in some respects, but both taxa were coded equally here because their condition is distinct from the "complete" post-orbital articulation of hexanchoids (Carvalho and Maisey, 1996). Although analyzed as one multi-state character, the complete articulation of hexanchoids is far more restrictive to jaw movement and protusability, reminiscent of many Paleozoic sharks (e.g., Xenacanthus; Maisey, 1980; Schaeffer, 1981). Alternatively, if this character is coded in binary form (i.e., as two separate characters), its presence in Chlamydoselachus is autapomorphic and cannot be used as a hexanchiform synapomorphy.

Sixth branchial unit present (character 20) [1.0]. This character has long been recognized as a defining feature of hexanchiforms, but that statement was severely criticized by Thies (1987) and more recently by Shirai (1992b). The arguments presented by Thies amount to the naive

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belief that if a character occurs outside of the group in question (i.e., is homoplastic) then it cannot be a reliable indicator of monophyly. Accordingly, Thies (1987) discards the extra branchial arch as a hexanchiform attribute because a sawshark (Pliotrema) and a myliobatidoid ray (Hexatrygon) also possess six branchial arches (the criticisms of Thies regarding other features putatively homologous for hexanchiforms are discussed below). Shirai (1992b) disagrees with this character on the basis of morphological dissimilarities in the extra branchial arches of hexanchoids and Chlamydoselachus. His detailed work demonstrates that a paired basibranchial is present in the anti-penultimate arch of Hexanchus, Notorynchus and Heptranchias, but absent in the corresponding arch of Chlamydoselachus. Hexanchoids also present the derived condition of having the arcualis dorsalis muscle originate from two distinct muscle slips on the pharyngobranchials, whereas, according to Shirai (1992b), Chlamydoselachus has a single head of origin for this muscle. These taxa also show different patterns in the dorsal aspect of the posteriormost arches. Shirai (1992b, c) believes these three distinctions are enough to render this character unreliable. In my view, these features simply highlight that hexanchoids and Chlamydoselachus are indeed distinct, but do not negate their monophyly. The differences described by Shirai amount to further synapomorphies of hexanchoids (the distinct pattern of the posteriormost dorsal elements?, the paired basibranchials of the anti-penultimate arch) or features defining a more inclusive group (double-headed origin of arcualis dorsalis). Shirai's argument breaks down to that because the extra arches of Chlamydoselachus and hexanchoids are not *identical*, then they cannot be scored as such in a matrix – as if there can be no minor distinctions in characters hypothesized to be homologous (this would render most characters in any matrix unusable). There is much

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variation in the shape of the jaws in elasmobranchs, but I doubt that anyone would not consider them homologous. Many earlier authors used this character as a hexanchiform feature (Regan, 1906; White, 1937; Berg, 1947), and this is the usage followed here.

Scapulocoracoids articulating (unfused) ventrally (character 37) [0.5]. Discussed above under Recent Elasmobranchs.

Pectoral propterygium not contacting radials (character 40) [1.0]. This character is free of homoplasy. Contact between the propterygium and radial elements is apparently a widespread condition in fossil sharks endowed with a tribasal pectoral fin, most notably Paleozoic ctenacanths (Zangerl, 1973, 1981) and hybodonts (Maisey, 1982) including the Pennsylvanian hybodont Hamiltonichthys (Maisey, 1989a). This is also the case in Recent chimaeroids (Patterson, 1965; Didier, 1995), although only two basal cartilages are present. However, Thies (1987) claims that radial elements are indeed articulating with the propterygium in Notorynchus, based on the description given by Daniel (1934: 50, 78). Examination of the exact text cited by Thies, however, does not lead to that conclusion, neither does Daniel's illustration of the pectoral endoskeleton of that species. The only other evidence cited by Thies reporting contact between the propterygium and radials in a hexanchiform (Gegenbaur, 1865) could not be examined. However, the species on which Gegenbaur apparently based his claim is Hexanchus griseus (Thies, 1987), which is figured by Shirai (1992c: pl. 48B) as clearly demonstrating the anterior mesopterygial expansion that does not permit contact between the propterygium and radial cartilages. The derived condition has been convincingly demonstrated

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in Chlamydoselachus and Notorynchus as well (Compagno, 1977; Shirai, 1992c). Partial dissection of an embryo Chlamydoselachus specimen (AMNH 59327, 317mm TL) revealed the mesopterygial anterior expansion figured by these authors. Regan (1906), White (1936a, 1937), Berg (1947), Compagno (1977) and Shirai (1992c) agreed that the hexanchiform condition is derived (or "diagnostic" for the former two authors), and this is the usage adopted here.

Only one dorsal fin present (character 50) [1.0]. The first usage of this character was by Rafinesque-Schmaltz (1810, for Hexanchus and Heptranchias; Gill, 1862). Among Recent elasmobranchs, a single dorsal fin is also present in a variety of rajiform taxa (Nishida, 1990), but the plesiomorphic condition for the rays is to have both dorsal fins present. The scyliorhinid Pentanchus, known only from the holotype, also has only one dorsal fin, but this specimen may be anomalous as the species is otherwise identical to Apristurus herklotsi (Compagno, 1984). This character is free of homoplasy for the tree presented here, but would certainly show incongruence in a phylogeny with more terminal rajiform groups included. Among Paleozoic taxa, the long dorsal fin of xenacanths (extending from just posterior to the cranium to the caudal fin, with which it can be confluent) cannot be considered the equivalent of the single dorsal in any other group. A single dorsal fin is seemingly common in many Paleozoic sharks, however. Symmoriid sharks have a single dorsal that is positioned slightly anterior to the pelvic fins and with an endoskeleton composed of radial cartilages only, not unlike the dorsals of galeomorphs (Zangerl, 1981). Sharks of the extinct order Eugeneodontida also possessed a single dorsal fin (Zangerl, 1981; the monophyly of this order

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is uncertain). These occurrences are independent from the state present in six- and seven-gilled sharks, irrespective of the phylogeny (of the afore-mentioned Paleozoic taxa) adopted. As with the extra gill arches, Thies (1987) disregards this character as a synapomorphy of hexanchiforms due to its occurrence in other taxa. Carvalho and Maisey (1996) placed this character as a squalean feature, with a reversal to the primitive condition occurring for the node uniting Echinorhinus and all other squaleans, because Hexanchiformes was not considered monophyletic. However, Compagno (1973, 1977, 1984), Maisey and Wolfram (1984) and Maisey (1986a) used the single dorsal fin as a defining feature of hexanchiforms, along with numerous previous authors, and this is corroborated by the present analysis.

Teeth devoid of labial and lingual "aprons" (character 59) [0.33]. Three steps are needed to accommodate this character. The "apron" is an expansion from the crown that covers the root from both labial and lingual view (Thies and Reif, 1985; Cappetta's [1987] "uvula" corresponds to the lingual apron), but is absent in hexanchiforms and higher galeomorphs (lamniforms and carcharhiniforms; see above). The distribution of this character needs further study, but is accepted here as described by Thies and Reif (1985).

Additional (fourth) column of heart valves present (character 45) [1.0]. Both Garman (1913) and White (1936b, 1937) have described and figured the valves of the conus arteriosus in a large number of taxa. White's comments directly support that the extra (fourth) column ("series") of valves present in the conus of hexanchiforms (her Hexanchea) is derived relative to the fewer number (three) of other Recent chondrichthyans. White (op. cit.) emphasized that

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the high number of rows is also derived in these sharks, even though three other species of sharks (a carcharhinoid and two squaliforms) and many rays were described as having four rows as well. Only the additional column was included here, but the additional rows are probably derived for hexanchiforms as White suggested (this character needs further scrutiny). As with the lack of propterygial radials (character 40 above), this feature is free of homoplasy.

SUBORDER CHLAMYDOSELACHOIDEI (Chlamydoselachus anguineus) (node **i** of Fig. 114). – Many characters define this taxon (Compagno, 1984) but those used here also occur, independently, in other taxa (listed in the figure legend of Fig. 114, cf. Table 46).

SUBORDER HEXANCHOIDEI (node **j** of Fig. 114). – Composed of the three remaining hexanchiform genera (Notorynchus, Hexanchus and Heptranchias), all of which are placed in the same family following Compagno (1984; cf. Shirai, 1992c). This clade is defined by seven characters.

Complete post-orbital articulation (character 12) [1.0]. If interpreted as one multi-state character (as done here), then the post-orbital suspension has been lost prior to the node uniting hybodonts and neoselachians, as the post-orbital articulation is present in many Paleozoic taxa. It is therefore reacquired here, and not lost twice (and retained by hexanchoids) as advocated by Maisey (once for hybodonts and once for neoselachians; Maisey, 1980: 7).

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Loss of the occipital hemicentrum (character 17) [0.33]. The presence of this feature defines Neoselachii, and not only extant elasmobranchs, and requires three steps: loss at nodes **j**, **o** and **c'** independently (Fig. 114). The presence of complete calcified vertebrae in fossil hexanchoids (Maisey, 1986a; Thies, 1987), does not change this optimization as no extra steps are required when fossil hexanchoids (for which this character is known, e.g., Notidanoides, "Hexanchus" gracilis) are added, as long as they remain basal to living hexanchoids, as is currently believed (Maisey, 1986a; Thies, 1987). If an alternative optimization is adopted, e.g., the independent gain of the occipital hemicentrum for Galeomorphii, Chlamydoselachus and node **p** (Fig. 114), then an extra step is required if fossil hexanchoids are included. The presence of the hemicentrum in these fossil taxa, however, is still questionable. Because the occipital hemicentrum is present in the basal neoselachian Palaeospinax (Late Jurassic; Maisey, 1977), the DELTRAN optimization is less parsimonious (more steps are also required to account for its absence in pristiophoroids + batoids in this scenario). The fossil genera Protospinax (Late Jurassic; Carvalho and Maisey, 1996) and Synechodus (Late Cretaceous; Maisey, 1985) also have this character, but they are systematically resolved as a basal hypnosqualean and galeomorph (?) respectively (the relationships of the latter are still problematical, which may be a basal neoselachian as suggested by previous authors; Carvalho and Maisey, unpubl.).

Seventh branchial unit present (character 21) [0.5]. Lost in Hexanchus.

Adductor mandibulae superficialis inserting on ectethmoid process (character 29) [1.0]. This character is adopted from Shirai (1992c), who considers the craniomandibular muscle of

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Heterodontus to be homologous (not coded as such here). Shirai (1992c) presents many different patterns associated with the origin and insertion of this muscle, which is here divided into two characters (28 and 29). Many of Shirai's (1992c) different conditions amount to autapomorphies (states 2 and 3 here, for batoids and Echinorhinus, respectively).

Constrictor hyoideus dorsalis inserting on palatoquadrate (character 31) [0.66]. Although there is homoplasy in this character, the state present in hexanchoids does not occur in other taxa.

Pectoral metapterygium contacts short proximal segment (character 42) [1.0]. The "short proximal segment" refers to the anterior portion of the metapterygium, which is divided into two sections in hexanchoids (Shirai, 1992c).

Linearly arranged tooth rows (character 58) [0.66]. This character is coded as in Shirai (1992c), with diagonally arranged tooth rows representing the primitive condition (seen in fossil outgroups, galeomorphs and, although somewhat distinctly, in Chlamydoselachus as well).

SUBFAMILY HEXANCHINAE (node **j** of Fig. 114). – This node contains Hexanchus and Heptranchias and is defined by four characters. The closed lateral line canal (character 2, ci = 0.33) is discussed above under Galeomorphii. The condition in Chlamydoselachus and Notorynchus (open lateral line canal) is a primitive feature, which renders the closed lateral line

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a *de novo* appearance for hexanchids. The ethmoidal canal is present but does not open on the dorsal surface of nasal capsules (character 5, 0.66). This character is differently optimized in Shirai (1992c; see his work and Carvalho and Maisey [1996] for further description). The subnasal fenetra is present (character 6, 0.33) and is characterized following Shirai (1992c). This character also defines Squaliformes (lost for Oxynotus, see Fig. 114). The presence of a concavity ventral to the hyomandibular fossa (character 15, 1.0), described by Holmgren (1941), also defines this component.

SUPERORDERS ECHINORHINOIDEA + SQUALOIDEA + HYPNOSQUALEA (node **n** of Fig. 114). – Includes Echinorhinus, all remaining "squaloids," Squatina, pristiophorids and all ray groups. Defined by five characters: an ethmoidal canal present but not opening on dorsal surface of nasal capsule (character 5, ci = 0.66; see Shirai [1992c] for a description of its alternative states), extrabranchial cartilages present on entire hyoid arch (character 19, 1.0; discussed above under Recent elasmobranchs), complete fusion of posterior dorsal gill arch elements (character 24, 0.5; see discussion above under Galeoidea), absence of mesonarial flap (character 56; 1.0), and lastly by the absence of the anal fin (character 66, 1.0). The anal fin is primitively present in neoselachians, and its absence here is derived (Compagno, 1984). Many Paleozoic sharks lack an anal fin, and this character has been used as a defining feature of a monophyletic group including Cladoselache, stethacanthids and symmoriids (Lund, 1985). As with the single dorsal fin discussed above, the lack of the anal fin is derived at this node irrespective of the relationships of the Paleozoic taxa that also lack this character.

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SUPERORDER ECHINORHINOIDEA (Order Echinorhiniformes: Echinorhinus) (node o of Fig. 114). Along with its many diagnostic characters (Compagno, 1984), this genus is further characterized by the loss of the occipital hemicentrum (character 17, 0.33; discussed above under Recent Elasmobranchs), adductor mandibulae superficialis inserting on mandibula (character 29, 1.0), all three basal cartilages of pectoral fin fused (character 39, 0.75; Shirai, 1992c), and linearly arranged tooth rows (character 58, 0.66), which is also present (homoplastically) in hexanchoids. Echinorhinus primitively retains an open lateral-line canal (Garrick, 1960). Placing Echinorhinus in an order of its own was advocated by Pfeil (1983) and further supported by Herman et al. (1989) on the basis of its distinctive teeth. The latter authors also mention the similarities between Echinorhinus and hexanchiforms (again on the basis of teeth morphology), a notion not entirely without support. Carvalho and Maisey (1996) found that the coding given to Echinorhinus for characters related to the ectethmoid process and suborbitalis muscle had an impact on hexanchiform monophyly, even though Echinorhinus and Hexanchiformes were not supported as monophyletic in any of the shortest trees they obtained. Molecular evidence also seems to support distinct ordinal placement for Echinorhinus (Bernardi and Powers, 1992).

SUPERORDERS SQUALOIDEA + HYPNOSQUALEA. – Eight characters support this node (p of Fig. 114), five of which were not considered by Shirai (1992c), who characterized this group with additional features that are differently optimized here.

Closed lateral line canal (character 2) [0.33]. Discussed above under Galeomorphii.

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Ectethmoid process lost (character 8) [0.5]. The discovery of the "membranous ectethmoid process" mentioned by Holmgren (1940) would fill in this "gap" in the tree, insofar as the ectethmoid process is reacquired higher in the phylogeny by pristiophoroids + Rajiformes (as the "antorbital cartilage").

Suborbitalis muscle originating from suborbital surface (character 26) [0.8]. Different states of the origin of the suborbitalis were described by Shirai (1992c). Further discussed under Galeomorphii.

Notochord constricted along entire vertebral column (character 44) [0.5]. See discussion under Squalea above.

Enlarged supraneurals preceding second dorsal fin (character 46) [0.66]. This multi-state character shows homoplasy in that the condition in dalatioids (see below) is a reversal to the state present in galeomorphs and basal squaleans (lack of obvious supraneurals). In squaloids, enlarged supraneurals are present anterior to the second dorsal fin, as in Squatina (Shirai, 1992c). The most apomorphic state of this character is seen in pristiophorids and rays (at least basally), where well developed supraneurals are present in precaudal tail and anterior to caudal fin. This character was used as evidence of a Squalidae + Hypnosqualea clade (Shirai, 1992c), but this is refuted here. This character can be used as a synapomorphy at this level, or independently acquired for squaloids and Squatina.

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Precaudal hemal processes as elongate as lower caudal skeleton (character 48) [0.5]. This character refers to the uniquely elongated hemal processes that fully partition the hypaxial musculature, contrasting to the primitive state in which the hemal processes are less expanded ventrally (Shirai, 1992c). This character is difficult to detect in fossil outgroups and Paleozoic taxa (Zangerl, 1981; Maisey, 1983).

Spiracle valve present (character 60) [0.5]. The coding of this character is after Shirai (1996, personal commun.).

Longitudinal precaudal keel present (character 63) [0.5]. According to Shirai (1992c), the derived condition of this character has the same distribution as the expanded supraneurals and elongated precaudal hemal processes discussed above, but this still was not enough to support a monophyletic Squalidae + Hypnosqualea, as defended by Shirai (1992c).

SUPERORDER SQUALOIDEA: SQUALIFORMES. – This component (node **q** of Fig. 114) is not the equivalent of Squaliformes of Compagno (1984) and is novel in this analysis, not present in the work of earlier authors including Shirai (1992c). The order is divided into two suborders, the Squaloidei and Dalatioidei. Four characters support its monophyly, all showing homoplasy. Three of these are described in Shirai (1992c), even though their optimization is different here (subnasal fenestra present – character 6, ci = 0.33; constrictor hyoideus dorsalis inserting partly on hyomandibula and partly on palatoquadrate – character 31, 0.66; linearly arranged tooth rows with teeth overlapping each other – character 58, 0.66).

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Dorsal fin endoskeleton composed of basal cartilage and finspine (character 49) [0.4]. Although this character is traditionally and correctly regarded as a primitive neoselachian feature, its placement here is a synapomorphy of squaliforms and is therefore derived. The finspine appears *de novo* at this node because basal squaleans (hexanchiforms and Echinorhinus) do not have a finspine. Further homoplasy is required as the clade Somniosidae + Dalatiidae lacks a finspine. Five steps are therefore minimally imposed by this character. A finspine appears in fossil "rhinobatoid" taxa (e.g., Belemnobatis and Spathobatis, Saint-Seine, 1949; Breviacanthus, Maisey, 1976; Cappetta, 1987), and in the basal hypnosqualean Protospinax (Carvalho and Maisey, 1996), therefore necessitating more homoplasy in a more inclusive matrix.

SUBORDER SQUALOIDEI (node **r** of Fig. 114). – Defined by two characters described in Shirai (1992c): a flexor caudalis muscle which extends to the origin of caudal fin (character 54, ci = 1.0) and the presence of an upper precaudal pit (character 62, 1.0).

SUBORDER DALATIOIDEI: CENTROPHORIDAE + ETMOPTERIDAE + OXYNOTIDAE + SOMNIOSIDAE + DALATIIDAE (node **s** of Fig. 114). – This node is supported by a suborbitalis muscle originating from the interorbital wall (character 26, ci = 0.8), and the reversal to the primitive condition for characters 46 (0.66), 48 (0.5) and 63 (0.5) (discussed above under Squaloidea + Hypnosqualea). The (unnamed) node Etmopteridae + Oxynotidae + Somniosidae + Dalatiidae and the rest of the components within this group

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(nodes **t** through **z** of Fig. 114) correspond to Shirai's (1992c) Dalatiiformes, and will not be discussed further (diagnosed in the figure legend of Fig. 114).

SUPERORDER HYPNOSQUALEA: Squatina + PRISTIOPHORIFORMES + RAJIFORMES (node **a'** of Fig. 114). – This component, considered a superorder by Carvalho and Maisey (1996), is defined here by seven features, all of which are present in the definition of this group given by Shirai (1992c). Three of these are from muscles (character 52, ci = 0.5; character 53, 1.0; character 54, 1.0). The anterior expansion of the pectoral fin (elongated propterygium, character 41, 0.5) is lost for pristiophoroids (along with character 53). Shirai (1992c) defines this group, novel in his earlier account (1992a), with additional characters not optimized in the same fashion here.

SQUATINIFORMES: Squatina (node **b'** of Fig. 114). – Squatina is defined by many autapomorphies (Compagno, 1984) as well as two homoplastic features: presence of nasoral groove (character 55, ci = 0.33) and loss of the spiracle valve (character 60, 0.5).

PRISTIOPHORIFORMES + RAJIFORMES: "PRISTIOBATEA" (node **c'** of Fig. 114). – This node, and those contained within it, are not further elaborated upon, except to note that the characters listed in Fig. 114 are those that occur homoplastically in other groups, or are states in multi-state series. Shirai (1992c; Carvalho and Maisey, 1996), and references he cites, provides explanations of some of those characters (figure legend of Fig. 114). Other characters

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defining nodes **d'** and **e'** (Fig. 114) can be found in Compagno (1973, 1977), Nishida (1990) and McEachran et al. (1996).

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DISCUSSION

Basal Squaleans: Hexanchiform Monophyly and Autapomorphy

Six- and seven-gilled sharks (cow sharks) are traditionally viewed as a primitive but natural group. Under one name or another, the group was included in the classifications of many earlier authors, such as Regan (1906), Goodrich (1909, 1986), Garman (1913), White (1936a, 1937) and Berg (1947). The first author to imply a possible close relationship between Chlamydoselachus and hexanchoids was Garman (1885; he described Chlamydoselachus the previous year), and this was followed by Gill (1893; cited in Compagno, 1984) and Jordan and Evermann (1896). Hexanchiform monophyly is entrenched in many volumes dealing with the identification and/or biology of elasmobranchs in general (Compagno, 1984; Smith and Heemstra, 1986; Cappetta, 1987; Springer and Gold, 1989; Ecshmeyer, 1990; J.S. Nelson, 1994), a notion that stems more recently from Compagno (1973, 1977) and supported by Maisey and Wolfram (1984) and Maisey (1986a). Ida et al. (1986) present karyological evidence in support of hexanchiform monophyly. The most outspoken recent opponents to this view are Thies (1987) and Shirai (1992b, c).

Compagno (1973) offers an extensive array of characters that occur in Chlamydoselachus and hexanchoids, however many represent characters primitive for elasmobranchs in general or for other higher-level groups (e.g., lack of calcification in the vertebral centra and unconstricted notochord, presence of ectethmoid processes, trough-like rostrum) or characters vaguely defined or spurious (e.g., eyes laterally situated on the head,

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head moderately depressed or conical but not greatly flattened). Compagno (1977) improved upon this by explicitly listing characters that are believed to be derived for hexanchiforms: extra gill arches, lack of lateral commissures on neurocranium, long ectethmoid processes on nasal capsules, no fin spines, a single dorsal fin (presumed to be the second dorsal fin), and propterygium not contacting any radial cartilages in the pectoral fin. Maisey (1986a) reduced this list, considering only the single dorsal fin and extra gill clefts as defining features (also Maisey and Wolfram, 1984). Along with these two characters, the present analysis identifies five additional synapomorphies for the order.

The criticisms of Thies (1987) and Shirai (1992b, c) have been partially considered above (under Notidanoidea). In his 1992 book, Shirai (1992c) coded the sixth gill arch of hexanchoids and Chlamydoselachus as *independent* characters, therefore eliminating any possibility of it becoming a synapomorphy of hexanchiforms (as was also true of the coding given to the single dorsal fin; cf. Carvalho and Maisey, 1996). This coding derives from an idiosyncratic a priori decision of considering the extra gill arch and single dorsal fin to be non-homologously distributed in hexanchoids and Chlamydoselachus, effectively prohibiting these characters from being homologous *before* any reference to a phylogeny. The determination of homology was based on Shirai (1992b) for the extra gill arch, a paper that does not present or make reference to a tree. Shirai's determination of homology was therefore a direct conclusion from observation and not from a phylogenetic analysis (also Shirai, 1996). As discussed above (Notidanoidea, character 20), the distinctions reported in the arches of Chlamydoselachus and hexanchoids by Shirai further characterize hexanchoids or define even more inclusive taxa, but do not affect the monophyly of Hexanchiformes. To further substantiate this, I experimentally

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coded Chlamydoselachus exactly as Shirai did for the extra gill arch (i.e., as not having it). Hexanchiformes was still monophyletic in the single tree obtained. The only way to decide if the extra gill arch is indeed independent is by congruence, not a direct conclusion from observation.

When in doubt if a feature is indeed homologous, a suspicious author should consider coding that character (believed to be independent but in which there is substantial doubt) equally for those taxa presenting it (as long as this is reasonable for a particular character in question, and there are not a great number of characters receiving this same treatment). In other words, if non-homology is believed to be likely, phylogenetic analysis should not be conducted in a manner that presumes non-homology, but in one that *tests* for it (Carpenter, 1994). I doubt that anyone seriously believes that there is no basis whatsoever for coding the extra gill arch and single dorsal fin equally for Chlamydoselachus and hexanchoids. If the result falsifies a monophyletic Hexanchiformes, then this is the necessary evidence that these characters are distinct (depending on the final topology, as different optimizations may still allow for their single origin).

The arguments presented by Thies (1987) in relation to the single dorsal fin and extra gill arch are reminiscent of compatibility (clique) analysis, wherein characters not congruent with the largest subset of mutually compatible characters (the clique) are discarded. In other words, he advocates that incongruent (homoplastic) characters are not accurate indicators of relationships and should be eliminated, as if homoplasy can be determined prior to a phylogenetic analysis (Farris, 1983). Any textbook on vertebrates cites homeothermy as a

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mammalian character (J. Z. Young, 1981), even though birds are homeothermic as well.[4] A character that is homoplastic is also diagnostic (see below). His rejection of the mesopterygial forward expansion which prevents the propterygium from contacting the radials was discussed above (Notidanoidea, character 45) and shown to be unfounded.

Other authors that have cast doubt upon a monophyletic Hexanchiformes include Bigelow and Schroeder (1948), Applegate (1974), Bass et al. (1975) and more recently Herman et al. (1993, 1994a). Bigelow and Schroeder (1948) chose to leave Chlamydoselachus in a separate suborder (Chlamydoselachoidea) due to differences in its suspensorium and vertebral column when compared to the "notidanoids" (their hexanchoids). However, their decision is symptomatic of a more encompassing issue, that of being mislead by data that have no real bearing on relationships (i.e., autapomorphy). Chlamydoselachus and hexanchoids differ in many attributes no doubt, and this has been used as an indication of their non-monophyly, but many of these attributes serve to distinguish these taxa from most or even all other elasmobranchs as well. The suspensorium of hexanchoids just mentioned is an example, as is the paired basibranchial of their antipenultimate arch, used by Shirai (1992b) as evidence for the non-monophyly of hexanchiforms. Both these characters are nothing but defining features of hexanchoids that do not help to clarify their relationships to other elasmobranchs.[5] Herman et al. (1993, 1994a) recommend isolating Chlamydoselachus into an order of its own because of distinctions in tooth structure (vascularization of the root) with hexanchoids. Even

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[4] This example does not hold if one accepts the Haematothermia of Gardiner (1982, 1993), but examples of homoplastic characters are abundant.

[5] Although the post-orbital articulation was herein interpreted as a multi-state character in which the condition of the frilled shark (state 1) is intermediate between the state in hexanchoids (2) and the primitive absence of the character (0) (implying a possible relationship between the hexanchoid condition and the incomplete post-orbital

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though they notice similarities in these features that suggest (to them) a possible close relationship between Chlamydoselachus and orectolobiforms, the great *distinctness* from hexanchoid tooth roots was more crucial in their judgement.

Autapomorphy has, in the past, misled many authors constructing classifications for elasmobranchs. For example, "sharks" were considered monophyletic without the rays (i.e., form a natural unit) due to the large number of derived features of the latter group (Müller and Henle, 1838-1841; Duméril, 1865; Günther, 1870; Regan, 1906; Garman, 1913; this dichotomy can still be seen in modern publications, even with much evidence to the contrary; Herman et al., 1987, 1994b; Dunn and Morrissey, 1995). This tradition was begun by Linnaeus (1758) who established a single genus for sharks and one for rays. Compagno (1973) was well aware of this tendency, noting that the "... ranking of modern elasmobranchs in two equal groups of sharks and rays places undue emphasis on unique characters of the rays while obscuring the many differences between the various shark groups" (p. 21). However, Compagno's (1973, 1977) interpretation of the phylogenetic placement of Squatina was no different, resulting from the many distinctions between angel sharks and all other elasmobranchs. Squatina was left in a superorder of its own, equal in rank to the three other superorders containing all other sharks and rays, and its relationships remained elusive. Another example can be seen in an unpublished manuscript by Dingerkus, in which he considered Chlamydoselachus to be the sister-group to all remaining elasmobranchs, heavily influenced by the peculiarities of its ("cladodont") tooth morphology (an autapomorphy, not a primitive condition as seen in certain Paleozoic taxa equivalent to the Cladodontida of Lund,

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connection), coding the post-orbital articulation in hexanchoids as a character separate from the incomplete articulation in Chlamydoselachus does not affect their phylogenetic position.

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1985). The relationships of Chlamydoselachus were problematical since its description, due to similarities shared with "cladodonts" (Garman, 1885; summarized in Gudger and Smith, 1933), even though these similarities are independently derived, not primitively retained by Chlamydoselachus or indicative of a monophyletic group comprised of the frilled shark and "cladodonts."

Homoplastic but Diagnostic

Intriguing character distributions suggested affinity, albeit falsified, between Heterodontus and most squaleans (character 28), hexanchiforms and "higher" galeoids (character 59), Chlamydoselachus and galeoids (galeomorphs minus Heterodontus; characters 49 and 51), orectolobiforms and rajiforms (character 30), and rajiforms and dalatiines (characters 33 and 34), among other interesting combinations. Intriguingly, many of these characters are from muscles.

Similar to the views of Shirai and Thies (cited above), Dingerkus (unpubl.) rejects hexanchiform monophyly on the basis that both the extra gill arch and single dorsal fin are "distinct." Hexanchiform monophyly is corroborated by more than these two characters, however. In any case, it is quite odd that Chlamydoselachus and hexanchoids share *two* features that require equal coding in a matrix, but were rejected as such beforehand by these authors, leaving no chance for a monophyletic Hexanchiformes. Rejecting these characters (single dorsal fin and extra gill arch) on the basis of their putative homoplastic distributions would require the rejection of a great many features as well, and derives from the misheld belief

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that homoplasy is a rare phenomenon, an expectation falsified by many published phylogenies created with large data matrices (Sanderson and Donoghue, 1989). Because phylogenetic analysis consists of minimizing homoplasy, "bad" data are not those with elevated levels of homoplasy *per se*, but those in which homoplasy is least minimizable (Goloboff, 1991). In other words, as long as there is resolution (congruence), then the (high) levels of homoplasy are just that, and not an indication of "bad" data. Furthermore, because there is much discordance (between characters and the tree), the discovery of additional characters that are congruent with homoplastic features already analyzed may change the topology in their favor once they are included, in which case they become synapomorphies. Discarding these characters beforehand would prohibit this.

For the resulting phylogeny (Fig. 114), almost one half of the characters (Tables 46 and 47) showed homoplastic distributions (either as reversals or independent gains). This was also the case in Carvalho and Maisey (1996) and Shirai (1992c; the matrices used in these papers are similar to the one compiled here), and has been reported in other studies dealing with different elasmobranch taxa (McEachran and Miyake, 1990). Almost every node contains characters that occur homoplastically elsewhere on the tree. This situation, clearly not restricted to (or uncommon in) chondrichthyans, makes careful character coding even more crucial, as the support for nodes is very sensitive to changes in particular coding strategies. Some of the nodes are supported only by homoplastic characters, and only very few nodes by characters perfectly congruent (Fig. 114).

The effects of homoplasy may be quite elusive, as evidenced by the otherwise excellent work of Nishida (1990) on the higher-level relationships of rays. Nishida's data were not

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subjected by him to a parsimony algorithm, even though he provides a character matrix. Analysis using Hennig86 (mh* and bb* options in conjunction) produces a strict consensus topology radically different from the tree Nishida presents, indicating that his data are much more complex than otherwise thought (Nishida's tree is not among the equally most parsimonious trees obtained either).

Compagno (1973, 1977, 1988) has extensively reviewed the relationships within galeomorphs, bringing much anatomical data into consideration. In those papers, he defended a sister-group relationship between Heterodontus and orectolobiforms, but without much conviction, as evidenced by his last review (Compagno, 1988). The characters incorporated in the present analysis do not support a Heterodontus + Orectolobiformes clade, and also reject Compagno's "second" choice phylogeny, in which orectolobiforms and carcharhiniforms are sister-groups. Characters shared by Heterodontus and orectolobiforms were included in my analysis, but are best optimized as defining features of Galeomorphii (with the secondary loss further supporting lamniforms + carcharhiniforms). However, it is unclear if the inclusion of additional characters putatively derived for Heterodontus and orectolobiforms will render this a monophyletic group. These taxa share the (or a) derived condition of characters 4 (downcurved ethmoidal area), 27 (insertion of the suborbitalis muscle anterior to adductor mandibulae) and 55 (presence of nasoral groove; also in Squatina). Because there is homoplasy in these characters for the tree (Fig. 114), it is possible that perhaps one more character shared by these taxa is enough to render them monophyletic. This situation occurs in many other branches of the tree, and is a function of the high number of discordant characters.

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As is now quite obvious, high levels of homoplasy render the use of parsimony algorithms to be a mandatory procedure when dealing with the phylogenetic relationships of elasmobranchs. This kind of analysis came relatively late in the field of chondrichthyan systematics, however, and Shirai (1992c) is definitively among the first to implement computer-based tree searches. The tardy application of more rigorous systematic methods (with or without parsimony algorithms), which are a routine practice in many groups, is intriguing, and may well be the result of few practicing elasmobranch systematists and the virtually unchallenged acceptance of Compagno's classifications by elasmobranch researchers.

Fossil Neoselachians

Fossil taxa are important when addressing relationships among basal Recent elasmobranchs. As used here, Neoselachii includes at least Palaeospinax (and possibly Synechodus), a taxon important for the optimization of characters previously restricted to living forms or their (mainly Tertiary) immediate relatives. Alternatively, if living chimaeroids are used as an outgroup, in an analysis of only Recent taxa (as did Dingerkus, unpubl.), the information contained in Paleozoic and Mesozoic sharks would be ignored, changing the interpretation of many features (e.g., fusion of posteriormost dorsal gill arch elements [gill pick-ax], fused coracoids, etc.). Because the objective of phylogenetic analysis is to determine the origin (and therefore distribution) of a character on a tree (i.e., relationships), data from fossil elasmobranchs must be included at this level, otherwise the origin of a specific feature may be (erroneously) hypothesized to be at a less inclusive node.

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The present analysis identified four characters in support of a group of "modern level elasmobranchs," less inclusive than Neoselachii, composed of Recent elasmobranchs and fossil taxa placed within extant groups (represented by Squalus in Fig. 113A). This distinction was present in the scheme put forth by Moy-Thomas (1939), and followed to a varying degree by subsequent authors (Arambourg and Bertin, 1958; Compagno, 1973, 1977; Schaeffer, 1981; Thies, 1983; Maisey, 1982, 1983, 1984a, b, 1986b). However, a more complete understanding of the anatomy of Palaeospinax (Schaeffer, 1967; Reif, 1974; Maisey, 1977) and Synechodus (Schweizer, 1964; Reif, 1973) has led to the belief that "So far, no convincing higher elasmobranch synapomorphies have been established that would exclude these fossils from a taxon consisting only of extant elasmobranchs" (Maisey, 1984a: 36). Of the four characters proposed here to unite "modern elasmobranchs" one concerns muscles (character 28), and one from cartilage that is at best very weakly calcified (character 19, extrabranchial cartilages on hyoid arch). Because this level of the phylogeny seems more subjected to the vagaries of preservation, Maisey's statement is to some degree still applicable in spite of these characters. The biochemical characters cited in Maisey (1986b; not included in my matrix) also are unavailable in stem-group neoselachians. Accordingly, Shirai (1992c: 14) does not recognize synapomorphies of Recent elasmobranchs, which he accepted as "traditional," even though his analysis contained characters that are optimized as synapomorphies of that group here.

A paradoxical aspect inherent in dealing with fossil and extant taxa together in the same analysis is the optimization of characters that are unpreserved in the fossils, such as muscles, "soft" anatomy, external coloration patterns, etc. The matrix in Table 47 has many features derived from muscles. When these characters involve transformations occurring at the base of

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the tree (i.e., at or close to the boundary that separates extant elasmobranchs from stem-group neoselachians), different options for their optimization exist that are ambiguous. Consider character 26 above. Character 26 (origin of suborbitalis) has five states, of which two (states 3 and 4) can be equally optimized at the root. There is really no basis for deciding which state best defines the ingroup (Recent elasmobranchs). Outgroup taxa certainly do not help here, but unquestionably Palaeospinax must have had some state of this character. Because this information is unavailable, an extra step is counted for the tree, due to the placement of both states at the nodes where they occur unequivocally (node **a** for state 4, node **g** for state 3) even though the actual placement of one of these states lies at a more inclusive node. In comparison, Hennig86 economized a step by placing one of these states at the outgroup node, thus assuming the "?" entry in the outgroup to be "1," pushing the character further down the tree.

The studies of Reif (1973, 1974, 1977, 1978) concerning the fine structure of tooth enameloid has led to more characters being proposed as defining features of Neoselachii, notably triple-layered enameloid (Maisey, 1984a, 1986b). Reif's (1974) own study of Palaeospinax, however, does not reveal three layers – the third and innermost layer (haphazardly fibered or "tangled" enameloid) apparently is absent. Synechodus is described as having all three layers (Reif, 1973; cf. Maisey, 1985), which might place it closer to Recent elasmobranchs than Palaeospinax, as suggested, on the basis of other evidence, by Maisey (1985). The presence of "shiny-layer" and "parallel-fibered" enameloid ("tooth type ß") are uncontested neoselachian characters, even though homoplasy is required as rajiforms apparently lack specialized enameloid layers (Reif, 1973, 1977). Curiously, Reif (1977)

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downplays the importance of haphazardly-fibered enameloid, stating that it is of "little diagnostic value" (p. 570), even though it is absent from the hybodont and ctenacanth fossils he examined. Confusingly, in a later study, Reif (1978) credits all neoselachians (his Euselachii) as having triple-layered enameloid. However stated, the enameloid ultrastructure is specialized for neoselachians, even though the condition in Palaeospinax regarding the third layer is unclear.

Fossil neoselachians are known for the most part from isolated teeth and incomplete skeletal remains (an exception is the neurocranium of Synechodus described by Maisey, 1985). The scarce anatomical data available leaves the position of these taxa open to some speculation, although they are without a doubt closer to Recent elasmobranchs than to other euselachians (Maisey, 1986b; Fig. 113A). Cappetta (1987: 128) and Cappetta et al. (1993) leave the Palaeospinacidae (in which they include Synechodus) as "Galeomorphii incertae ordinis." Maisey (1985) considered two alternatives regarding the phylogenetic placement of Synechodus, either as the sister-group to all Recent elasmobranchs or as the most basal galeomorph. Palaeospinax and Synechodus are known to possess characters diagnostic of "higher" or "modern" elasmobranchs (e.g., occipital hemicentrum, primary calcification of notochord, specialized enameloid layering in teeth). However, only Synechodus has been determined to share similarities with galeomorphs that are possibly derived (Maisey, 1985), even though this remains unresolved. Hence, Palaeospinax is interpreted as a basal neoselachian in this study (cf. Schaeffer, 1967), a situation that may change once more information is available.

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Other contenders for neoselachian membership are the orthacodontids and anacoracids, which are known almost exclusively from isolated teeth (the exception is Sphenodus nitidus [= S. macer?] from Solnhofen; Beaumont, 1960). In recent reviews, these taxa have been considered to be hexanchoids and lamniforms, respectively (Cappetta, 1987; Cappetta et al., 1993), but it is not very clear if the similarities on which these assignments are based are in fact derived, primitive or homoplastic. These taxa are perhaps best considered *incertae sedis* at present.

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CONCLUSIONS

The classification resulting from the analysis presented here, summarized below, is somewhat intermediate when compared to the previous classifications of Compagno (1973, 1977, 1984) and Shirai (1992c). Shirai's Squalea is corroborated, but his components (hexanchoids + (Echinorhinus + (Dalatiiformes + (Squalidae + Hypnosqualea)))) and (Squalidae + Hypnosqualea) are not. Instead, Hexanchiformes and a slightly modified Squaliformes (without Echinorhinus) are defended as monophyletic groups. Recent elasmobranchs are divided into 10 monophyletic orders. The relationships among the four superorders of Compagno are fully resolved, corroborating further the work of Shirai at this level. The following hierarchic summary of ordinal groups includes only living forms although, as mentioned, some fossil groups are well corroborated systematically.

Class Chondrichthyes

Subclass Elasmobranchii

Infraclass Neoselachii

Division Galeomorphii

Superorder Heterodontoidea

Order Heterodontiformes

Superorder Galeoidea

Order Orectolobiformes

Order Lamniformes

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Order Carcharhiniformes

Division Squalea

Superorder Notidanoidea

Order Hexanchiformes

Suborder Chlamydoselachoidei

Suborder Hexanchoidei

Superorder Echinorhinoidea

Order Echinorhiniformes

Superorder Squaloidea

Order Squaliformes

Suborder Squaloidei

Suborder Dalatioidei

Superorder Hypnosqualea

Order Squatiniformes

Order Pristiophoriformes

Order Rajiformes

As with any analysis of this kind, coding and comparing the distribution of a character across a wide range of taxa proved to be difficult when the character required division into more than two states and many "intermediate" conditons exist. For example, coding secondary calcifications of the vertebral centra proved extremely complex, and this character was not included (Compagno, 1988). This is not to say that this character has no potential for

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synapomorphy or phylogenetic significance. What is implied by this exclusion is that this character, and others similar to it, can be included confidently only in a matrix containing more terminal taxa such that coding is straightforward. It is difficult to code a single terminal that represents an entire order for a character with such a scattered distribution (e.g., secondary calcification patterns for Carcharhiniformes).

This paper presented a broad overview of recent developments in elasmobranch phylogeny. As such, much emphasis was given to the work of Shirai (1992c), who has made substantial progress in creating a more rigorous and modern footing for the systematics of certain shark groups, and especially how these groups are related to the rays. Particular to Shirai's contributions is the demise of a taxon variously denoted "Squaliformes" or "Squaloidei," which, although lacking defining characters, was entrenched. The major problem in establishing a monophyletic Squaliformes, however, was more an outcome of the cryptic effects of homoplasy as opposed to the "right" character(s) never having been found by those authors supporting it. The substantial amount of incongruence exhibited by any phylogeny constructed with the taxa in question is capable of misleading any systematist not equipped with parsimony algorithms. The matrix used here contains characters that were used by previous authors, but the novel placement of some of these characters derives from a more fuller exploration of their interactions, which is only possible with the application of computer-based parsimony procedures.

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A

A SYSTEMATIC REVISION OF THE ELECTRIC RAY GENUS NARCINE HENLE, 1834 (CHONDRICHTHYES: TORPEDINIFORMES: NARCINIDAE), AND THE HIGHER-LEVEL PHYLOGENETIC RELATIONSHIPS OF THE ORDERS OF ELASMOBRANCH FISHES (CHONDRICHTHYES)

(Parts I and II)

by

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VOLUME II (TABLES AND ILLUSTRATIONS)

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TABLES

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PART I

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Table 1. List of nominal and valid genera of Torpediniformes. The 32 nominal genera of Torpediniformes are arranged in chronological order. Column on right indicates present status. Compiled from original descriptions, Gill (1895), Fowler (1941), Bigelow and Schroeder (1953) and Eschmeyer (1990; 1998). Spelling is maintained as in original publications. The number in parentheses for valid genera indicates number of nominal species presently available in each genus (Eschmeyer, 1998; Carvalho, unpubl.).

Torpedo Houttuyn, 1764	valid (46)
Narcacion Klein, 1776	not available[6]
Torpedo Duméril, 1806	synonym of Torpedo Houttuyn, 1764
Torpedo Rafinesque, 1810	synonym of Torpedo Houttuyn, 1764
Apturus Rafinesque, 1815	not available[7]
Megabatus Rafinesque, 1815	not available[7]
Sephenia Rafinesque, 1815	not available[7]
Narcobatus Blainville, 1816	synonym of Torpedo Houttuyn, 1764
Narke Kaup, 1826	valid (6)
Temera Gray, 1831	valid (1)
Narcine Henle, 1834	valid (26)
Astrape Müller and Henle, 1837	synonym of Narke Kaup, 1826
Syrraxis Jourdan, 1841[8]	synonym of Narcine Henle, 1834
Discopyge Heckel, 1846	valid (3)
Hypnos Duméril, 1852	valid (2)
Narcacion Gill, 1862[6]	synonym of Torpedo Houttuyn, 1764
Tetronarce Gill, 1862[9]	synonym of Torpedo Houttuyn, 1764
Cyclonarce Gill, 1862	synonym of Narcine Henle, 1834
Gonionarce Gill, 1862	synonym of Narcine Henle, 1834

[6] According to Opinion no. 1938 of the ICZN (published in 1910, see reference in Bigelow and Schroeder, 1953: 90, footnote 42), Klein's (1775) genera and the revival of them by Walbaum (1792) are not permissable. Hence, Narcacion dates from Gill (1862), the first to define the genus subsequently.

[7] Rafinesque-Schmalz (1815) used these generic names without species, intended for eletric rays (Eschmeyer, 1990: 36, 239, 377).

[8] Published in Bonaparte (1841, no pagination). Type species: Narcine indica Henle, 1834 (Bigelow and Schroeder, 1953: 107).

[9] According to Gill (1895: 163), Tetranarce was the intended original spelling – Tetronarce being an error by the printer. However, the original spelling as printed and not as intended is adopted here (ICZN).

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Table 1 (cont.).

Fimbriotorpedo Fritsch, 1884	synonym of Torpedo Houttuyn, 1764
Gymnotorpedo Fritsch, 1884	synonym of Torpedo Houttuyn, 1764
Benthobatis Alcock, 1898	valid (3)
Hypnarce Waite, 1902[10]	synonym of Hypnos Duméril, 1852
Tetronarcine Tanaka, 1908	synonym of Torpedo Houttuyn, 1764
Typhlonarke Waite, 1909	valid (2)
Bengalichthys Annandale, 1909	synonym of Narke Kaup, 1826
Eunarce Fowler, 1910	synonym of Torpedo Houttuyn, 1764
Heteronarce Regan, 1921	valid (6)
Notastrape Whitley, 1932	synonym of Torpedo Houttuyn, 1764
Narcinops Whitley, 1940	synonym of Narcine Henle, 1834
Diplobatis Bigelow and Schroeder, 1948	valid (6)
Crassinarke Takagi, 1951	uncertain[11]

[10] Waite (1902: 180) published Hypnarce as a replacement name for Hypnos Duméril, 1852, which he erroneously believed was occupied in Lepidoptera.

[11] The type-species of Crassinarke, Crassinarke dormitor Takagi, 1951, is included in the species count of Narke. See footnote for "Key to the Genera of Torpdeiniformes" for more information concerning the validity of Crassinarke.

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Table 2. Nominal species of Torpedinidae and Hypnidae and their present status. Nominal species arranged chronologically within genera.

NOMINAL SPECIES	STATUS
Torpedo Houttuyn, 1764:	
Raja torpedo Linnaeus, 1758	valid
Torpedo marmorata Risso, 1810	valid
Torpedo galvani Risso, 1810	?syn. of T. marmorata Risso, 1810
Torpedo ocellata Risso, 1810	syn. of R. torpedo Linnaeus, 1758
Torpedo narke Risso, 1810	syn. of R. torpedo Linnaeus, 1758
Torpedo unimaculata Risso, 1810	syn. of R torpedo Linnaeus, 1758
Torpedo immaculata Rafinesque, 1810	?syn. of T. marmorata Risso, 1810
Torpedo punctata Rafinesque, 1810	?syn. of T. marmorata Risso, 1810
Torpedo variegata Rafinesque, 1810	?syn. of T. nobiliana Bonaparte, 1835
Torpedo vulgaris Fleming, 1828	?syn. of T. marmorata Risso, 1810
Torpedo panthera von Olfers, 1831	valid
Torpedo sinuspersici von Olfers, 1831	syn. of T. panthera von Olfers, 1831
Torpedo pardalis von Olfers, 1831	?syn.of T. marmorata Risso, 1810
Torpedo diversicolor Davy, 1834	?syn.of T. marmorata Risso, 1810
Torpedo oculata Davy, 1834	?
Torpedo nobiliana Bonaparte, 1835	valid
Torpedo electrica Swainson, 1838	?
Torpedo emarginata McCoy, 1841	?syn. of T. nobiliana Bonaparte, 1835
Torpedo occidentalis Storer, 1843	?syn. of T. nobiliana Bonaparte, 1835
Torpedo picta Lowe, 1843	?syn. of T. marmorata Risso, 1810
Torpedo hebitans Valenciennes, 1841	?syn. of T. marmorata Risso, 1810
Torpedo trepidans Valenciennes, 1843	?syn. of T. marmorata Risso, 1810
Torpedo nigra Guichenot, 1850	?syn. of T. marmorata Risso, 1810

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Table 2 (cont.).

Torpedo oculata Duméril, 1852	primary hom. of T. oculata Davy, 1834
Torpedo californica Ayres, 1855	valid
Torpedo fuscomaculata Peters, 1855	valid
Torpedo walshii Thompson, 1856	?syn. of T. nobiliana Bonaparte, 1835
Narcacion polleni Bleeker, 1866	?valid
Torpedo smithii Gunther, 1870	syn. of T. sinuspersici von Olfers, 1831
Torpedo fairchildi Hutton, 1872	valid
Torpedo fusca Parker, 1884	syn. of T. fairchildi Hutton, 1872
Torpedo suessii Steindachner, 1898	?valid
Torpedo torpedo atlantica Pietschmann, 1906	syn. of R. torpedo Linnaeus, 1758
Torpedo torpedo mediterranea Pietschmann, 1906	syn. of R. torpedo Linnaeus, 1758
Tetranarcine tokionis Tanaka, 1908	valid
Torpedo zugmayeri Engelhardt, 1912	?
Torpedo mackayana Metzelaar, 1919	valid
Torpedo puelcha Lahille, 1928	valid
Notastrape macneilli Whitley, 1932	valid
Torpedo tremens de Buen, 1959	valid
Torpedo andersoni Bullis, 1962	valid
Torpedo tremens peruana Chirichigno, 1963	?valid
Torpedo bauchotae Cadenat, Capapé and Desoutter, 1978	valid
Torpedo microdiscus Parin and Kotylar, 1985	?valid
Torpedo semipelagica Parin and Kotylar, 1985	?valid
Torpedo alexandriensis Mazhar, 1987	?valid
Hypnos Duméril, 1852:	
Lophius monopterygius Shaw and Nodder, 1796	valid
Hypnos subnigrum Duméril, 1852	syn. of L. monopterygius Shaw and Nodder, 1796

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Table 3. Nominal species of Narkidae and their present status. Nominal species of Narkidae (including Narke, Temera, Typhlonarke and Heteronarce) arranged according to genus and by chronological order within genera.

NOMINAL SPECIES	STATUS
Narke Kaup, 1826:	
Raja capensis Gmelin, 1789	valid
Raja dipterygia Bloch and Schneider, 1801	valid
Torpedo (Astrape) japonica Schlegel, 1850	valid
Torpedo capensis Gronow, 1854	synonym of R. capensis Gmelin, 1789
Bengalichthys impennis Annandale, 1909	?syn.of R. dipetrygia Bloch and Schneider, 1801
Crassinarke dormitor Takagi, 1951	?syn.of T. (Astrape) japonica Schlegel, 1850
Temera Gray, 1831:	
Temera hardwickii Gray, 1831	valid
Typhlonarke Waite, 1909:	
Astrape aysoni Hamilton, 1902	valid
Typhlonarke tarakea Phillips, 1929	?valid
Heteronarce Regan, 1921:	
Narcine mollis Lloyd, 1907	valid
Heteronarce garmani Regan, 1921	valid
Heteronarce regani von Bonde and Swart, 1923	syn. of H. garmani Regan, 1921
Narcine natalensis Fowler, 1925	syn. of H. garmani Regan, 1921
Heteronarce prabhui Talwar, 1981	?syn.of H. garmani or H. mollis; ?valid
Narcine bentuviai Baranes and Randall, 1989	valid

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Table 4. Nominal species of Narcinidae, exclusive of Narcine Henle, 1834 and their present status. Nominal species arranged according to genera and in chronological order within genera.

NOMINAL SPECIES	STATUS
Discopyge Heckel, 1846:	
Discopyge tschudii Heckel, 1846	valid
Torpedo chilensis Guichenot, 1848	synonym of D. tschudii Heckel, 1846
Narcine nigra Duméril, 1852	?valid
Benthobatis Alcock, 1898:	
Benthobatis moresbyi Alcock, 1898	valid
B. marcida Bean and Weed, 1909	valid
B. cervina Bean and Weed, 1909	syn. of B. marcida Bean and Weed, 1909
Diplobatis Bigelow and Schroeder, 1948:	
Discopyge ommata Jordan and Gilbert, 1890	valid
Narcine ommata Clark, 1936	syn. of D. ommata Jordan and Gilbert, 1890
Diplobatis pictus Palmer, 1950	valid
Diplobatis guamachensis Martin, 1957	synonym of D. pictus Palmer, 1950
Diplobatis altenai Boeseman, 1963	valid
Diplobatis colombiensis Fechhelm and McEachran, 1984	valid

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Table 5. Chronology of nominal species available in the Recent genus Narcine Henle, 1834. Spelling of names and generic assignment is maintained as in original publications. Refer to species accounts for more information on the status of each nominal species.

NOMINAL SPECIES	STATUS
Raja timlei Bloch and Schneider, 1801	valid
Raja maculata Shaw, 1804[12]	valid
Raja bicolor Shaw, 1804[12]	synonym of R. maculata Shaw, 1804
Torpedo ocellata Quoy and Gaimard, 1824	homonym of T. ocellata Rafinesque, 1810
Torpedo brasiliensis von Olfers, 1831	valid
Narcine indica Henle, 1834	synonym of R. timlei Bloch and Schneider, 1801
Torpedo bancroftii Griffith, 1834[13]	valid
Narcine tasmaniensis Richardson, 1841	valid
Narcine lingula Richardson, 1846[14]	valid
Narcine macrura Valenciennes, 1852[15]	synonym of R. timlei Bloch and Schneider, 1801
Narcine maculata Duméril, 1852	secondary homonym of R. maculata Shaw, 1804
Narcine microphthalma Valenciennes, 1852[15]	synonym of R. timlei Bloch and Schneider, 1801
Torpedo pictus Gray, 1854[16]	synonym of T. bancroftii Griffith, 1834
Narcine corallina Garman, 1881	synonym of T. bancroftii Griffith, 1834
Narcine punctata Garman, 1881	synonym of T. bancroftii Griffith, 1834
Narcine umbrosa Jordan, 1884	synonym of T. bancroftii Griffith, 1834
Narcine entemedor Jordan and Starks, 1895	valid
Narcine brunnea Annandale, 1909	synonym of R. timlei Bloch and Schneider, 1801
Narcine firma Garman, 1913	synonym of R. maculata Shaw, 1804
Narcine brachypleura Miranda Ribeiro, 1923	synonym of T. brasiliensis von Olfers, 1831
Narcine vermiculatus Breder, 1928	valid
Narcine schmitti Hildebrand, 1948	synonym of N. vermiculatus Breder, 1928

[12] Species based on plates and descriptions of P. Russell (1803).
[13] Species based on a plate by Bancroft, published by Griffith in Cuvier (1834).
[14] Species based on plate by J. Reeves.
[15] Published in Duméril (1852).

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Table 5 (cont.).

Narcine brevilabiata Bessednov, 1966	valid
Narcine prodorsalis Bessednov, 1966	synonym of N. lingula Richardson, 1846
Narcine westraliensis McKay, 1966	valid
Heteronarce rierai Lloris and Rucabado, 1991	valid

[16] Species based on manuscript of L.T. Gronovius, edited by Gray (1854) who proposed the specific name.

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Table 6. Measurements taken on specimens of Narcine brasiliensis (von Olfers, 1831). A) Lectotype of Torpedo brasiliensis von Olfers, 1831 (ZMB 4577); B) Paralectotype of Torpedo ocellata Quoy and Gaimard, 1824 (MNHN 7891); C) Paralectotype of Torpedo ocellata Quoy and Gaimard, 1824 (MNHN 7891); D) Lectotype of Torpedo ocellata Quoy and Gaimard, 1824 (MNHN 7516); E) Holotype of Narcine brachypleura Miranda Ribeiro, 1923 (MNRJ 548). Ranges given do not include types (A – E); N is number of specimens, including types, from which means and standard deviations (SD) were taken.

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	A	B	C	D	E	NON-TYPES	N	MEAN	SD
TL (mm)	235.0	110.0	103.0	107.0	321.0	107.0 – 445.0	35	--	--
DW (%)	51.4	50.0	43.7	52.6	44.5	45.2 – 55.3	35	51.0	2.8
DL (%)	48.5	48.2	48.5	49.0	48.0	45.7 – 56.0	35	50.2	2.5
PCSL (%)	10.5	11.1	--	11.9	9.4	8.9 – 14.2	34	11.1	1.1
POSL (%)	12.5	12.8	11.2	14.4	12.0	11.0 – 16.5	35	13.3	1.2
PNSL (%)	9.4	9.6	--	10.9	9.0	8.3 – 12.8	34	10.4	1.1
SDW (%)	31.1	28.2	--	31.0	28.0	24.1 – 39.9	34	28.9	3.1
IOD (%)	6.0	7.5	6.1	7.7	5.5	4.8 – 8.9	35	6.7	0.8
EL (%)	3.4	3.3	3.7	3.8	2.4	2.2 – 3.9	35	3.1	0.4
ISD (%)	6.6	7.5	7.5	8.8	6.0	4.7 – 9.6	35	7.0	0.9
SPL (%)	1.8	2.8	1.9	2.6	1.9	1.5 – 2.5	35	2.0	0.3
SPW (%)	1.6	2.8	1.9	2.6	2.1	1.4 – 2.6	35	2.0	0.4
MW (%)	7.1	6.6	6.7	5.7	5.8	5.6 – 9.6	35	6.8	0.7
UTBW (%)	2.6	3.8	4.0	2.6	3.1	2.4 – 3.4	35	3.1	0.3
LTBW (%)	2.5	3.7	2.7	2.9	2.6	2.3 – 3.3	34	2.8	0.3
NCW (%)	6.0	6.5	--	6.1	6.3	5.2 – 6.7	34	6.0	0.4
NCL (%)	2.6	2.3	--	2.5	2.8	1.7 – 3.1	34	2.2	0.4
DBN (%)	6.4	6.6	--	5.7	5.7	5.4 – 6.7	34	6.2	0.4
DBFGO(%)	12.2	13.5	--	13.7	13.2	12.4 – 16.1	34	14.3	0.9
DBLGO(%)	8.0	7.6	--	9.3	7.0	6.6 – 11.5	34	8.8	1.2
BBL (%)	8.6	10.3	--	12.2	8.8	6.9 – 10.7	34	9.4	1.1
PFL (%)	26.4	20.0	--	19.7	31.2	15.4 – 27.2	34	24.0	2.7
PFW (%)	33.3	--	--	29.9	24.9	29.6 – 38.4	33	33.1	2.8
ALPF (%)	14.0	12.8	--	12.7	9.7	8.9 – 17.1	34	13.1	1.9
PLPF (%)	18.2	17.7	--	14.1	19.3	15.6 – 24.6	34	19.8	2.6
TW (%)	21.3	14.8	16.0	20.2	23.1	16.3 – 25.4	35	20.5	2.6
HFD (%)	10.9	9.0	--	9.5	9.0	6.5 – 12.3	34	9.7	1.2
LFD (%)	6.7	6.9	--	7.0	6.7	5.8 – 7.8	34	6.9	0.4
HSD (%)	10.4	9.5	--	9.2	8.8	8.1 – 12.4	34	10.3	1.2
LSD (%)	6.9	6.5	--	6.6	7.1	5.6 – 7.8	34	7.0	0.5
LDLC (%)	13.7	13.2	--	12.9	10.1	9.8 – 14.3	34	12.5	1.0
LVLC (%)	15.1	14.1	--	11.4	11.6	11.3 – 15.7	34	13.1	1.1
HDLC (%)	5.8	5.7	--	4.2	5.0	3.6 – 8.4	34	6.0	1.0
HVLC (%)	4.7	4.3	--	4.0	4.2	2.7 – 5.7	34	4.6	0.6
HC (%)	12.3	11.4	--	10.1	9.7	8.3 – 14.4	34	11.9	1.4
DBD (%)	4.3	5.5	--	4.8	6.4	3.3 – 7.3	34	4.9	0.9
DSDC (%)	5.3	5.7	--	5.7	5.2	3.3 – 6.6	33	4.9	0.8
SCL (%)	48.9	50.9	--	54.8	45.8	46.7 – 53.6	34	50.3	2.1
CLCF (%)	46.8	50.9	--	46.8	47.7	42.0 – 51.3	34	46.3	2.0
SFD (%)	62.6	63.6	--	65.8	63.9	58.4 – 68.5	34	64.0	1.9
EOL (%)	23.4	29.1	--	23.2	23.7	21.5 – 32.3	34	24.9	2.4
EOW (%)	9.8	9.8	--	10.5	6.3	7.5 – 13.4	34	10.0	1.5
CL (%)	20.4	10.5	--	11.2	18.1	11.5 – 20.9	33	17.6	3.0

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Table 7. Counts for Narcine brasiliensis (von Olfers, 1831). A) Lectotype of Torpedo brasiliensis von Olfers, 1831 (ZMB 4577; Rio de Janiero); B) Lectotype of Torpedo ocellata Quoy and Gaimard, 1824 (MNHN 7516); C) Paralectotype of T. ocellata Quoy and Gaimard, 1824 (MNHN 7891, 110 mm TL); D) Paralectotype of T. ocellata Quoy and Gaimard, 1824 (MNHN 7891, 103 mm TL); E) MCZ 164 (Rio de Janeiro); F) MCZ 643 (Rio de Janeiro); G) MCZ 643 (Rio de Janiero); H) MNHN 1992-1288 (Rio de Janeiro); I) MNHN 1992-1289 (Rio de Janeiro); J) MNHN 1991-55 (Rio de Janeiro); K) MCP 3381 (Rio Grande do Sul). Values that are approximate include PROP, DCR, VCR and TCR for column A and DCR for column C. Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	G	H	I	J	K	RANGE
PROP	21	21	19	20	18	20	22	20	19	19	21	18 – 22
MESO	9	8	8	8	8	8	7	8	7	7	8	7 – 9
META	8	10	6	6	9	12	10	11	11	11	10	6 – 12
TPR	38	39	33	34	35	40	39	39	37	37	39	33 – 40
PVR	18	18	20	19	18	21	18	19	21	19	22	18 – 22
FDR	–	10	–	–	11	9	9	–	8	9	10	8 – 11
SDR	8	–	–	11	10	9	11	11	9	–	9	8 – 11
DCR	20	22	17	–	26	24	23	–	–	22	27	17 – 27
VCR	26	24	24	–	25	26	–	–	–	27	27	24 – 27
TCR	46	46	41	–	51	50	–	–	–	49	54	41 – 54
TC	26	32	28	27	26	28	30	28	31	30	28	26 – 32
PC	67	70	64	75	64	66	71	72	67	64	67	64 – 75
CC	26	25	26	26	26	24	25	–	23	26	24	23 – 26
TV	119	127	118	128	116	118	126	–	121	120	119	116 – 128
R	8	9	10	8	8	9	8	8	9	8	9	8 – 10

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Table 8. Measurements taken on specimens of Narcine bancroftii (Griffith, 1834). A) Holotype of N. punctata Garman, 1881 (MCZ 752); B) Lectotype of N. corallina Garman, 1881 (MCZ 44); C) Paralectotype of N. corallina Garman, 1881 (MCZ 44); D) Lectotype of N. umbrosa Jordan, 1884 (CAS 18246); E) Paralectotype of N. umbrosa Jordan, 1884 (USNM 36940). Ranges given do not include types (A – E); N is number of specimens, including types, from which means and standard deviations (SD) were taken.

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	A	B	C	D	E	NON-TYPES	N	MEAN	SD
TL (mm)	234.0	249.0	195.0	250.0	279.0	135.0 – 561.0	117	--	--
DW (%)	50.0	45.0	51.3	46.4	45.2	43.0 – 59.7	117	51.7	3.4
DL (%)	53.4	48.6	49.2	47.2	45.2	44.9 – 56.9	116	51.0	2.5
PCSL (%)	12.7	11.7	12.7	10.6	10.2	9.7 – 16.5	117	12.4	1.2
POSL (%)	15.6	13.8	14.9	12.7	12.1	11.4 – 18.1	117	14.5	1.3
PNSL (%)	12.9	11.0	12.5	9.9	9.4	9.0 – 16.5	117	11.5	1.2
SDW (%)	33.8	36.1	35.4	28.0	26.9	22.6 – 39.3	117	30.9	3.1
IOD (%)	7.4	6.7	6.9	5.7	6.0	5.2 – 8.1	117	6.7	0.6
EL (%)	3.2	4.3	4.6	3.4	2.9	1.1 – 4.4	117	3.1	0.5
ISD (%)	7.9	6.7	7.4	6.3	6.3	4.9 – 7.8	117	6.5	0.5
SPL (%)	2.2	1.8	2.1	2.2	2.4	1.7 – 3.1	117	2.2	0.3
SPW (%)	2.2	2.9	2.6	2.0	2.3	1.5 – 3.1	116	2.3	0.3
MW (%)	7.0	6.6	6.7	6.4	7.3	5.2 – 7.8	116	6.3	0.5
UTBW (%)	3.3	2.9	3.1	3.4	2.8	2.0 – 3.8	116	3.0	0.3
LTBW (%)	3.1	2.9	2.8	3.1	2.7	2.0 – 6.8	116	2.9	0.5
NCW (%)	6.1	5.6	5.8	5.4	5.1	3.7 – 6.6	117	5.4	0.5
NCL (%)	2.1	2.2	1.7	2.4	1.6	1.4 – 5.8	116	2.3	0.6
DBN (%)	5.9	5.6	6.1	5.6	5.4	2.4 – 6.7	116	5.6	0.5
DBFGO(%)	15.9	12.5	13.3	12.4	12.2	10.1 – 17.3	116	13.8	1.3
DBLGO(%)	9.7	7.6	9.5	8.8	6.5	6.1 – 12.7	116	8.5	1.2
BBL (%)	10.6	8.1	9.9	8.0	8.6	6.5 – 14.1	116	9.2	1.0
PFL (%)	24.8	21.8	23.5	23.2	20.8	15.6 – 27.5	117	23.8	1.9
PFW (%)	36.2	29.4	31.7	31.2	32.3	26.5 – 39.4	117	33.0	2.2
ALPF (%)	12.1	13.8	14.6	11.6	13.6	9.5 – 17.0	117	12.4	1.6
PLPF (%)	24.3	18.6	16.8	20.0	16.1	12.3 – 25.7	117	20.1	2.8
TW (%)	22.4	17.8	19.5	18.4	20.1	16.1 – 27.8	117	21.3	2.4
HFD (%)	9.6	11.4	9.8	9.3	--	7.2 – 12.1	116	9.7	0.9
LFD (%)	6.2	7.0	6.6	6.4	6.2	4.8 – 8.6	117	6.5	0.6
HSD (%)	9.8	11.3	11.6	9.4	8.9	8.3 – 12.2	116	10.3	0.8
LSD (%)	7.1	7.3	6.7	6.6	6.2	5.7 – 7.8	116	6.8	0.4
LDLC (%)	13.6	13.5	13.9	12.4	--	9.0 – 14.3	116	11.8	1.1
LVLC (%)	13.4	14.0	13.3	11.2	--	9.9 – 14.3	116	12.1	1.0
HDLC (%)	6.7	6.3	5.0	4.4	--	3.5 – 7.5	116	5.3	0.8
HVLC (%)	6.1	4.9	4.4	4.2	--	3.1 – 5.5	115	4.3	0.5
HC (%)	13.4	11.9	11.3	9.0	--	7.0 – 14.9	115	11.7	1.3
DBD (%)	4.4	4.3	5.2	6.1	5.8	3.0 – 6.0	117	4.4	0.7
DSDC (%)	3.5	4.0	4.6	4.9	5.8	3.0 – 6.1	116	4.5	0.7
SCL (%)	53.5	49.0	50.3	48.0	47.7	45.7 – 56.1	116	50.5	2.0
CLCF (%)	43.7	47.8	46.7	46.8	48.0	41.0 – 50.0	117	45.7	1.8
SFD (%)	64.5	61.8	63.6	64.0	63.8	58.1 – 71.0	116	64.4	2.1
EOL (%)	25.7	25.0	23.5	19.2	25.1	19.8 – 29.2	117	24.6	1.6
EOW (%)	10.8	9.4	11.6	7.2	7.5	7.2 – 14.1	117	10.2	1.4
CL (%)	--	18.9	20.7	17.6	18.6	11.1 – 20.4	54	17.5	2.1

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Table 9. Counts for Narcine bancroftii (Griffith, 1834). A) Holotype of Narcine punctata Garman, 1881 (MCZ 752, 234 mm TL; St. Vincent); B) Lectotype of Narcine corallina Garman, 1881 (MCZ 44, 249 mm TL; Key West, Florida); C) Paralectotype of N. corallina Garman, 1881 (MCZ 44, 195 mm TL; Key West, Florida); D) Lectotype of Narcine umbrosa Jordan, 1884 (CAS 18246, 250 mm TL; Key West, Florida); E) Paralectotype of N. umbrosa Jordan, 1884 (USNM 36940, 279 mm TL; Key West, Florida); F) AMNH 9054 (North Carolina); G) AMNH 77069 (South Carolina); H) MCZ 37143 (Florida); I) MCZ 42475 (Alabama); J) FMNH 65830 (Alabama); K) FMNH 31784 (Mississippi); L) – M) MCZ 147915 (Texas); N) FMNH 111898 (Texas); O) USNM 187944 (Jamaica); P) FMNH 2803 (Jamaica); Q) USNM 222484 (Dominica); R) MCZ 47448 (Colombia); S) – T) ISH 251-1981 (Surinam); U) USNM 186411 (Surinam); V) USNM 222472 (French Guiana); W) – X) USNM 216829 (N Brazil). Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
PROP	22	22	21	21	19	22	21	21	20	21	20	21	23	18
MESO	8	8	9	7	7	6	7	8	9	8	8	7	7	8
META	9	8	7	10	7	10	8	7	–	8	9	9	9	8
TPR	39	38	37	38	33	38	36	36	–	37	31	37	39	34
PVR	22	18	17	18	18	19	19	20	21	20	20	18	18	21
FDR	10	10	7	9	–	7	8	8	10	7	5	8	–	8
SDR	11	11	9	9	10	9	10	7	11	11	8	–	10	10
DCR	24	20	21	19	–	21	20	18	20	–	–	21	–	–
VCR	29	25	25	–	–	26	23	23	25	–	–	27	–	–
TCR	53	45	46	–	–	47	43	41	45	–	–	48	–	–
TC	30	24	24	23	26	28	28	27	27	31	28	26	27	25
PC	70	65	68	73	68	65	65	68	66	64	65	68	72	67
CC	28	32	27	25	27	30	26	21	25	28	22	23	22	18
TV	128	121	119	121	121	123	119	116	118	123	115	117	121	110
R	8	8	8	9	8	7	9	8	8	9	8	9	8	8

	O	P	Q	R	S	T	U	V	W	X	RANGE
PROP	22	20	20	22	22	23	23	21	22	23	18 – 23
MESO	8	7	9	7	8	7	7	7	8	7	6 – 9
META	10	9	10	11	10	11	10	9	10	11	7 – 11
TPR	40	36	39	40	40	41	40	39	40	41	31 – 41
PVR	19	18	22	21	22	22	21	18	19	21	17 – 22
FDR	9	8	7	8	9	8	9	10	–	8	5 – 10
SDR	10	10	9	–	10	10	11	9	11	10	7 – 11
DCR	21	–	20	–	21	21	–	21	21	–	18 – 24
VCR	27	–	22	21	26	29	–	27	27	–	21 – 29
TCR	48	–	42	–	47	50	–	48	48	–	41 – 53
TC	27	29	29	27	29	25	32	31	29	30	23 – 32
PC	66	74	66	65	74	70	67	63	71	68	63 – 74
CC	26	20	23	24	25	26	26	26	28	26	18 – 32
TV	119	123	118	116	128	126	125	120	128	124	110 – 128
R	7	8	7	8	8	9	9	8	8	8	7 – 9

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Table 10. Measurements for Narcine brevilabiata Bessednov, 1966. N indicates number of specimens from which means and standard deviations (SD) were taken.

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	SPECIMENS	N	MEAN	SD
TL (mm)	82.0 – 322.0	15	--	--
DW (%)	47.8 – 57.7	9	53.6	3.1
DL (%)	48.7 – 58.1	9	51.8	2.8
PCSL (%)	12.5 – 15.2	9	14.0	0.8
POSL (%)	14.7 – 17.8	9	16.3	1.1
PNSL (%)	10.9 – 13.1	9	12.3	0.8
SDW (%)	29.0 – 33.9	9	31.2	1.6
IOD (%)	5.7 – 7.1	9	6.1	0.5
EL (%)	2.9 – 3.5	9	3.2	0.2
ISD (%)	4.8 – 7.0	9	5.6	0.8
SPL (%)	2.0 – 2.9	9	2.4	0.3
SPW (%)	2.7 – 3.4	9	3.1	0.2
MW (%)	6.7 – 9.1	9	7.5	0.8
UTBW (%)	1.7 – 2.4	8	2.2	0.2
LTBW (%)	1.0 – 1.6	8	1.2	0.2
NCW (%)	5.6 – 7.9	6	6.3	0.9
NCL (%)	2.2 – 3.1	5	2.6	0.3
DBN (%)	5.3 – 6.4	9	5.8	0.4
DBFGO (%)	12.2 – 15.5	9	13.5	1.1
DBLGO (%)	6.0 – 9.5	9	8.2	1.1
BBL (%)	8.4 – 11.5	9	9.4	1.0
PFL (%)	17.0 – 19.6	9	18.1	0.8
PFW (%)	29.7 – 37.5	9	33.8	2.6
ALPF (%)	10.4 – 13.9	9	12.4	1.2
PLPF (%)	13.4 – 20.2	9	17.0	2.3
TW (%)	14.7 – 20.0	9	18.9	2.0
HFD (%)	8.5 – 11.5	9	9.9	0.9
LFD (%)	5.2 – 7.4	9	6.4	0.7
HSD (%)	8.1 – 10.2	9	9.1	0.8
LSD (%)	5.3 – 7.6	9	6.4	0.7
LDLC (%)	14.0 – 16.8	9	15.1	0.9
LVLC (%)	13.1 – 16.6	9	14.8	1.0
HDLC (%)	5.0 – 7.0	9	6.0	0.7
HVLC (%)	5.0 – 7.1	9	6.0	0.7
HC (%)	12.3 – 15.9	9	13.5	1.1
DBD (%)	4.5 – 6.4	9	5.6	0.6
DSDC (%)	4.9 – 7.8	9	6.4	1.0
SCL (%)	49.6 – 53.0	9	51.0	1.2
CLCF (%)	40.7 – 48.3	9	45.5	2.5
SFD (%)	57.8 – 60.3	9	59.1	1.0
EOL (%)	23.1 – 25.9	9	24.7	0.9
EOW (%)	9.1 – 13.8	9	11.0	1.5
CL (%)	11.1 – 14.5	6	12.9	1.4

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Table 11. Meristics for Narcine brevilabiata Bessednov, 1966. A) CAS 40887 (Hong Kong); B) CAS 114138 (China, Guangdong Prov.); C) CAS 98233, female (Hong Kong); D) CAS 98233, male (Hong Kong); E) FMNH 46990 (Hong Kong); F) USNM 26545 (Hong Kong); G) ZRC 679 (Malaysia, Borneo); H) CAS 98158 (Thailand); I) – N) CAS 98234 (Viet Nam). Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	RANGE
PROP	18	16	–	16	17	17	15	16	18	19	17	16	18	15	15 – 19
MESO	9	8	–	8	8	8	10	8	9	9	9	9	7	8	7 – 10
META	5	5	–	4	4	4	3	4	5	6	4	3	4	3	3 – 6
TPR	32	29	–	28	29	29	28	28	32	34	30	28	29	26	26 – 34
PVR	14	18	16	14	14	15	19	14	17	16	14	18	15	15	14 – 19
FDR	10	7	–	9	9	9	6	8	6	7	8	8	9	7	6 – 10
SDR	9	8	11	9	9	11	9	8	9	–	9	7	5	7	5 – 11
DCR	20	21	21	21	16	20	19	20	23	23	22	20	19	22	16 – 23
VCR	26	30	31	28	22	27	28	31	28	27	27	27	26	25	22 – 31
TCR	46	51	52	49	38	47	47	51	51	50	49	47	45	47	38 – 52
TC	24	27	25	24	25	21	24	24	24	25	21	23	23	25	21 – 27
PC	58	54	57	57	63	62	59	57	59	58	59	55	54	59	54 – 63
CC	26	24	28	24	19	24	31	22	25	25	25	20	23	22	19 – 31
TV	108	105	110	104	107	107	114	103	108	108	105	98	100	106	98 – 114
R	7	6	6	6	6	6	7	5	8	8	8	6	8	6	5 – 8

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Table 12. Measurements for Narcine entemedor Jordan and Starks, 1895. N is number of specimens from which means and standard deviations (SD) were extracted, and includes holotype of N. entemedor (CAS 11699).

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	HOLOTYPE	NON-TYPES	N	MEAN	SD
TL (mm)	421.0	222.0 – 750.0	24	--	--
DW (%)	53.0	44.7 – 53.0	24	49.5	2.3
DL (%)	48.5	43.3 – 52.3	24	48.7	1.9
PCSL (%)	13.1	10.7 – 14.4	24	12.7	1.0
POSL (%)	14.0	12.0 – 17.0	24	14.4	1.3
PNSL (%)	11.6	9.7 – 13.0	24	11.5	0.9
SDW (%)	28.5	24.1 – 33.3	24	28.0	2.0
IOD (%)	7.6	6.6 – 9.0	24	7.5	0.6
EL (%)	2.9	2.3 – 3.6	24	2.9	0.3
ISD (%)	7.2	6.1 – 8.1	24	7.2	0.6
SPL (%)	2.9	1.5 – 3.1	24	2.3	0.4
SPW (%)	2.6	1.8 – 2.9	24	2.3	0.4
MW (%)	7.4	4.5 – 7.9	24	6.6	0.6
UTBW (%)	2.7	2.3 – 3.3	24	2.9	0.3
LTBW (%)	2.8	2.1 – 3.2	24	2.8	0.3
NCW (%)	5.2	4.5 – 5.6	24	5.0	0.3
NCL (%)	1.7	1.5 – 3.0	24	2.0	0.3
DBN (%)	5.3	4.7 – 5.8	24	5.3	0.3
DBFGO (%)	14.0	12.7 – 19.3	24	14.8	1.4
DBLGO (%)	9.5	8.1 – 11.5	23	10.0	0.8
BBL (%)	7.8	7.7 – 10.4	24	9.0	0.8
PFL (%)	20.7	19.1 – 25.4	24	22.0	1.7
PFW (%)	34.7	27.3 – 36.9	24	31.6	2.4
ALPF (%)	9.3	9.2 – 15.1	24	11.1	1.4
PLPF (%)	20.4	13.6 – 23.5	24	18.8	2.7
TW (%)	23.3	16.7 – 29.4	24	21.5	2.7
HFD (%)	11.0	8.5 – 11.4	24	10.1	0.8
LFD (%)	7.0	5.7 – 7.7	24	6.8	0.5
HSD (%)	11.1	8.6 – 11.4	24	10.3	0.8
LSD (%)	7.0	5.9 – 7.6	24	6.7	0.5
LDLC (%)	12.2	10.9 – 13.8	24	12.2	0.8
LVLC (%)	12.6	11.0 – 14.8	24	12.7	0.9
HDLC (%)	6.7	4.1 – 6.3	23	5.7	0.6
HVLC (%)	5.0	2.7 – 5.7	24	4.6	0.7
HC (%)	13.3	10.3 – 14.3	23	12.3	1.1
DBD (%)	5.9	3.2 – 5.9	24	4.7	0.8
DSDC (%)	5.6	3.4 – 7.1	24	5.5	0.7
SCL (%)	51.3	44.9 – 53.2	23	50.0	2.2
CLCF (%)	47.5	42.0 – 50.6	23	46.9	2.1
SFD (%)	62.9	55.8 – 64.9	23	62.2	2.0
EOL (%)	25.9	18.1 – 26.6	24	22.9	2.1
EOW (%)	8.6	6.4 – 12.1	24	8.7	1.2
CL (%)	--	9.8 – 19.3	10	15.6	3.2

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Table 13. Counts for Narcine entemedor Jordan and Starks, 1895. A) Holotype of N. entemedor (CAS-SU 11699; Sinaloa, Mexico); B) USNM 222505 (Gulf of California); C) YPM 1132 (Gulf of California); D) AMNH 15694 (Gulf of California); E) AMNH 15695 (Gulf of California); F) AMNH 11800 (Gulf of California);G) – K) ISH 263-1975 (southern Mexico); L) SIO 73-61 (Revillagigedos Is.); M) USNM 222466 (Colombia); N) USNM 128385 (Panama); O) USNM 94615 (Costa Rica). Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	RANGE
PROP	21	20	21	20	20	--	22	24	21	24	23	24	21	18	21	18 – 24
MESO	10	7	7	9	8	--	10	8	9	8	8	9	8	9	7	7 – 10
META	9	12	10	12	8	--	11	12	8	11	10	9	11	10	8	8 – 12
TPR	40	39	38	41	36	--	43	44	38	43	41	42	40	37	36	36 – 44
PVR	20	20	20	20	20	20	23	23	19	19	21	23	21	19	21	19 – 23
FDR	7	9	9	8	10	8	9	12	11	10	12	11	11	9	12	7 – 12
SDR	10	7	10	8	11	8	10	11	11	11	12	11	9	11	13	7 – 13
DCR	23	20	20	21	21	--	20	24	21	21	23	24	22	--	--	20 – 24
VCR	28	27	24	25	24	--	26	27	27	25	26	29	24	--	--	24 – 29
TCR	51	47	44	46	45	--	46	51	48	46	49	53	46	--	--	44 – 53
TC	32	33	31	32	34	30	33	32	33	30	32	32	28	35	30	28 – 35
PC	71	75	77	73	72	72	75	78	74	80	76	71	78	78	78	71 – 80
CC	28	25	22	21	21	24	25	25	24	24	25	27	21	21	24	21 – 28
TV	131	133	130	126	127	126	133	135	131	134	133	130	127	134	132	126 – 135
R	8	7	9	9	9	9	9	9	8	9	9	9	9	9	9	7 – 9

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Table 14. Measurements for Narcine lingula Richardson, 1846. N indicates number of specimens from which means and standard deviations (SD) were taken.

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	SPECIMENS	N	MEAN	SD
TL (mm)	128.0 – 496.0	30	--	--
DW (%)	43.1 – 56.9	30	51.1	3.3
DL (%)	42.6 – 52.9	30	48.9	2.5
PCSL (%)	10.4 – 14.7	30	12.9	1.2
POSL (%)	11.1 – 15.2	29	13.1	1.0
PNSL (%)	9.0 – 12.2	30	10.8	0.8
SDW (%)	21.7 – 33.1	30	27.6	2.7
IOD (%)	5.0 – 7.0	30	6.1	0.6
EL (%)	1.6 – 3.4	30	2.6	0.4
ISD (%)	4.5 – 6.4	30	5.6	0.5
SPL (%)	1.3 – 2.6	30	2.0	0.3
SPW (%)	1.9 – 3.4	30	2.5	0.3
MW (%)	5.0 – 6.5	30	5.8	0.4
UTBW (%)	1.7 – 2.9	30	2.3	0.3
LTBW (%)	1.7 – 2.8	30	2.2	0.3
NCW (%)	4.0 – 6.0	30	4.9	0.6
NCL (%)	1.0 – 2.5	30	1.6	0.3
DBN (%)	4.1 – 5.7	30	5.0	0.4
DBFGO (%)	11.3 – 16.0	29	13.1	1.3
DBLGO (%)	7.3 – 12.3	29	9.0	1.3
BBL (%)	8.3 – 12.0	30	9.4	1.0
PFL (%)	15.3 – 21.2	30	18.6	1.6
PFW (%)	23.9 – 35.7	30	30.8	2.5
ALPF (%)	9.5 – 15.4	30	11.8	1.3
PLPF (%)	11.5 – 19.4	30	16.2	2.4
TW (%)	13.7 – 21.5	30	17.7	1.8
HFD (%)	7.1 – 11.0	30	8.9	0.9
LFD (%)	5.6 – 7.7	30	6.8	0.6
HSD (%)	8.0 – 10.3	30	9.1	0.5
LSD (%)	6.2 – 8.1	30	7.3	0.5
LDLC (%)	12.3 – 16.5	30	14.3	1.0
LVLC (%)	11.6 – 15.7	30	14.1	1.0
HDLC (%)	3.6 – 6.0	30	4.8	0.6
HVLC (%)	3.0 – 5.5	30	4.0	0.6
HC (%)	7.8 – 12.0	30	9.7	1.0
DBD (%)	3.4 – 7.1	30	5.0	0.9
DSDC (%)	3.0 – 8.2	30	5.8	1.3
SCL (%)	47.1 – 55.4	30	50.3	1.9
CLCF (%)	44.8 – 51.1	30	47.7	1.5
SFD (%)	56.5 – 61.9	30	59.7	1.5
EOL (%)	21.1 – 27.7	30	24.0	1.5
EOW (%)	8.9 – 12.6	30	10.5	1.0
CL (%)	9.0 – 17.0	10	12.2	2.5

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Table 15. Counts taken on specimens of Narcine lingula Richardson, 1846. A) – C) USNM 192574 (Taiwan); D) NTUM 01642 (Taiwan); E) NTUM 01648 (Taiwan); F) NTUM 00006 (Taiwan); G) NTUM 04455 (Taiwan); H) NTUM 04454 (Taiwan); I) NTUM 00023 (Taiwan); J) ANSP 76544 (Hong Kong, China); K) MCZ 45 (China); L) ZMH 10431 (China, Shanghai); M) SIO 65-473 (Gulf of Thailand); N) SMF 4589 (Madras, eastern India). Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	RANGE
PROP	16	18	16	–	16	15	15	–	16	17	16	18	15	16	15 – 18
MESO	10	10	10	–	9	9	8	–	9	9	10	9	11	9	8 – 11
META	6	6	8	–	4	6	7	–	–	8	6	6	5	7	4 – 8
TPR	32	34	34	–	29	30	30	–	–	34	32	33	31	32	29 – 34
PVR	17	20	19	17	18	20	18	18	17	17	20	19	19	17	17 – 20
FDR	8	8	8	7	9	6	–	–	–	–	–	8	7	–	6 – 9
SDR	9	10	10	–	11	8	9	–	10	8	7	–	–	–	7 – 11
DCR	22	19	24	19	23	24	19	22	24	22	24	19	22	22	19 – 24
VCR	28	30	31	25	28	28	24	25	27	29	28	23	27	28	23 – 31
TCR	50	49	55	44	51	52	43	47	51	51	52	42	49	50	42 – 55
TC	26	30	30	25	24	29	29	26	29	22	29	28	23	25	23 – 30
PC	60	66	62	64	63	67	65	65	62	69	65	62	56	59	56 – 69
CC	26	29	28	23	27	28	25	25	26	25	27	25	27	22	22 – 29
TV	112	125	120	112	114	124	119	116	117	116	121	115	106	106	106 – 125
R	–	8	8	–	8	8	10	–	–	8	8	7	7	–	8 – 10

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Table 16. Measurements for specimens of Narcine maculata (Shaw, 1804). A) Holotype of Narcine maculata Duméril, 1852 (MNHN 1336; Java); B) Holotype of Narcine firma Garman, 1913 (MCZ 75; Sri Lanka); C) Paralectotype of Raja timlei Bloch and Schneider, 1801 (ZMB 7588; Tranquebar, eastern India). Number of specimens (N) on which means and standard deviations (SD) are based includes all type, excluding paralectotype of Raja timlei (column C). ZMB 7588 is excluded because specimen is stuffed and heavily distorted.

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	A	B	C	SPECIMENS	N	MEAN	SD
TL (mm)	330.0	401.0	364.0	246.0 – 391.0	12	--	--
DW (%)	53.9	50.4	44.5	42.4 – 52.4	12	49.3	3.4
DL (%)	50.0	49.1	40.4	43.3 – 51.2	12	48.1	2.3
PCSL (%)	14.5	12.5	11.3	11.5 – 13.4	12	12.7	0.8
POSL (%)	14.8	12.5	10.2	12.1 – 13.5	12	13.0	0.7
PNSL (%)	10.7	9.9	8.5	9.1 – 10.8	12	10.2	0.6
SDW (%)	26.1	32.7	20.6	25.2 – 30.8	12	28.1	2.3
IOD (%)	6.2	7.3	6.9	5.0 – 6.7	12	6.0	0.7
EL (%)	2.5	2.1	--	1.8 – 2.7	12	2.3	0.3
ISD (%)	6.1	6.3	7.4	4.6 – 6.9	12	5.7	0.6
SPL (%)	1.8	2.0	--	1.6 – 2.3	12	1.9	0.2
SPW (%)	2.4	2.6	--	2.1 – 2.8	12	2.4	0.2
MW (%)	6.7	6.4	5.5	5.4 – 6.8	12	6.1	0.5
UTBW (%)	3.0	2.8	--	2.0 – 3.0	12	2.6	0.3
LTBW (%)	2.7	2.5	2.5	1.9 – 2.8	12	2.4	0.3
NCW (%)	5.7	5.4	--	4.7 – 6.0	12	5.5	0.4
NCL (%)	2.0	2.1	--	1.6 – 2.3	11	1.7	0.3
DBN (%)	34.2	5.4	--	4.9 – 6.2	11	5.5	0.4
DBFGO (%)	12.1	13.2	--	10.9 – 14.9	12	12.8	1.2
DBLGO (%)	8.8	9.2	--	8.1 – 10.0	12	9.1	0.6
BBL (%)	9.0	9.3	--	8.1 – 10.4	12	9.3	0.6
PFL (%)	18.2	19.7	14.8	13.1 – 19.8	12	17.7	1.8
PFW (%)	34.2	29.3	26.1	25.2 – 31.3	12	29.5	2.5
ALPF (%)	12.1	11.0	9.6	9.2 – 13.1	12	11.4	1.2
PLPF (%)	15.2	18.3	13.2	8.6 – 19.5	12	15.0	3.0
TW (%)	18.2	16.7	18.7	14.9 – 21.2	12	17.8	1.7
HFD (%)	9.5	9.6	9.6	7.7 – 10.0	12	8.8	0.7
LFD (%)	6.8	7.6	5.5	6.1 – 7.2	12	6.8	0.4
HSD (%)	9.4	10.4	10.7	8.0 – 10.4	11	9.3	0.7
LSD (%)	7.0	8.8	5.2	6.5 – 7.7	12	7.2	0.7
LDLC (%)	13.6	16.1	11.5	12.6 – 15.5	12	14.6	0.9
LVLC (%)	13.6	12.1	9.6	12.3 – 14.7	12	13.4	0.8
HDLC (%)	4.3	4.0	3.6	4.0 – 5.3	12	4.6	0.4
HVLC (%)	4.6	4.0	2.2	2.8 – 5.4	12	4.1	0.7
HC (%)	11.5	9.7	8.2	9.2 – 11.1	12	10.1	0.7
DBD (%)	6.7	3.7	7.4	4.0 – 6.5	12	4.9	0.9
DSDC (%)	7.2	5.1	8.0	5.1 – 7.0	12	5.8	0.7
SCL (%)	52.4	47.6	--	44.2 – 54.9	12	49.9	2.7
CLCF (%)	51.8	50.8	--	45.1 – 50.8	12	48.5	1.9
SFD (%)	59.4	60.6	60.4	57.9 – 61.4	12	59.5	1.1
EOL (%)	22.7	24.0	--	21.0 – 25.1	12	23.5	1.3
EOW (%)	10.0	10.1	--	8.0 – 11.8	12	10.2	1.1
CL (%)	16.1	14.3	--	11.6 – 15.2	8	14.2	1.4

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Table 17. Counts for specimens of Narcine maculata (Shaw, 1804). A) Paralectotype of Raja timlei Shaw, 1804 (Tranquebar, eastern India); B) Holotype of Narcine maculata Duméril, 1852 (Java); C) Holotype of Narcine firma Garman, 1913 (Sri Lanka); D) ZRC 2101, female (Singapore); E) ZRC 2101, male (Singapore). Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	RANGE
PROP	--	17	18	16	16	16 – 17
MESO	--	9	10	10	10	9 – 10
META	--	6	6	5	4	4 – 6
TPR	--	32	34	31	30	30 – 34
PVR	21	17	16	19	16	16 – 21
FDR	--	6	9	8	7	6 – 7
SDR	--	7	10	9	--	7 – 10
DCR	20	18	24	20	19	18 – 24
VCR	--	25	28	24	24	24 – 28
TCR	--	43	53	44	43	43 – 52
TC	--	26	26	26	25	25 – 26
PC	--	64	67	63	63	63 – 67
CC	--	22	27	26	25	22 – 27
TV	--	112	120	115	113	112 – 120
R	--	8	9	9	7	7 – 9

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Table 18. Measurements for Narcine rierai (Lloris and Rucabado, 1991). N is number of specimens, type and non-type, from which means and standard deviations (SD) were extracted. Of the five paratypes, one (IIPB 579/1986) was not examined and is excluded from table.

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	PARATYPES	NON-TYPES	N	MEAN	SD
TL (mm)	269.0 – 293.0	213.0 – 272.0	8	--	--
DW (%)	35.8 -- 40.3	35.2 -- 38.6	8	37.1	1.6
DL (%)	37.0 -- 42.4	37.2 -- 40.3	8	39.6	1.9
PCSL (%)	7.7 -- 8.8	8.6 -- 9.3	8	8.5	0.6
POSL (%)	10.0 -- 11.3	10.8 -- 12.0	8	11.0	0.6
PNSL (%)	6.9 -- 7.7	7.2 -- 8.2	8	7.4	0.4
SDW (%)	20.4 -- 30.2	28.7 -- 32.4	8	27.6	3.9
IOD (%)	4.7 -- 5.5	4.8 -- 5.3	8	5.1	0.3
EL (%)	2.8 -- 3.5	3.0 -- 3.5	8	3.2	0.3
ISD (%)	5.5 -- 6.2	6.0 -- 7.1	8	6.2	0.5
SPL (%)	0.9 -- 1.6	2.4 -- 2.6	8	1.9	0.7
SPW (%)	2.1	1.7 -- 2.9	8	2.1	0.3
MW (%)	5.5 -- 6.3	5.0 -- 6.2	8	5.6	0.5
UTBW (%)	1.7 -- 2.2	2.1 -- 2.4	8	2.1	0.3
LTBW (%)	1.2 -- 2.2	1.5 -- 1.6	6	1.6	0.4
NCW (%)	2.2 -- 2.9	2.1 -- 2.5	8	2.4	0.3
NCL (%)	3.0 -- 3.3	2.3 -- 2.8	8	2.9	0.4
DBN (%)	2.5 -- 3.1	2.1 -- 3.3	8	2.8	0.4
DBFGO (%)	9.1 -- 11.7	9.9 -- 10.9	8	10.3	0.9
DBLGO (%)	7.3 -- 9.0	7.4 -- 8.6	8	8.0	0.6
BBL (%)	6.7 -- 7.6	8.1 -- 8.5	8	7.8	0.6
PFL (%)	14.2 -- 17.3	14.0 -- 15.7	8	15.2	1.1
PFW (%)	24.2 -- 26.2	24.5 -- 27.4	8	25.8	1.0
ALPF (%)	6.9 -- 11.9	4.4 -- 11.1	8	8.6	2.4
PLPF (%)	11.8 -- 17.6	12.8 -- 19.5	8	14.6	2.7
TW (%)	14.7 -- 16.7	13.9 -- 19.7	8	16.5	1.8
HFD (%)	7.8 -- 9.7	9.1 -- 9.6	8	9.0	0.6
LFD (%)	5.8 -- 6.5	5.4 -- 8.3	8	6.4	0.9
HSD (%)	8.1 -- 9.8	8.2 -- 9.2	8	8.9	0.6
LSD (%)	6.8 -- 7.4	5.4 -- 7.7	8	6.8	0.8
LDLC (%)	13.6 -- 15.1	11.8 -- 15.3	8	14.1	1.1
LVLC (%)	14.2 --15.0	10.1 -- 13.9	8	13.4	1.9
HDLC (%)	2.9 -- 3.4	2.7 -- 3.9	8	3.3	0.3
HVLC (%)	2.8 -- 3.6	2.5 -- 3.3	8	2.9	0.4
HC (%)	6.7 -- 8.3	6.5 -- 7.6	8	7.2	0.6
DBD (%)	9.7 -- 10.8	9.1 -- 10.4	8	9.9	0.6
DSDC (%)	7.3 -- 9.7	7.2 -- 9.3	8	8.3	0.9
SCL (%)	39.5 -- 41.6	38.6 -- 42.3	8	40.5	1.2
CLCF (%)	53.7 -- 56.7	53.8 -- 55.3	8	54.8	1.1
SFD (%)	48.8 -- 52.4	49.4 -- 52.6	8	50.9	1.5
EOL (%)	20.4 -- 21.0	17.4 -- 22.4	8	20.6	1.5
EOW (%)	6.2 -- 10.6	7.0 -- 8.4	8	8.1	1.3
CL (%)	--	11.6	1	11.6	--

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Table 19. Counts for Narcine rierai (Lloris and Rucabado, 1991). A) Holotype IIPB 82/1987; B) Paratype IIPB 577/1986; C) ISH 255-1975; D) RUSI 48256; E) ZMA 113.398 (male); F) ZMA 113.398 (female). The available radiograph of the holotype was not properly exposed, and did not permit most counts to be taken (tooth row counts for holotype extracted from slide). Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	RANGE
PROP	--	10	10	12	14	13	10 – 14
MESO	--	6	6	6	5	3	3 – 6
META	--	3	3	9	7	6	3 – 9
TPR	--	19	19	27	26	22	19 – 27
PVR	--	16	13	17	13	16	13 – 17
FDR	--	8	--	8	8	9	8 – 9
SDR	--	8	7	6	--	6	6 – 8
DCR	--	24	26	23	23	23	23 – 26
VCR	--	30	25	19	23	24	19 – 30
TCR	--	54	51	42	46	47	42 – 54
TC	15	16	17	17	17	16	15 – 17
PC	66	67	66	62	62	66	62 – 67
CC	--	31	28	27	25	26	25 – 31
TV	--	114	111	106	104	108	104 – 114
R	6	6	6	6	6	6	6

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Table 20. Measurements for Narcine tasmaniensis Richardson, 1841. N indicates number of specimens, including type and non-type, from which means and standard deviations (SD) were taken.

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	HOLOTYPE	NON-TYPES	N	MEAN	SD
TL (mm)	276.0	201.0 -- 482.0	63	--	--
DW (%)	39.9	32.7 -- 51.8	63	43.4	4.6
DL (%)	41.7	34.5 -- 46.8	63	41.6	2.9
PCSL (%)	7.7	6.9 -- 9.4	63	7.8	0.6
POSL (%)	11.4	9.7 -- 13.1	63	11.3	0.7
PNSL (%)	7.7	6.6 -- 8.9	63	7.7	0.6
SDW (%)	30.8	24.9 -- 35.1	63	30.6	1.9
IOD (%)	5.2	4.4 -- 6.9	62	5.4	0.5
EL (%)	3.1	2.3 -- 4.7	63	3.6	0.4
ISD (%)	5.8	4.9 -- 6.8	63	5.7	0.4
SPL (%)	1.9	1.5 -- 2.9	63	2.3	0.3
SPW (%)	2.5	1.8 -- 3.8	63	2.6	0.3
MW (%)	5.9	5.3 -- 7.7	63	6.1	0.4
UTBW (%)	1.5	1.5 -- 2.6	63	2.1	0.3
LTBW (%)	1.4	1.0 -- 2.1	63	1.6	0.3
NCW (%)	4.5	4.2 -- 6.8	62	5.3	0.6
NCL (%)	1.7	1.5 -- 3.6	58	2.5	0.5
DBN (%)	4.7	4.0 -- 5.8	63	4.9	0.4
DBFGO (%)	12.5	9.8 -- 15.1	63	12.7	1.0
DBLGO (%)	9.7	6.0 -- 11.5	63	9.1	1.1
BBL (%)	9.3	6.6 -- 10.0	63	8.4	0.9
PFL (%)	15.0	13.3 -- 21.6	63	18.3	2.2
PFW (%)	23.9	19.8 -- 30.9	63	26.5	2.2
ALPF (%)	8.5	6.9 -- 12.0	63	9.2	1.1
PLPF (%)	11.8	8.5 -- 20.6	63	15.3	2.3
TW (%)	17.3	14.0 -- 22.5	63	17.4	2.0
HFD (%)	9.5	6.0 -- 11.1	63	8.9	0.9
LFD (%)	6.6	4.9 -- 7.6	63	6.2	0.6
HSD (%)	9.0	6.1 -- 10.6	63	8.9	0.9
LSD (%)	6.9	4.6 -- 7.9	63	6.5	0.5
LDLC (%)	13.1	11.1 -- 15.7	63	13.8	1.0
LVLC (%)	12.1	11.8 -- 16.3	63	14.2	1.0
HDLC (%)	3.4	3.0 -- 5.6	63	4.2	0.5
HVLC (%)	2.7	2.7 -- 5.1	63	3.9	0.5
HC (%)	7.9	7.2 -- 14.5	63	9.8	1.3
DBD (%)	7.6	5.7 -- 9.7	63	7.8	0.8
DSDC (%)	6.3	6.3 -- 11.1	63	8.6	0.9
SCL (%)	42.0	38.5 -- 46.7	63	42.3	1.8
CLCF (%)	53.3	49.4 -- 57.0	63	53.3	1.5
SFD (%)	55.8	50.0 -- 54.5	62	55.2	2.3
EOL (%)	20.7	17.5 -- 23.7	63	21.0	1.3
EOW (%)	8.6	5.3 -- 10.4	63	8.0	1.1
CL (%)	--	9.9 -- 14.2	25	12.2	1.1

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Table 21. Counts for Narcine tasmaniensis Richardson, 1841. A) Holotype of N. tasmaniensis BMNH 1898. B) NMV A1606; C) – D) CSIRO T 1051; E) CSIRO 3528; F) NMV A2165; G) NMV 11289; H) NMV 11290; I) – K) AMS 19091-005. Dashes represent counts not readable in available radiographs. For FDR in column G, there are at least six radials, but radiograph does not permit a complete count.

	A	B	C	D	E	F	G	H	I	J	K	RANGE
PROP	15	19	17	12	16	--	17	16	12	12	12	12 – 19
MESO	6	6	6	7	7	6	6	7	4	6	6	4 – 7
META	7	8	7	7	7	8	8	8	5	6	5	5 – 8
TPR	28	33	30	26	30	--	31	31	19	24	23	19 – 33
PVR	22	20	20	19	19	19	20	21	15	20	20	15 – 22
FDR	--	8	8	8	--	8	--	--	--	8	--	8
SDR	--	9	--	10	--	9	9	--	7	8	9	7 – 10
DCR	26	21	23	23	25	25	29	22	22	31	28	21 – 31
VCR	30	21	28	32	29	28	29	26	30	31	31	21 – 32
TCR	56	42	51	55	54	53	58	48	52	62	59	42 – 62
TC	16	15	14	15	16	17	17	16	16	17	17	14 – 17
PC	75	79	76	76	69	69	70	75	76	70	76	69 – 79
CC	25	21	26	30	29	31	29	26	30	28	32	21 – 31
TV	116	115	116	121	114	117	116	117	122	115	125	114 – 125
R	6	6	5	6	6	5	6	6	6	7	7	5 – 7

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Table 22. Measurements for Narcine timlei (Bloch and Schneider, 1801). A) Lectotype of Raja timlei (MZB 4581); Paralectotype of R. timlei and holotype of Narcine indica (ZMB 4582); C) Holotype of N. microphthalma (MNHN 1342); D) Holotype of N. macrura (MNHN 2095); E) Paralectotype of N. brunnea (BMNH 1909.7.12.10); F) Paralectotype of N. brunnea (BMNH 1909.7.12.11); G) Lectotype of N. brunnea (ZMN 112.827). N is number or specimens from which means and standard deviations (SD) were taken, and includes type- and non-type specimens.

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	A	B	C	D	E	F	G	NON-TYPES	N	MEAN	SD
TL (mm)	154	166	175	135	135	225	182	122.0 – 237.0	28	--	--
DW (%)	44.2	57.2	60.6	45.2	49.6	46.7	58.8	40.2 – 59.8	28	50.7	5.2
DL (%)	42.9	45.8	48.6	41.5	51.1	45.8	52.2	39.0 – 53.9	28	47.0	3.1
PCSL (%)	11.7	12.7	13.4	11.6	13.8	14.0	14.6	10.0 – 15.0	28	12.9	1.3
POSL (%)	13.2	14.5	17.0	12.2	15.0	--	16.8	10.3 – 16.5	27	14.1	1.6
PNSL (%)	9.8	9.6	11.5	8.0	11.6	11.7	12.6	7.2 – 12.9	28	10.7	1.4
SDW (%)	19.5	24.1	22.9	21.5	34.8	28.1	27.5	20.6 – 35.5	28	26.3	3.7
IOD (%)	5.5	6.2	6.9	6.2	6.3	6.0	6.5	5.0 – 7.4	28	6.2	0.6
EL (%)	2.2	2.0	2.1	3.0	2.4	2.1	2.4	1.5 – 2.6	28	2.1	0.3
ISD (%)	5.1	6.7	6.7	7.0	6.2	6.5	5.8	5.0 – 6.8	28	5.8	0.6
SPL (%)	2.8	2.6	2.5	1.9	2.4	1.6	1.9	1.7 – 3.2	28	2.4	0.4
SPW (%)	2.4	2.3	2.3	2.1	1.9	1.8	2.3	1.8 – 3.0	28	2.3	0.3
MW (%)	6.6	10.7	5.9	--	7.5	--	7.5	3.9 – 7.7	27	6.5	1.2
UTBW (%)	3.1	3.4	3.1	--	3.1	--	3.1	2.3 – 3.8	23	3.0	0.4
LTBW (%)	2.6	3.4	2.9	--	3.0	--	2.6	2.1 – 3.5	23	2.7	0.4
NCW (%)	6.0	5.5	4.9	--	7.3	6.2	7.3	4.3 – 7.2	28	5.8	0.8
NCL (%)	2.3	2.2	2.1	--	2.8	2.5	3.1	1.1 – 5.0	27	2.3	0.7
DBN (%)	6.0	5.8	5.0	--	6.3	6.0	6.2	1.9 – 6.3	28	5.3	0.9
DBFGO (%)	13.6	12.1	13.8	13.0	13.6	11.7	13.7	10.8 – 14.5	28	13.2	1.0
DBLGO (%)	7.9	7.0	7.9	7.4	8.8	6.5	8.9	4.9 – 10.1	28	8.1	1.2
BBL (%)	8.9	9.4	12.5	11.2	11.3	9.5	9.2	7.5 – 12.9	28	10.4	1.3
PFL (%)	18.2	20.5	17.7	--	20.2	19.3	22.0	15.9 – 22.0	28	18.9	1.6
PFW (%)	32.6	33.7	37.1	--	29.2	34.2	32.4	28.9 – 40.4	28	33.3	2.8
ALPF (%)	13.2	15.1	13.6	--	13.5	11.3	13.7	10.4 – 16.2	28	13.2	1.4
PLPF (%)	11.8	12.7	15.3	--	14.9	13.6	16.5	11.9 – 24.8	28	15.5	2.7
TW (%)	18.8	18.7	17.8	16.1	16.4	16.4	22.0	11.1 – 21.2	28	17.5	2.5
HFD (%)	7.3	8.7	9.5	9.5	8.7	9.1	8.7	6.3 – 10.1	28	8.1	1.0
LFD (%)	5.9	5.9	5.8	5.6	6.2	5.6	7.2	3.8 – 7.0	28	6.0	0.8
HSD (%)	9.4	8.1	9.4	9.3	8.4	10.2	9.5	6.9 – 10.1	28	8.8	0.9
LSD (%)	6.6	6.1	5.9	7.0	6.6	7.6	7.9	4.6 – 7.9	28	6.5	0.8
LDLC (%)	14.1	12.9	15.9	14.4	15.4	16.8	14.6	10.9 – 16.0	28	13.9	1.3
LVLC (%)	--	12.5	15.9	14.0	13.2	16.6	15.3	9.5 – 15.5	27	13.5	1.5
HDLC (%)	3.8	4.3	5.1	4.5	5.6	5.4	5.3	3.4 – 6.0	28	4.7	0.7
HVLC (%)	--	3.7	4.6	4.5	4.6	3.8	4.8	3.1 – 5.3	27	4.0	0.6
HC (%)	--	8.7	10.3	9.3	10.6	12.0	12.4	7.3 – 14.2	27	10.2	1.7
DBD (%)	3.8	4.6	3.9	5.3	5.0	3.5	4.3	2.6 – 6.2	28	4.6	0.8
DSDC (%)	5.1	4.2	5.3	6.1	4.1	3.4	5.0	3.4 – 6.3	28	5.0	1.0
SCL (%)	48.7	50.0	52.6	44.4	51.9	50.2	48.9	43.3 – 53.9	28	49.9	2.3
CLCF (%)	44.2	45.2	45.7	48.1	45.9	46.2	41.8	41.8 – 49.1	28	45.5	2.0
SFD (%)	60.4	62.0	61.7	60.0	61.5	60.0	60.4	56.1 – 65.6	28	61.4	1.9
EOL (%)	24.9	22.9	23.4	24.0	24.7	21.1	25.3	18.4 – 28.7	28	23.1	2.4
EOW (%)	8.3	9.0	8.0	9.6	9.5	8.4	9.3	6.5 – 12.7	28	8.8	1.4
CL (%)	13.8	14.5	14.3	8.4	13.0	13.1	14.3	9.1 – 15.1	19	13.4	1.3

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Table 23. Counts for Narcine timlei (Bloch and Schneider, 1801). A) Lectotype of Raja timlei (ZMB 4581; Tranquebar, India); B) Paralectotype of R. timlei and holotype of Narcine indica (ZMB 4582; Tranquebar, India); C) Holotype of N. microphthalma (MNHN 1342; Malabar coast, India); D) Holotype of N. macrura (MNHN 2095; "mer des Indes" [Indian Ocean]); E) Paralectotype of N. brunnea (BMNH 1909.7.12.10; Bay of Bengal, India); F) Paralectotype of N. brunnea (BMNH 1909.7.12.11; Bay of Bengal, India); G) Lectotype of N. brunnea (ZMA 112.827; Bay of Bengal, India); H) USNM 222479, male (Sri Lanka); I) USNM 222479, female (Sri Lanka); J) USNM 222478 (Sri Lanka); K) MNHN 7893, 237 mm TL (Pondicherry, India); L) MNHN 7893, 206 mm TL (Pondicherry, India); M) FMNH 47257 (Selangor, Malaysia); N) ZMH 10432 (Sumatra, Indonesia); O) ZMH 4466 (Pakistan); P) USNM 222474 (Pakistan). For columns A, E and F, it was not possible to separate pre-caudal and caudal centra, and number for pre-caudal centra indicates both counts combined (ranges given for pre-caudal and caudal centra does not include data from these three columns). Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	RANGE
PROP	–	17	18	–	18	19	21	19	14	20	17	17	16	15	14	16	14–21
MESO	–	8	10	–	8	8	8	8	8	7	8	9	8	8	8	8	7–10
META	–	5	5	–	6	5	5	6	7	7	6	6	6	5	5	6	5–7
TPR	–	30	32	–	32	32	34	32	29	34	31	30	30	28	27	30	27–34
PVR	15	15	15	–	15	15	17	17	19	15	16	16	17	15	18	19	15–19
FDR	–	–	6	–	–	7	7	6	6	6	–	6	5	6	–	6	5–7
SDR	–	–	8	–	–	–	–	6	7	6	7	8	6	8	8	–	6–8
DCR	–	–	19	17	–	–	19	19	–	19	20	20	17	15	18	–	15–20
VCR	–	–	19	–	–	–	21	22	–	24	26	22	21	19	23	–	19–26
TCR	–	–	38	–	–	–	40	41	–	43	46	42	38	34	41	–	34–46
TC	24	24	25	23	24	26	24	23	28	26	27	25	22	21	25	27	21–28
PC	77	58	54	63	77	78	52	57	56	55	54	58	52	51	54	54	51–63
CC		19	19	18			20	22	18	22	21	22	18	16	22	26	16–26
TV	101	101	98	104	101	104	96	102	100	103	102	105	92	88	101	107	88–107
R	7	8	6	6	7	8	7	8	7	8	7	7	5	5	7	7	5–8

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Table 24. Measurements for Narcine vermiculatus Breder, 1928. A) Holotype of N. vermiculatus Breder, 1928 (YPM 1142); B) Holotype of Narcine schmitti Hildebrand, 1948 (USNM 94044). N indicates number of specimens, including type and non-type, from which means and standard deviations (SD) were taken.

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	A	B	NON-TYPES	N	MEAN	SD
TL (mm)	204.0	220.0	107.0 – 203.0	23	--	--
DW (%)	48.5	44.1	44.9 – 51.5	23	47.5	2.3
DL (%)	51.5	47.7	43.9 – 51.4	23	48.4	1.8
PCSL (%)	13.3	11.9	11.9 – 15.3	23	13.5	0.9
POSL (%)	16.0	14.6	14.2 – 17.0	23	15.6	0.8
PNSL (%)	12.4	10.7	11.3 – 14.1	23	12.7	0.8
SDW (%)	31.9	28.6	25.5 – 33.3	23	30.0	2.0
IOD (%)	8.0	7.1	6.0 – 8.0	23	7.2	0.5
EL (%)	2.3	2.3	1.9 – 3.0	23	2.3	0.2
ISD (%)	6.7	6.8	5.3 – 8.3	23	6.7	0.7
SPL (%)	2.3	2.3	2.1 – 3.5	23	2.7	0.4
SPW (%)	2.7	2.1	1.7 – 3.0	23	2.3	0.3
MW (%)	6.2	6.6	5.4 – 7.7	23	6.5	0.6
UTBW (%)	3.0	3.5	2.4 – 3.8	23	3.3	0.4
LTBW (%)	2.6	3.5	2.2 – 3.5	23	2.8	0.3
NCW (%)	5.9	--	4.8 – 6.4	22	5.5	0.5
NCL (%)	2.4	--	1.6 – 2.8	22	2.1	0.3
DBN (%)	6.1	--	5.0 – 6.9	22	6.0	0.5
DBFGO (%)	14.3	--	10.8 – 15.6	22	14.2	1.0
DBLGO (%)	7.5	--	6.6 – 11.0	22	8.2	1.0
BBL (%)	9.9	10.4	5.3 – 11.1	23	9.7	1.2
PFL (%)	21.6	18.8	16.0 – 24.3	23	20.3	1.8
PFW (%)	30.0	26.9	25.1 – 35.0	23	30.3	2.2
ALPF (%)	13.0	12.5	10.5 – 14.0	23	12.2	1.0
PLPF (%)	17.8	16.3	11.4 – 23.8	23	15.2	2.7
TW (%)	17.3	15.4	15.0 – 24.6	23	18.6	2.2
HFD (%)	10.0	8.2	7.3 – 9.0	23	8.3	0.7
LFD (%)	6.2	6.6	5.2 – 6.8	23	6.0	0.5
HSD (%)	10.8	9.3	8.4 – 10.0	23	9.4	0.5
LSD (%)	6.8	6.9	5.6 – 7.2	23	6.6	0.4
LDLC (%)	13.0	12.0	10.6 – 14.4	23	12.8	0.9
LVLC (%)	14.2	12.5	10.5 – 14.4	23	12.9	0.9
HDLC (%)	5.7	4.9	4.1 – 6.2	23	5.1	0.6
HVLC (%)	4.5	4.2	3.4 – 5.2	23	4.3	0.5
HC (%)	11.2	10.5	9.0 – 13.4	23	11.6	1.0
DBD (%)	4.3	4.6	2.9 – 5.7	23	4.3	0.7
DSDC (%)	6.6	5.5	3.7 – 6.9	23	4.8	0.9
SCL (%)	51.0	50.9	47.9 – 52.5	23	50.4	1.2
CLCF (%)	47.1	46.8	42.9 – 47.1	23	45.2	1.4
SFD (%)	62.5	63.6	62.1 – 66.5	23	64.1	1.1
EOL (%)	24.0	24.5	18.4 – 28.2	23	23.9	1.9
EOW (%)	9.3	10.9	6.6 – 11.7	23	9.1	1.4
CL (%)	15.7	17.7	13.8 – 17.0	13	15.2	1.2

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Table 25. Counts for Narcine vermiculatus Breder, 1928. A) Holotype of N. vermiculatus (YPM 1143; Mexico); B) Holotype of N. schmitti (USNM 94044; Mexico); C) FMNH 62372 (Mexico); D) USNM 181305 (Mexico); E) – H) FMNH 63711 (Mexico); I) ZMH 10410 (Costa Rica). Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	G	H	I	RANGE
PROP	15	16	15	15	16	18	15	15	18	15 – 18
MESO	6	7	6	6	7	7	6	8	6	6 – 8
META	9	11	11	9	10	11	9	9	10	9 – 11
TPR	30	34	32	30	33	36	30	32	34	30 – 36
PVR	15	16	18	17	16	18	16	18	16	15 – 18
FDR	--	--	6	6	6	--	6	7	6	6 – 7
SDR	9	8	8	9	--	8	8	8	9	8 – 9
DCR	21	21	20	20	21	20	20	19	17	17 – 21
VCR	24	24	21	22	26	22	23	24	23	21 – 26
TCR	45	45	41	42	47	42	43	43	40	40 – 47
TC	21	27	27	27	24	28	22	25	26	21 – 28
PC	62	61	59	60	60	58	63	56	57	56 – 63
CC	20	22	21	21	20	22	19	22	21	19 – 22
TV	103	110	107	108	104	108	104	103	104	103 – 110
R	6	8	6	6	6	6	7	6	6	6 – 8

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Table 26. Measurements for Narcine westraliensis McKay, 1966. A) Holotype of N. westraliensis McKay, 1966 (WAM P 6963-001); B) Paratypes of N. westraliensis. N indicates number of specimens, including type and non-type, from which means and standard deviations (SD) were taken.

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	A	B	NON-TYPES	N	MEAN	SD
TL (mm)	211	106 – 270	134 -- 252	64	--	--
DW (%)	42.2	37.7 -- 46.0	35.3 -- 43.5	64	41.1	2.4
DL (%)	41.2	35.8 -- 44.3	29.5 -- 45.1	64	39.4	3.3
PCSL (%)	8.0	6.7 -- 10.0	6.7 -- 9.5	64	8.5	0.7
POSL (%)	12.8	10.8 -- 13.7	10.0 -- 12.8	64	12.1	0.8
PNSL (%)	8.3	6.9 -- 8.9	6.5 -- 8.6	64	8.1	0.5
SDW (%)	28.0	23.6 -- 30.5	21.5 -- 29.7	64	26.6	2.1
IOD (%)	5.0	4.3 -- 6.5	4.9 -- 6.4	64	5.6	0.4
EL (%)	3.6	3.1 -- 4.4	2.5 -- 4.2	64	3.5	0.4
ISD (%)	5.3	4.3 -- 9.4	5.2 -- 7.8	64	6.3	0.7
SPL (%)	2.6	1.9 -- 2.9	1.9 -- 3.0	64	2.5	0.3
SPW (%)	2.3	2.0 -- 3.1	2.2 -- 3.6	64	2.5	0.3
MW (%)	7.2	5.8 -- 8.3	5.4 -- 8.1	64	6.9	0.5
UTBW (%)	2.6	2.0 -- 3.1	2.9 -- 3.1	64	2.6	0.3
LTBW (%)	2.2	1.8 -- 2.6	1.5 -- 2.5	64	2.1	0.2
NCW (%)	5.9	4.1 -- 6.0	3.6 -- 5.5	62	4.8	0.5
NCL (%)	4.0	2.5 -- 4.1	2.2 -- 3.6	62	3.1	0.4
DBN (%)	4.7	3.7 -- 4.7	3.2 -- 4.7	64	4.0	0.4
DBFGO (%)	11.2	9.1 -- 12.5	7.5 -- 12.8	64	10.7	1.1
DBLGO (%)	8.0	7.5 -- 10.2	5.7 -- 9.5	63	7.9	0.8
BBL (%)	8.5	5.5 -- 8.5	6.2 -- 9.2	63	7.4	0.7
PFL (%)	19.5	15.7 -- 23.6	13.9 -- 24.1	64	19.2	2.1
PFW (%)	27.8	24.5 -- 34.5	23.2 -- 31.3	64	28.1	2.1
ALPF (%)	10.0	8.4 -- 13.3	6.6 -- 11.8	64	9.9	1.2
PLPF (%)	16.7	13.1 -- 24.1	9.1 -- 22.7	64	17.0	2.9
TW (%)	15.6	16.0 -- 22.0	14.2 -- 23.1	64	18.2	1.9
HFD (%)	9.6	7.0 -- 10.8	6.7 -- 10.0	64	9.0	0.8
LFD (%)	8.1	6.4 -- 8.6	5.5 -- 9.6	64	7.4	0.7
HSD (%)	9.5	6.9 -- 10.1	6.8 -- 10.6	64	8.9	0.8
LSD (%)	8.2	6.9 -- 9.1	6.9 -- 9.4	64	8.2	0.6
LDLC (%)	14.8	13.0 -- 17.2	11.8 -- 17.3	64	14.7	1.3
LVLC (%)	15.4	12.7 -- 17.2	11.9 -- 17.5	64	15.1	1.3
HDLC (%)	3.9	3.0 -- 4.7	2.7 -- 4.7	64	3.9	0.5
HVLC (%)	3.4	2.6 -- 4.5	2.2 -- 4.1	64	3.3	0.5
HC (%)	8.6	7.4 -- 10.4	6.4 -- 9.9	64	8.5	0.9
DBD (%)	7.1	5.3 -- 8.5	5.2 -- 9.0	64	6.8	0.9
DSDC (%)	5.6	4.7 -- 8.3	5.8 -- 9.2	64	6.8	0.9
SCL (%)	41.7	39.2 -- 46.6	37.7 -- 46.8	64	42.0	1.7
CLCF (%)	54.0	45.7 -- 56.6	41.2 -- 56.6	64	53.2	2.2
SFD (%)	54.5	40.9 -- 57.9	50.8 -- 58.2	64	54.4	2.4
EOL (%)	21.3	18.6 -- 25.0	15.8 -- 24.0	64	21.6	1.7
EOW (%)	7.1	5.6 -- 10.0	4.4 -- 10.0	64	7.8	1.2
CL (%)	14.2	9.1 -- 15.3	12.1 -- 15.5	27	13.4	1.4

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Table 27. Counts for Narcine westraliensis McKay, 1966. A) Holotype of N. westraliensis (WAM P6963-001); B) Paratype WAM P7033-001; C) Paratype WAM P6990-001; D) Paratype WAM P6997-001; E) Paratype WAM P6998-001; F) Paratype WAM P6999-001; G) Paratype WAM P6962-001; H) Paratype WAM P6961-001; I) Paratype WAM P6960-001; J) – K) NTM 11670; L) WAM 29334; M) – N) WAM 14801; O) WAM 23837. Dashes represent counts not readable in available radiographs. Value for PC in column B is approximate as structure is not properly exposed in radiograph. Ranges exclude column I (juvenile specimen).

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	RANGE
PROP	17	13	15	14	15	16	13	16	9	13	14	14	14	14	14	13 – 17
MESO	8	6	7	7	6	6	7	7	5	6	6	6	7	8	7	6 – 8
META	8	8	6	7	7	7	7	7	8	8	9	9	8	7	8	6 – 9
TPR	33	27	28	28	28	29	27	30	22	27	29	29	29	29	29	27 – 33
PVR	16	16	17	15	17	18	17	16	18	17	16	17	17	17	17	15 – 18
FDR	8	8	8	–	7	–	8	6	–	9	7	8	–	–	6	6 – 9
SDR	8	8	9	–	–	–	6	7	9	–	7	9	8	8	9	6 – 9
DCR	–	–	24	–	–	–	–	–	–	26	22	21	23	24	21	21 – 26
VCR	–	–	26	–	–	–	–	35	–	30	27	23	26	29	27	23 – 35
TCR	–	–	50	–	–	–	–	–	–	56	49	43	49	53	48	43 – 56
TC	17	16	17	15	16	13	17	15	16	16	17	15	17	15	15	13 – 17
PC	61	58	68	60	64	59	62	58	64	71	64	64	60	61	62	58 – 71
CC	29	30	25	27	29	33	27	33	19	26	23	21	25	28	24	21 – 33
TV	107	104	110	102	109	105	106	106	99	113	104	100	102	104	101	100 – 113
R	7	6	6	7	6	5	7	7	5	5	6	6	5	6	5	5 – 7

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Table 28. Measurements for Narcine sp. nov. A. N is number of specimens from which means and standard deviations (SD) were extracted.

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	SPECIMENS	N	MEAN	SD
TL (mm)	155 -- 241	24	--	--
DW (%)	30.4 -- 42.8	24	36.9	3.7
DL (%)	36.5 -- 44.0	24	40.2	2.2
PCSL (%)	7.5 -- 11.6	24	9.5	0.9
POSL (%)	12.0 -- 14.0	24	12.7	0.6
PNSL (%)	7.2 -- 9.8	24	8.5	0.7
SDW (%)	22.1 -- 30.7	24	25.8	2.4
IOD (%)	4.7 -- 7.5	24	5.9	0.7
EL (%)	2.3 -- 3.9	24	3.0	0.4
ISD (%)	4.6 -- 7.1	24	6.2	0.6
SPL (%)	1.5 -- 3.0	24	2.2	0.3
SPW (%)	2.0 -- 3.7	24	2.5	0.3
MW (%)	6.0 -- 8.1	24	7.1	0.6
UTBW (%)	2.0 -- 3.4	24	2.6	0.3
LTBW (%)	1.5 -- 3.0	24	2.0	0.4
NCW (%)	4.1 -- 6.6	24	5.1	0.6
NCL (%)	1.8 -- 4.1	24	2.7	0.7
DBN (%)	1.9 -- 6.0	24	4.5	0.9
DBFGO (%)	10.2 -- 14.5	24	11.8	1.1
DBLGO (%)	7.2 -- 10.7	24	8.6	1.0
BBL (%)	6.9 -- 10.5	24	8.5	0.9
PFL (%)	13.7 -- 19.3	24	17.3	1.6
PFW (%)	20.8 -- 31.9	24	28.0	2.9
ALPF (%)	7.5 -- 16.9	24	10.6	1.9
PLPF (%)	9.2 -- 17.8	24	13.2	2.4
TW (%)	14.1 -- 22.0	24	17.2	2.1
HFD (%)	8.2 -- 11.5	24	9.5	1.0
LFD (%)	5.6 -- 9.0	24	7.3	1.0
HSD (%)	7.1 -- 11.1	24	9.2	1.0
LSD (%)	5.7 -- 9.5	24	7.9	0.9
LDLC (%)	6.1 -- 16.7	24	14.5	2.0
LVLC (%)	6.6 -- 16.5	24	13.9	2.1
HDLC (%)	2.9 -- 4.5	24	3.7	0.4
HVLC (%)	2.6 -- 4.4	24	3.3	0.4
HC (%)	6.9 -- 11.4	24	8.6	1.1
DBD (%)	4.4 -- 9.3	24	6.8	1.3
DSDC (%)	4.8 -- 8.8	24	6.9	1.1
SCL (%)	39.2 -- 45.6	24	42.3	1.5
CLCF (%)	49.5 -- 58.4	24	53.3	2.0
SFD (%)	48.8 -- 58.6	24	53.7	2.6
EOL (%)	12.9 -- 24.8	24	20.8	2.8
EOW (%)	5.4 -- 10.2	24	7.1	1.2
CL (%)	10.2 -- 15.2	12	13.0	1.5

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Table 29. Counts for Narcine sp. nov. A. A) – B) QM 23187; C) QM 25766; D) QM 27918; E) – F) NTM 13576; G) NTM 13400; H) NTM 12924; I) NTM 13329; J) NTM 11680-012; K) NTM 12983-002; L) NTM 12262-003; M) NTM 12264-003. Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	G	H	I	J	K	L	M	RANGE
PROP	15	15	15	14	15	--	15	15	15	15	15	15	17	14 – 17
MESO	6	7	7	7	8	8	8	8	8	6	8	6	6	6 – 9
META	9	7	7	8	6	9	9	9	8	7	6	6	6	6 – 9
TPR	30	29	29	28	29	--	32	32	31	28	29	27	29	27 – 32
PVR	17	19	19	16	16	14	17	16	17	15	17	15	14	14 – 19
FDR	9	9	9	7	--	7	8	7	7	--	8	6	7	6 – 9
SDR	11	9	9	8	--	9	--	8	11	--	8	--	8	8 – 11
DCR	28	28	28	25	23	21	24	31	22	24	25	26	27	21 – 31
VCR	32	32	32	31	27	27	31	32	30	29	31	26	29	26 – 32
TCR	60	60	60	56	50	48	55	63	52	53	56	52	56	48 – 63
TC	16	17	17	17	15	16	16	16	18	16	17	17	16	15 – 18
PC	58	63	63	59	59	64	67	61	59	61	63	63	61	58 – 67
CC	26	30	30	26	26	23	26	28	29	24	26	24	26	23 – 30
TV	100	110	110	102	100	103	109	105	106	101	106	104	103	100 – 110
R	7	5	5	6	6	6	5	6	5	6	6	5	6	5 – 7

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Table 30. Measurements for Narcine sp. nov. B. N is number of specimens from which means and standard deviations (SD) were taken.

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	SPECIMENS	N	MEAN	SD
TL (mm)	115.6 -- 365.0	53	--	--
DW (%)	34.1 -- 45.2	53	40.3	2.1
DL (%)	38.2 -- 48.6	53	42.1	1.9
PCSL (%)	8.5 – 12.6	53	10.1	0.8
POSL (%)	11.4 – 15.7	53	13.4	0.9
PNSL (%)	8.4 – 12.0	53	9.8	0.7
SDW (%)	29.1 – 35.6	53	32.1	1.7
IOD (%)	4.4 -- 6.9	53	5.7	0.5
EL (%)	2.6 -- 4.5	53	3.3	0.4
ISD (%)	4.5 -- 7.0	53	6.0	0.5
SPL (%)	1.6 -- 3.0	53	2.2	0.3
SPW (%)	1.7 -- 3.6	53	2.4	0.3
MW (%)	5.3 -- 7.5	53	6.3	0.4
UTBW (%)	1.4 -- 2.9	53	2.1	0.3
LTBW (%)	1.0 -- 2.3	52	1.6	0.3
NCW (%)	4.1 -- 6.5	52	5.3	0.5
NCL (%)	1.7 -- 5.0	46	2.4	0.6
DBN (%)	3.2 -- 6.2	53	5.1	0.5
DBFGO (%)	10.2 – 14.5	53	12.7	0.9
DBLGO (%)	6.1 – 10.4	53	8.5	1.0
BBL (%)	6.4 -- 9.9	53	8.5	1.0
PFL (%)	12.3 – 18.9	53	15.7	1.7
PFW (%)	19.6 – 25.2	53	25.2	2.1
ALPF (%)	6.2 -- 12.2	52	8.8	1.3
PLPF (%)	7.9 -- 18.8	52	12.8	2.4
TW (%)	10.8 -- 19.7	53	16.5	1.9
HFD (%)	5.9 -- 10.6	53	8.6	1.0
LFD (%)	5.2 -- 6.9	53	5.8	0.4
HSD (%)	7.0 -- 10.4	53	8.6	0.9
LSD (%)	4.9 -- 7.5	53	6.3	0.5
LDLC (%)	11.5 -- 16.7	53	13.3	1.1
LVLC (%)	11.5 -- 17.2	53	14.3	1.1
HDLC (%)	2.5 -- 4.6	53	3.6	0.4
HVLC (%)	2.2 -- 4.5	53	3.5	0.5
HC (%)	6.4 -- 10.0	53	8.2	0.9
DBD (%)	4.0 -- 9.9	53	7.7	0.9
DSDC (%)	7.1 -- 11.3	53	9.1	0.9
SCL (%)	37.9 -- 47.6	53	42.5	1.8
CLCF (%)	50.0 -- 57.1	53	53.7	1.6
SFD (%)	50.3 -- 59.0	53	55.3	1.6
EOL (%)	16.7 -- 24.0	53	20.1	1.5
EOW (%)	5.0 -- 9.4	53	7.5	1.0
CL (%)	7.2 -- 13.9	19	11.4	2.1

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Table 31. Counts for Narcine sp. nov. B. A) CSIRO 2597; B) NMV A9656; C) CSIRO 2274; D) NTM 13579-004; E) NTM 12641; F) CSIRO 4367; G) NMV 1798; H) NTM 13578; I) NMV 1798; J) CSIRO 1036; K) MNHN 1996-1556. Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	G	H	I	J	K	RANGE
PROP	18	16	15	16	15	14	16	16	16	15	14	14 – 18
MESO	5	5	5	6	6	6	6	6	6	6	6	5 – 6
META	10	9	9	7	8	9	9	8	7	8	9	7 – 10
TPR	33	30	29	29	29	29	31	30	29	29	29	29 – 33
PVR	18	18	16	19	17	17	19	17	18	19	17	16 – 19
FDR	--	7	8	8	10	--	--	--	7	9	9	7 – 10
SDR	9	--	9	9	10	9	--	--	8	--	9	8 – 10
DCR	24	26	21	25	26	29	27	24	25	27	26	21 – 29
VCR	27	29	--	27	29	30	30	26	29	31	29	26 – 31
TCR	51	55	--	52	55	59	57	50	54	58	55	50 – 59
TC	16	17	16	16	17	17	16	16	16	17	17	16 – 17
PC	76	71	68	72	71	71	71	71	72	71	73	68 – 76
CC	27	28	23	27	29	31	26	25	26	30	27	23 – 31
TV	119	116	107	115	117	119	113	112	114	118	117	107 – 119
R	6	6	5	5	6	6	6	6	6	7	7	5 – 7

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Table 32. Measurements for Narcine sp. nov. C. N indicates number of specimens from which means and standard deviations (SD) were extracted.

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	SPECIMENS	N	MEAN	SD
TL (mm)	135.0 -- 348.0	67	--	--
DW (%)	28.6 -- 43.7	67	38.4	3.3
DL (%)	35.6 -- 44.9	67	40.2	2.0
PCSL (%)	8.6 -- 11.1	67	9.7	0.7
POSL (%)	11.8 -- 15.9	67	13.5	0.9
PNSL (%)	8.1 -- 15.8	67	9.7	1.1
SDW (%)	26.3 -- 35.9	64	31.7	2.1
IOD (%)	4.7 -- 7.1	67	5.5	0.5
EL (%)	2.5 -- 4.4	67	3.4	0.4
ISD (%)	4.8 -- 6.4	67	5.7	0.4
SPL (%)	1.7 -- 2.8	67	2.2	0.2
SPW (%)	1.6 -- 2.9	67	2.3	0.3
MW (%)	4.4 -- 7.1	67	6.0	0.5
UTBW (%)	1.4 -- 2.8	67	2.0	0.3
LTBW (%)	1.0 -- 1.8	67	1.4	0.2
NCW (%)	4.0 -- 7.8	54	5.3	0.6
NCL (%)	1.6 -- 3.3	51	2.4	0.4
DBN (%)	4.2 -- 5.9	67	5.0	0.3
DBFGO (%)	9.4 -- 14.4	67	12.6	1.1
DBLGO (%)	6.2 -- 10.4	67	8.5	0.9
BBL (%)	7.1 -- 10.7	67	8.5	0.8
PFL (%)	9.8 -- 19.0	67	15.1	2.0
PFW (%)	21.3 -- 30.0	67	25.2	1.8
ALPF (%)	5.8 -- 11.6	67	8.4	1.3
PLPF (%)	6.2 -- 17.6	67	12.8	2.4
TW (%)	12.7 -- 20.0	67	16.0	1.5
HFD (%)	6.7 -- 10.5	67	8.6	0.8
LFD (%)	4.7 -- 6.6	67	5.7	0.4
HSD (%)	6.6 -- 9.9	67	8.4	0.7
LSD (%)	4.7 -- 7.5	67	6.2	0.5
LDLC (%)	10.5 -- 14.8	67	12.8	0.8
LVLC (%)	11.3 -- 15.4	67	13.2	0.8
HDLC (%)	2.4 -- 6.1	67	3.8	0.6
HVLC (%)	2.1 -- 5.1	67	3.4	0.5
HC (%)	5.8 -- 12.2	67	8.5	1.1
DBD (%)	7.7 -- 11.4	67	9.1	0.8
DSDC (%)	7.4 -- 10.5	67	9.1	0.7
SCL (%)	40.0 -- 45.0	67	42.2	1.3
CLCF (%)	50.5 -- 56.6	67	54.1	1.5
SFD (%)	49.8 -- 60.3	67	54.7	1.7
EOL (%)	14.3 -- 23.5	67	19.5	1.5
EOW (%)	5.1 -- 9.4	67	7.2	1.1
CL (%)	6.2 -- 15.4	30	11.6	2.1

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Table 33. Counts for Narcine sp. nov. C. A) – C) QM 25296; D) – E) NTM 11750-003; F) QM 21583. Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	RANGE
PROP	22	18	16	17	18	15	15 – 22
MESO	7	5	7	8	7	7	5 – 8
META	12	7	8	8	8	8	7 – 12
TPR	41	30	31	33	33	30	30 – 41
PVR	20	--	19	20	19	21	19 – 21
FDR	8	--	8	7	9	8	7 – 9
SDR	9	--	10	9	11	9	9 – 11
DCR	26	27	23	25	21	28	23 – 28
VCR	33	26	27	29	31	29	26 – 33
TCR	59	53	50	54	52	57	50 – 59
TC	18	17	16	17	16	17	16 – 18
PC	75	76	73	77	74	75	73 – 77
CC	32	26	31	26	29	27	26 – 32
TV	125	119	120	120	119	119	119 – 125
R	6	6	6	6	6	6	6

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Table 34. Measurements for Narcine sp. nov. D. N indicates number of specimens from which means and standard deviations (SD) were extracted.

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	SPECIMENS	N	MEAN	SD
TL (mm)	240.0 -- 350.0	--	--	--
DW (%)	41.9 -- 47.7	4	44.9	2.9
DL (%)	40.5 -- 46.7	4	43.8	2.9
PCSL (%)	7.5 -- 9.7	4	8.7	1.1
POSL (%)	11.9 -- 13.1	4	12.7	0.6
PNSL (%)	8.1 -- 10.0	4	9.1	0.9
SDW (%)	22.3 -- 32.3	4	26.1	4.4
IOD (%)	5.9 -- 7.5	4	6.6	0.7
EL (%)	3.1 -- 3.7	4	3.4	0.3
ISD (%)	4.5 -- 5.4	4	4.8	0.4
SPL (%)	2.5 -- 3.2	4	2.9	0.3
SPW (%)	2.9 -- 4.0	4	3.5	0.4
MW (%)	6.0 -- 6.9	4	6.6	0.4
UTBW (%)	2.8 -- 3.2	4	3.0	0.2
LTBW (%)	2.8 -- 3.1	4	2.9	0.1
NCW (%)	4.8 -- 5.4	4	5.1	0.3
NCL (%)	1.75 -- 1.82	4	1.78	0.4
DBN (%)	4.9 -- 5.3	4	5.1	0.2
DBFGO (%)	10.0 -- 12.1	4	11.5	1.0
DBLGO (%)	6.0 -- 7.2	4	6.6	0.6
BBL (%)	8.0 -- 10.2	4	9.3	1.0
PFL (%)	13.8 -- 19.2	4	16.6	2.2
PFW (%)	24.4 -- 32.8	4	28.1	3.8
ALPF (%)	9.5 -- 12.5	4	11.4	1.5
PLPF (%)	10.2 -- 17.4	4	13.9	3.1
TW (%)	13.7 -- 20.6	4	17.1	2.9
HFD (%)	11.3 -- 14.3	4	13.1	1.4
LFD (%)	7.5 -- 8.4	4	8.0	0.4
HSD (%)	11.8 -- 13.0	4	12.3	0.6
LSD (%)	7.7 -- 8.4	4	8.1	0.3
LDLC (%)	13.3 -- 18.2	4	16.0	2.1
LVLC (%)	11.6 -- 15.0	4	13.2	1.4
HDLC (%)	4.2 -- 8.4	4	6.4	2.2
HVLC (%)	3.7 -- 5.3	4	4.5	0.8
HC (%)	10.0 -- 15.8	4	13.5	2.5
DBD (%)	6.0 -- 7.9	4	7.0	0.8
DSDC (%)	5.9 -- 8.9	4	7.0	1.4
SCL (%)	43.0 -- 45.8	4	44.5	1.2
CLCF (%)	48.9 -- 53.4	4	52.1	2.1
SFD (%)	49.1 -- 53.8	4	50.7	2.1
EOL (%)	19.8 -- 24.0	4	21.6	1.8
EOW (%)	7.8 -- 9.2	4	8.4	0.7
CL (%)	10.7 -- 13.0	3	11.9	1.2

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Table 35. Counts for Narcine sp. nov. D. CAS specimens from Gulf of Oman, TCWC and BMNH specimens from Gulf of Aden. Dashes represent counts not readable in available radiographs.

	CAS 66838	CAS 58368	TCWC	BMNH	RANGE
PROP	14	17	14	14	14 -- 17
MESO	9	10	13	13	9 --13
META	5	6	7	6	5 -- 7
TPR	28	33	34	33	28 -- 34
PVR	19	16	18	18	16 -- 19
FDR	9	8	9	6	6 -- 9
SDR	10	9	--	9	9 -- 10
DCR	19	20	20	22	19 -- 22
VCR	26	26	25	27	25 -- 27
TCR	45	46	45	49	45 -- 49
UTR	27	22	23	27	22 -- 27
LTR	30	20	24	23	20 -- 30
TC	26	24	31	22	22 -- 31
PC	68	64	67	65	64 -- 68
CC	25	27	21	26	21 -- 27
TV	119	115	109	113	109 -- 119
R	7	6	10	8	6 -- 10

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Table 36. Measurements for Narcine sp. nov. E. N is number of specimens from which means and standard deviations (SD) were extracted.

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	SPECIMENS	N	MEAN	SD
TL (mm)	135 -- 356	7	--	--
DW (%)	40.4 -- 54.9	7	48.0	5.3
DL (%)	43.5 -- 50.9	7	47.5	2.3
PCSL (%)	8.7 -- 11.4	7	10.2	0.9
POSL (%)	12.3 -- 15.6	7	14.2	1.1
PNSL (%)	9.0 -- 11.6	7	10.7	0.8
SDW (%)	26.3 -- 32.5	7	28.8	2.2
IOD (%)	5.6 -- 7.8	7	7.0	0.7
EL (%)	3.3 -- 4.7	7	4.0	0.5
ISD (%)	5.2 -- 6.0	7	5.6	0.2
SPL (%)	2.3 -- 4.1	7	3.2	0.6
SPW (%)	2.8 -- 3.8	7	3.2	0.4
MW (%)	6.6 -- 7.6	7	7.1	0.4
UTBW (%)	2.5 -- 3.4	7	3.0	0.3
LTBW (%)	2.5 -- 3.4	7	2.9	0.3
NCW (%)	4.6 -- 5.5	7	5.3	0.3
NCL (%)	2.1 -- 2.9	7	2.5	0.3
DBN (%)	5.0 -- 5.9	7	5.5	0.3
DBFGO (%)	10.3 -- 13.6	7	11.8	1.3
DBLGO (%)	5.9 -- 9.0	7	7.3	1.1
BBL (%)	7.7 -- 9.2	7	8.2	0.5
PFL (%)	13.2 -- 21.4	7	17.9	2.8
PFW (%)	26.5 -- 35.8	7	32.0	3.4
ALPF (%)	10.1 -- 15.6	7	12.5	1.8
PLPF (%)	12.6 -- 17.1	7	15.1	1.9
TW (%)	15.4 -- 19.7	7	16.7	1.6
HFD (%)	11.3 -- 16.9	7	13.9	1.9
LFD (%)	7.6 -- 10.7	7	9.1	1.0
HSD (%)	8.3 -- 13.3	7	10.8	1.7
LSD (%)	6.2 -- 8.5	7	7.2	0.7
LDLC (%)	14.6 -- 19.4	7	17.2	1.7
LVLC (%)	14.6 -- 17.3	7	16.2	1.0
HDLC (%)	4.1 -- 7.2	7	5.4	1.2
HVLC (%)	4.6 -- 7.3	7	5.7	1.0
HC (%)	10.2 -- 16.2	7	13.3	2.5
DBD (%)	6.9 -- 8.7	7	7.8	0.7
DSDC (%)	5.5 -- 9.0	7	6.6	1.1
SCL (%)	43.5 -- 47.1	7	45.6	1.2
CLCF (%)	47.7 -- 50.6	7	49.5	1.1
SFD (%)	48.3 -- 53.0	7	50.3	1.7
EOL (%)	19.3 -- 23.2	7	21.7	1.4
EOW (%)	7.9 -- 11.7	7	10.2	1.5
CL (%)	7.3 -- 12.8	4	9.7	2.4

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Table 37. Counts for Narcine sp. nov. E. A) MNHN 1996-1554; B) MNHN 1996-1555; C) MNHN 1996-1552; D) MNHN 1996-1551; E) MNHN 1996-1550; F) MNHN 1996-1549. All specimens are from Madagascar. Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	RANGE
PROP	14	14	15	16	16	17	14 -- 17
MESO	10	10	11	8	11	10	8 -- 11
META	5	5	6	3	3	2	2 -- 6
TPR	29	29	32	27	30	29	27 -- 32
PVR	16	20	19	19	18	17	16 -- 20
FDR	10	9	9	9	8	9	8 -- 10
SDR	10	--	6	6	9	6	6 -- 10
DCR	22	22	19	19	19	19	19 -- 22
VCR	29	24	22	23	26	28	22 -- 29
TCR	51	46	41	42	55	47	41 -- 55
UTR	23	24	19	18	19	14	14 -- 24
LTR	23	21	23	18	19	11	11 -- 23
TC	28	29	27	28	25	27	25 -- 29
PC	68	70	70	71	68	78	68 -- 71
CC	25	23	22	24	26	22	22 -- 26
TV	121	122	119	123	119	127	119 -- 127
R	6	7	7	6	7	6	6 -- 7

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Table 38. Measurements for Narcine sp. nov. F. N is number of specimens from which means and standard deviations (SD) were extracted.

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	SPECIMENS	N	MEAN	SD
TL (mm)	110.0 – 277.0	13	--	--
DW (%)	46.6 – 57.3	13	52.0	3.5
DL (%)	50.0 – 58.2	13	53.4	2.3
PCSL (%)	12.7 – 15.7	13	14.6	1.0
POSL (%)	14.5 – 17.5	13	15.5	1.1
PNSL (%)	12.0 – 14.4	13	13.0	0.9
SDW (%)	21.1 – 41.0	13	32.3	3.0
IOD (%)	6.0 – 8.5	13	7.4	0.8
EL (%)	1.8 – 3.0	13	2.4	0.4
ISD (%)	5.8 – 8.5	13	7.1	0.8
SPL (%)	2.1 – 3.0	13	2.4	0.3
SPW (%)	1.6 – 2.7	13	2.1	0.3
MW (%)	5.3 – 6.7	13	5.9	0.4
UTBW (%)	2.3 – 3.2	13	2.6	0.3
LTBW (%)	1.9 – 2.8	13	2.3	0.3
NCW (%)	5.0 – 6.6	8	5.7	0.7
NCL (%)	1.0 – 2.4	11	1.8	0.4
DBN (%)	5.5 – 7.3	13	6.1	0.5
DBFGO (%)	11.5 – 14.5	13	13.3	0.8
DBLGO (%)	5.9 – 9.5	13	7.1	0.9
BBL (%)	7.2 – 11.0	13	9.8	1.0
PFL (%)	17.8 – 23.5	13	20.7	1.9
PFW (%)	26.7 – 36.8	13	33.5	3.0
ALPF (%)	11.3 – 14.2	13	12.4	0.8
PLPF (%)	15.5 – 23.2	13	19.5	2.6
TW (%)	15.4 – 21.6	13	18.9	1.8
HFD (%)	6.8 – 9.3	13	8.2	0.8
LFD (%)	4.5 – 7.6	13	5.9	0.7
HSD (%)	7.5 – 9.9	13	8.8	0.6
LSD (%)	5.5 – 7.3	13	6.2	0.5
LDLC (%)	11.8 – 13.1	13	12.3	0.4
LVLC (%)	11.0 – 14.1	13	12.7	1.0
HDLC (%)	3.2 – 5.0	13	4.4	0.5
HVLC (%)	2.2 – 4.7	13	3.7	0.8
HC (%)	7.5 – 12.5	13	10.3	1.3
DBD (%)	2.2 – 3.4	13	2.6	0.4
DSDC (%)	2.5 – 3.9	13	3.3	0.5
SCL (%)	50.0 – 54.8	13	52.6	1.3
CLCF (%)	39.7 – 47.0	13	42.6	2.0
SFD (%)	65.0 – 70.1	13	68.0	1.6
EOL (%)	22.8 – 29.2	13	25.0	1.9
EOW (%)	9.8 – 12.1	13	10.7	0.7
CL (%)	15.7 – 17.0	3	16.2	0.7

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Table 39. Counts for Narcine sp. nov. F. A) USNM 222500; B) USNM 222498; C) USNM 222200; D) USNM 235519; E) USNM 222199 (163 mm TL); F) USNM 222199 (167 mm TL). All specimens from Colombia. Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	RANGE
PROP	17	17	18	17	--	18	17 – 18
MESO	6	6	6	5	--	6	5 – 6
META	10	12	11	9	--	--	9 – 12
TPR	33	35	35	31	--	--	31 – 35
PVR	17	19	19	19	20	19	17 – 20
FDR	8	6	8	8	--	8	6 – 8
SDR	9	7	10	10	10	10	7 – 10
DCR	17	23	26	21	--	--	17 – 26
VCR	22	24	27	25	--	--	22 – 27
TCR	39	47	53	46	--	--	39 – 53
TC	24	24	28	26	28	24	24 – 28
PC	59	59	59	59	60	59	59 – 60
CC	20	23	24	22	24	23	20 – 24
TV	103	106	111	107	112	106	103 – 112
R	8	7	8	8	7	8	7 – 8

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Table 40. Measurements (column on left) and counts (column on right) for Narcine sp. nov. G. Number in parenthesis indicates that both sides of specimen differed in relation to the count, and both values are given (probably an artifact of exposure during radiography).

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	BMNH 1984.4.11.2		BMNH 1984.4.11.12
TL (mm)	306.0	PROP	17 (18)
DW (%)	51.3	MESO	10
DL (%)	47.1	META	6
PCSL (%)	11.5	TPR	33 (34)
POSL (%)	13.8	PVR	18
PNSL (%)	11.0	FDR	8
SDW (%)	27.8	SDR	6
IOD (%)	6.8	DCR	21
EL (%)	3.0	VCR	28
ISD (%)	5.8	TCR	49
SPL (%)	2.8	UTR	26
SPW (%)	1.5	LTR	21
MW (%)	7.1	TC	24
UTBW (%)	3.1	PC	59
LTBW (%)	2.7	CC	22
NCW (%)	5.1	TV	105
NCL (%)	1.7	R	8
DBN (%)	5.2		
DBFGO (%)	11.5		
DBLGO (%)	7.7		
BBL (%)	8.7		
PFL (%)	20.2		
PFW (%)	37.4		
ALPF (%)	11.8		
PLPF (%)	19.5		
TW (%)	22.2		
HFD (%)	10.7		
LFD (%)	7.1		
HSD (%)	10.8		
LSD (%)	7.4		
LDLC (%)	15.0		
LVLC (%)	14.3		
HDLC (%)	5.7		
HVLC (%)	4.3		
HC (%)	13.1		
DBD (%)	4.9		
DSDC (%)	5.6		
SCL (%)	49.3		
CLCF (%)	47.4		
SFD (%)	57.5		
EOL (%)	22.9		
EOW (%)	9.3		
CL (%)	--		

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Table 41. Measurements for Narcine sp. nov. H. N is number of specimens from which means and standard deviations (SD) were extracted.

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	SPECIMENS	N	MEAN	SD
TL (mm)	103.0 – 336.0	13	--	--
DW (%)	46.0 – 56.3	12	52.6	3.7
DL (%)	45.4 – 56.5	12	51.2	3.0
PCSL (%)	12.1 – 14.4	12	13.3	0.7
POSL (%)	15.1 – 19.7	12	16.3	1.3
PNSL (%)	10.0 – 13.5	12	11.6	1.0
SDW (%)	29.6 – 38.8	12	32.2	2.8
IOD (%)	5.5 – 7.5	12	6.6	0.5
EL (%)	2.3 – 4.2	12	3.0	0.6
ISD (%)	5.4 – 7.1	12	6.1	0.5
SPL (%)	1.9 – 3.6	12	2.7	0.6
SPW (%)	2.3 – 4.2	12	3.0	0.6
MW (%)	6.5 – 8.6	12	7.3	0.6
UTBW (%)	1.8 – 2.8	12	2.2	0.3
LTBW (%)	1.2 – 1.8	12	1.4	0.2
NCW (%)	4.9 – 6.1	12	5.5	0.5
NCL (%)	1.8 – 2.9	12	2.2	0.3
DBN (%)	4.5 – 6.4	12	5.5	0.6
DBFGO (%)	11.3 – 15.1	12	12.8	1.2
DBLGO (%)	5.5 – 9.1	12	7.4	1.1
BBL (%)	8.0 – 10.3	12	9.2	0.7
PFL (%)	15.6 – 19.9	12	17.7	1.4
PFW (%)	29.8 – 38.9	12	34.3	3.0
ALPF (%)	11.2 – 13.9	11	12.6	1.2
PLPF (%)	11.7 – 19.4	11	15.2	2.1
TW (%)	15.3 – 22.4	12	18.4	2.1
HFD (%)	8.8 – 12.4	12	10.1	1.0
LFD (%)	5.3 – 7.2	12	6.3	0.5
HSD (%)	8.4 – 11.5	12	9.6	0.9
LSD (%)	5.6 – 7.1	12	6.2	0.5
LDLC (%)	13.2 – 19.6	12	16.6	1.7
LVLC (%)	13.4 – 18.8	12	15.5	1.6
HDLC (%)	4.1 – 7.1	12	5.2	1.0
HVLC (%)	3.4 – 6.2	12	4.8	0.9
HC (%)	10.0 – 15.3	12	11.7	1.5
DBD (%)	4.2 – 6.5	12	5.5	0.8
DSDC (%)	2.7 – 7.9	12	5.8	1.4
SCL (%)	44.7 – 54.8	12	50.2	2.6
CLCF (%)	44.4 – 48.5	12	45.9	1.4
SFD (%)	51.8 – 62.5	12	57.7	2.5
EOL (%)	22.7 – 28.7	12	25.2	2.0
EOW (%)	9.9 – 14.8	12	11.6	1.4
CL (%)	12.0 – 14.4	5	13.5	1.0

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Table 42. Meristics of Narcine sp. nov. H. A) CAS 58358, female; B) CAS 58358, male; C) CAS 58359; D) USNM 236394; E) USNM 263398; F) USNM 263400, 250 mm TL; G) USNM 263400, 257 mm TL; H) USNM 263402, 233 mm TL; I) USNM 263402, 230 mm TL. Dashes represent counts not readable in available radiographs.

	A	B	C	D	E	F	G	H	I	RANGE
PROP	16	16	15	15	15	16	16	15	16	15 – 16
MESO	11	9	7	8	8	8	8	8	7	7 – 11
META	4	4	5	3	5	5	4	5	--	3 – 5
TPR	31	29	27	26	28	29	28	28	--	26 – 31
PVR	17	15	15	15	14	18	17	15	15	14 – 18
FDR	--	7	8	--	8	6	9	9	--	6 – 9
SDR	--	7	9	9	8	8	9	8	8	7 – 9
DCR	22	20	22	22	20	--	19	21	22	19 – 22
VCR	31	32	30	26	27	--	28	27	25	25 – 32
TCR	51	52	52	48	47	--	47	48	47	47 – 52
TC	27	25	25	20	19	25	27	22	25	19 – 27
PC	56	54	59	59	60	64	63	55	56	54 – 64
CC	29	28	26	27	27	25	25	24	29	24 – 29
TV	112	107	110	106	106	114	115	101	110	101 – 115
R	6	5	5	9	6	6	6	6	6	5 – 9

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Table 43. Measurements taken on specimens of Narcine sp. nov. I. N is number of specimens from which means and standard deviations (SD) were extracted.

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	SPECIMENS	N	MEAN	SD
TL (mm)	298.0 – 360.0	3	--	--
DW (%)	52.2 – 58.4	3	54.8	3.2
DL (%)	47.0 – 54.2	3	50.4	3.6
PCSL (%)	10.9 – 12.8	3	12.1	1.1
POSL (%)	14.1 – 15.3	3	14.9	0.7
PNSL (%)	7.1 – 12.0	3	9.8	2.5
SDW (%)	24.2 – 30.6	3	27.0	3.3
IOD (%)	5.9 – 6.8	3	6.2	0.5
EL (%)	2.6 – 3.2	3	2.8	0.3
ISD (%)	5.1 – 5.8	3	5.4	0.4
SPL (%)	2.3 – 2.8	3	2.5	0.3
SPW (%)	2.9 – 3.4	3	3.2	0.3
MW (%)	7.0 – 7.3	3	7.1	0.2
UTBW (%)	1.8 – 2.9	3	2.4	0.6
LTBW (%)	1.5 – 2.6	3	2.0	0.8
NCW (%)	4.5 – 5.6	3	5.0	0.5
NCL (%)	1.6 – 2.2	3	2.0	0.3
DBN (%)	4.6 – 5.1	3	4.9	0.2
DBFGO (%)	13.6 – 15.3	3	14.3	0.9
DBLGO (%)	7.5 – 8.8	3	8.3	0.7
BBL (%)	9.3 – 10.4	3	9.9	0.6
PFL (%)	16.3 – 21.3	3	18.1	2.8
PFW (%)	33.6 – 39.0	3	35.6	3.0
ALPF (%)	11.3 – 13.5	3	12.4	1.1
PLPF (%)	16.1 – 17.9	3	17.2	1.0
TW (%)	16.4 – 18.7	3	17.9	1.3
HFD (%)	9.8 – 11.6	3	10.9	1.0
LFD (%)	6.4 – 8.5	3	7.5	1.0
HSD (%)	8.5 – 9.6	3	9.0	0.6
LSD (%)	5.6 – 7.3	3	6.2	0.9
LDLC (%)	14.6 – 15.7	3	15.2	0.6
LVLC (%)	13.4 – 14.8	3	14.0	0.7
HDLC (%)	5.5 – 6.5	3	6.0	0.5
HVLC (%)	5.7 – 6.8	3	6.3	0.6
HC (%)	12.0 – 15.8	3	13.6	2.0
DBD (%)	5.9 – 7.4	3	6.6	0.8
DSDC (%)	6.4 – 6.8	3	6.7	0.2
SCL (%)	50.0 – 53.2	3	51.6	1.6
CLCF (%)	47.1 – 47.7	3	47.3	0.3
SFD (%)	55.6 – 60.0	3	57.9	2.3
EOL (%)	21.1 – 24.5	3	22.8	1.7
EOW (%)	9.4 – 12.3	3	10.5	1.6
CL (%)	--	--	--	--

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Table 44. Counts for specimens of Narcine sp. nov. I. A) BPBM 21418 (Oman); B) CAS 58398 (Sri Lanka). Value for lower tooth rows (LTR) for CAS 58398 is estimated, as mouth is heavily flattened and more tooth rows than normal are exposed. Dashes represent counts not readable in available radiographs.

	A	B
PROP	16	15
MESO	10	8
META	4	7
TPR	31	30
PVR	19	17
FDR	8	8
SDR	10	6
DCR	23	23
VCR	26	27
TCR	49	50
UTR	20	20
LTR	19	19
TC	28	27
PC	63	60
CC	26	26
TV	117	113
R	8	8

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PART II

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Table 45. List of Recent elasmobranch specimens used for Part II of this study. Specimens are housed in the Department of Ichthyology, AMNH (except for the Jurassic Palaeospinax priscus, which is housed in the Department of Vertebrate Paleontology, AMNH VP7085). CS = cleared and stained preparations; SW = wet skeletons; AMNH = American Museum of Natural History.

Galeomorphii

Carcharhinus leucas, AMNH 55610 (CS).

Galeocerdo cuvieri, AMNH 55042 (CS).

Prionace glauca, AMNH 49517 (CS), AMNH 32701 (CS).

Scyliorhinus retifer, AMNH 36777 (CS).

Scyliorhinus canicula, AMNH 4120 (CS).

Mustelus cf. dorsalis, AMNH 5579 (CS).

Mustelus laevis, AMNH 4138 (CS).

Pseudotriakis microdon, AMNH 71983 (CS).

Sphyrna lewini, AMNH 12464 (CS), embryo.

Sphyrna tiburo, AMNH 53030 (CS), gill and hyoid arches only.

Pseudocarcharias kamoharai, AMNH 71984 (CS).

Cetorhinus maximus, AMNH 38141 (SW), 57264 (SW).

Chiloscyllium punctatum, AMNH 44013 (CS), gill and hyoid arches only.

Ginglymostoma cirratum, AMNH uncatalogued (CS).

Hemiscyllium ocellatum, AMNH 38151 (CS).

Heterodontus francisci, AMNH 96795 (SW).

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Squalea

Chlamydoselachus anguineus, AMNH 13814, 13815, 38149, 59327.

Heptranchias perlo, AMNH (uncatalogued adult male).

Hexanchus griseus, AMNH 38185, 53092, 78170, 78172, 97382, 98254.

Hexanchus vitulus, AMNH 33474 (SW).

Notorynchus cepedianus, AMNH 55711, 55712, 55748.

Centroscymnus coelolepis, AMNH 78237 (SW), chondrocranium only.

Centroscymnus crepidator, AMNH 55521 (CS).

Etmopterus princeps, AMNH 78343 (SW), chondrocranium only.

Dalatias licha, AMNH 19446 (CS).

Squaliolus laticaudus, AMNH 15731 (CS).

Squalus acanthias, AMNH 38136 (2 specimens) (CS), 55513 (SW), chondrocranium only.

Pliotrema warreni, AMNH 44012 (CS), gill and hyoid arches only.

Pristiophorus cirratus, AMNH 30169 (CS).

Squatina californica, AMNH 55686 (CS).

Anoxypristis cuspidata, AMNH 3268 (CS).

Pristis pristis, AMNH 44011 (CS), gill arches only.

Pristis zijsron, AMNH 44048 (CS), gill arches only.

Platyrhina sinensis, AMNH 44055 (CS).

Rhinobatos percellens, AMNH 55622 (CS).

Narcine brasiliensis, AMNH 2488 (CS).

Torpedo torpedo, AMNH 4128 (CS).

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Holocephali

Callorhynchus capensis, AMNH 36943 (CS).

Hydrolagus colliei, AMNH 40801 (CS), AMNH 44129 (2 specimens) (CS).

Hydrolagus alberti, AMNH 39108 (CS).

Chimaera monstrosa, AMNH 55040 (CS).

Harriotta raleighana, AMNH 55039 (CS).

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Table 46. List of characters and their states coded for the matrix in Table 47.

1. Rostral process ("rostrum") a single (ventral) projection, formed solely by the trabecula (0); tripodal rostral cartilages (1); absence of rostral process (2).
2. Open lateral line canal (0); closed lateral line canal (1).
3. Precerebral fossa absent or uncovered (0); precerebral fossa roofed (1).
4. Ethmoidal region of neurocranium not downcurved (0); downcurved ethmoidal area (1).
5. Ethmoidal canal absent (0); present (1); present with exit on dorsal surface of nasal capsules (2).
6. Subnasal fenestra absent (0); present (1).
7. Superficial ophthalmic nerve exits neurocranium through prootic foramen (0); separate foramen for superficial ophthalmic nerve (1).
8. Ectethmoid process absent (0); present (as in Carvalho and Maisey, 1996) (1); present as "unchondrified antorbital cartilage" (2); antorbital cartilage (3).
9. Orbital articulation absent (0); present (1).
10. Suborbital shelf present (0); absent (1).
11. Basitrabecular process absent (0); present (1).
12. Post-orbital articulation absent (0); present but without complete articular facet (1); present with complete articular facet (2).
13. Hyomandibular fossa in the posterior part of otic region (0); hyomandibular fossa anteriorly situated in otic region (1).

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Table 46 (cont.).

14. Hyomandibular fossa not composed of two horizontally adjacent concavities (0); articular fossa for hyomandibula composed of two horizontally arranged concavities (1).
15. Concavity ventral to hyomandibular fossa absent (0); present (1).
16. Basioccipital fovea present (0); absent (1).
17. Occipital hemicentrum present (0); absent (1).
18. Obliquus inferior ß absent (0); present (1).
19. Absence of extrabranchial cartilages on hyoid arch (0); extrabranchials on dorsal side only (1); extrabranchials present on entire arch (2).
20. Sixth branchial unit absent (0); present (1).
21. Seventh branchial unit absent (0); present (1).
22. Anterior basibranchials present (0); absent (1).
23. Hypobranchial bar absent (0); present (1).
24. Posteriormost elements of dorsal gill arches not completely fused (0); complete fusion of posterior dorsal gill arch elements ("gill pick-ax") (1).
25. Adductor mandibulae composed of dorsal and ventral components (0); composed of "lateralis i and ii" (1).
26. Suborbitalis muscle originating on suborbital surface (0); originating on interorbital wall (1); originating on posterior aspect of nasal capsule (2); originating on ectethmoid process (3); originating on upper preorbital wall (4).

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Table 46 (cont.).

27. Suborbitalis inserting on adductor mandibulae and/or dermal tissues around mouth corner (0); suborbitalis inserting directly on mandibula anterior to adductor mandibulae (1); suborbitalis inserting on mandibula via elongate tendon (2).
28. Adductor mandibulae superficialis absent (0); present (1).
29. Adductor mandibulae superficialis inserting on subcutaneous tissue around the eye opening (0); inserting on ectethmoid process (1); inserting on posterior aspect of nasal capsule (2); inserting on mandibula (3).
30. Levator palatoquadrati muscle not separated from spiracularis (0); separated (1).
31. Constrictor hyoideus dorsalis inserting on hyomandibula (0); inserting on palatoquadrate (1); inserting partly on both (2).
32. Arcualis dorsalis muscle with single origin (0); originating from two heads (1).
33. Subspinalis muscle absent (0); present (1).
34. Interpharyngobranchialis muscles present (0); absent (1).
35. Genio-coracoideus originating on fascia covering coraco-arcualis (rectus cervicis) (0); genio-coracoideus originating from coracoid or pericardial membrane (1).
36. Coraco-hyomandibularis muscle absent (0); present and originating on the coraco- arcualis muscle (1).
37. Right and left coracoids separate (0); fused (1).

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Table 46 (cont.).

38. Single facet for the articulation of pectoral basals (0); separate articular condyle for pectoral metapterygium present (1); all three basals with separate condyles for articulation with scapulocoracoid (2).
39. Tribasal pectoral fin (0); propterygium and mesopterygium fused (1); mesopterygium and metapterygium fused (2); all three basals fused (3).
40. Pectoral propterygium articulating with radials (0); propterygium not contacting radials (1).
41. Pectoral propterygium not elongated anteriorly (0); propterygium extended forward (1).
42. Pectoral metapterygium without short proximal segment (0); metapterygium contacts short proximal segment (1).
43. Ventral marginal cartilage of clasper not elongated (0); elongated (1).
44. Notochord constricted along entire vertebral column (0); constricted only anteriorly and posteriorly, or primarily absent (1).
45. Three columns of heart valves (0); four columns (1).
46. Supraneurals not enlarged anterior to second dorsal fin (0); enlarged supraneurals preceding second dorsal fin (1); enlarged supraneurals also in abdominal and precaudal regions (2).
47. Hemal spines not forming complete arches in precaudal region (0); complete hemal arches in precaudal region (1).

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Table 46 (cont.).

48. Precaudal hemal process not elongate (0); elongate similar to lower caudal skeleton (1).
49. Dorsal fin endoskeleton composed of basal cartilage with a finspine (0); dorsal fin endoskeleton with basal cartilage and no finspine (1); dorsal endoskeleton composed of radials only (no finspine) (2).
50. Two dorsal fins (0); one dorsal fin (1).
51. Anal fin skeleton composed of basal cartilage and radials (0); composed of radials only (1).
52. Inclinator dorsalis muscle originating on epaxial musculature (0); originating from vertebrae (1).
53. Ventral tail muscle bundle not developed (0); well developed (1).
54. Flexor caudalis muscle restricted to hemal processes of caudal fin (0); flexor caudalis extending to origin of caudal fin (1); flexor caudalis extending anterior to origin of caudal fin (2).
55. Nasoral groove absent (0); present (1).
56. Mesonarial flap present (0); absent (1).
57. Circumnarial folds and grooves absent (0); present (1).
58. Diagonal tooth rows (0); linearly arranged tooth rows (1); linearly arranged rows with teeth overlapping each other (2).
59. Teeth devoid of "aprons" (0); with "aprons" (1).
60. Spiracle valve absent (0); present (1).
61. Luminous organs absent from body surface (0); present (1).

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Table 46 (cont.).

62. Upper precaudal pit absent (0); present (1).

63. Longitudinal precaudal keel absent (0); present (1).

64. Intestinal spiral valve (0); intestinal ring valve (1).

65. Basihyal elongated (0); basihyal as broad as long (1).

66. Anal fin present (0); absent (1).

67. Pharyngobranchial blade absent (0); present (1).

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Table 47. Matrix of characters and taxa derived from Table 46. This matrix was used for the phylogenetic analyses presented in Part II.

Outgroup
0000000000 0000000??0 0000?????? ??????0000 0000?00000
0??????00? ????700

Heterodontus
2101000000 0010000010 0000041100 0000001000 0000000000
0000101010 0000001

Orectolobiformes
0101001000 0010000010 0001?410?1 0000001000 0010000020
100010?010 000?001

Lamniformes
1100001000 0010000010 000102007?0 0000001000 0010000020
1000000000 0??1001

Carcharhiniformes
1100001000 0010000010 000102007?0 0000001000 0010000020
1000000000 0000001

Chlamydoselachus
0000000111 1100000001 000003007?0 0000000001 0001100021
1000000000 0000100

Hexanchus
0100110111 1200101011 0000030110 1100000001 0101101011
0000000100 0000000

Notorynchus
0000000111 1200001011 1000030110 1100000001 0101101011
0000000100 0000000

Heptranchias
0100110111 1200101011 1000030110 1100000001 0101101011
0000000100 0000100

Echinorhinus
0000100111 1000001020 0001030130 0100001030 0001001010
?000010110 0000010

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Table 47 (cont.).

Etmopteridae
0100110011 1000000020 0001010100 2100101000 0000001000
?000010211 1000010

Somniosidae
0100110011 1000000020 0011011100 2100101010 0000001010
?000010211 1000010

Oxynotus
0100100011 1000000020 0011011100 2100101010 0000001000
?000010211 1000010

Dalatiinae
0100110011 1000000020 0011011100 2111101030 0000001010
?000010211 1000010

Euprotomicrininae
0100110011 1000000020 0011011100 2100101030 0000001010
?000010211 1000010

Centrophoridae
0100110011 1000000020 0001010100 2100001020 0000001000
?000010211 0000010

Squalidae
0100110011 1000000020 0001000100 2100001000 0000011100
?001010211 0110010

Squatina
0100200011 1000010020 00010??100 0100?01100 1000011110
?112110010 0010010

Pristiophoridae
0110200211 1001011120 0101102100 2100011200 0000021110
?102010011 0010010

Batoidea
0110200300 0001011120 0101102121 0011011200 1000021110
?112010011 0010010

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ILLUSTRATIONS

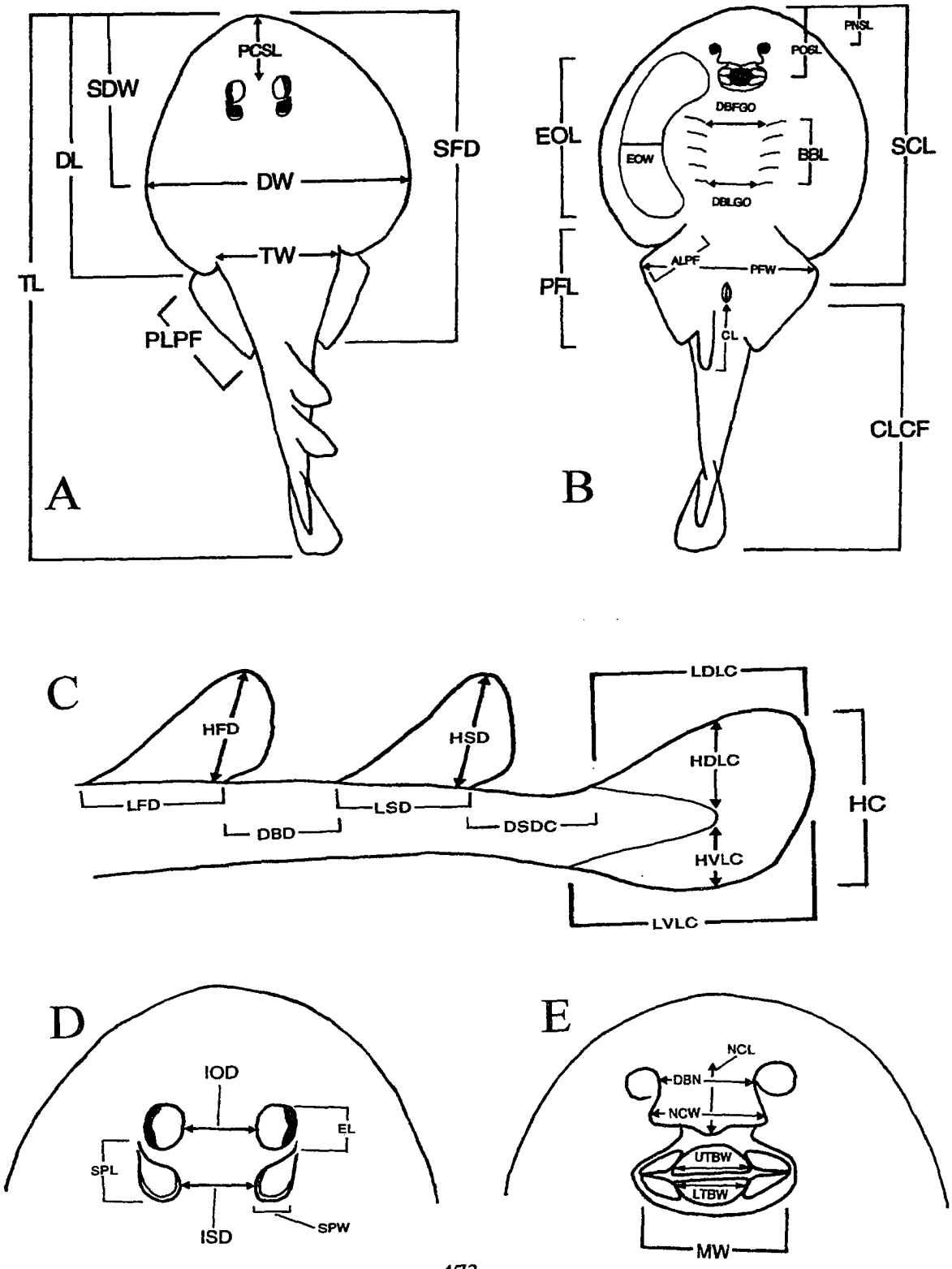
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PART I

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Figure 1. Measurements taken on specimens of Narcine. A) entire specimen in dorsal view; B) entire specimen in ventral view; C) lateral view of tail with measurements of dorsal and caudal fins; D) dorsal view of anterior disc region depicting measurements of eyes and spiracles; E) ventral view of snout region with measurements of nasal curtain and mouth region. Abbreviations are listed in the "Material and Methods" section under "Measurements".

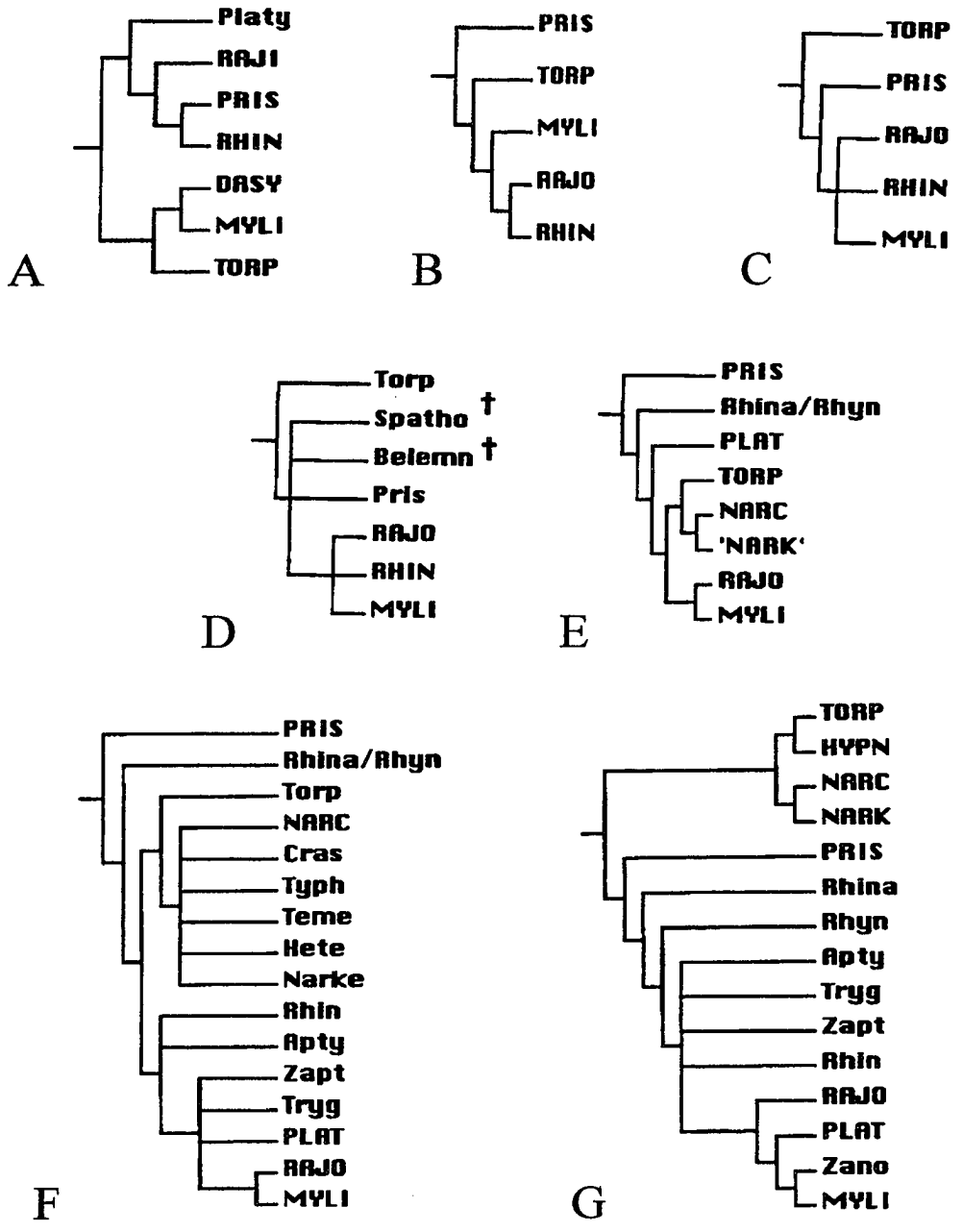
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Figure 2. Previous phylogenetic hypotheses concerning the relationships of electric rays. A) Holmgren , 1941; B) Compagno, 1973 and Heemstra and Smith, 1980; C) Compagno, 1977; D) Maisey, 1984; E) Shirai, 1996; F) Nishida, 1990; G) McEachran et al., 1996. Apty = Aptychotrema; Belemn = Belemnobatis; DASY = Dasyatidae; Cras = Crassinarke; Hete = Heteronarce; HYPN = Hypnidae; MYLI = Myliobatidae; NARC = Narcinidae; NARK and 'NARK' = Narkidae; Platy = Platyrhina; PLAT = Platyrhinidae; Pris = Pristis; PRIS = Pristidae; RAJI = Rajiformes; RAJO = Rajoidei; Rhin = Rhinobatos; RHIN = Rhinobatidae; Rhyn = Rhyncobatus; Teme = Temera; Torp = Torpedo; TORP = Torpedinidae; Tryg = Trygonorhina; Typh = Typhlonarke; Zano = Zanobatus; Zapt = Zapteryx. Daggers indicate fossil taxa; names in figures not included in abbreviations are spelled in their entirety (lower case indicative of generic level taxa).

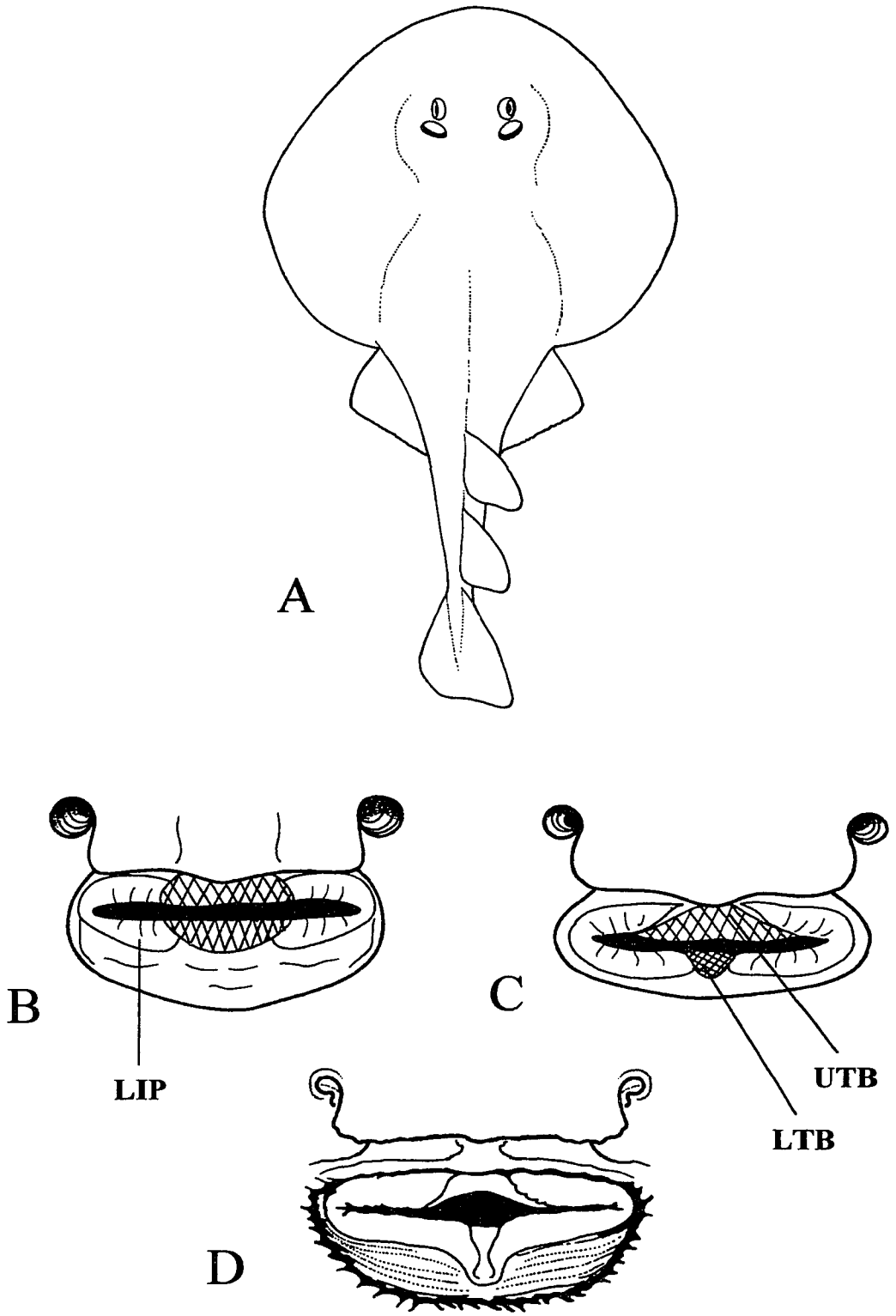
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Figure 3. Outline illustrations of entire specimen and nasoral regions of a generalized member of the Narcinidae.

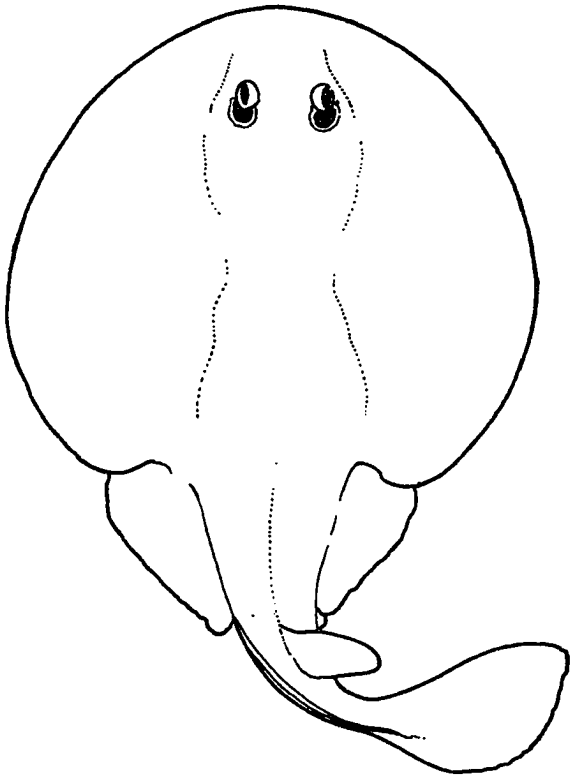
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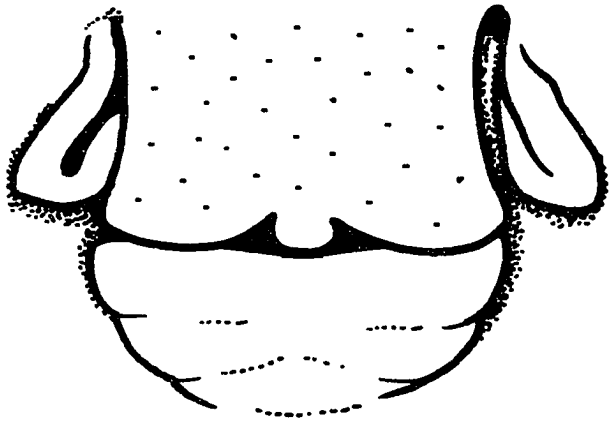
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Figure 4. Outline illustrations of entire specimen and nasoral region of a generalized member of the Narkidae.

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A

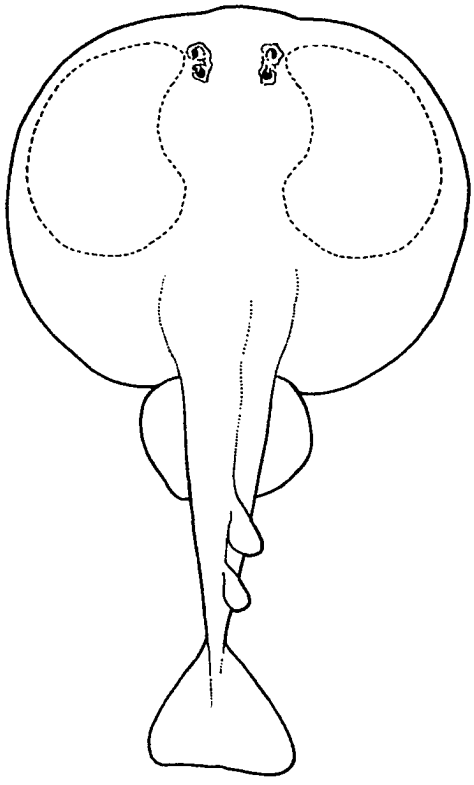


B

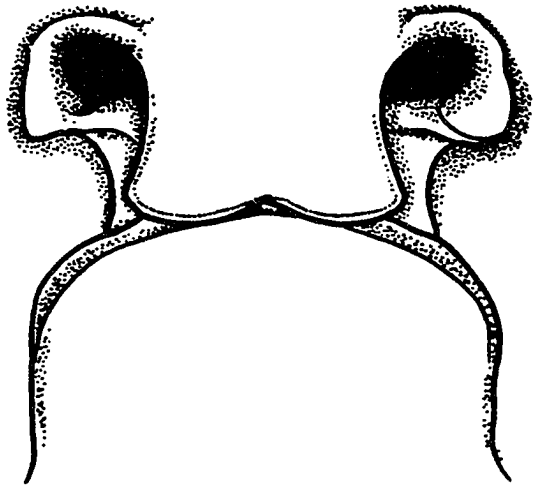
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Figure 5. Outline illustrations of entire specimen and nasoral region of a generalized member of the Torpedinidae.

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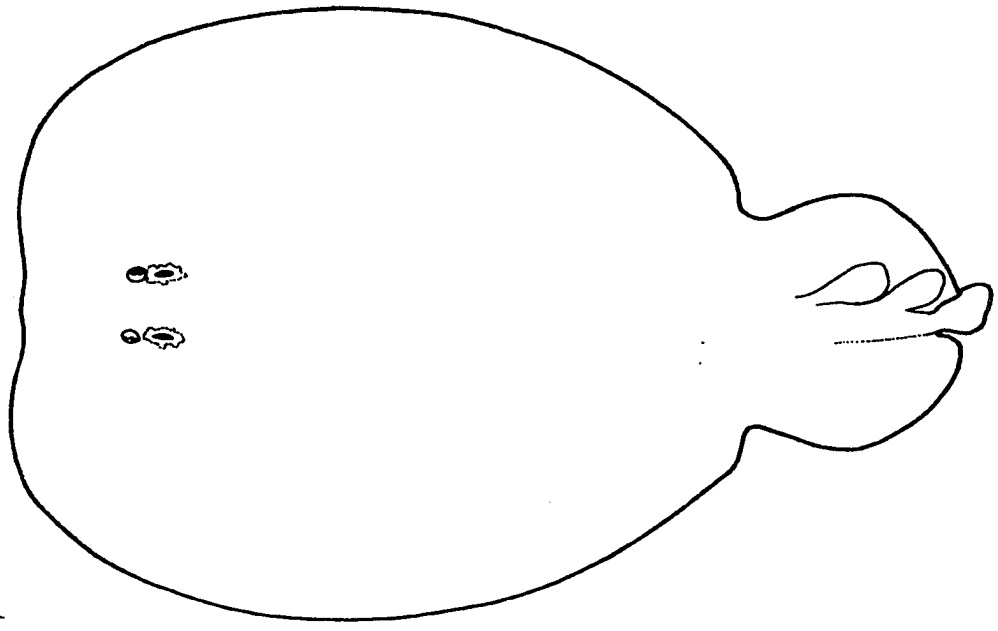


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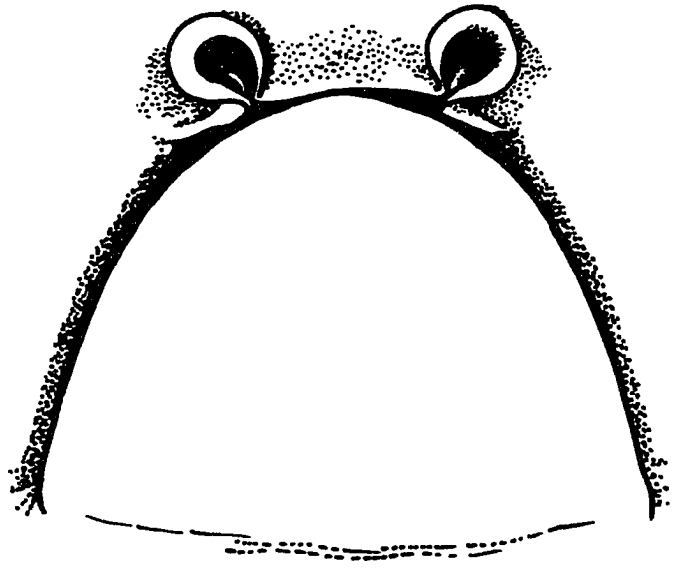
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Figure 6. Outline illustrations of entire specimen and nasoral region of a generalized member of the Hypnidae.

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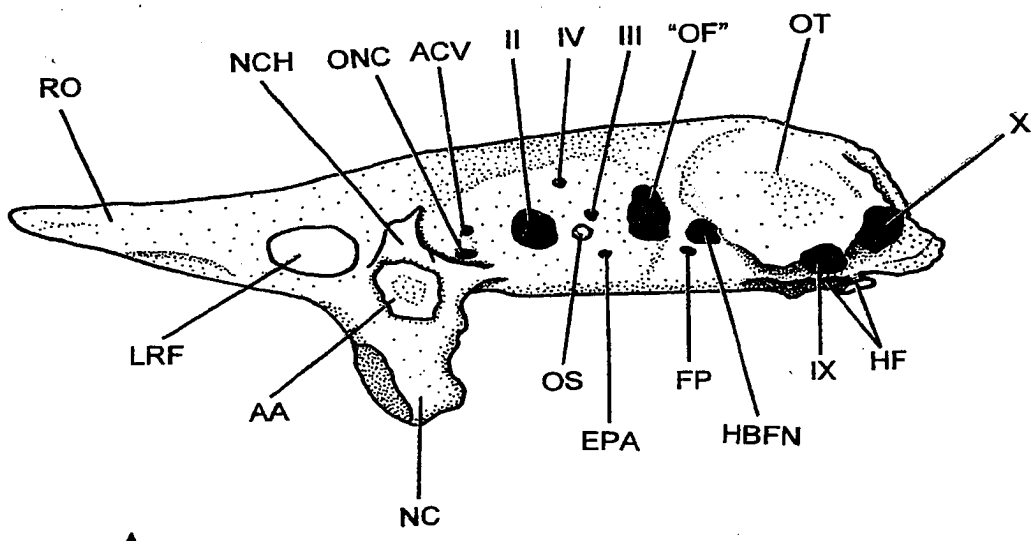


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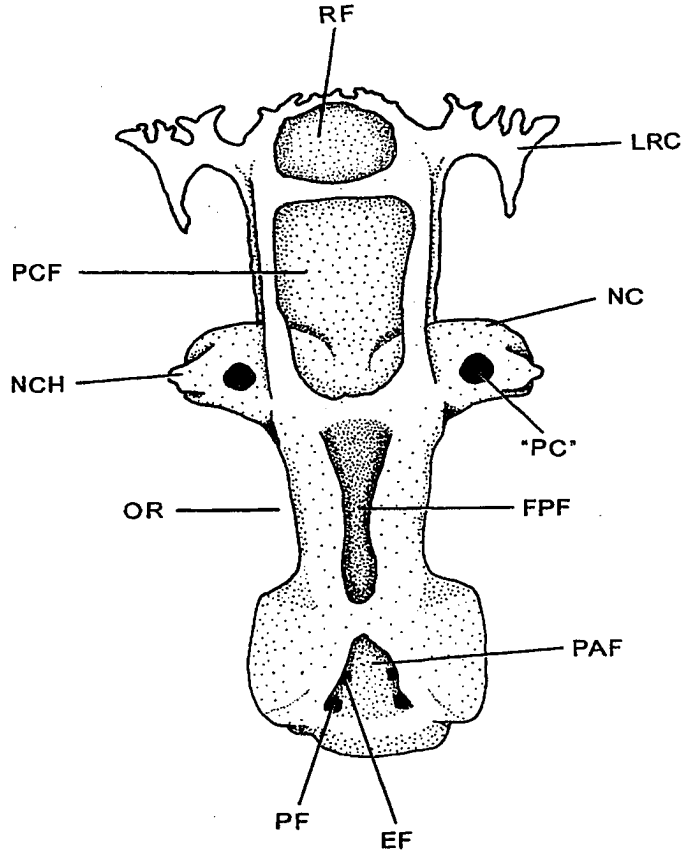
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Figure 7. Neurocranium of Narcine brasiliensis (DBAV-UERJ 1176.4, Cananéia, SP, Brazil) in A) lateral and, B) dorsal views; anterior to top for B), anterior to left in A). Scale bar = 1cm.

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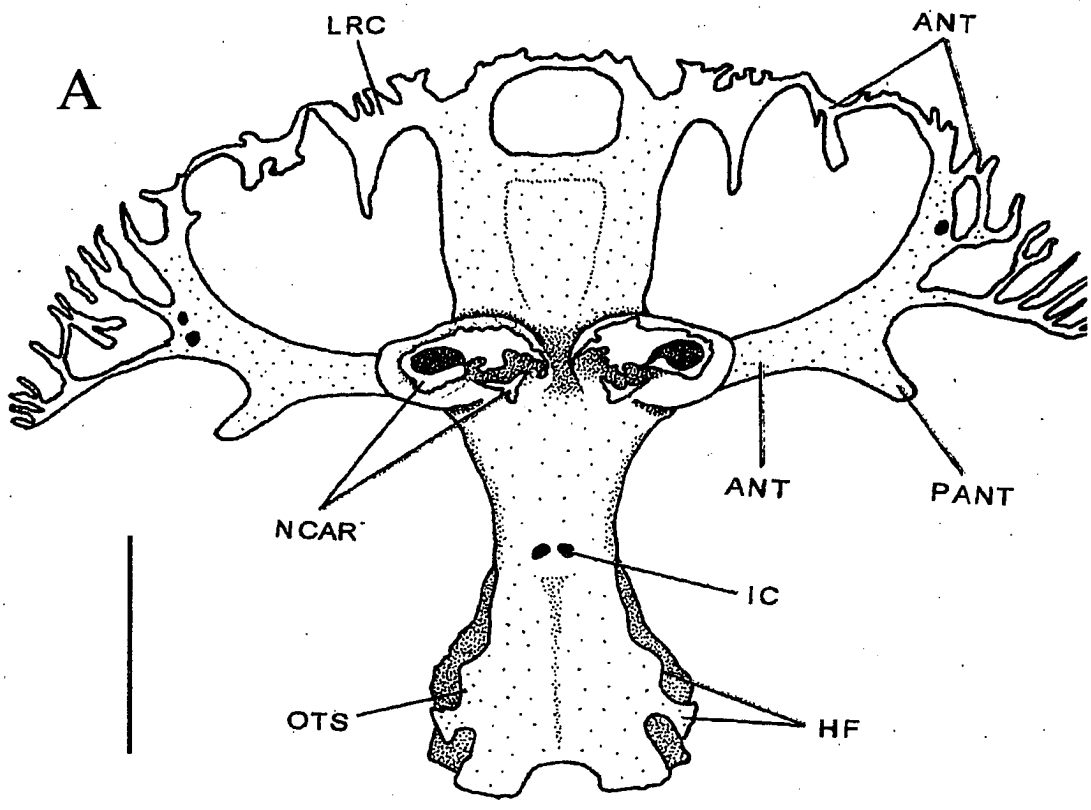


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Figure 8. A) Neurocranium of Narcine brasiliensis in ventral view (DBAV-UERJ 1176.4, Cananéia, SP, Brazil), anterior to top; B) Neurocranium of N. bancroftii in dorsal views (AMNH 2488, Florida), anterior to top. Scale bar = 1 cm.

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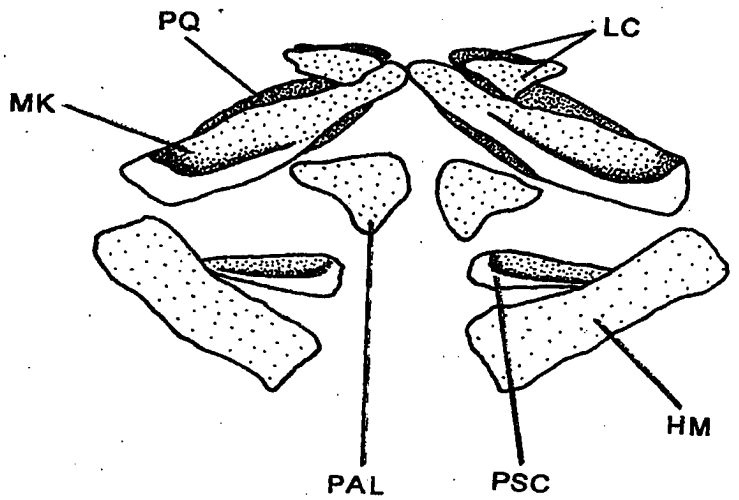




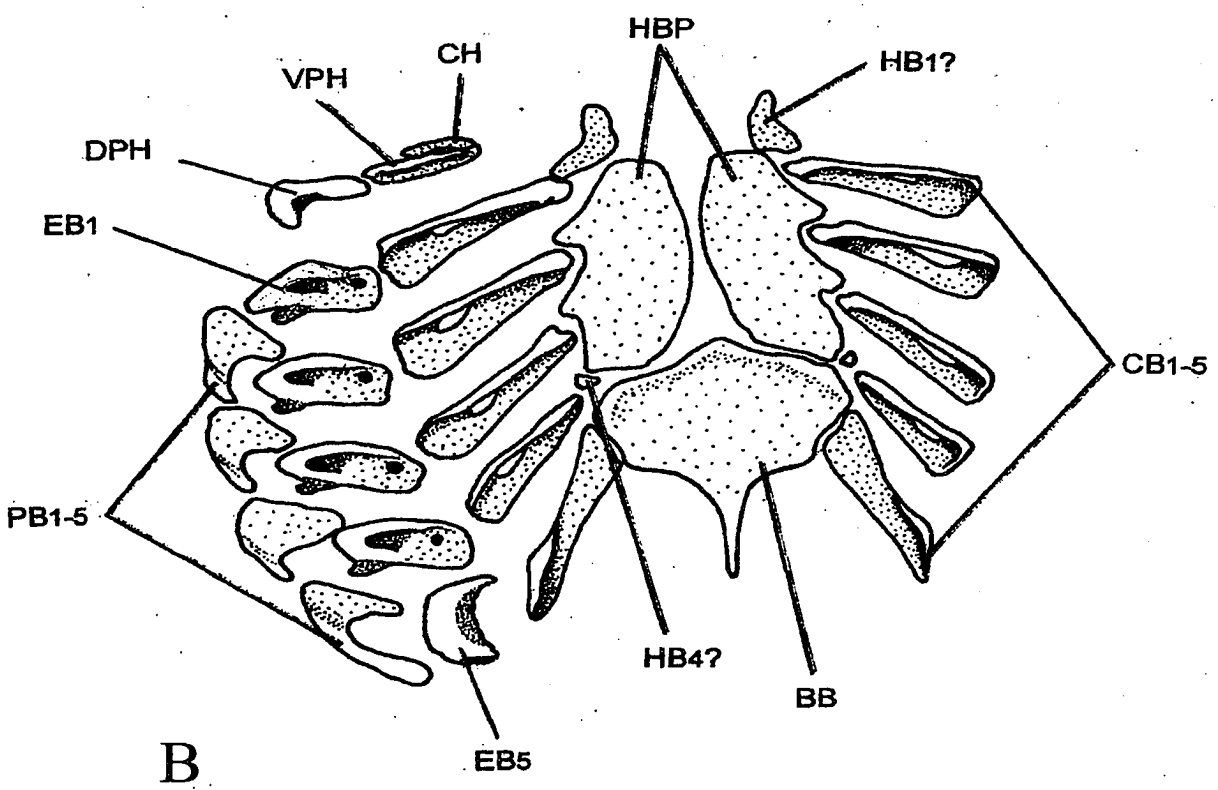
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Figure 9. A) Mandibular and hyoid arches of Narcine brasiliensis (DBAV-UERJ 1176.4, Cananéia, SP, Brazil) in ventral view, anterior to top. Components depicted are slightly pulled apart. B) Branchial arches of Narcine brasiliensis (DBAV-UERJ 1176.4, Cananéia, SP, Brazil) in dorsal view, anterior to top. Dorsal gill arch elements pulled toward left; right dorsal gill arch elements and right ceratohyal and pseudohyal arch not shown. Gill arch structures are naturally closer together than depicted. Scale bar = 1cm.

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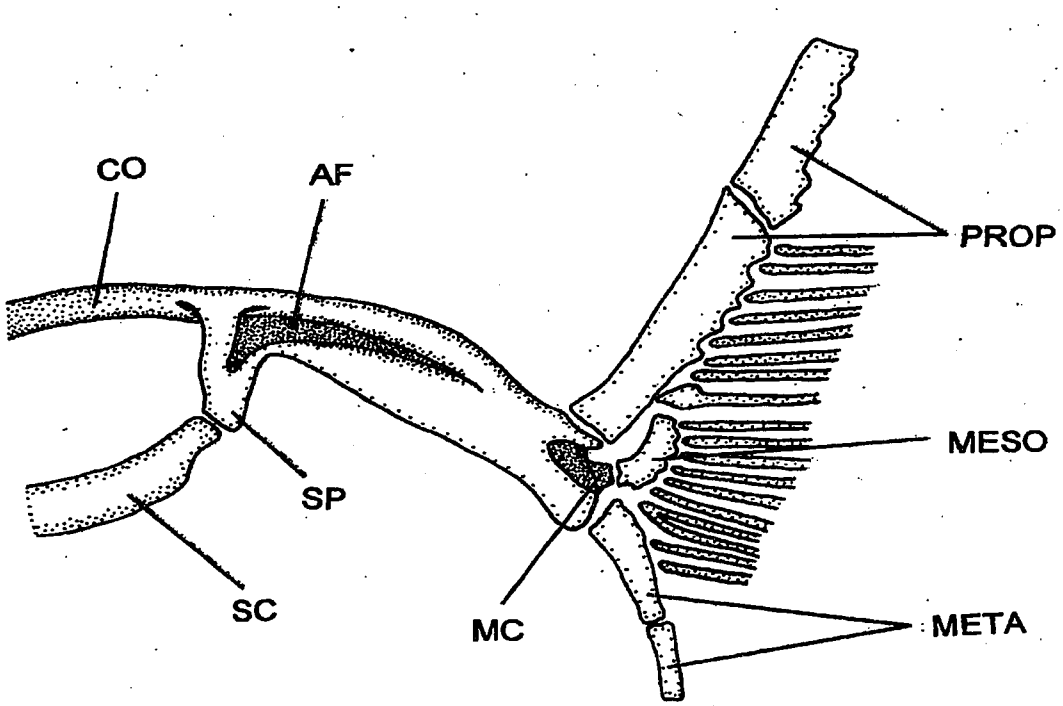


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Figure 10. Dorsal view of right half of scapulocoracoid of Narcine brasiliensis (DBAV-UERJ 1176.4, Cananéia, SP, Brazil); anterior to top. Scale bar = 1 cm.

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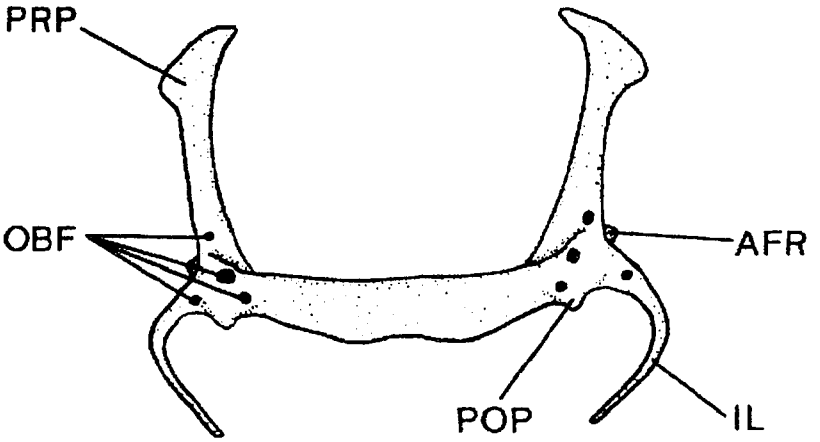


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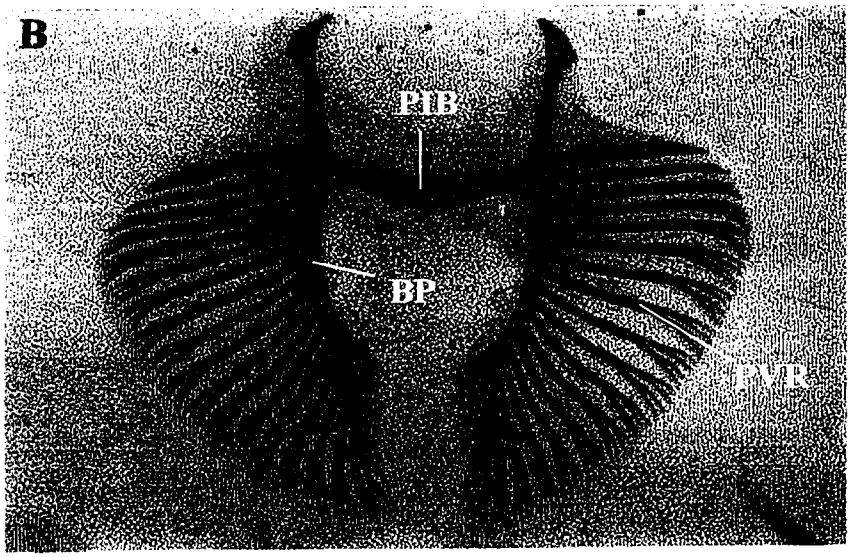
Figure 11. A) Dorsal view of pelvic girdle of Narcine brasiliensis (DBAV-UERJ 1176.4, Cananéia, SP, Brazil); anterior to top. Radial elements, including first compound radial, and basipterygium not shown. B) Pelvic girdle of N. bancroftii (AMNH 2488, Florida). Scale bar = 1cm.

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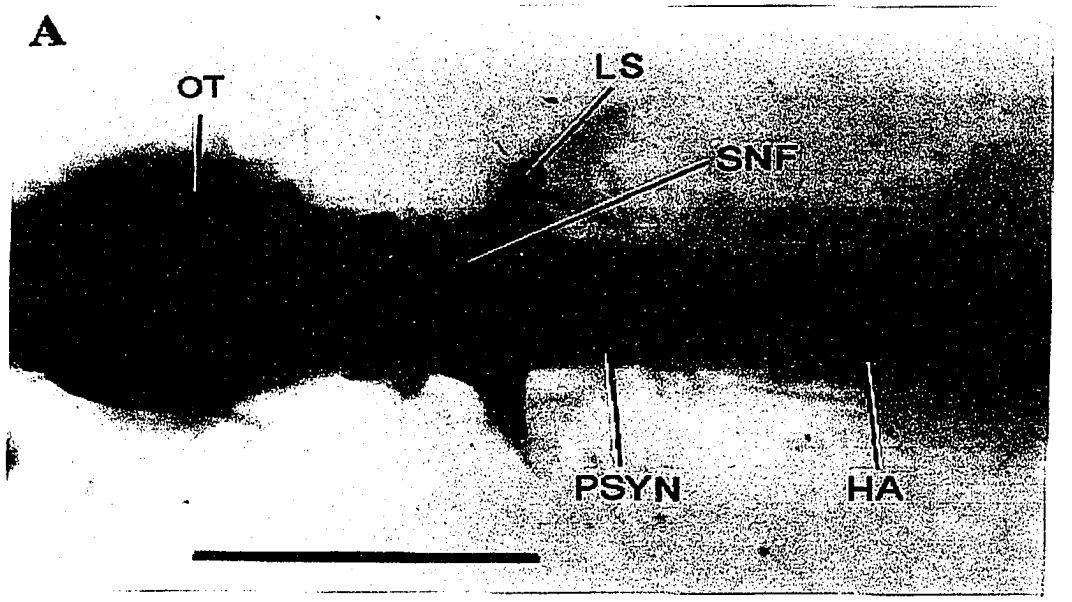
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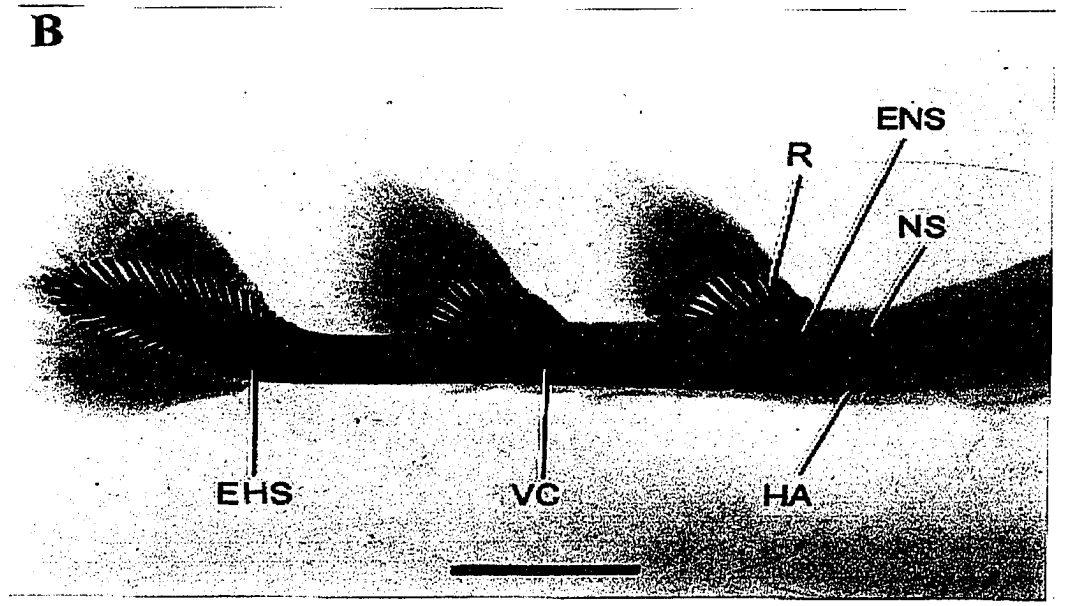


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Figure 12. A) Dorsal view of posterior neurocranial region of Narcine bancroftii (AMNH 2488, Florida) showing synarcual cartilage and beginning of vertebral column; anterior to left. B) Lateral view of posterior vertebral column depicting skeleton of dorsal and caudal fins; anterior to left. Scale bar = 1cm.

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Figure 13. Dorsal (A) and ventral (B) views of lectotype of Torpedo brasiliensis von Olfers, 1831 (ZMB 4577, 235 mm TL; Rio de Janeiro); C) lateral view of tail of lectotype (ZMB 4577).

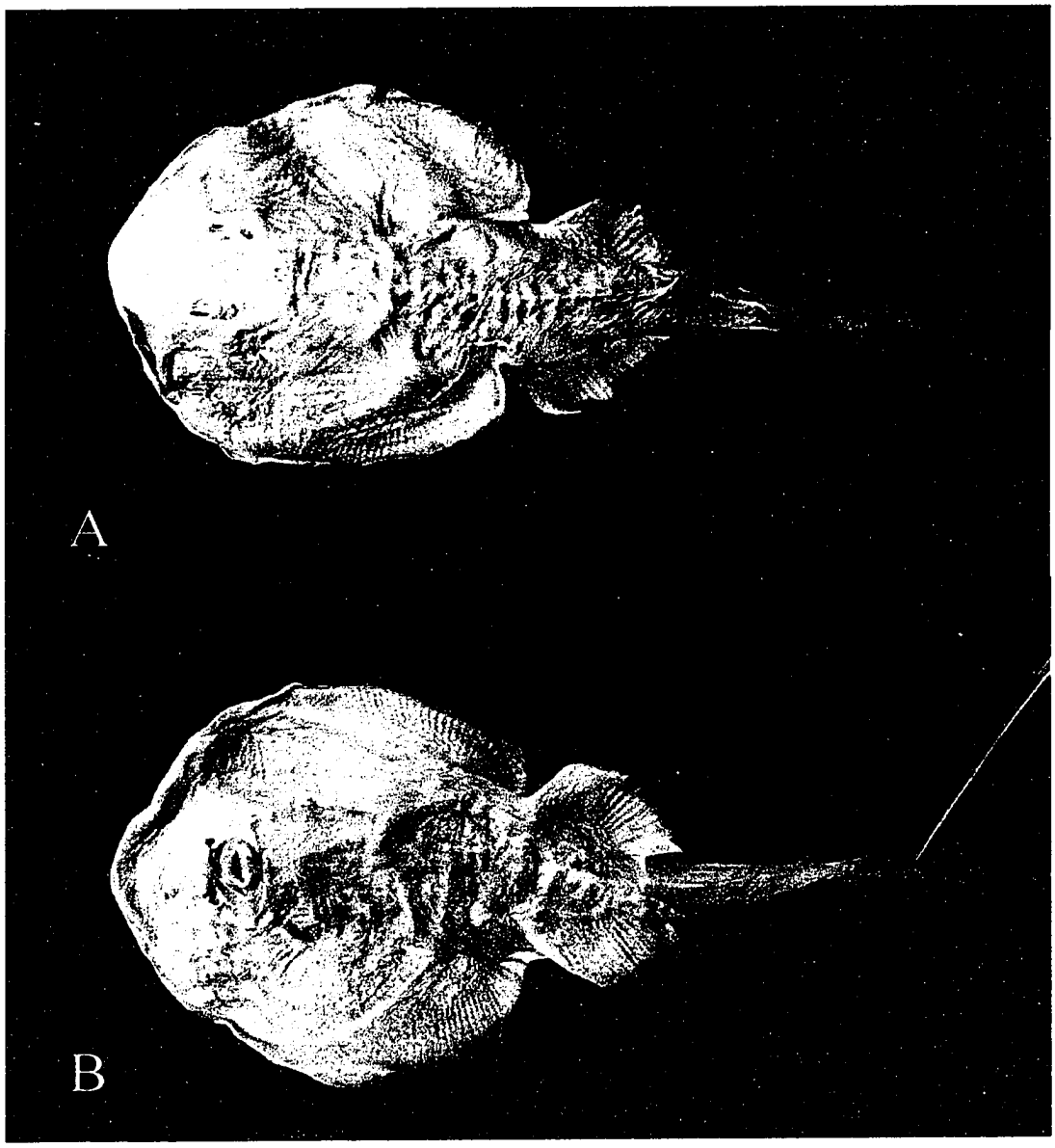
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Figure 14. Lectotype of Torpedo ocellata Quoy and Gaimard, 1824 in dorsal (A) and ventral (B) view (MNHN 7516, 107 mm TL).

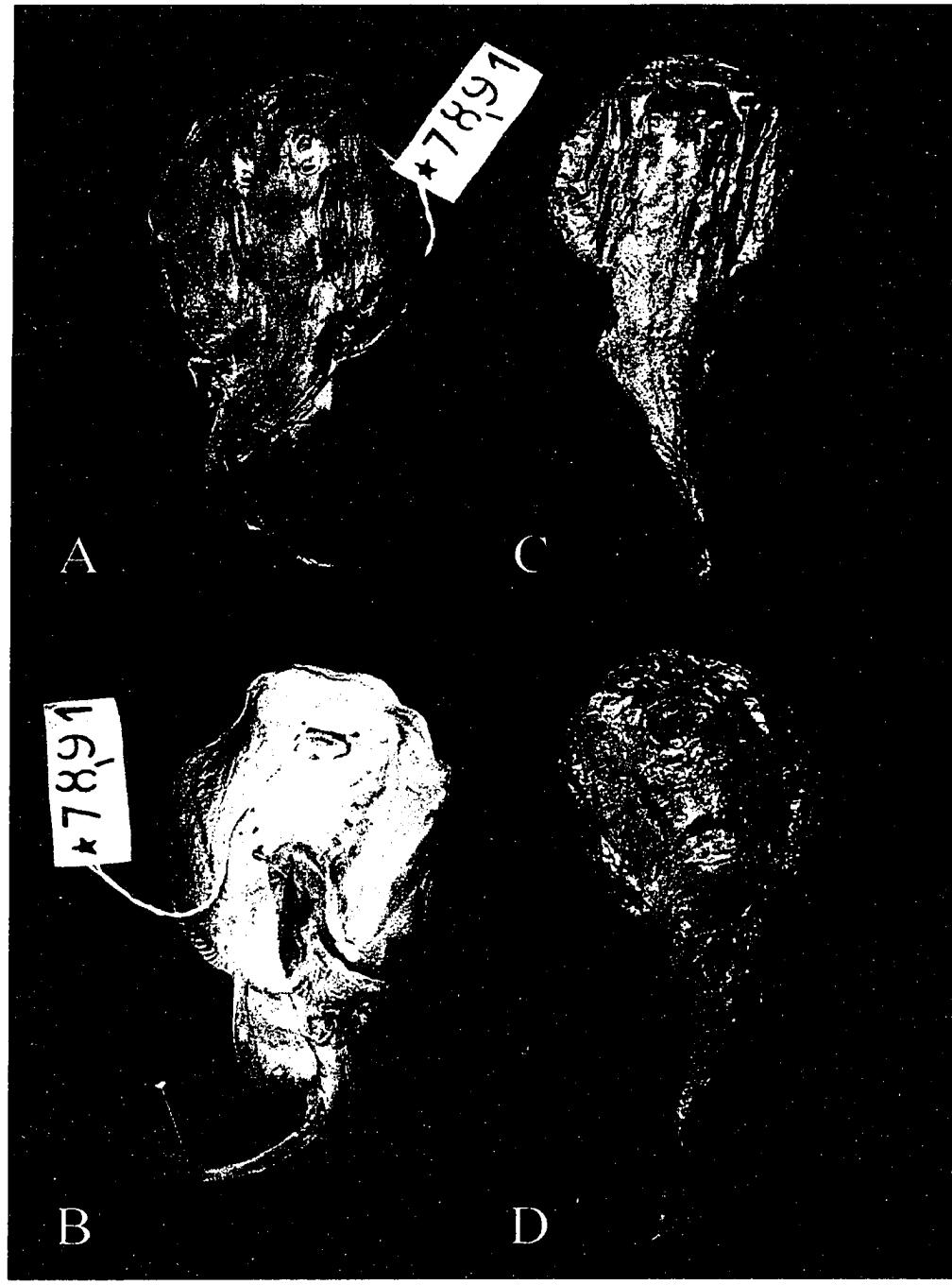
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Figure 15. Paralectotypes of Torpedo ocellata Quoy and Gaimard, 1824. A and B MNHN 7891 (110 mm TL), C and D MNHN 7891 (103 mm TL).

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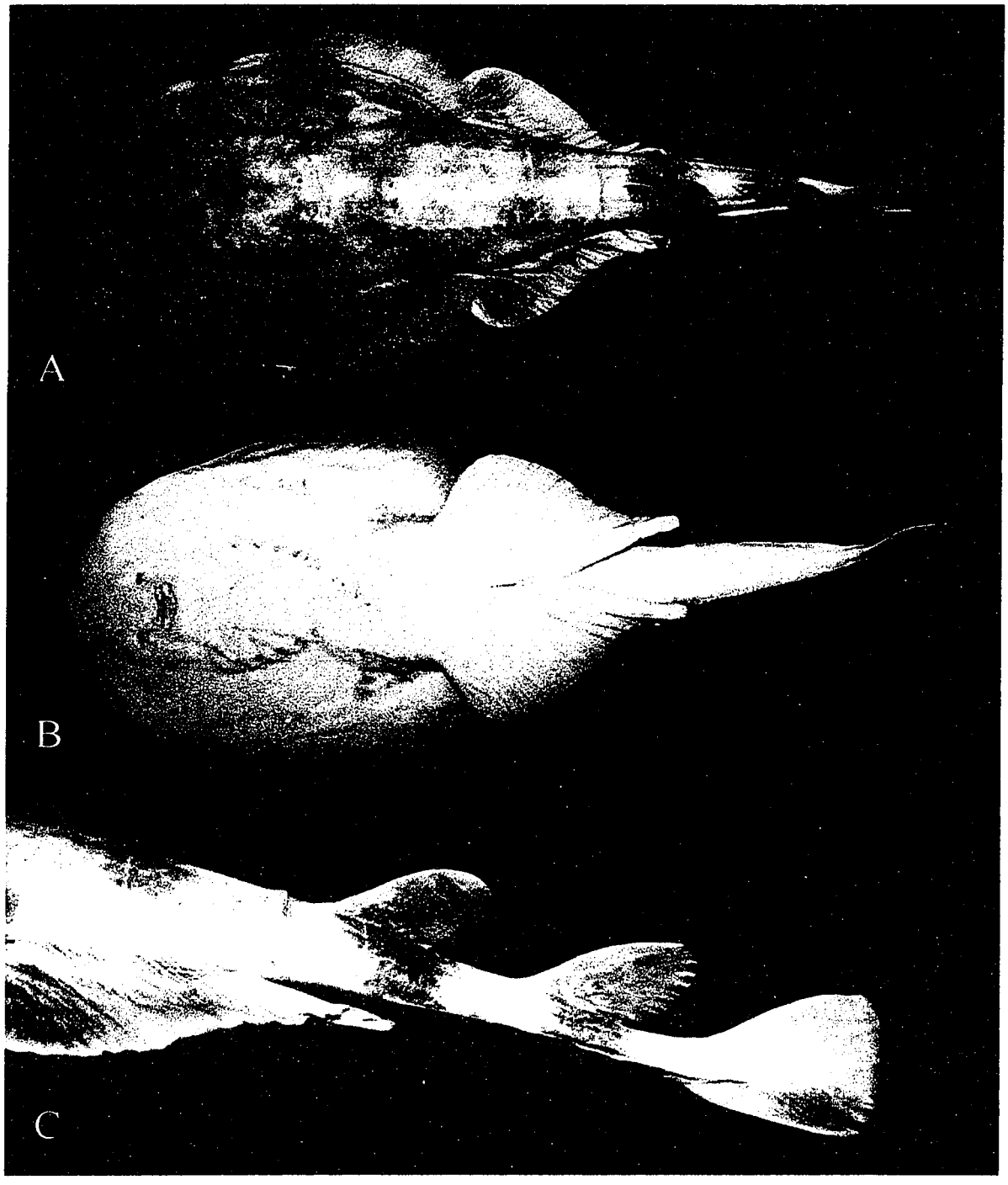


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Figure 16. Holotype of Narcine brachypleura Miranda Ribeiro, 1923 (MNRJ 548, 321 mm TL; Rio de Janeiro) in dorsal (A), ventral (B) and lateral view of tail (C).

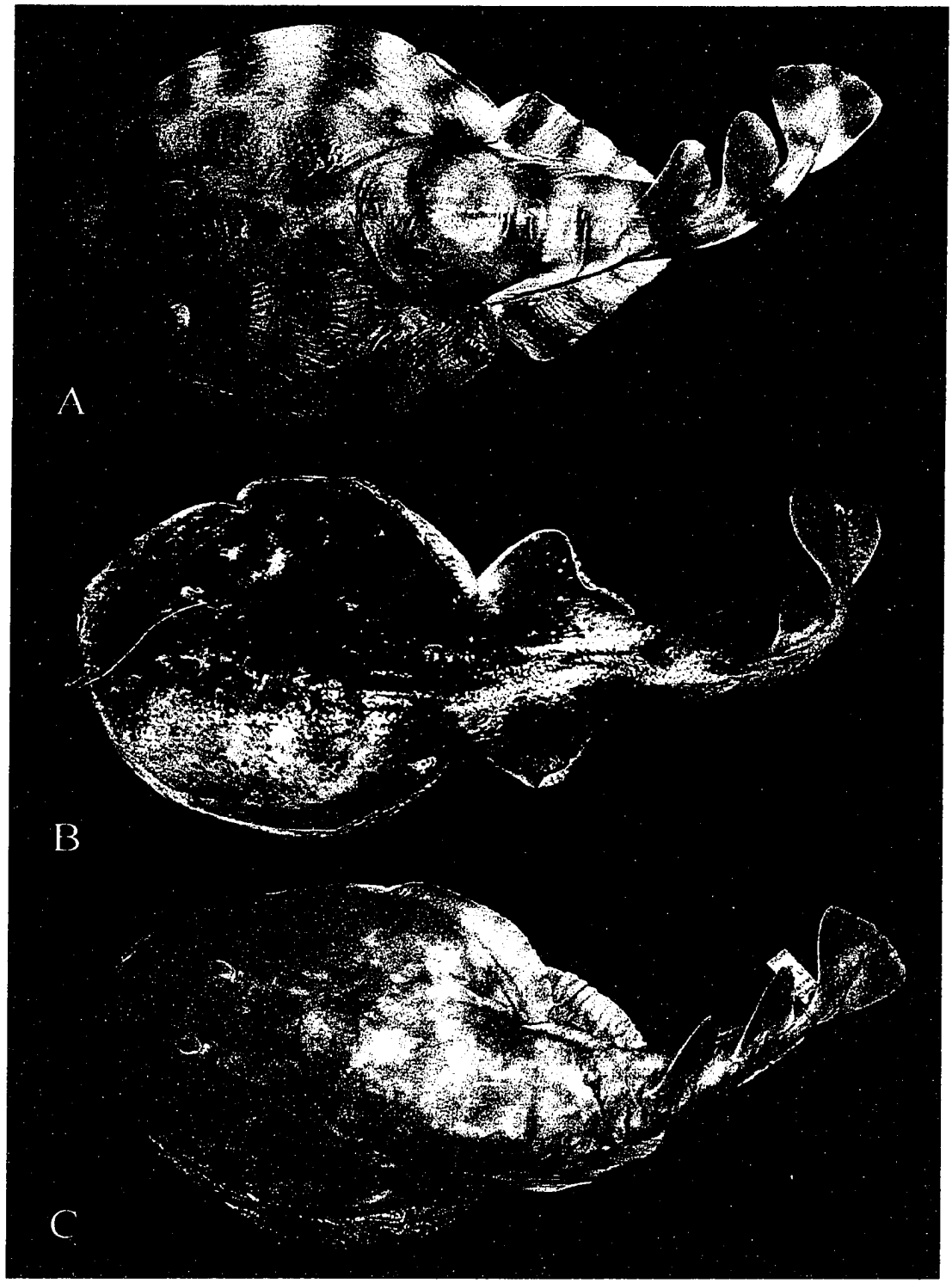
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Figure 17. Dorsal views of specimens of N. brasiliensis. A) MZUSP uncat. (262 mm TL; Espírito Santo); B) DBAV-UERJ 1571 (515 mm TL; Rio de Janeiro, specimen greatly shrunken); C) MCP 1435 (355 mm TL; Rio Grande do Sul).

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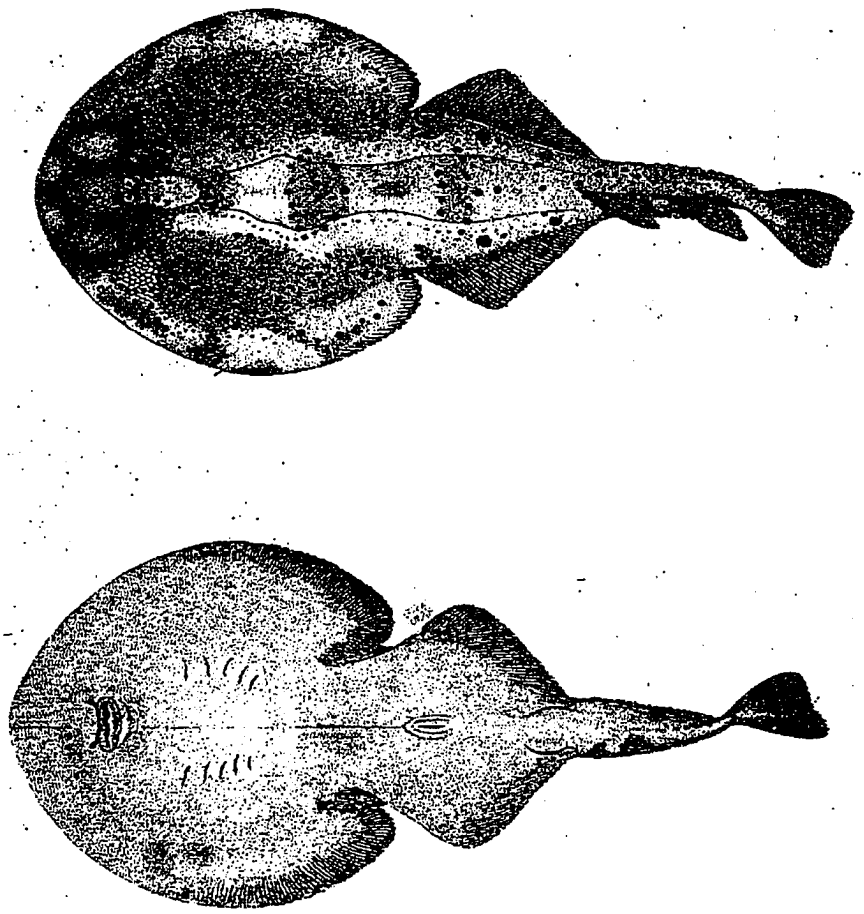


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Figure 18. Reproduction of illustration by Dr. Bancroft on which Griffith (in Cuvier,1834) published the new species Torpedo bancroftii Griffith, 1834, by indication.

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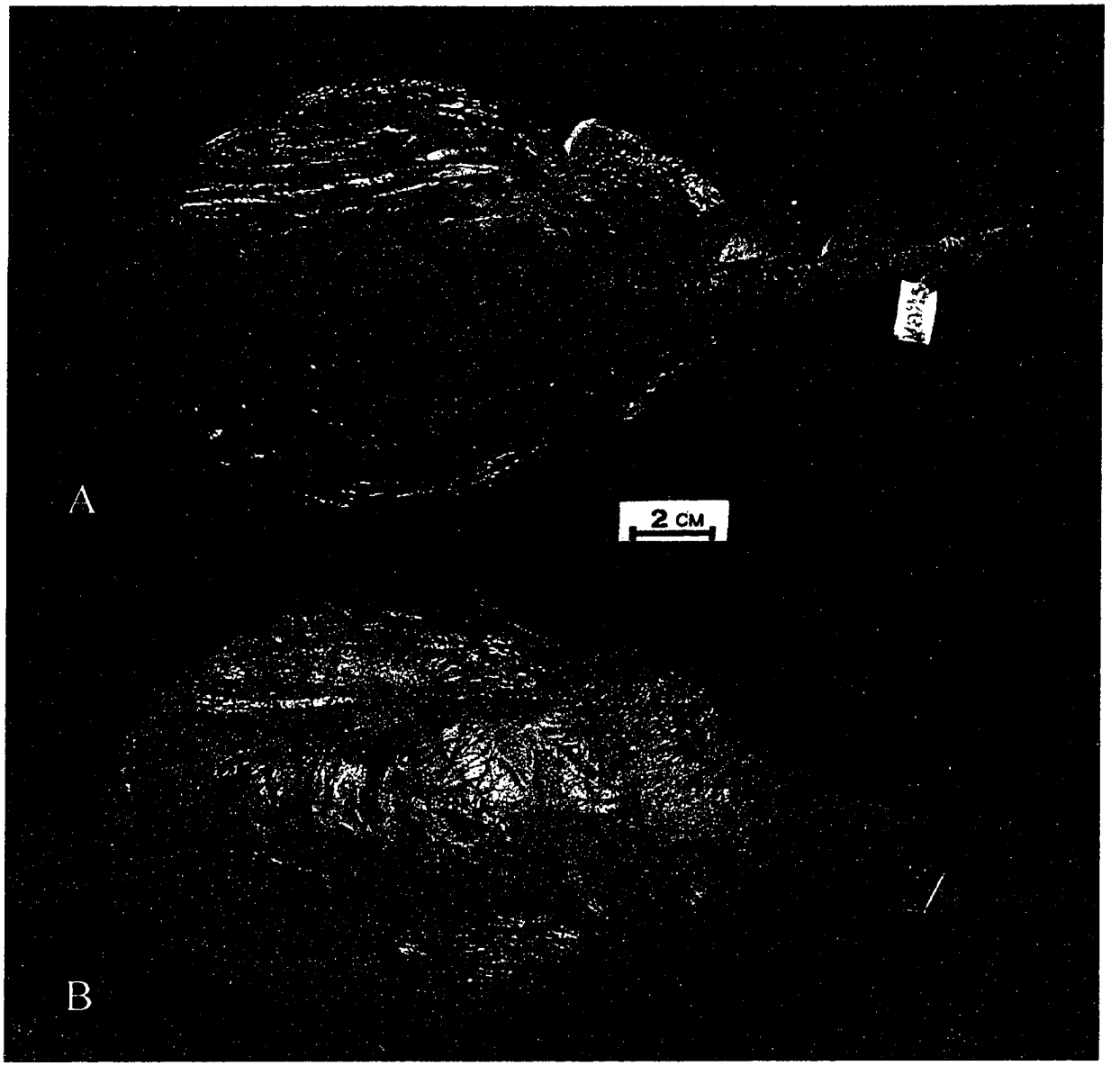
Torpedo Bancroftii.

London, Published by Taylor & Co 64 Ave Maria Lane 1829

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Figure 19. Dorsal (A) and ventral (B) view of holotype of Narcine punctata Garman,, 1881 (MCZ 752, 234 mm TL; St. Vincent).

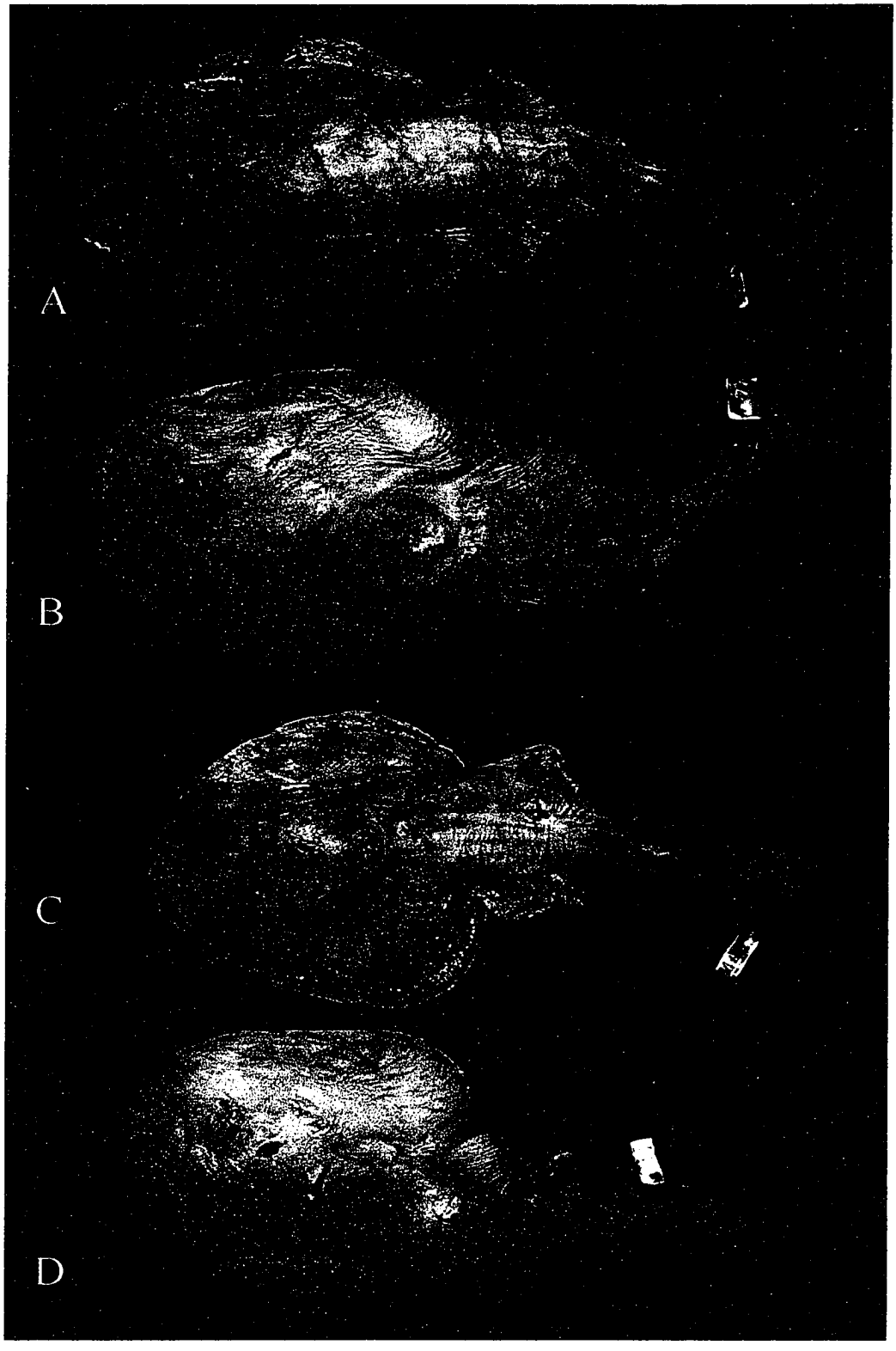
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Figure 20. Dorsal (A) and ventral (B) view of lectotype of Narcine corallina Garman, 1881 (MCZ 44, 249 mm TL; Key West, Florida); and dorsal (C) and ventral (D) view of paralectotype of Narcine corallina Garman, 1881 (MCZ 44, 195 mm TL; Key West, Florida).

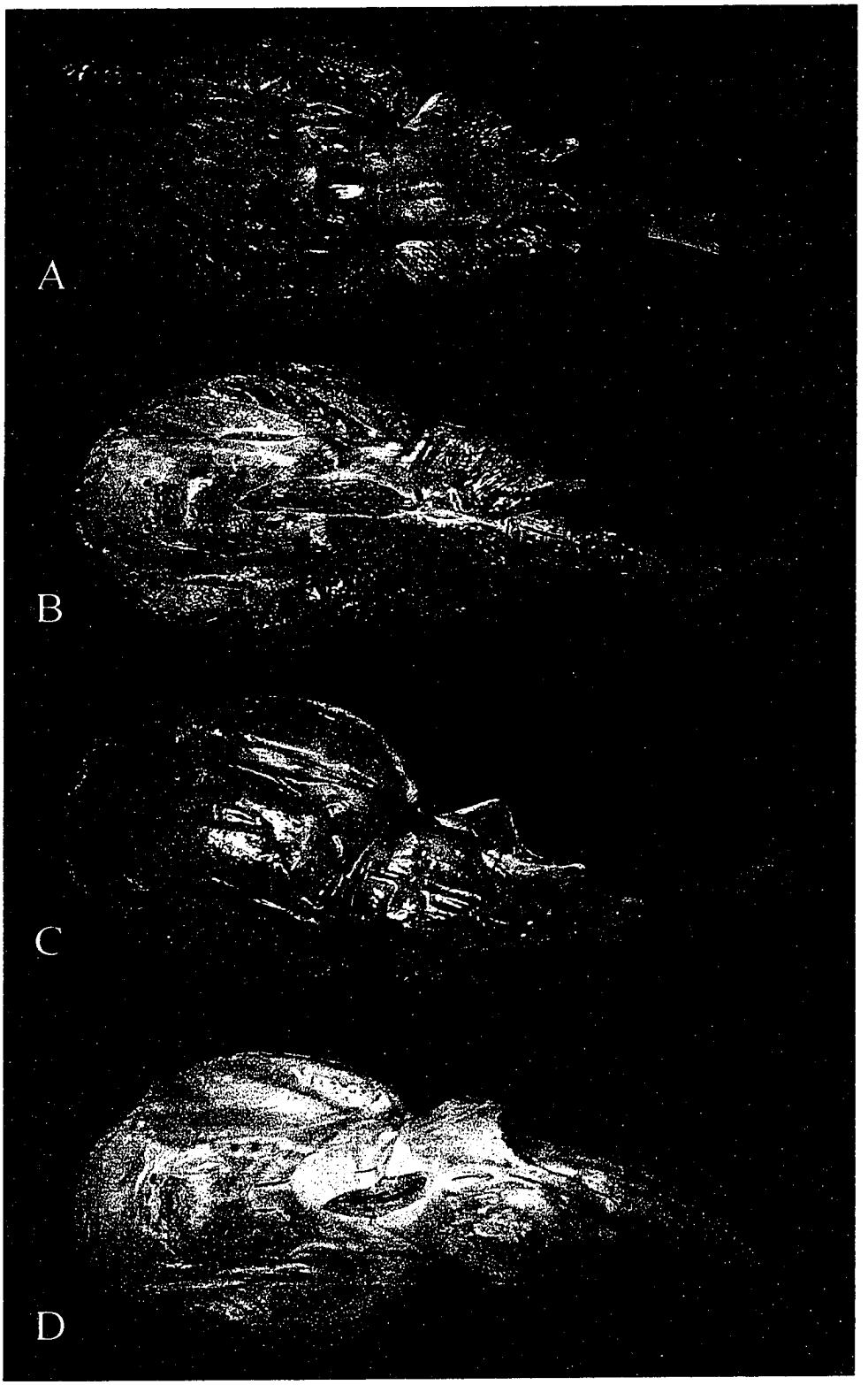
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Figure 21. Dorsal (A) and ventral (B) view of lectotype of Narcine umbrosa Jordan, 1884 (CAS 18246, 250 mm TL; Key West, Florida); dorsal (C) and ventral (D) view of paralectotype of Narcine umbrosa Jordan, 1884 (USNM 36940, 279 mm TL; Key West, Florida).

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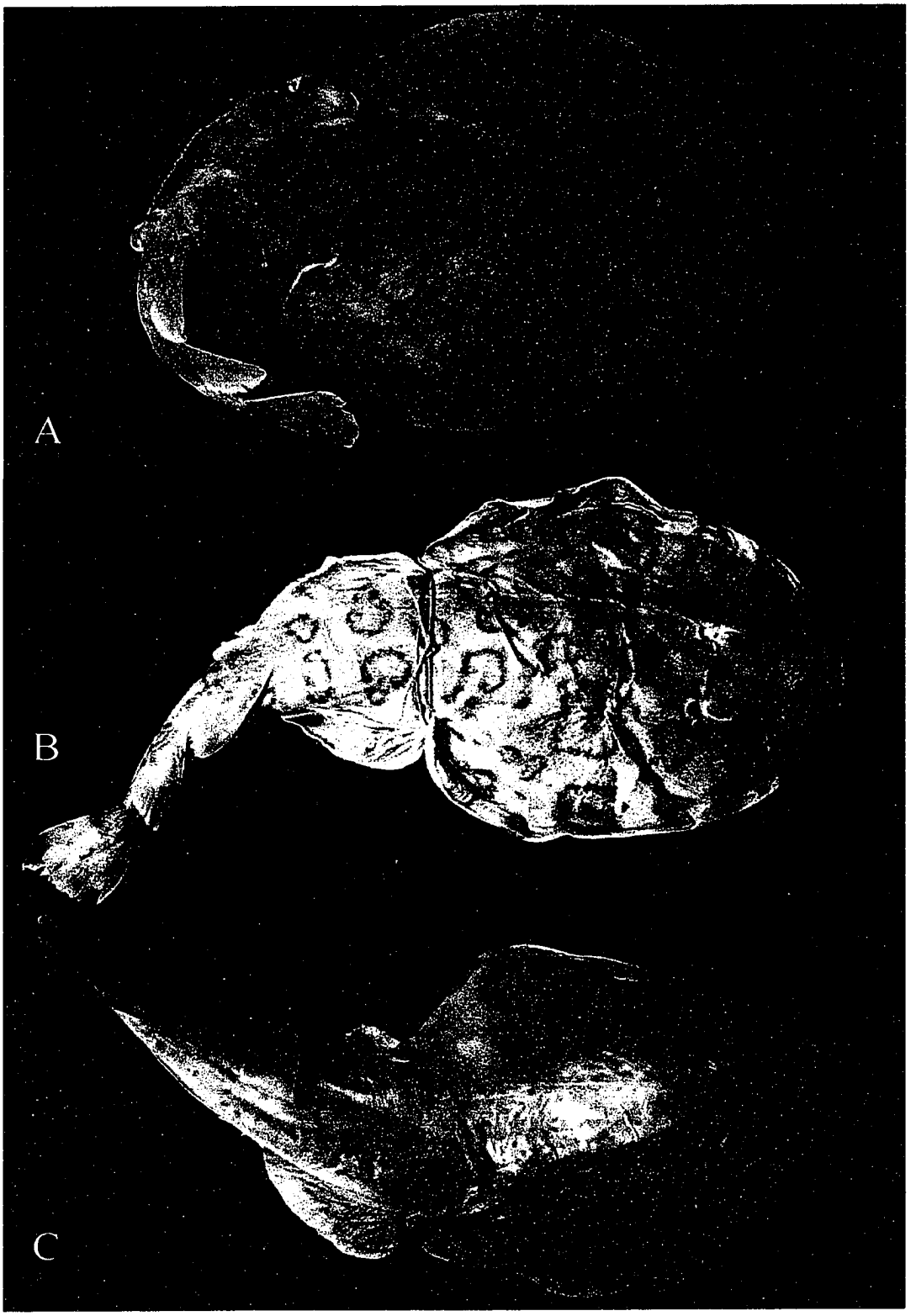


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Figure 22. Representative specimens of N. bancroftii, in dorsal view. A) BMNH 1913.12.8.2 (231 mm TL; North Carolina); B) BMNH 1909.2.26.14-15 (429 mm TL; Jamaica); C) BMNH 1853.12.26.63 (226 mm TL; Cuba).

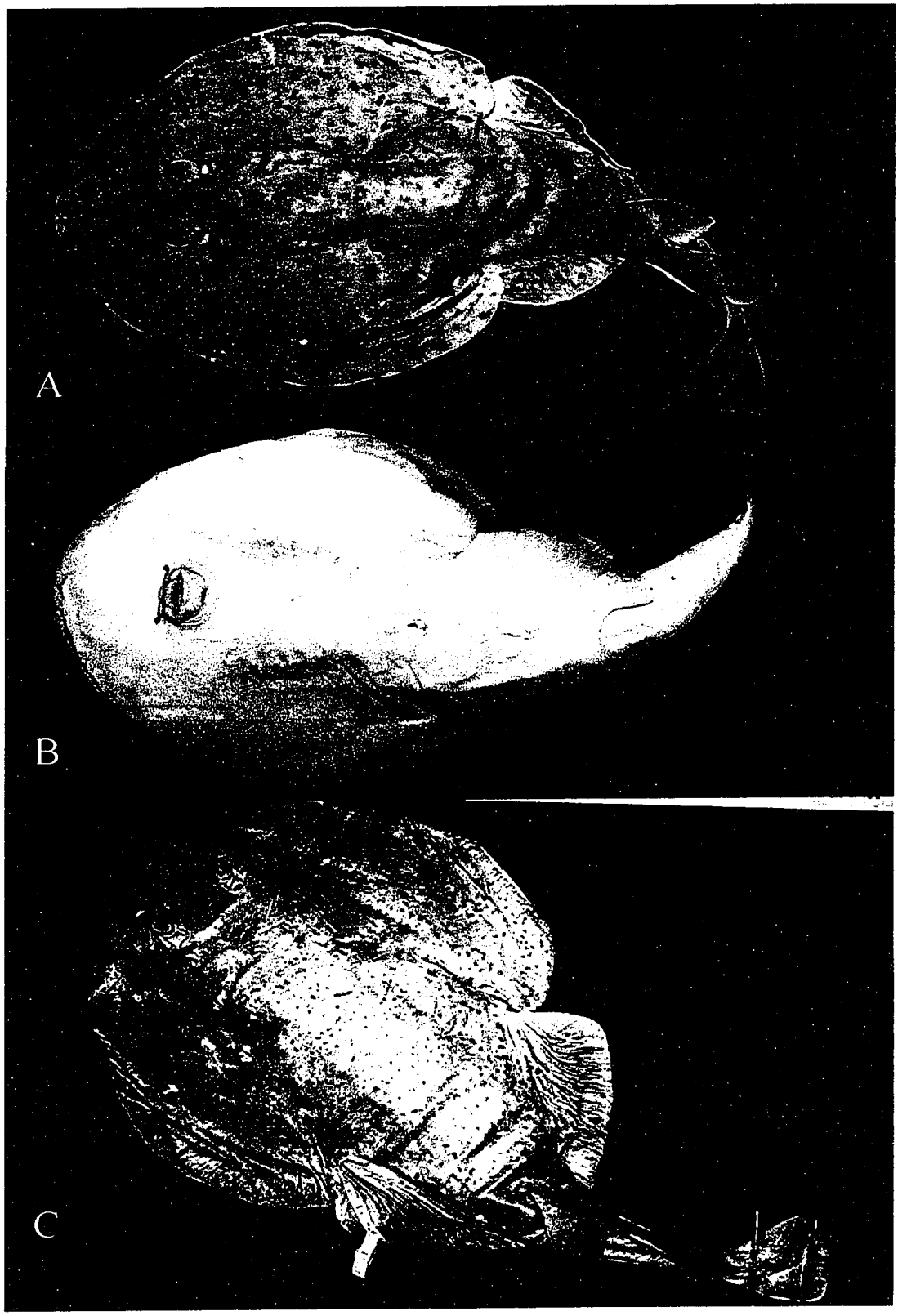
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Figure 23. Representative specimens from northern South America, provisionally identified as N. bancroftii. A) USNM 216829 (281 mm TL; Maranhão) in dorsal view; B) ventral view of specimen in A; C) NSMT P40033 (615 mm TL).

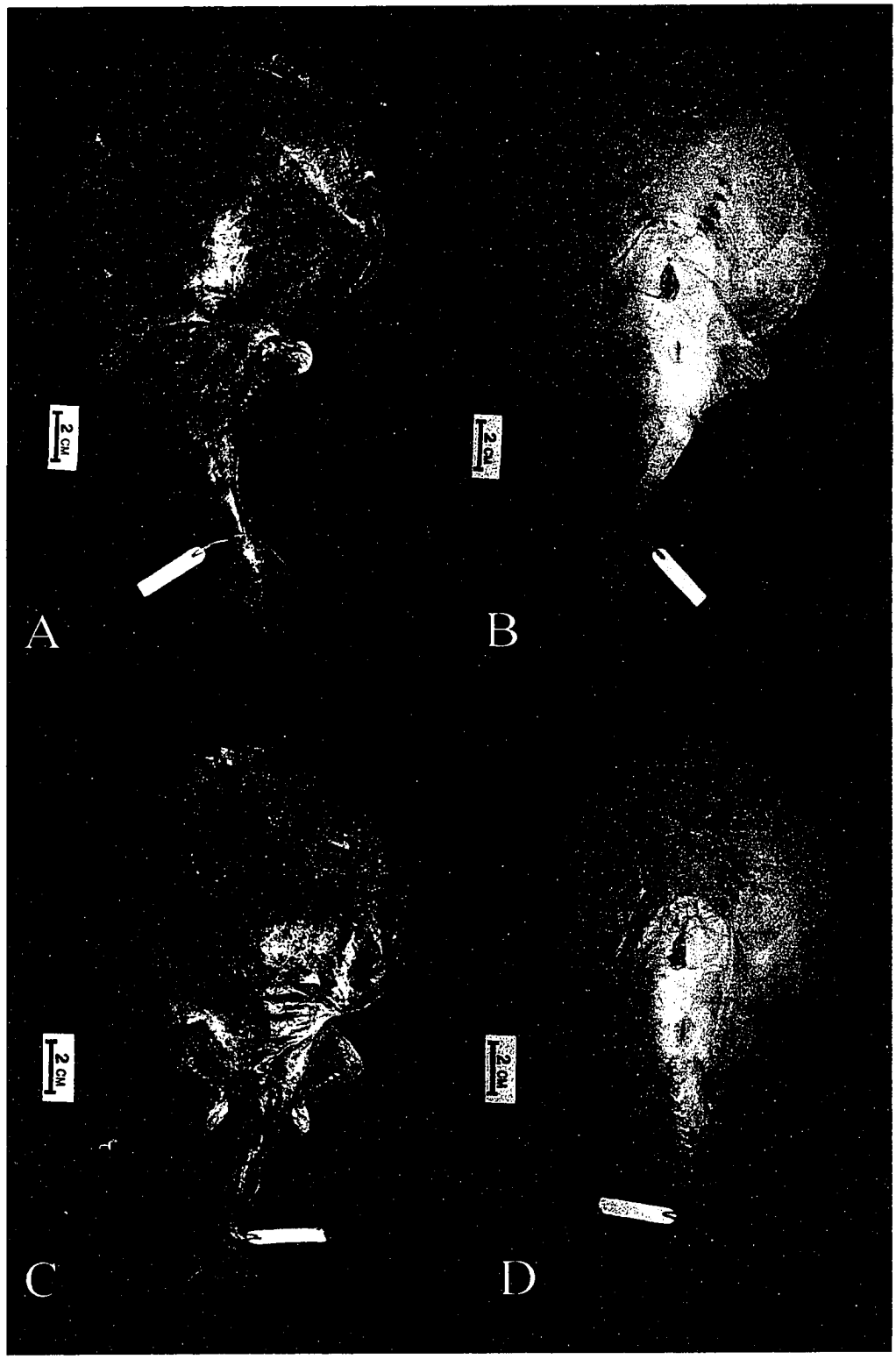
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Figure 24. Representative specimens of N. brevilabiata. A and B) dorsal and ventral views of CAS 98234 (257 mm TL; Viet Nam); C and D) Neotype of Narcine brevilabiata in dorsal and ventral views of CAS 98234 (234 mm TL; Viet Nam).

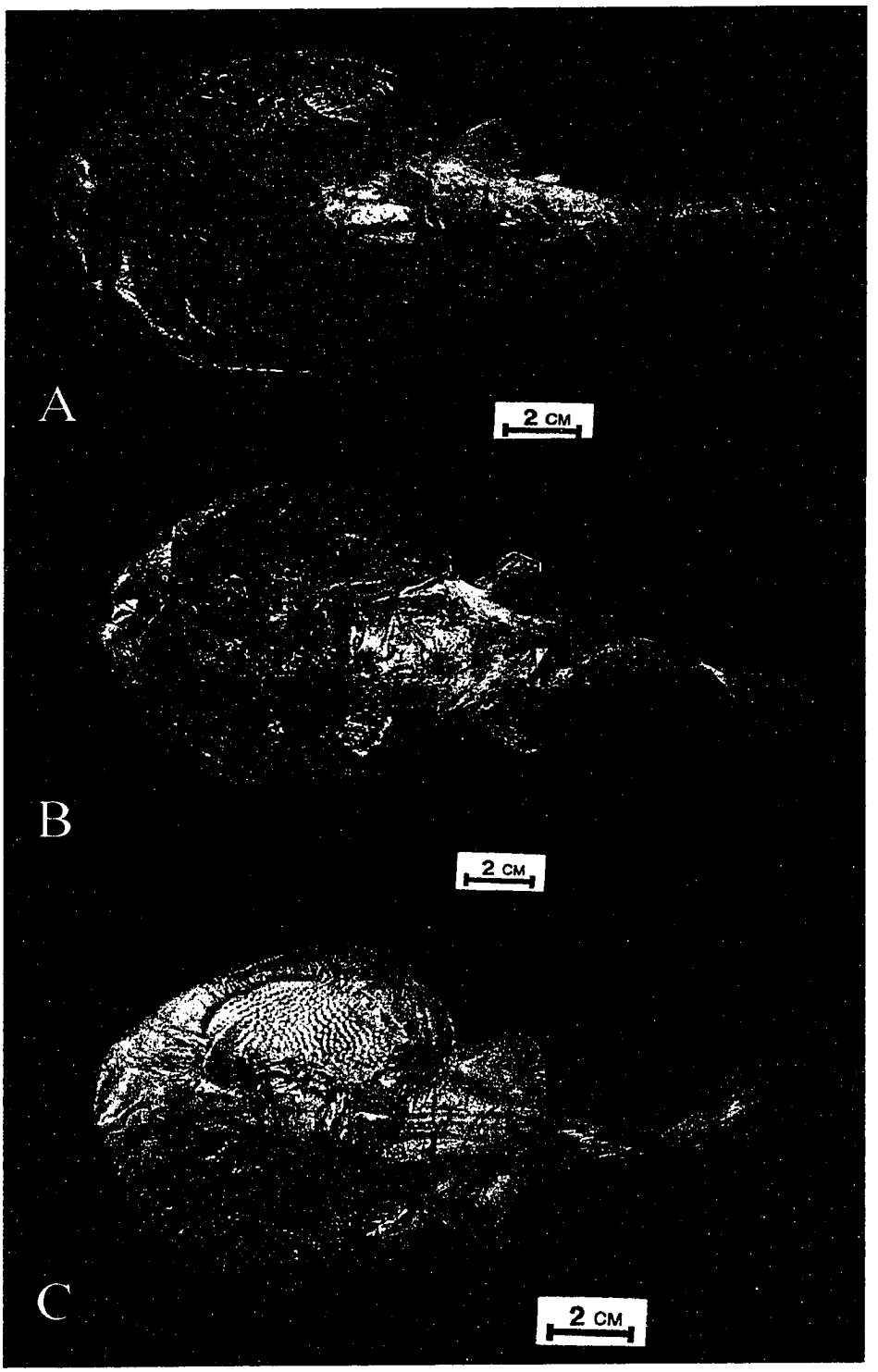
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Figure 25. Dorsal views of representative specimens of N. brevilabiata. A) CAS 98234 (218 mm TL; Viet Nam); B) CAS 98234 (225 mm TL; Viet Nam); C) ZRC 679 (173 mm TL; Borneo).

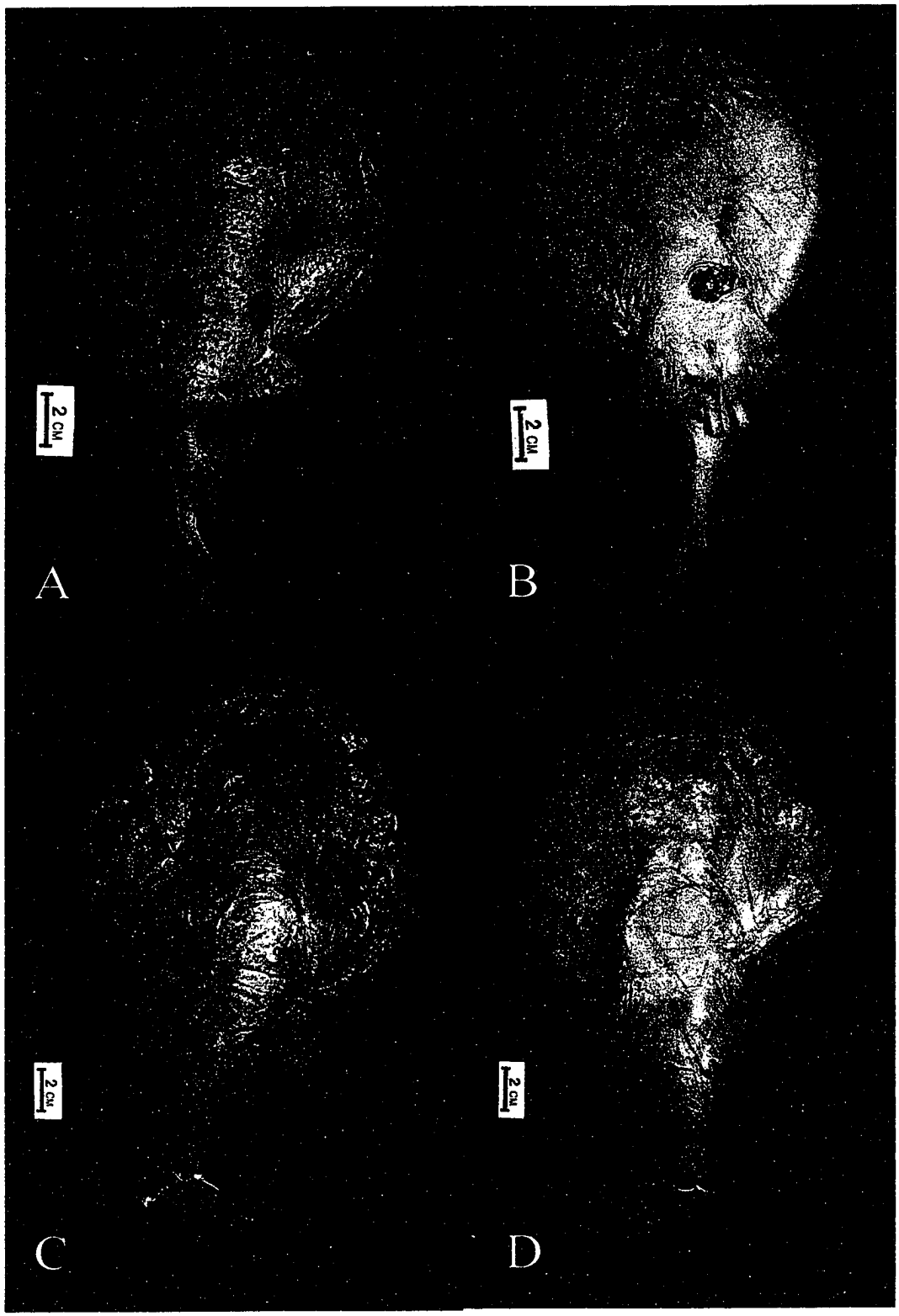
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Figure 26. N. brevilabiata from the Gulf of Thailand (CAS 98158, 230 mm TL) in dorsal (A) and ventral (B) views; and from China (CAS 14138, 298 mm TL; Guangdong Province) in dorsal (C) and ventral (D) views.

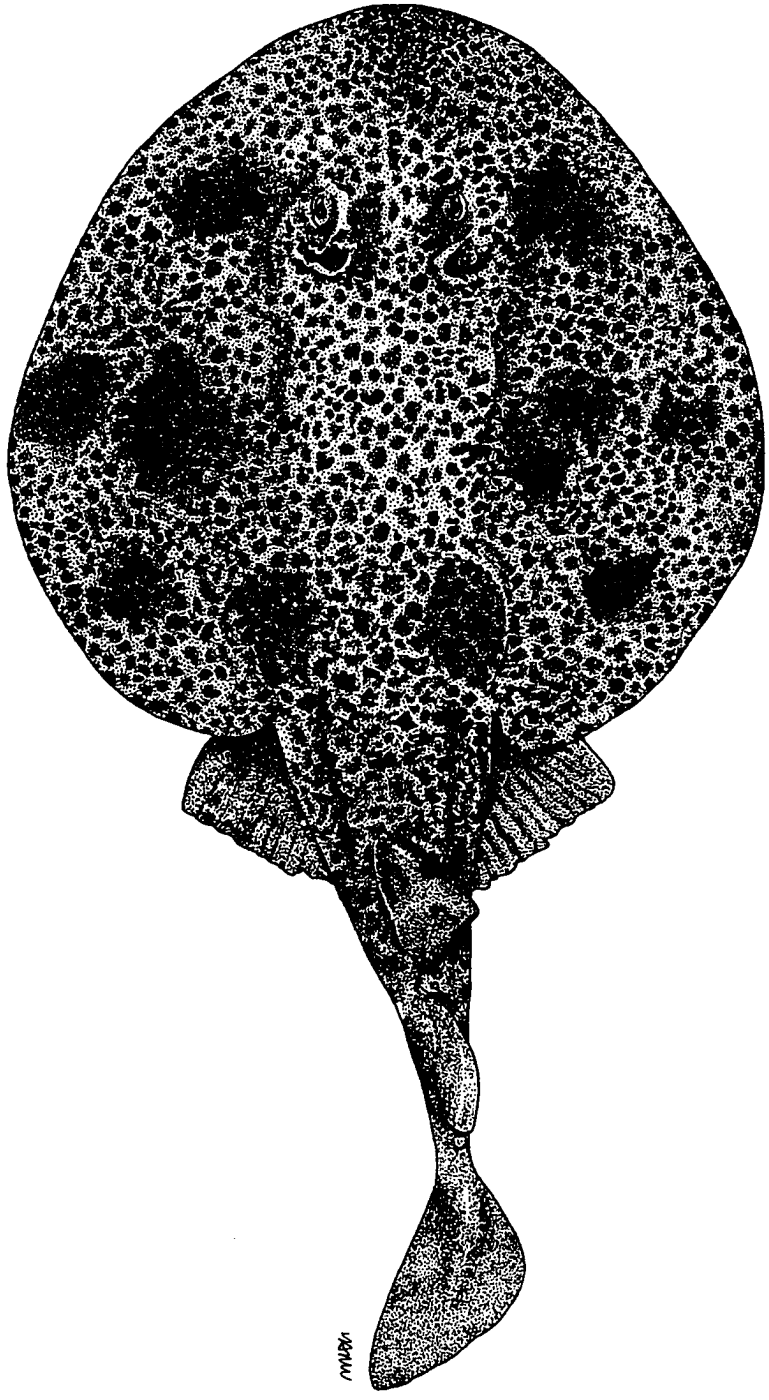
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Figure 27. Illustration of N. brevilabiata based on specimen from Gulf of Thailand. Reproduced from FAO (Rome), with permission (originally published in Carvalho et al., in press).

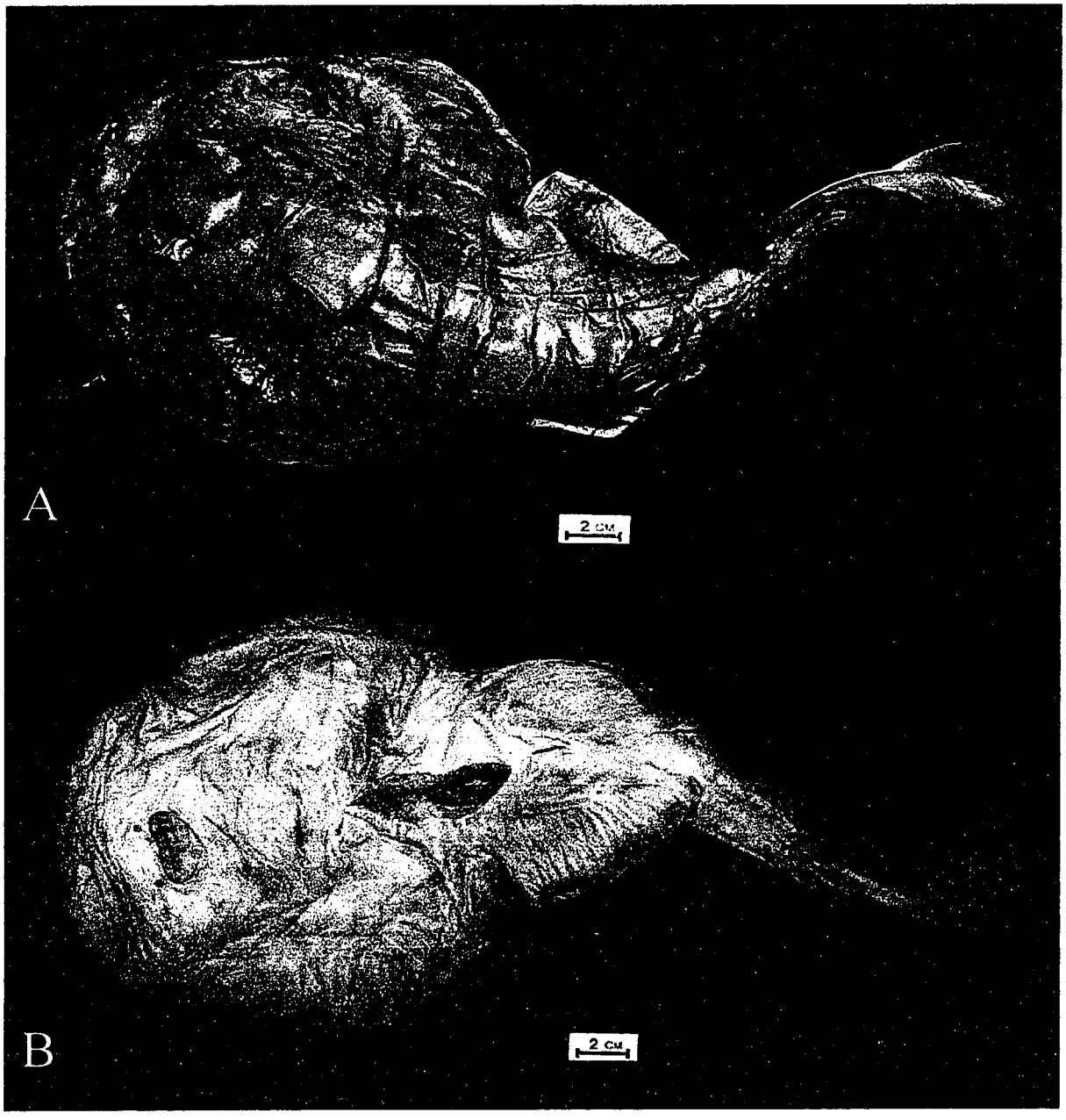
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Figure 28. Dorsal (A) and ventral (B) views of holotype of Narcine entemedor Jordan and Starks, 1895 (CAS 11699, 421 mm TL; Mazatlán, Sinaloa state, Mexico).

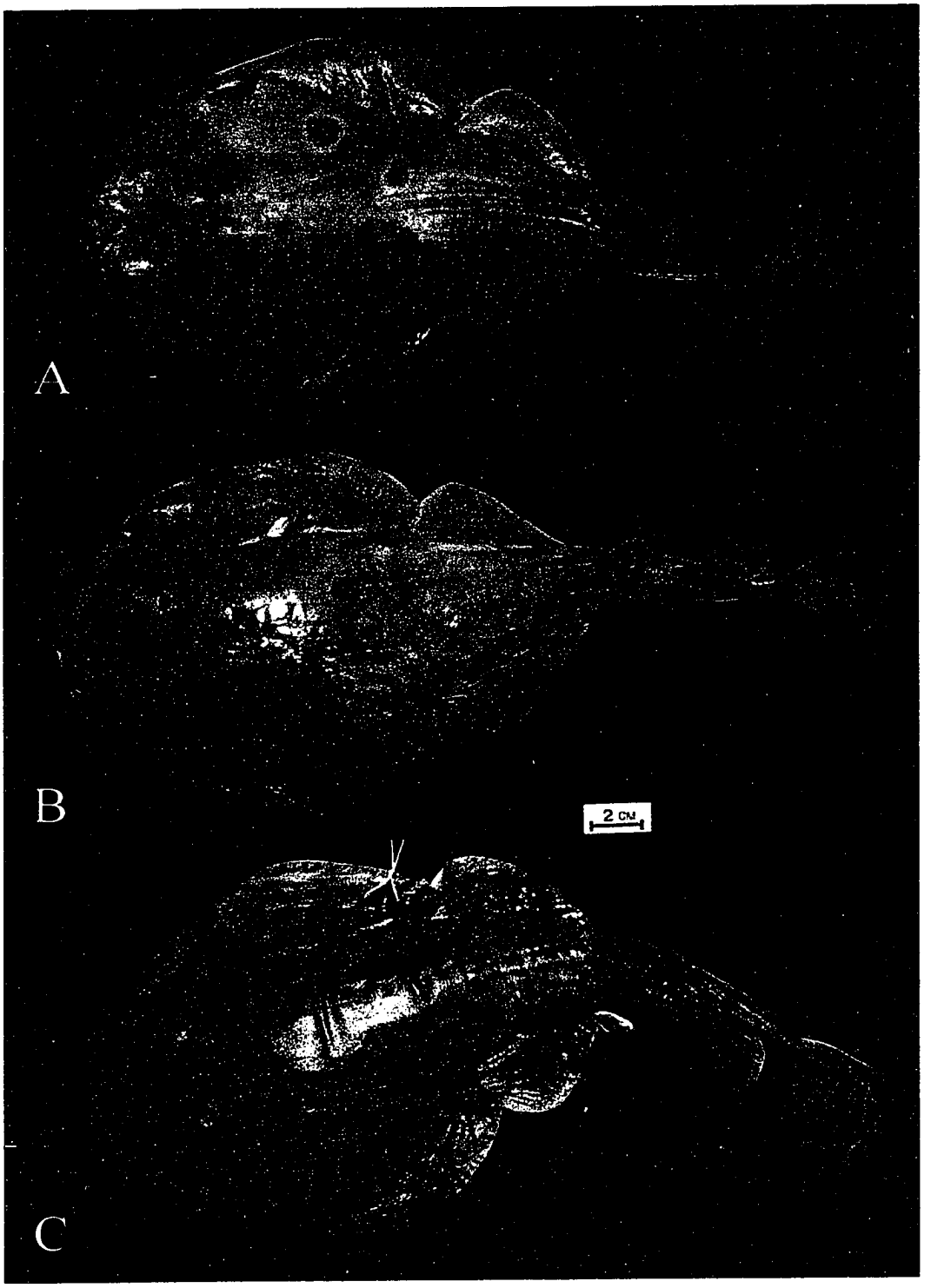
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Figure 29. Dorsal views of representative specimens of N. entemedor. A) YPM 1142 (222 mm TL; Gulf of California); B) YPM 1132 (334 mm TL; Gulf of California); C) CAS uncat. ("W57-36"; 342 mm TL; Baja California).

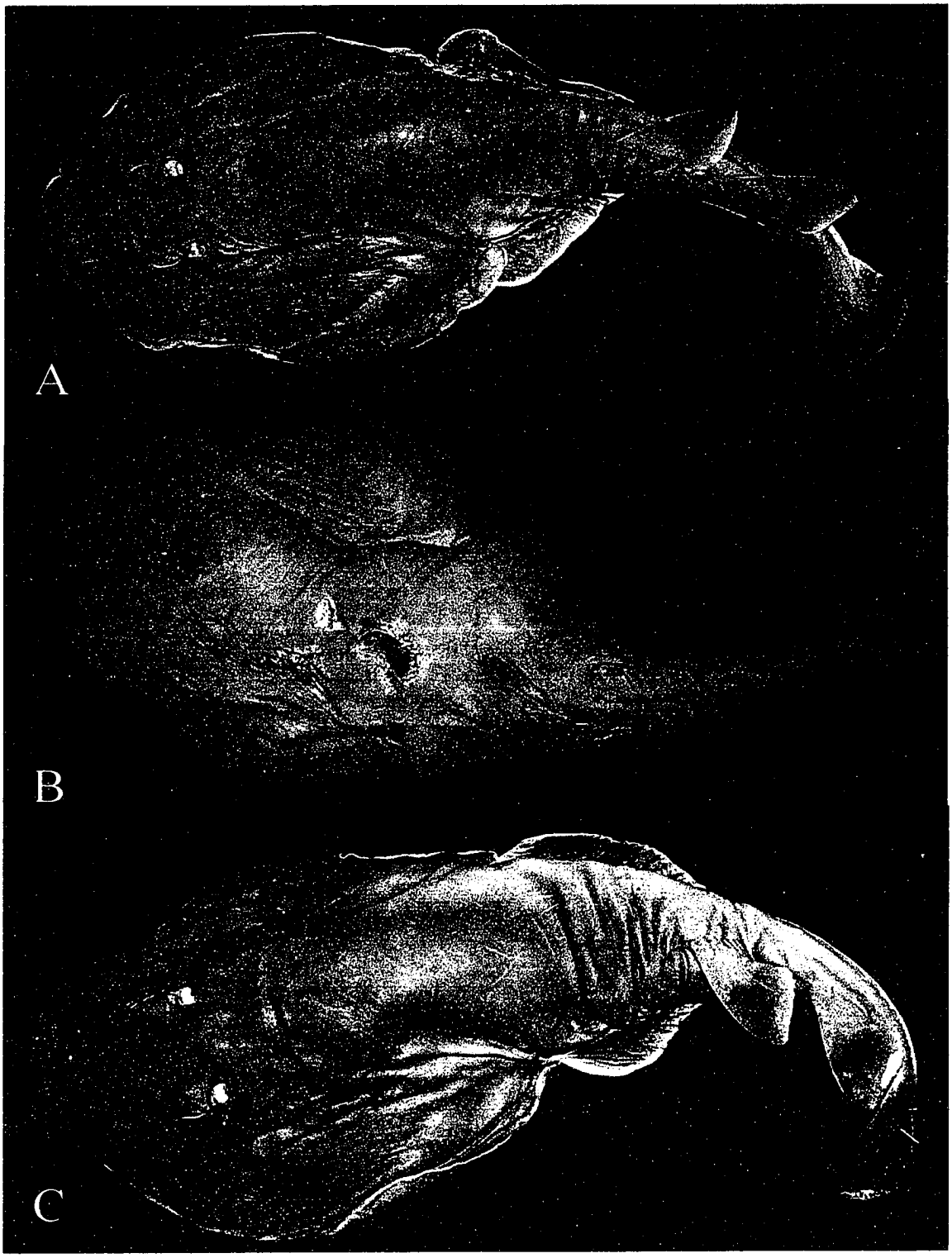
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Figure 30. Representatives of N. entemedor. A and B) dorsal and ventral views of CAS 58354 (457 mm TL; Colombia); C) dorsal view of CAS 58354 (588 mm TL; Colombia).

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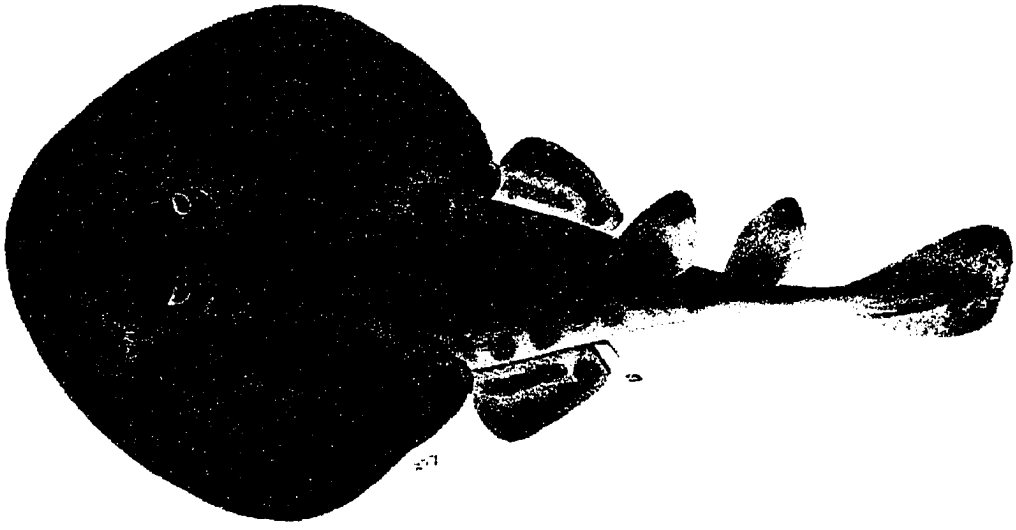
Figure 31. Representatives of N. entemedor. A and B) USNM 165519 (425 mm TL; Gulf of California); C and D) SIO 73-61 (484 mm TL; Revillagigedos Is.).

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Figure 32. Black and white reproduction of illustration executed for J. Reeves, from which Narcine lingula Richardson, 1846 was described (from Whitehead, 1970).

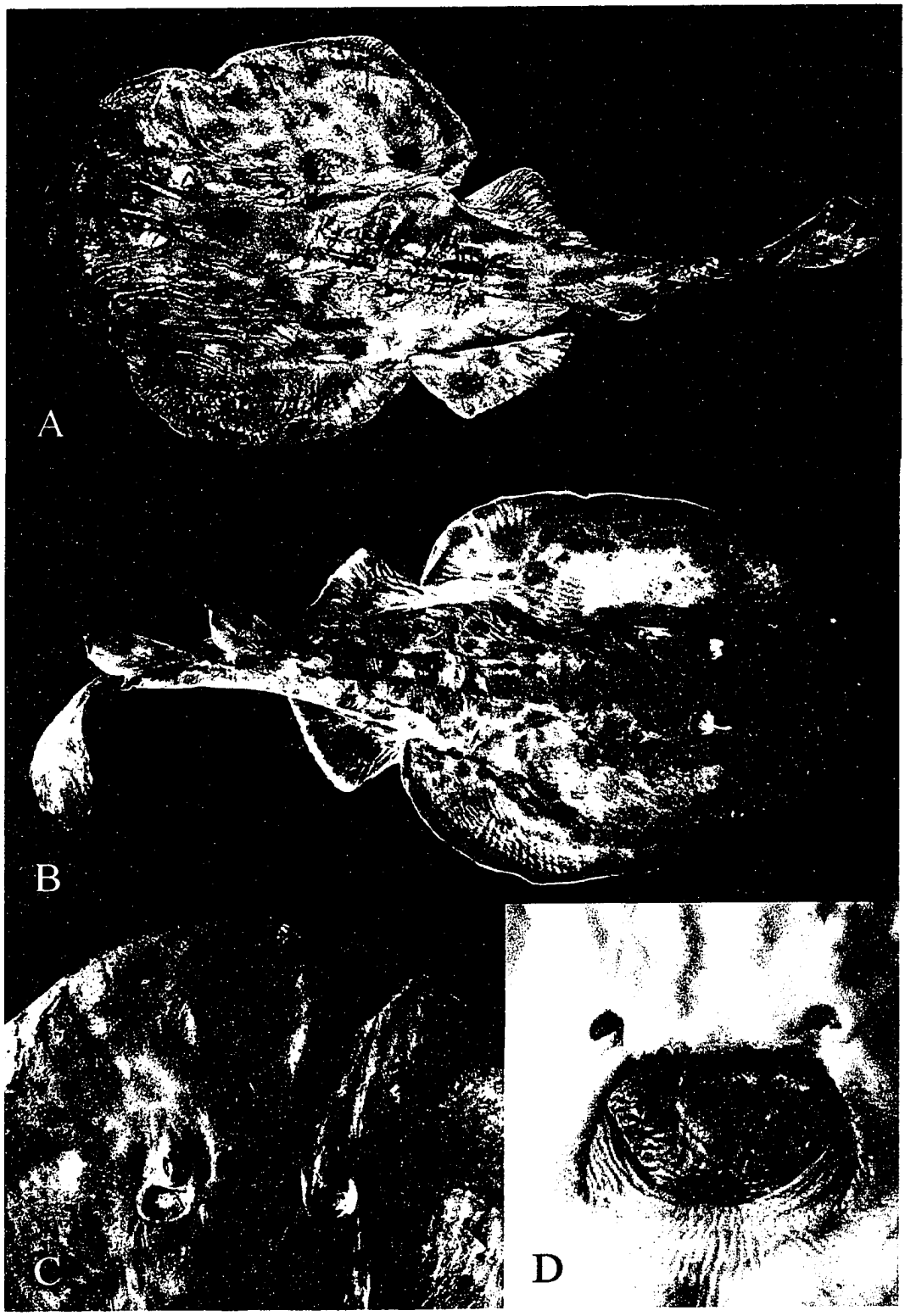
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Figure 33. Representative specimens of N. lingula. A) dorsal view of SIO 65-473 (325 mmTL; Gulf of Thailand); B, C and D) dorsal view, dorsal snout and nasoral region, respectively, of BMNH 1892.6.17.10 (264 mm TL; India).

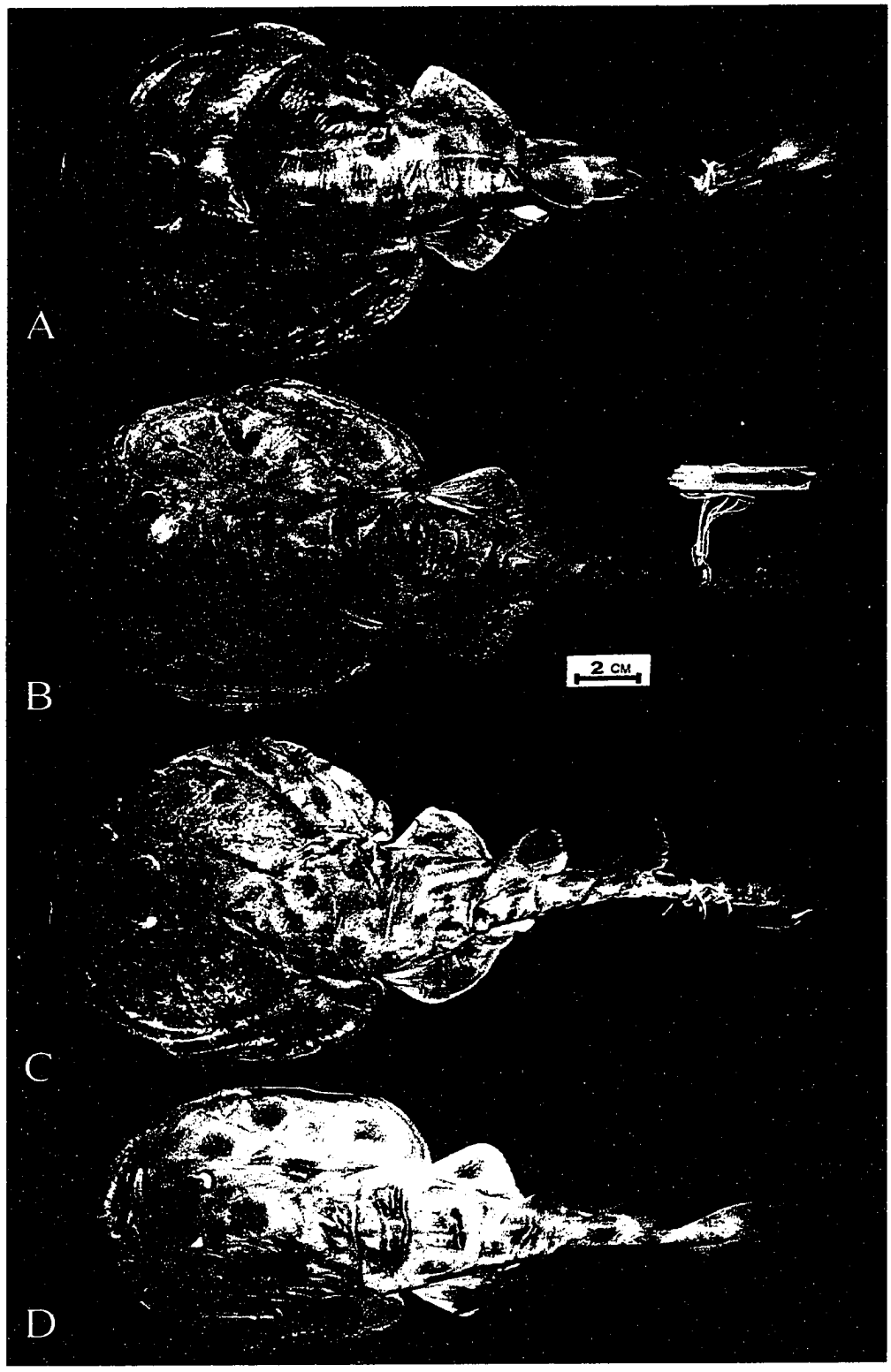
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Figure 34. Representatives of N. lingula from Taiwan Province of China. A) NTUM 01648 (270 mm TL); B) NTUM 00023 (258 mm TL); C) NTUM 01642 (285 mm TL); D) USNM 192574 (200 mm TL).

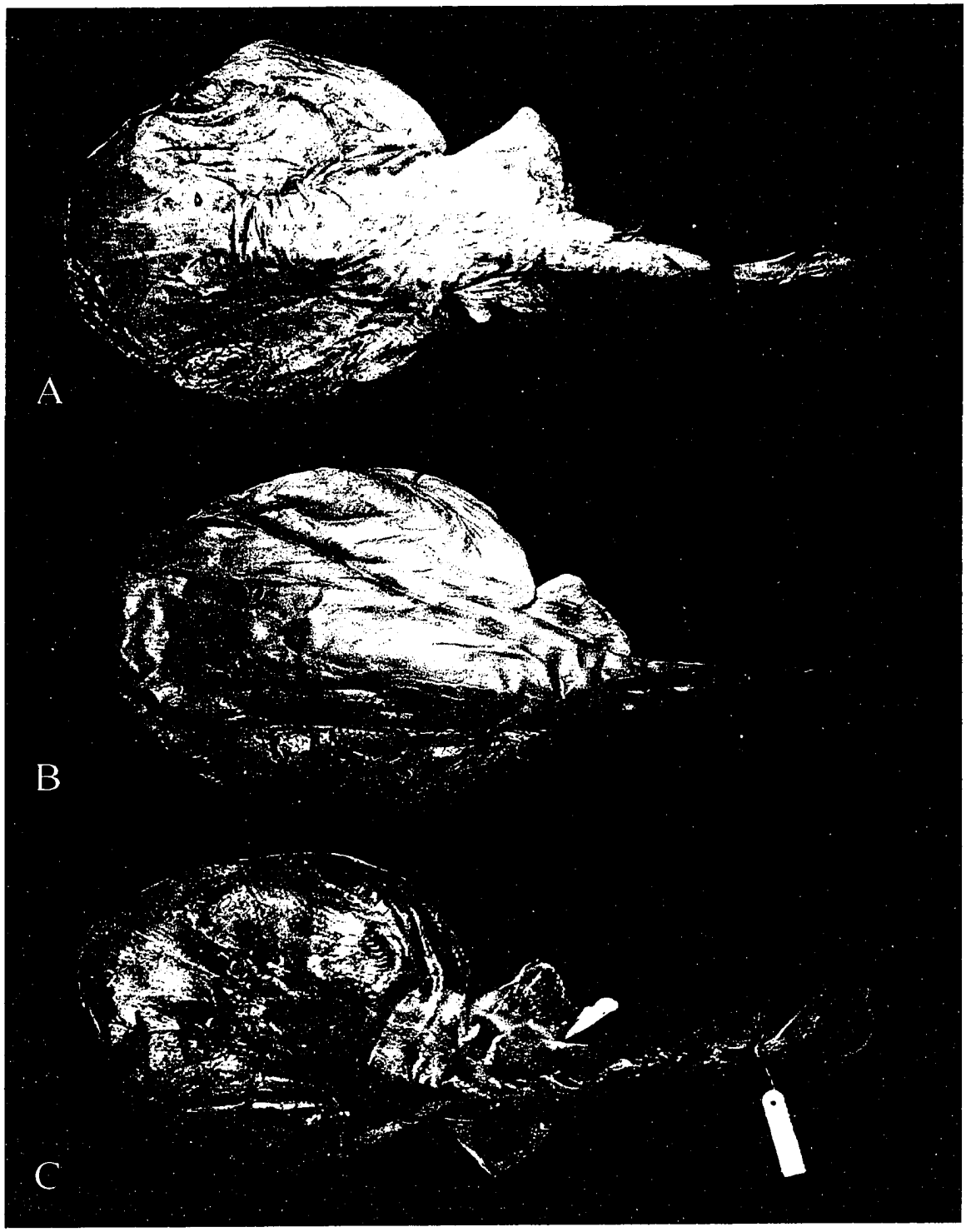
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Figure 35. Specimens of N. lingula from: A) Shanghai, China (ZMH 10431; 281 mm TL); B) Myanmar (CAS 58361; 206 mm TL); C) Viet Nam (CAS 33898; 241 mm TL).

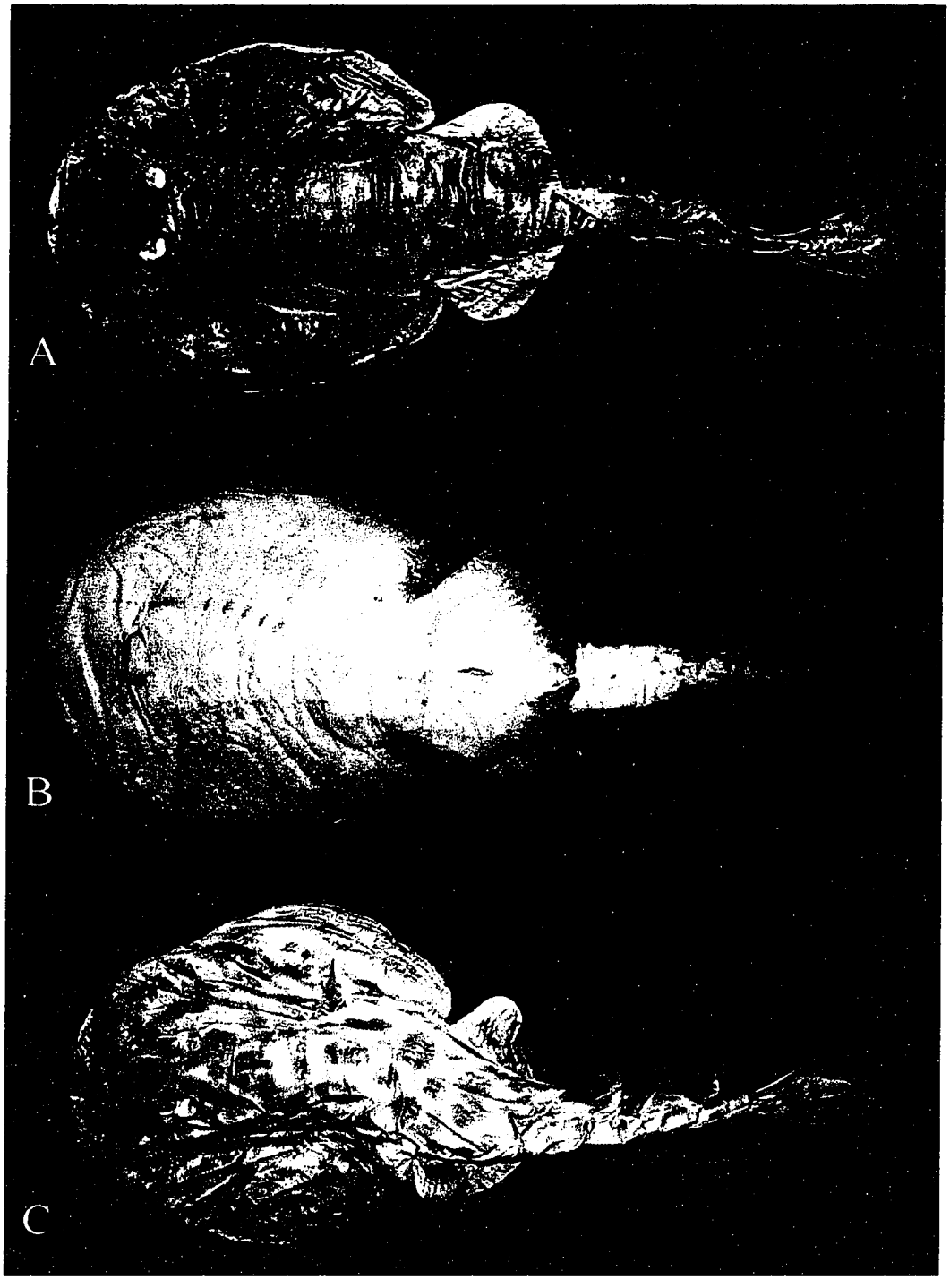
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Figure 36. Representatives of N. lingula. A and B) dorsal and ventral views of NTUM 04455 (369 mm TL; Taiwan); C) ANSP 76544 (320 mm TL; Hong Kong).

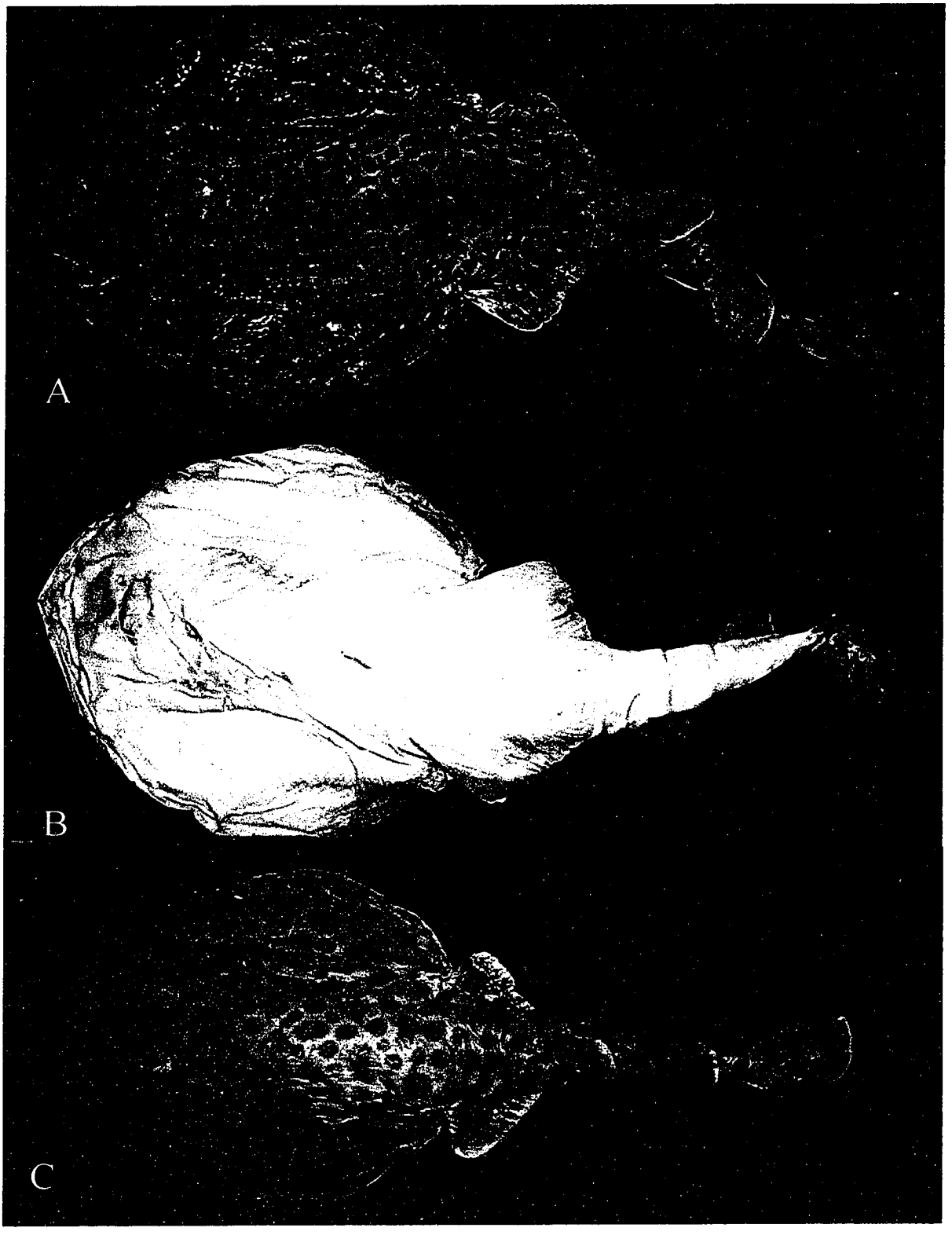
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Figure 37. Specimens tentatively identified as N. lingula from Madras, India. A and B) dorsal and ventral views of CAS 58353 (496 mm TL); C) CAS 58353 (324 mm TL).

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Figure 38. Reproduction of original illustration of "Temeree" published in Russell (1803) on which Shaw (1804) based the new species Raja maculata Shaw, 1804.

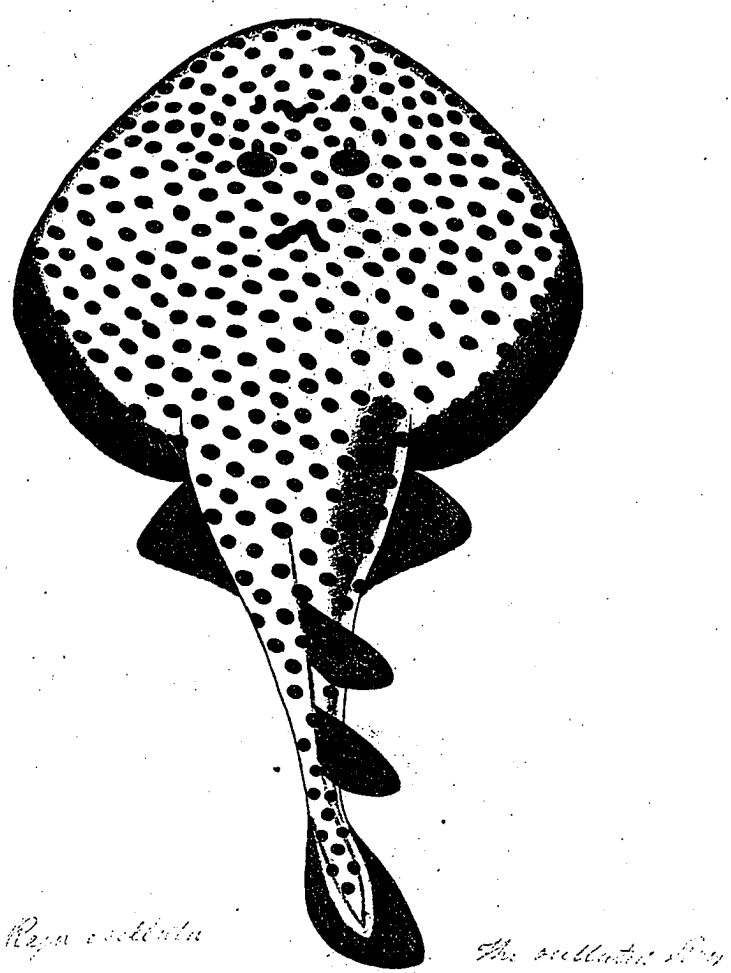
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Figure 39. Reproduction of original illustration of "Nalla Temeree" published in Russell (1803) on which Shaw (1804) based the new species Raja bicolor Shaw, 1804.

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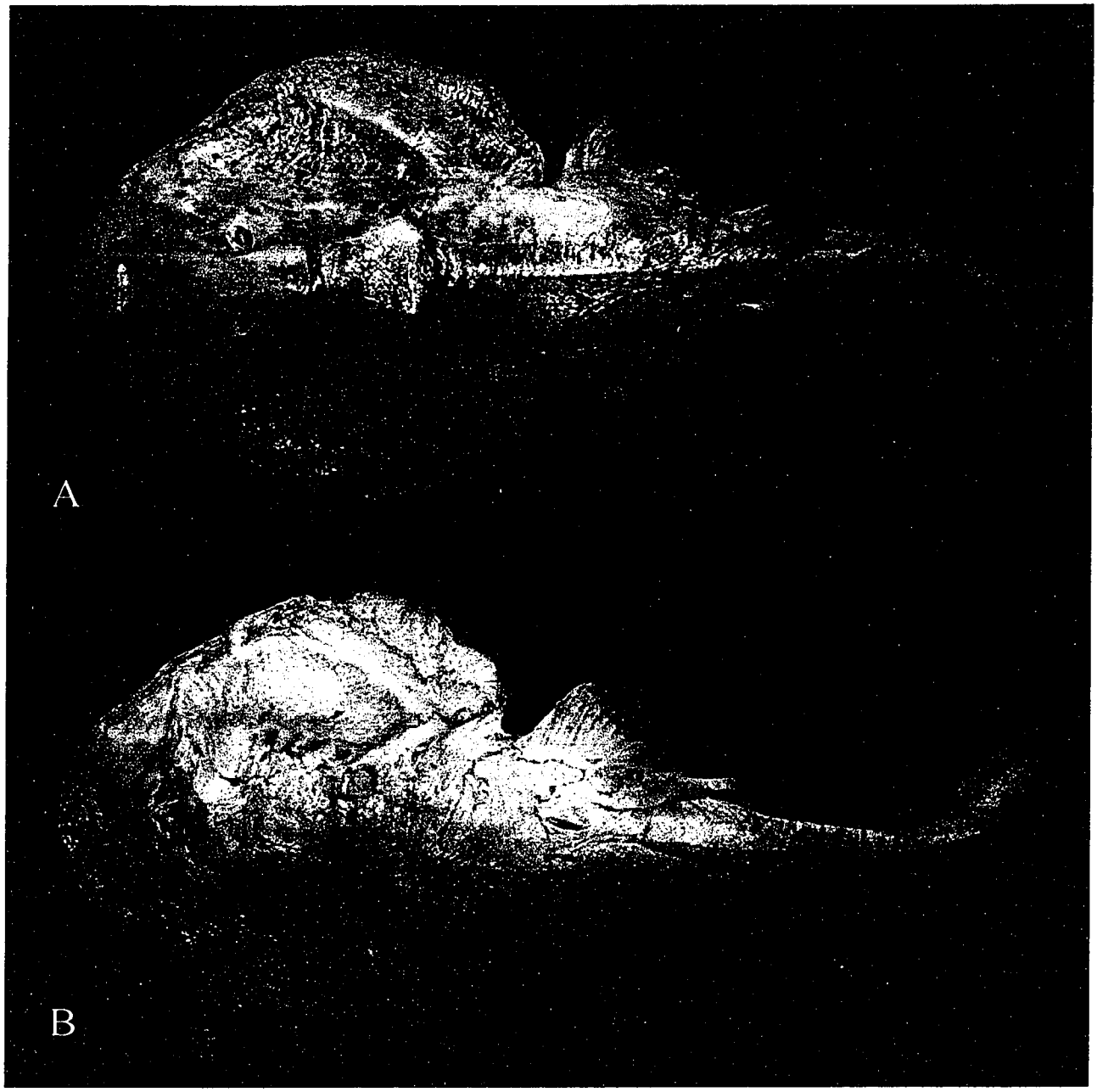


NALLA TEMEREE.

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Figure 40. Holotype of Narcine maculata Duméril, 1852 (MNHN 1336, 330 mm TL; Java, Indonesia).

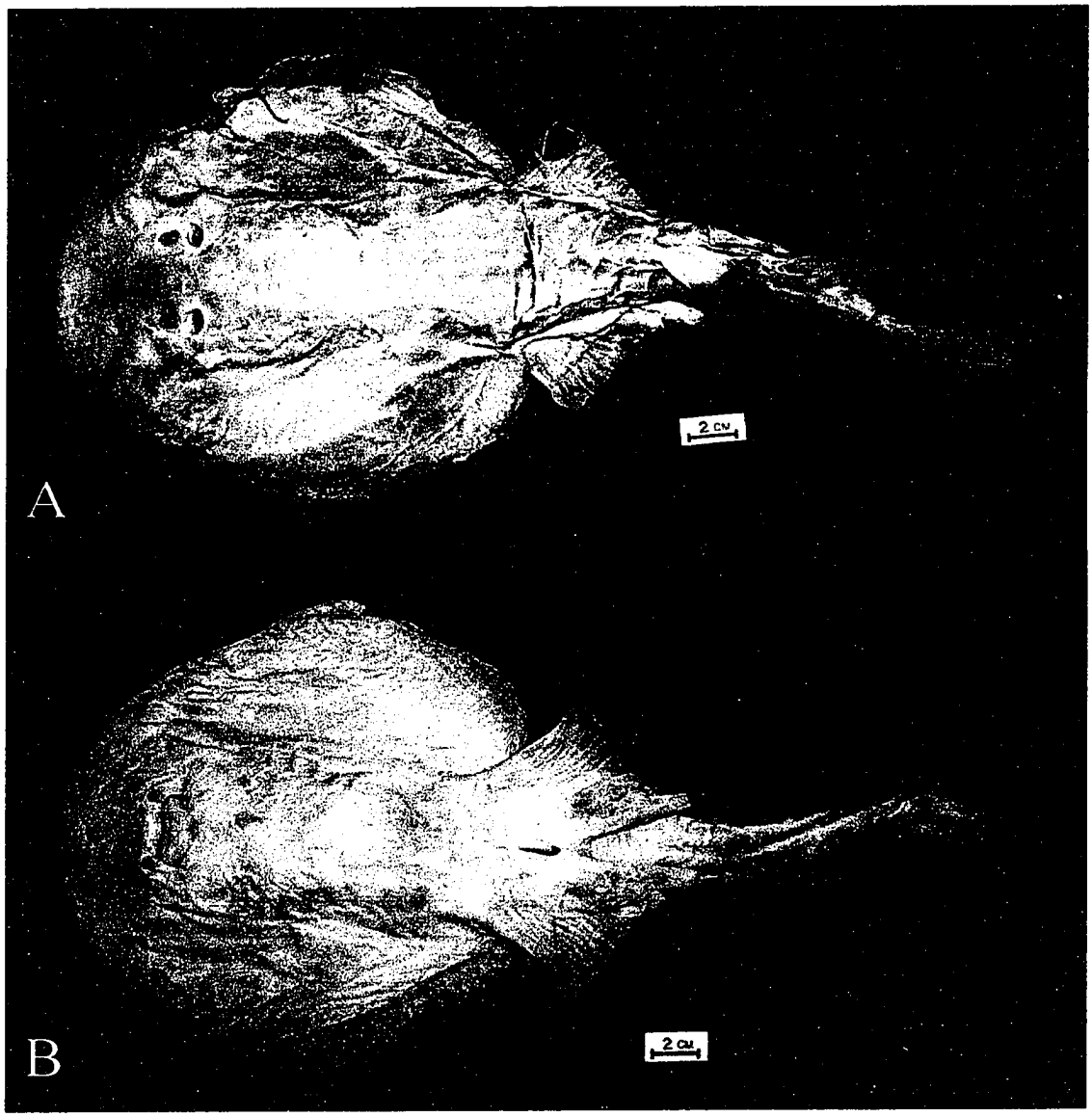
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Figure 41. Holotype of Narcine firma Garman, 1913 (MCZ 75, 401 mm TL; Sri Lanka).

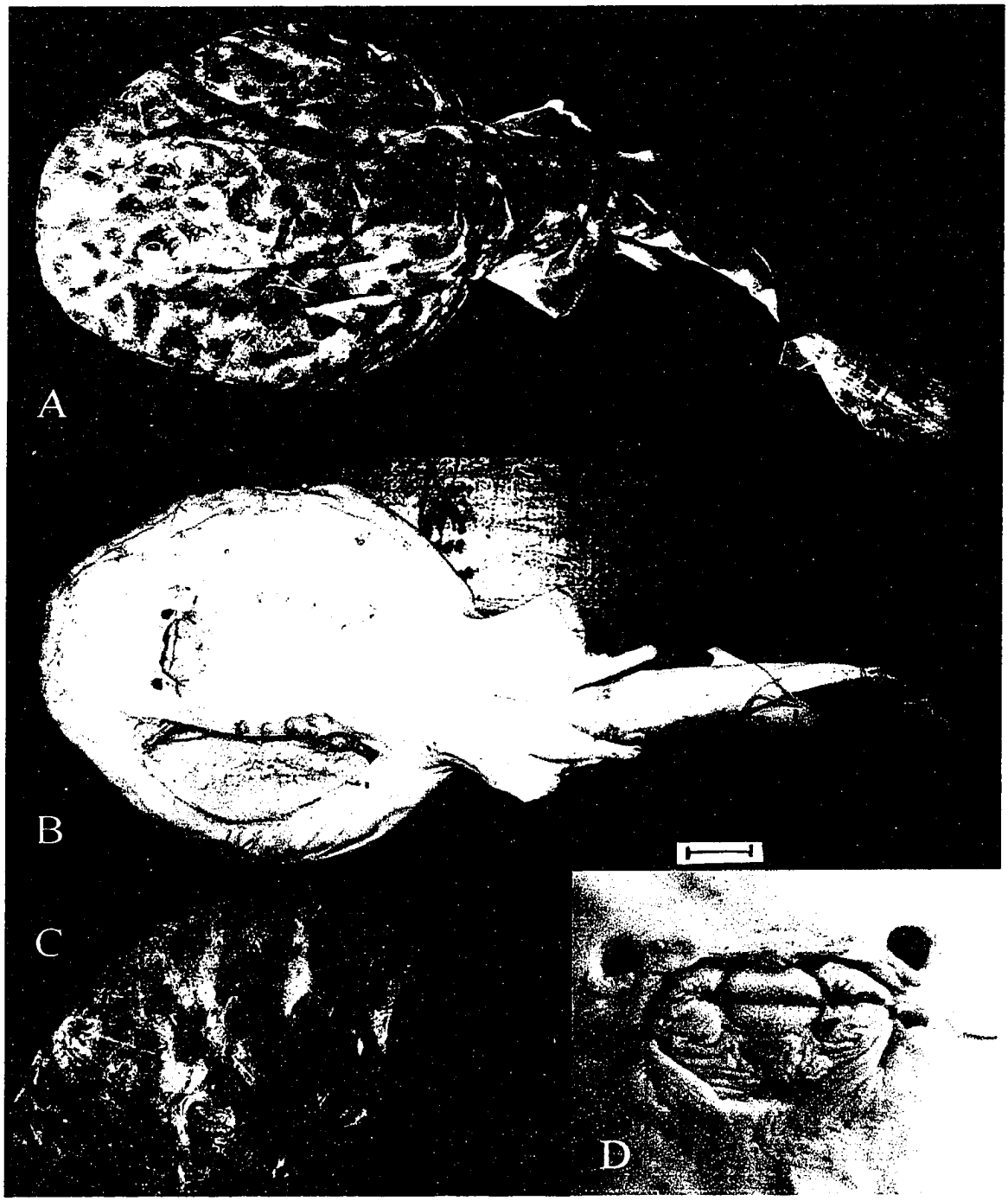
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Figure 42. Representative specimen of N. maculata. A) dorsal; B) ventral; C) dorsal snout; D) nasoral area (all BMNH 1909.7.12.8, 321 mm TL; Myanmar).

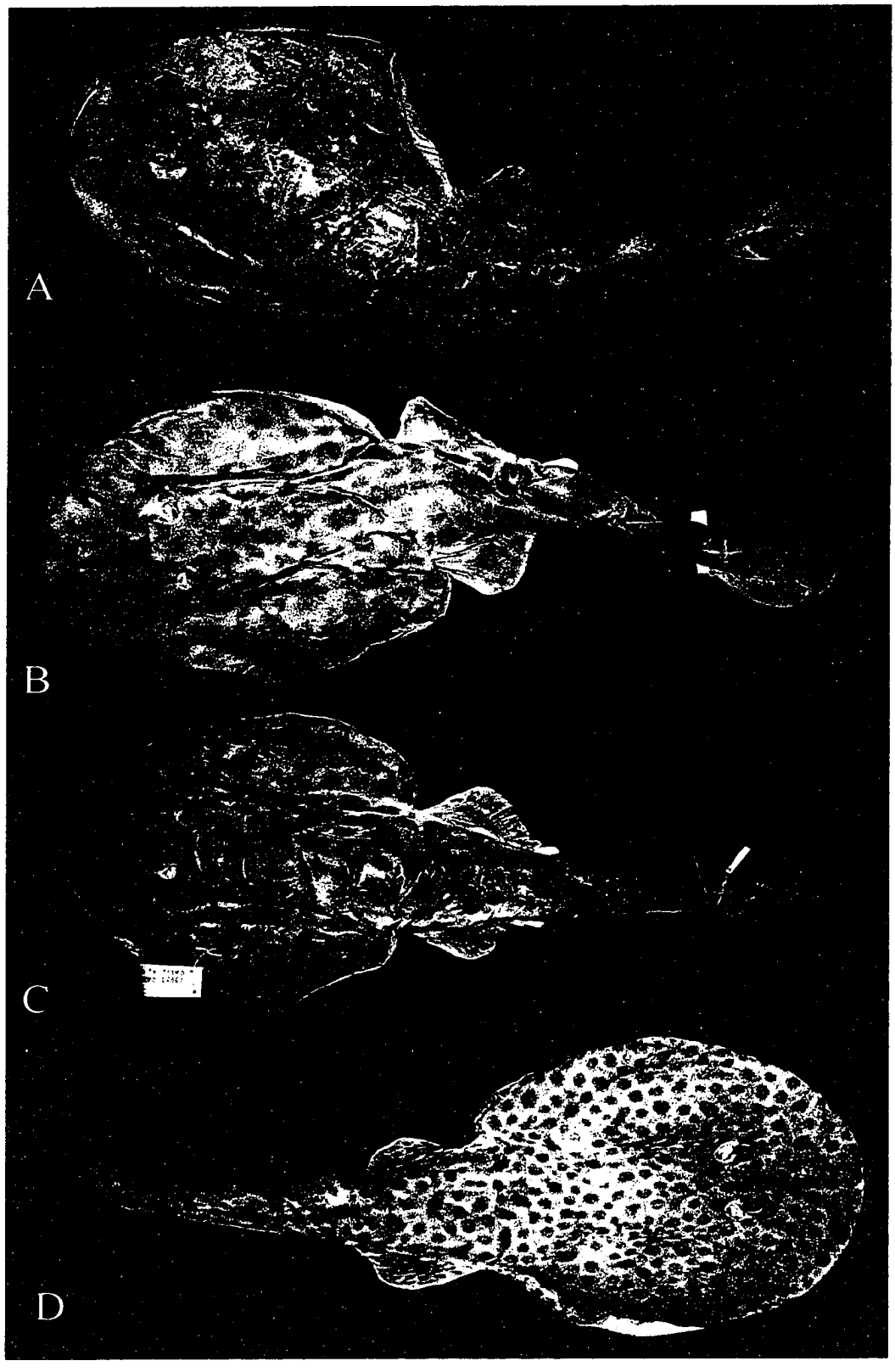
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Figure 43. Representative specimens of N. maculata in dorsal view. A) CAS 27722 (331 mm TL; Sandakan, Borneo, Malaysia); B) CAS 13931 (391 mm TL, Hong Kong); C) CAS 41715 (282 mm TL, Orissa coast, India); D) BMNH 1888.11.6.87-89 (382 mm TL; Madras, India).

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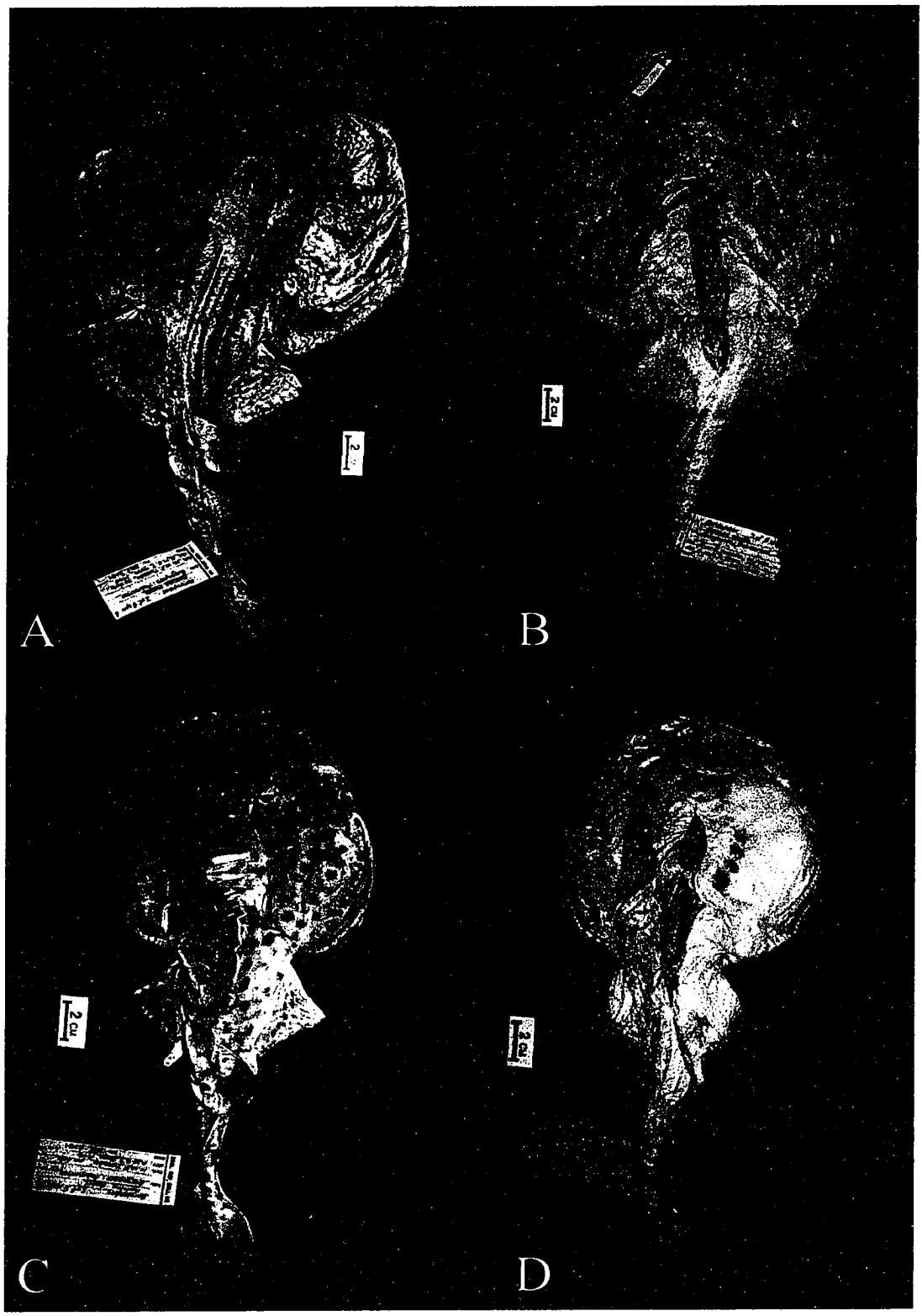


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Figure 44. Representatives of N. maculata fom Singapore. A and B) dorsal and ventral views of ZRC 2101 (390 mm TL); C and D) dorsal and ventral views of ZRC 2101 (302 mm TL).

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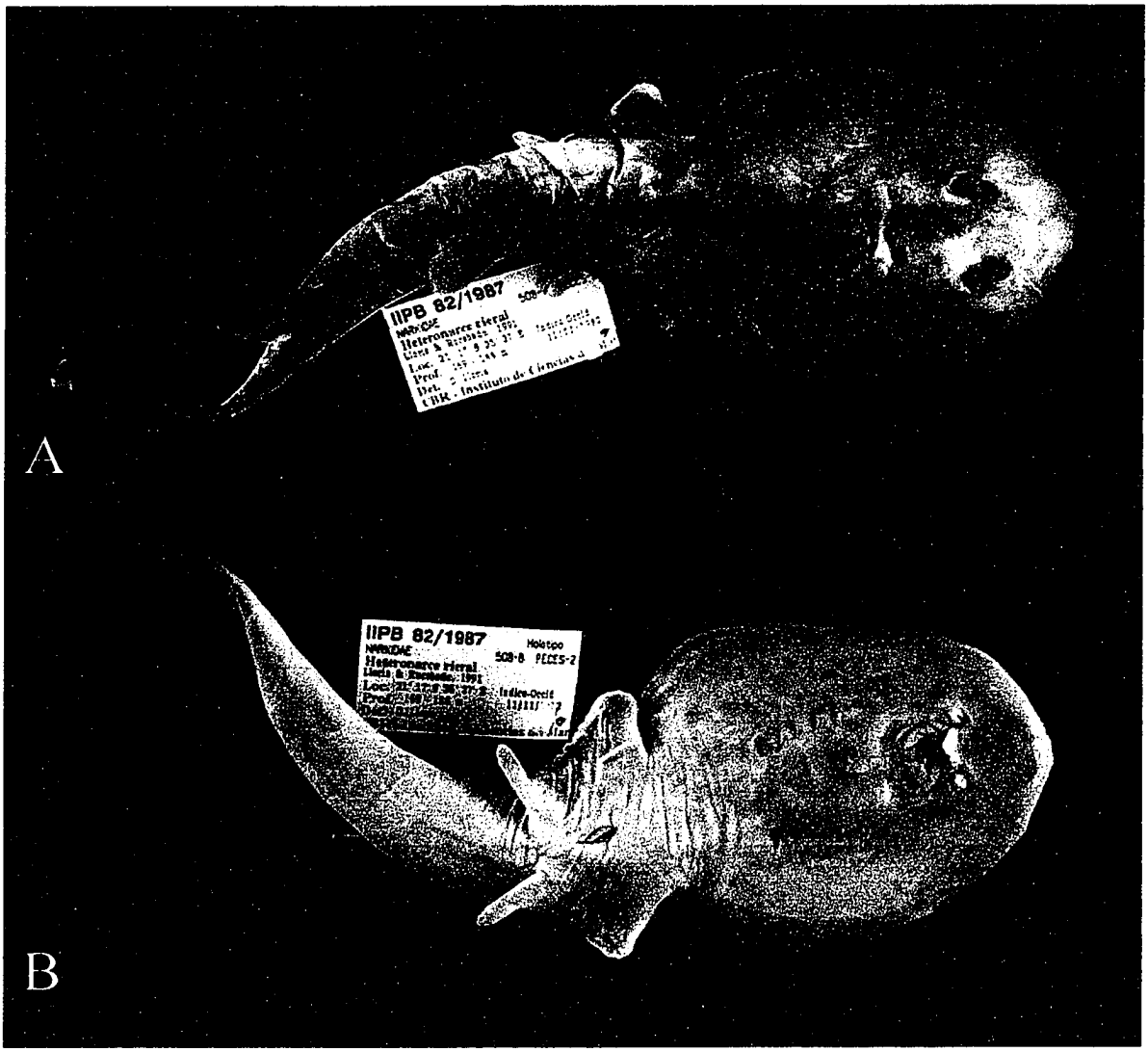


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Figure 45. Dorsal (A) and ventral (B) view of holotype of Heteronarce rierai Lloris and Rucabado, 1991 (= Narcine rierai) (IIPB 82/1987, 257 mm TL; Mozambique). Courtesy of C. Allué (IIPB).

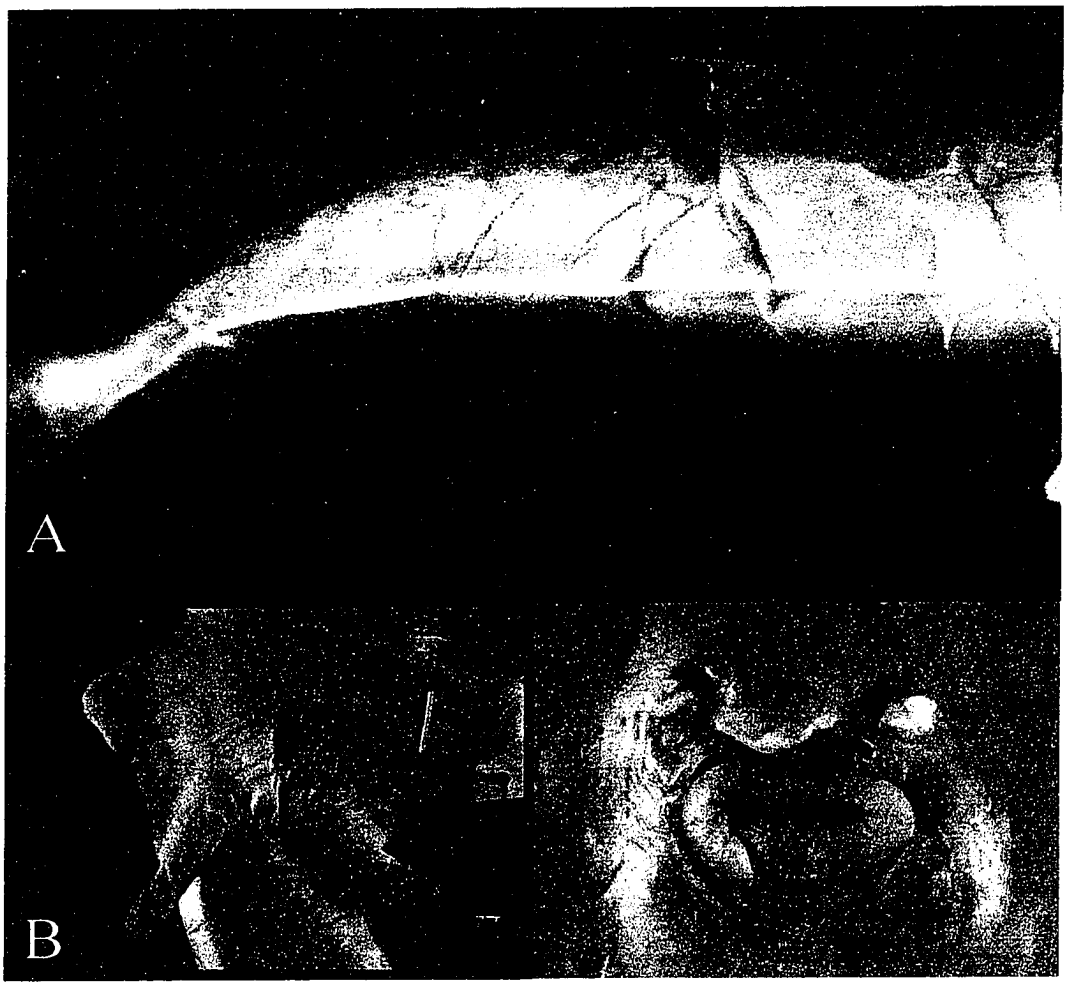
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Figure 46. Holotype of Heteronarce rierai Llorias and Rucabado, 1991 (IIPB 82/1987, 257 mm TL). A) Lateral view of post-pelvic tail region of holotype; B) ventral view of pelvic fins and clasper; C) close-up view of nasoral region. Courtesy of C. Allué (IIPB).

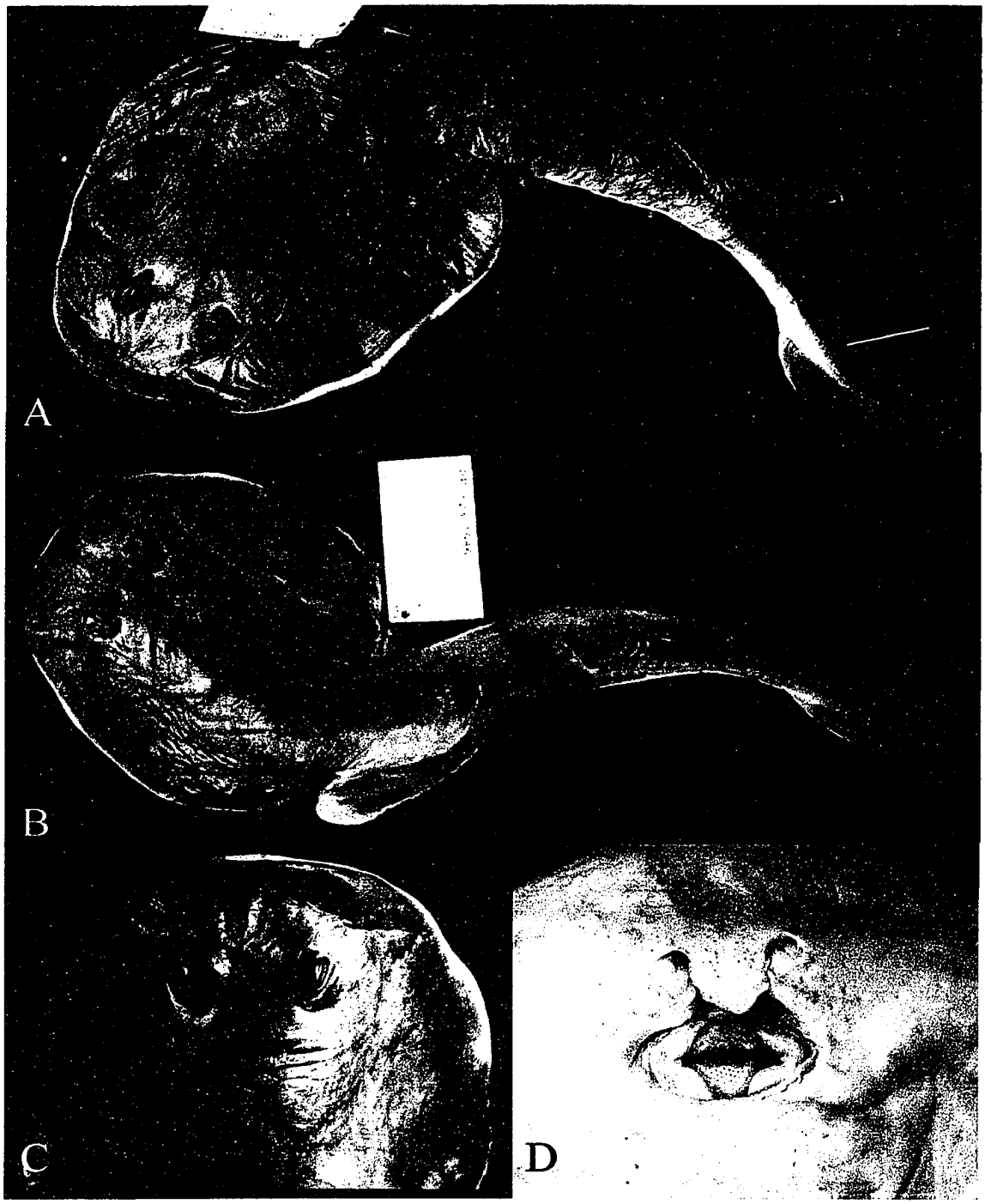
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Figure 47. Paratypes of Heteronarce rierai Lloris and Rucabado, 1991. A) IIPB 577/1986 (288 mm TL; Mozambique); B) IIPB 528/1986 (293 mm TL; Mozambique); C) dorsal snout region of IIPB 528/1986; D) nasoral region of IIPB 528/1986.

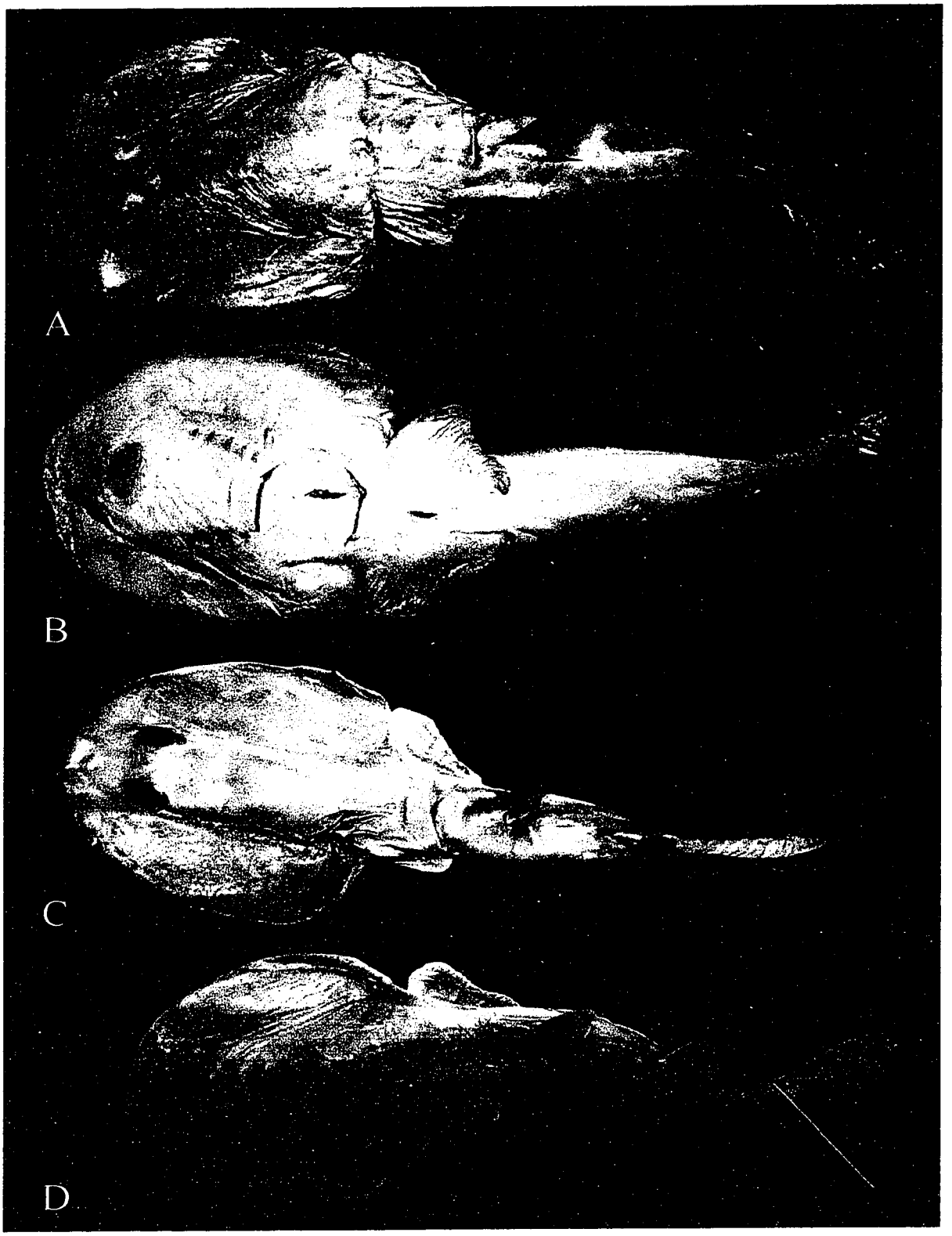
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Figure 48. Representative specimens of N. rierai. A) RUSI 48526 (272 mm TL); B) ventral view of same; C) ZMA 113.398 (213 mm TL; Tanzania); D) ISH 255-75 (223 mm TL; Somalia).

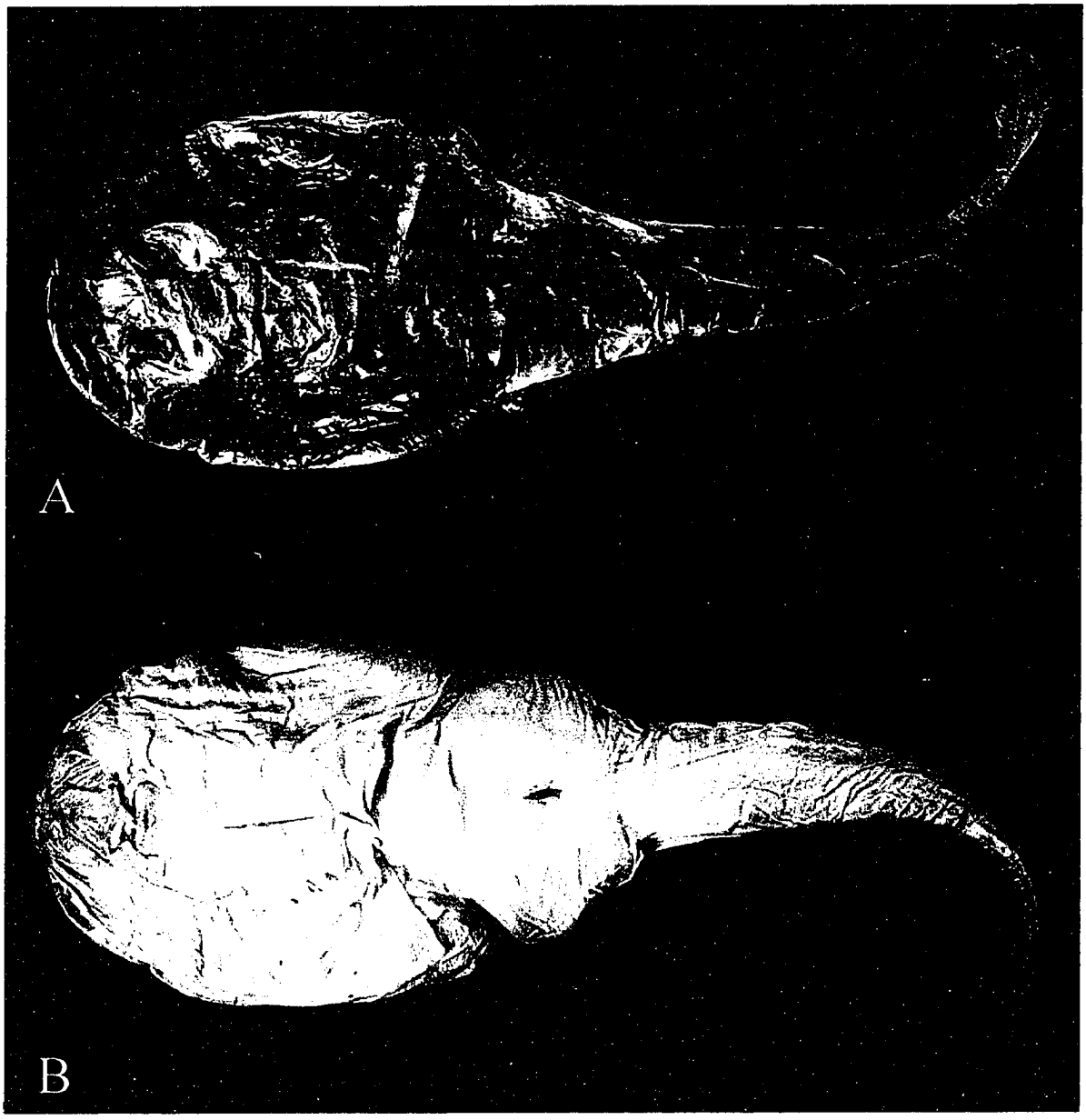
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Figure 49. Holotype of Narcine tasmaniensis Richardson, 1841 in dorsal (A) and ventral (B) views (BMNH 1848.3.18.16, 276 mm TL; Port Arthur, Tasmania).

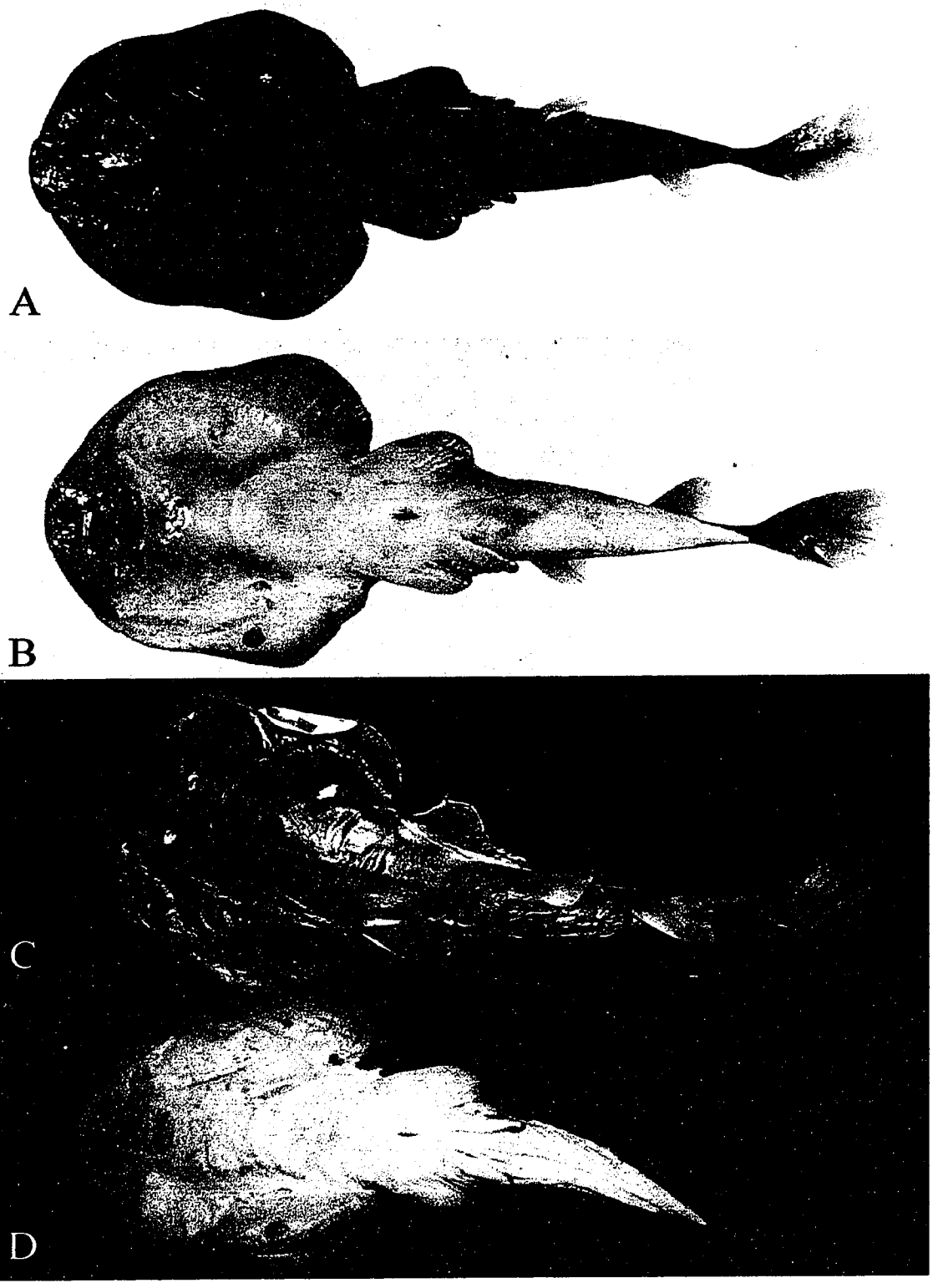
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Figure 50. Representative specimens of N. tasmaniensis. A and B) CSIRO H949-12 (360 mm TL; New South Wales) in dorsal and ventral views at time of capture; C and D) dorsal and ventral views of sam specimen in preservative. A and B courtesy of CSIRO.

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Figure 51. N. tasmaniensis in dorsal view. A) CSIRO T1051 (201 mm TL; Tasmania); B) CSIRO H857-03 (291 mm TL; Tasmania); C) CSIRO H1265-01 (Tasmania). Courtesy of CSIRO.

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A



B

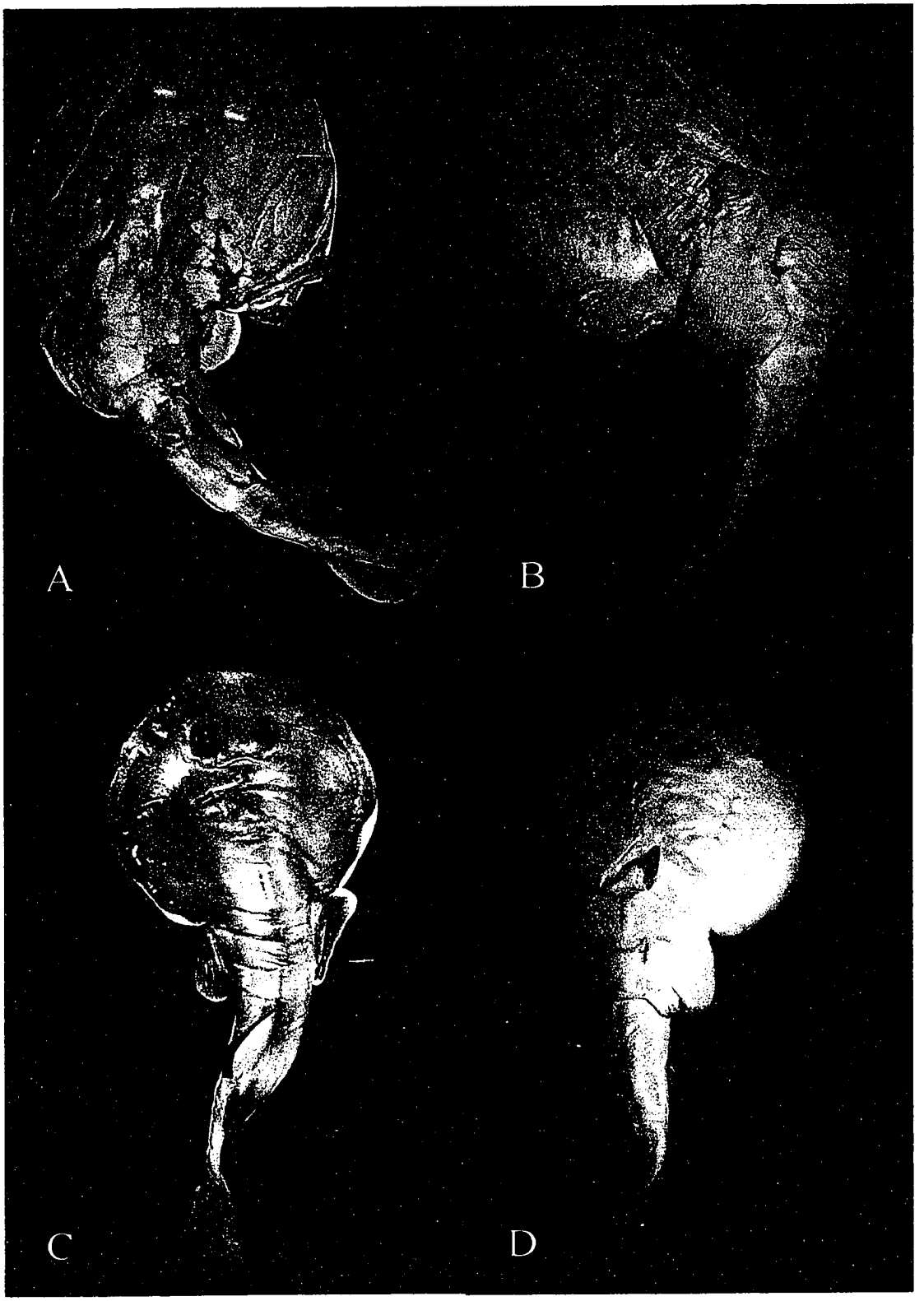


C

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Figure 52. Representative specimens of N. tasmaniensis. A and B) NMV 11289 (444 mm TL; Western Australia); C and D) AMS 19091-005 (285 mm TL; New South Wales).

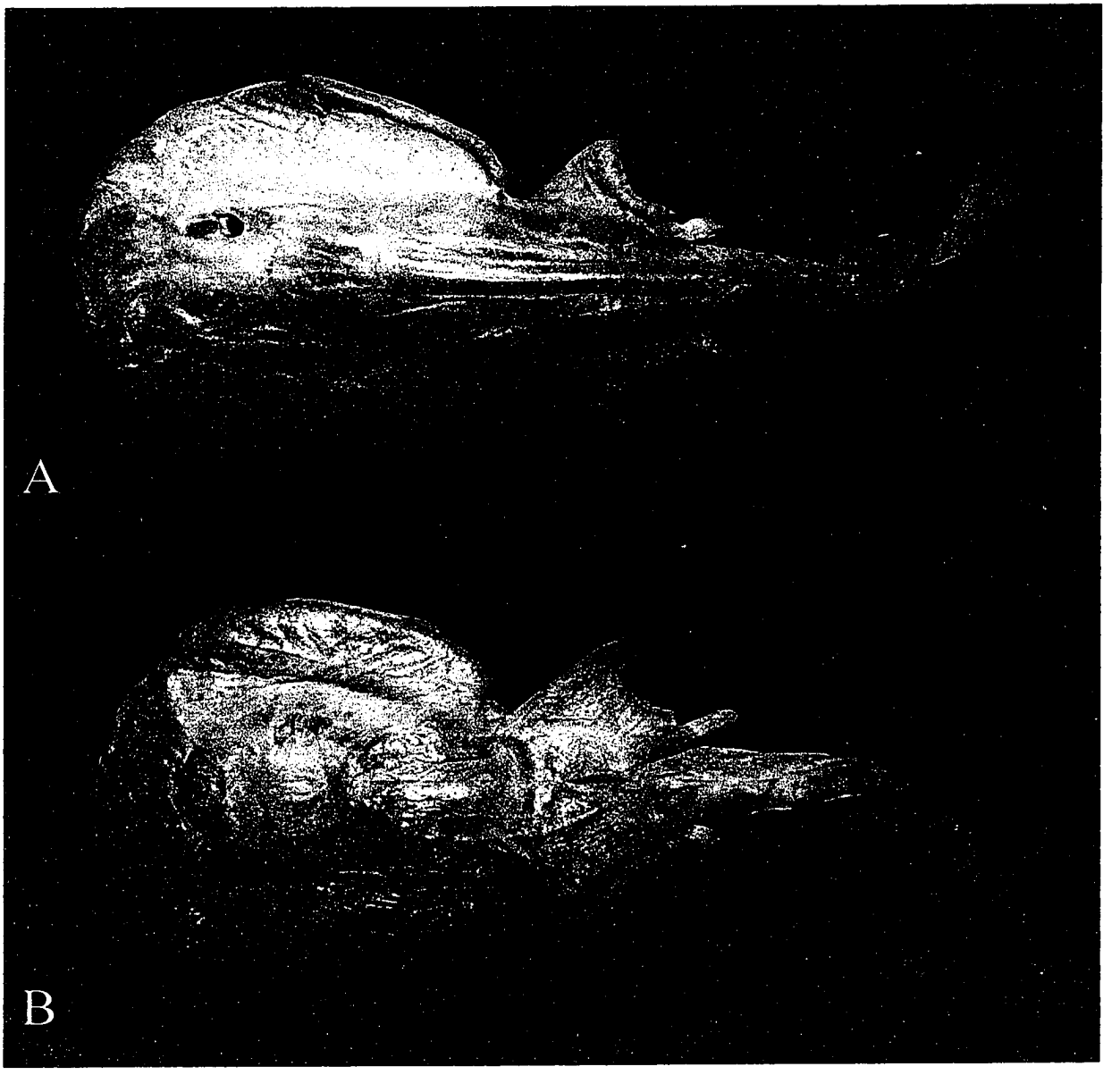
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Figure 53. Lectotype of Raja timlei Bloch and Schneider, 1801 (ZMB 4581, 154 mm TL; Tranquebar, India) in dorsal (A) and ventral (B) views.

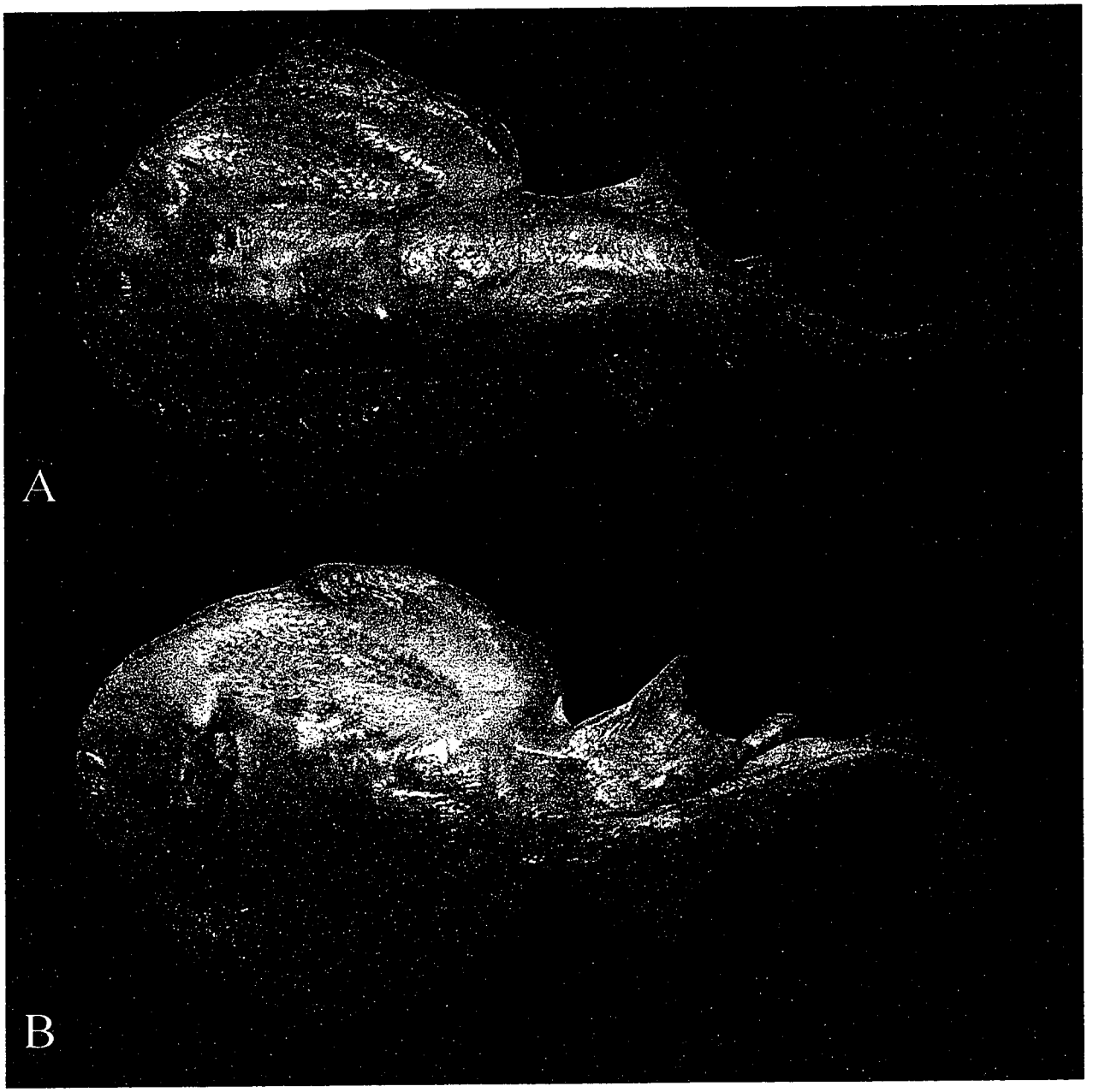
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Figure 54. Paralectotype of Raja timlei Bloch and Schneider, 1801 and holotype of Narcine indica Henle. 1834 (ZMB 4582, 166 mm TL; Tranquebar, India) in dorsal (A) and ventral (B) views.

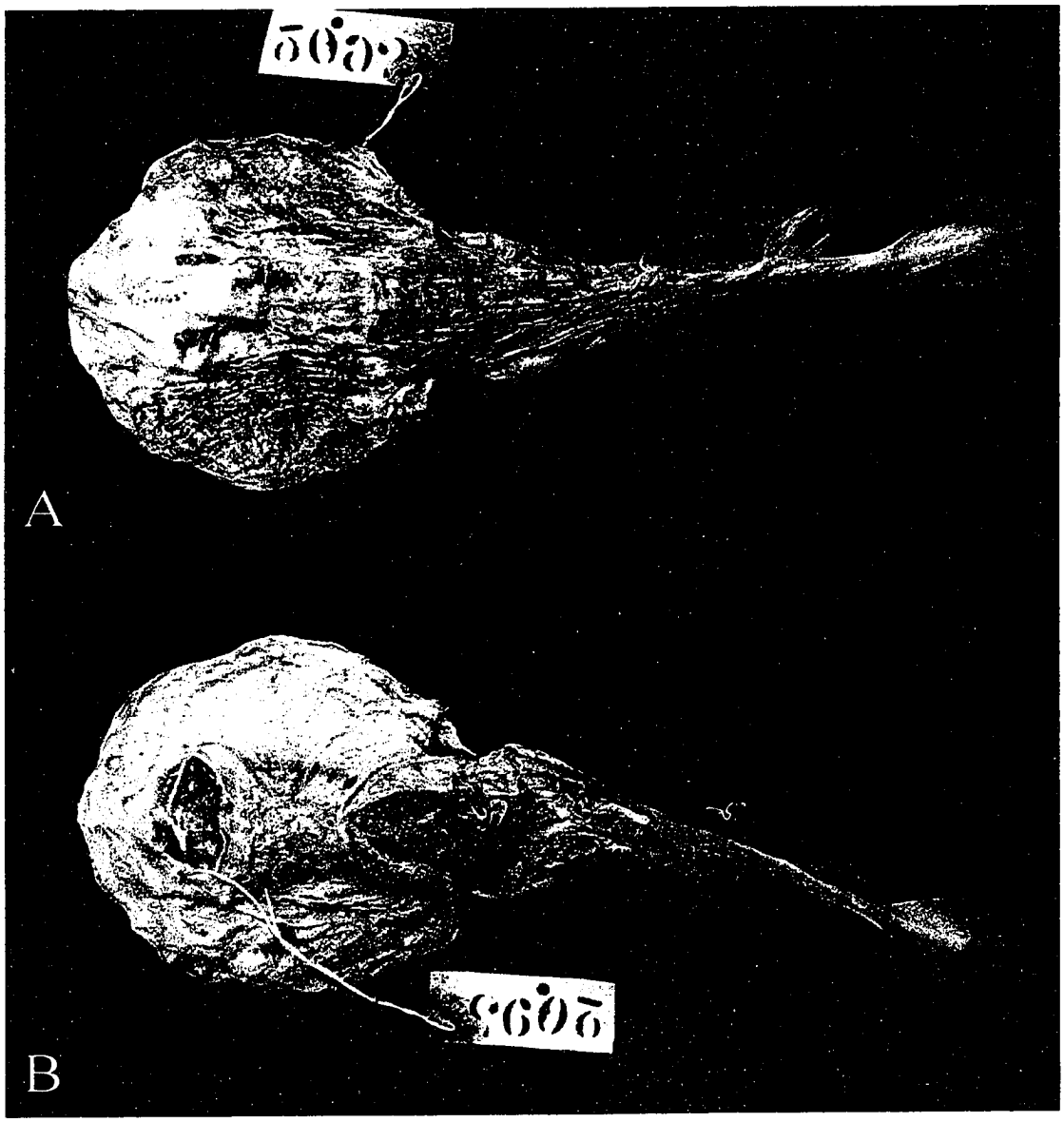
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Figure 55. Holotype of Narcine macrura Valenciennes, 1852 (MNHN 2095, 135 mm TL; "mer des Indes") in dorsal (A) and ventral (B) views.

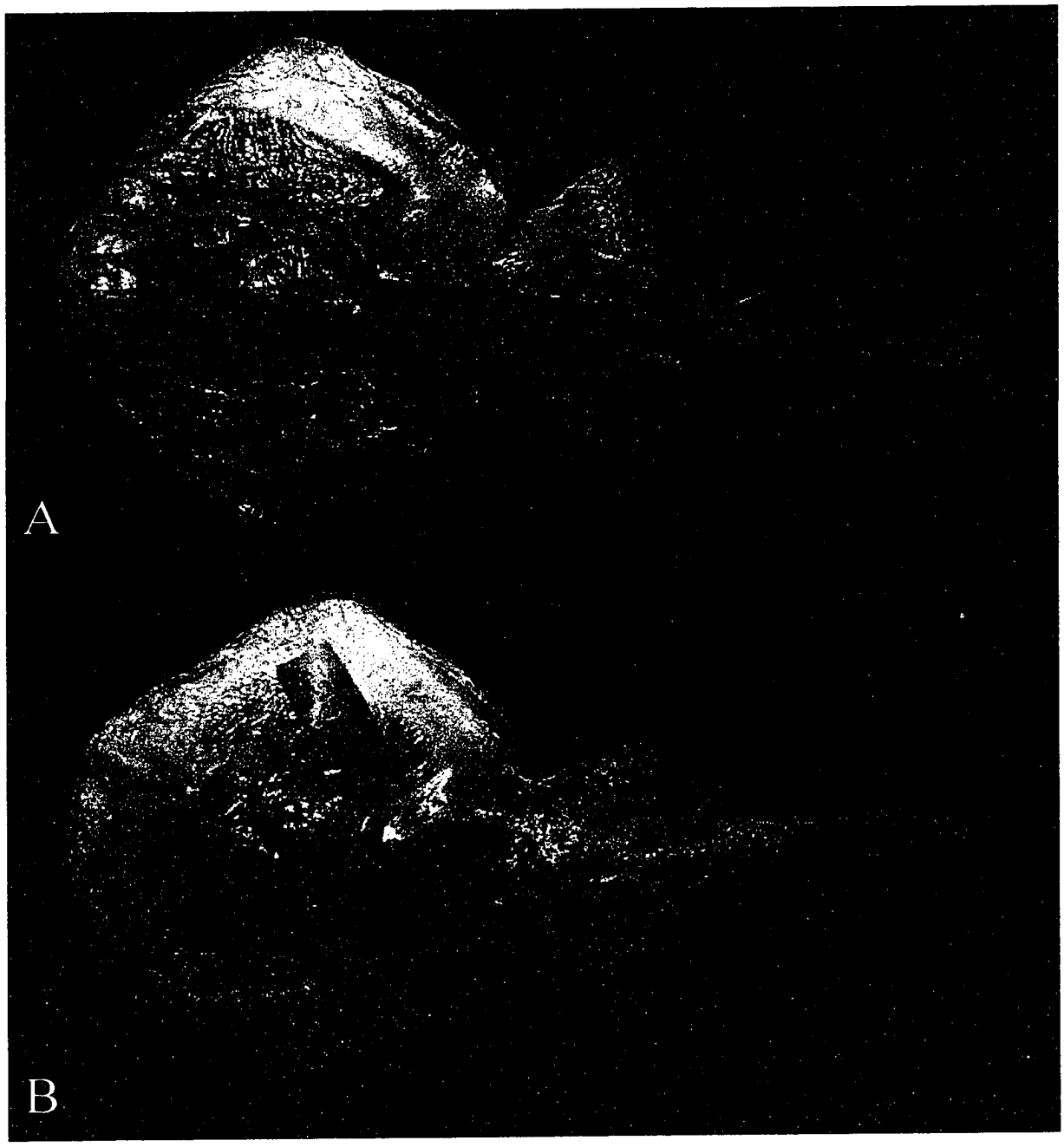
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Figure 56. Holotype of Narcine microphthalma Valenciennes, 1852 (MNHN 1342, 175 mm TL; Malabar coast, India) in dorsal (A) and ventral (B) views.

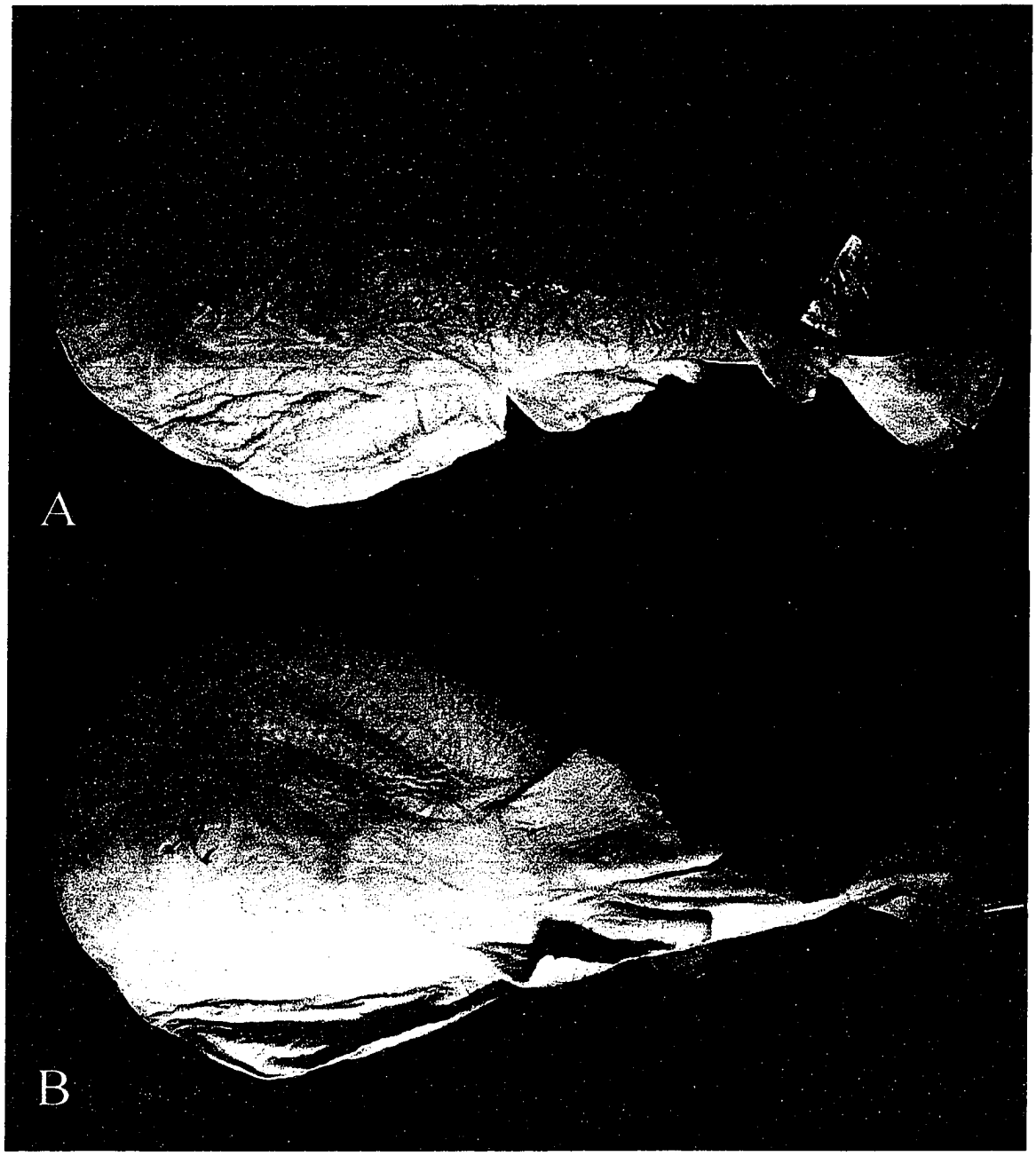
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Figure 57. Lectotype of Narcine brunnea Annandale, 1909 (ZMA 112.827, 182 mm TL; Orissa coast, India) in dorsal (A) and ventral (B) views.

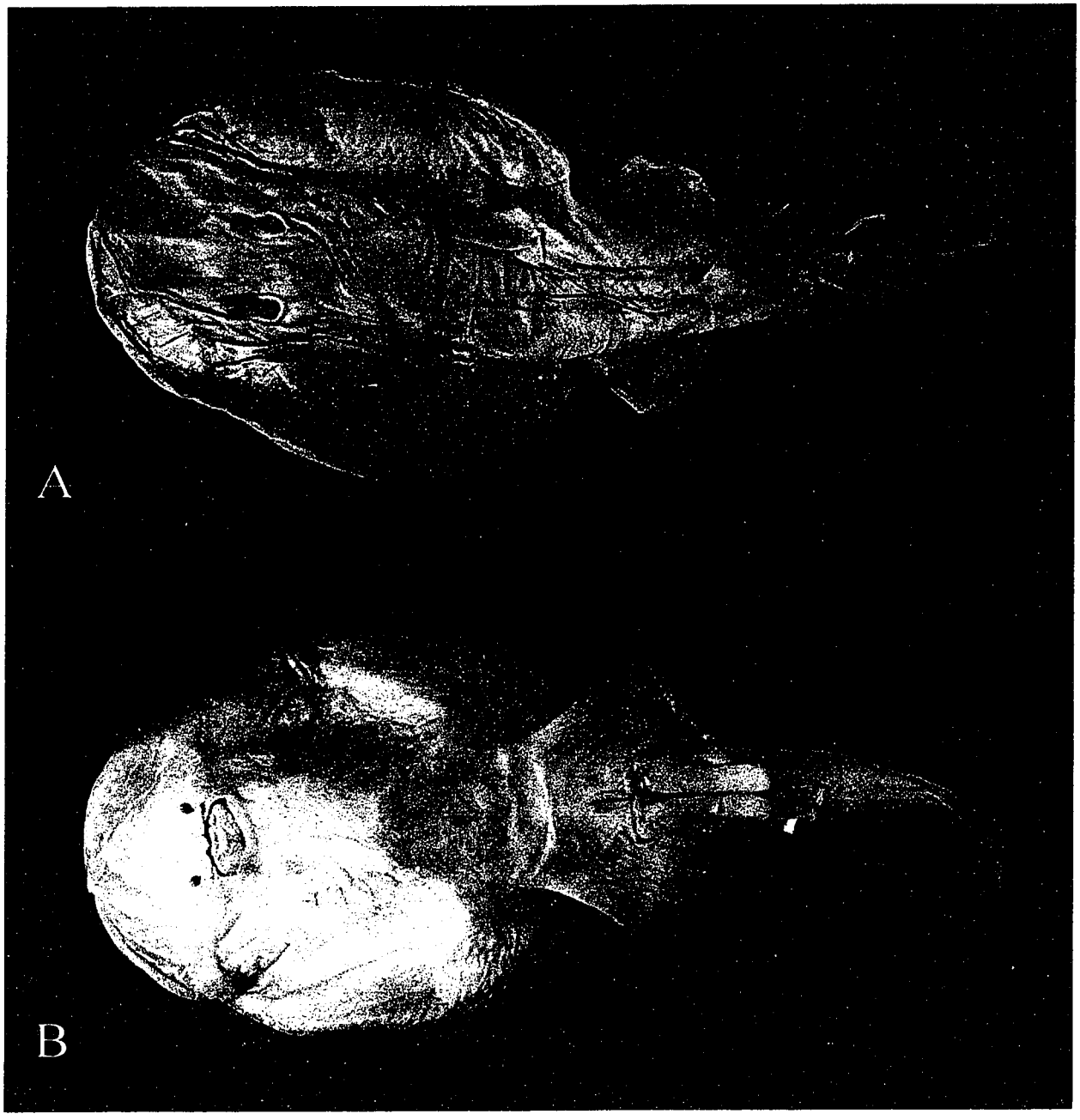
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Figure 58. Paralectotype of Narcine brunnea Annandale, 1909 (BMNH 1909.7.12.10, 135 mm TL; Orissa coast, India) in dorsal (A) and ventral (B) views.

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Figure 59. Paralectotype of Narcine brunnea Annandale, 1909 (BMNH 1909.7.12.11, 225 mm TL; Orissa coast, India) in dorsal (A) and ventral (B) views.

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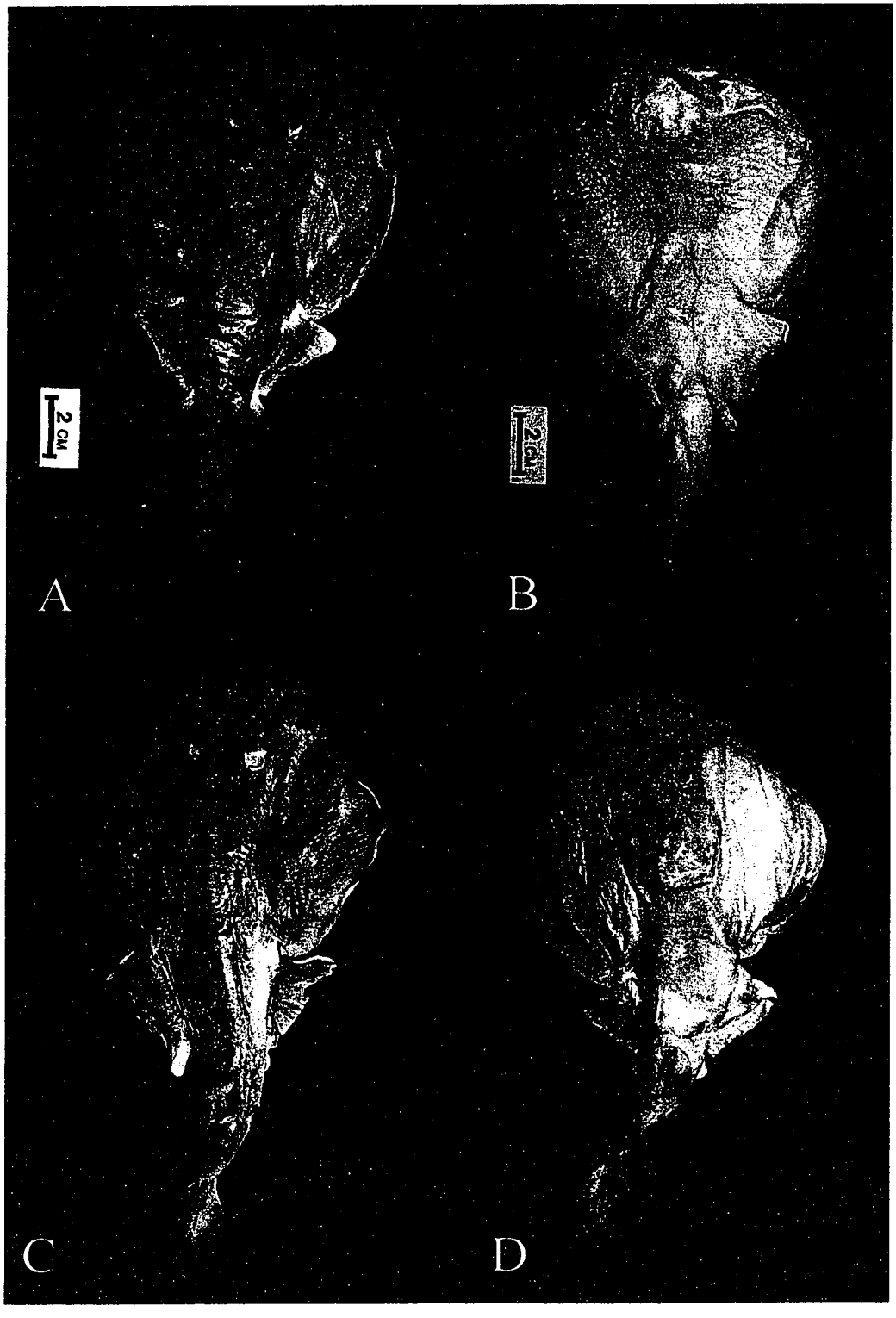


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Figure 60. Representative specimens of N. timlei. A and B) dorsal and ventral views of USNM 222479 (187 mm TL; Sri lanka); C) dorsal view of USNM 222478 (216 mm TL; Sri Lanka); D) dorsal view of CAS 58355 (164 mm TL, western coast of India).

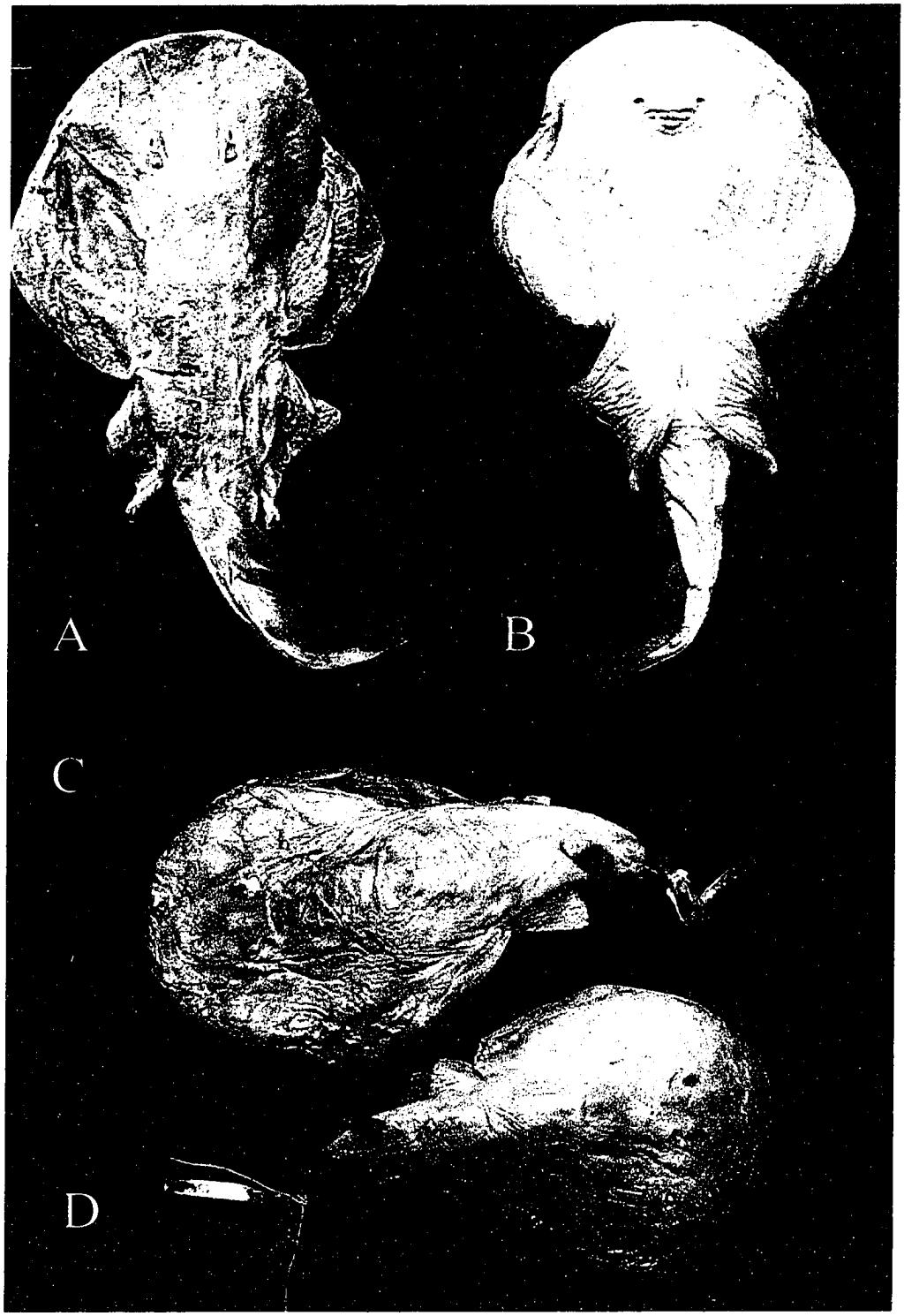
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Figure 61. Representative specimens of N. timlei. A and B) BMNH 1848.3.18.178-179 (215 mm TL; China) in dorsal and ventral views; C and D) dorsal views of CAS 30983 (151 and 108 mm TL; Ketam Island, Malaysia).

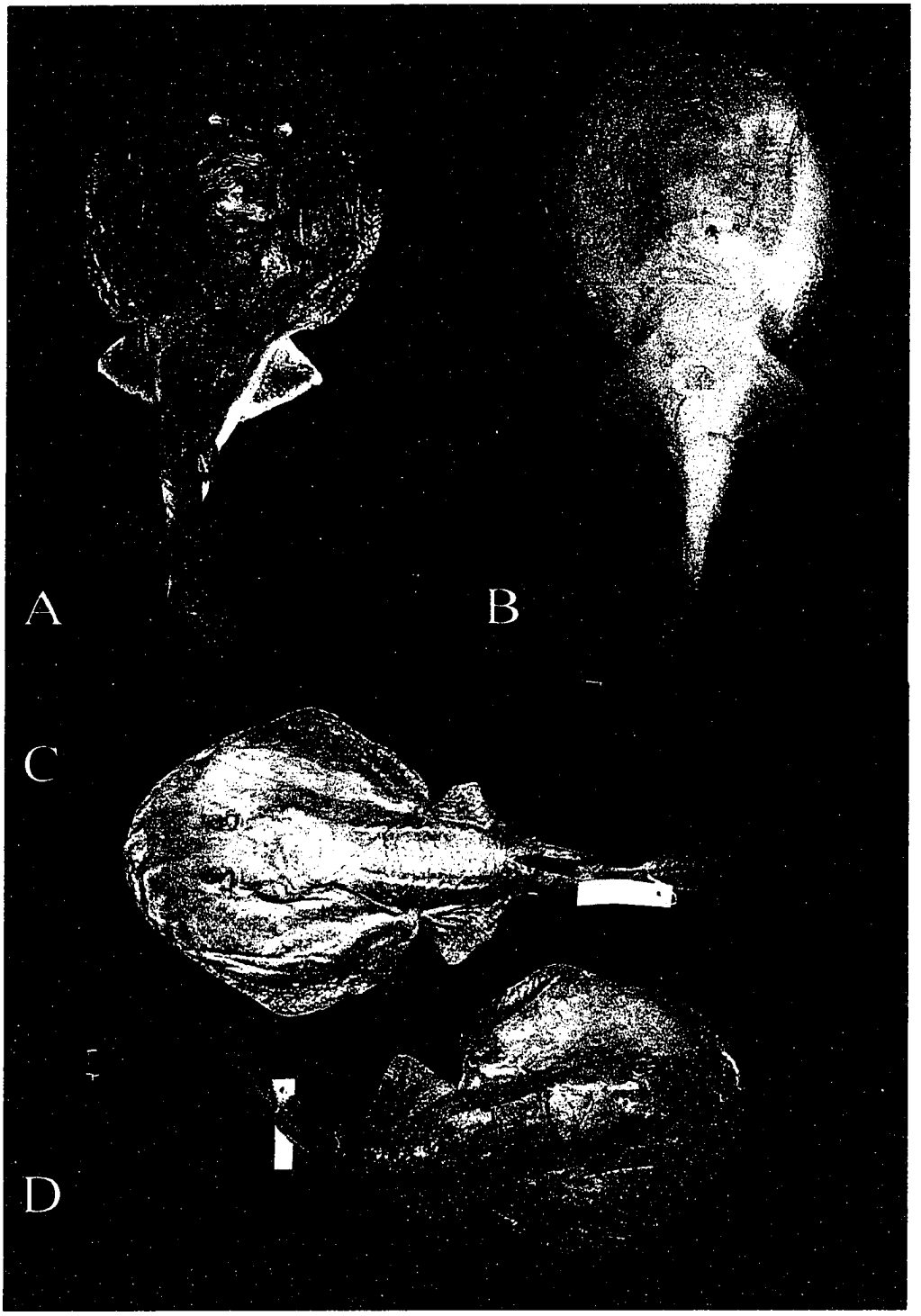
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Figure 62. Specimens of N. timlei. A and B) CAS 98159 (196 mm TL; Myanmar) in dorsal and ventral view; C and D) dorsal view of CAS 41712 (170 and 155 mm TL; Madras, India).

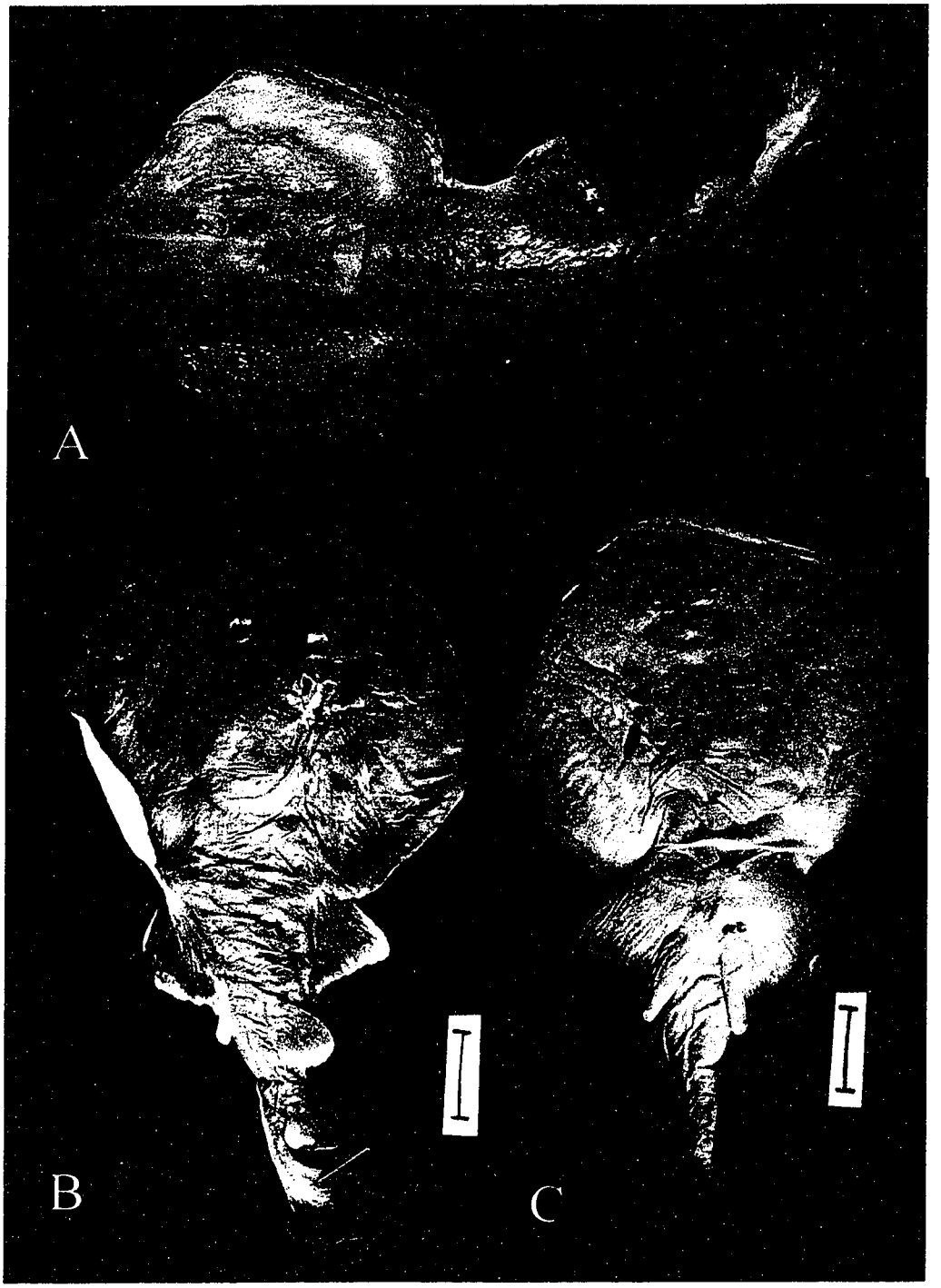
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Figure 63. Representatives of N. timlei. A) MNHN 1340 (234 mm TL; Pondicherry, India); B and C) BMNH 1979.3.21.409-410 (190 mm TL; Bombay, India).

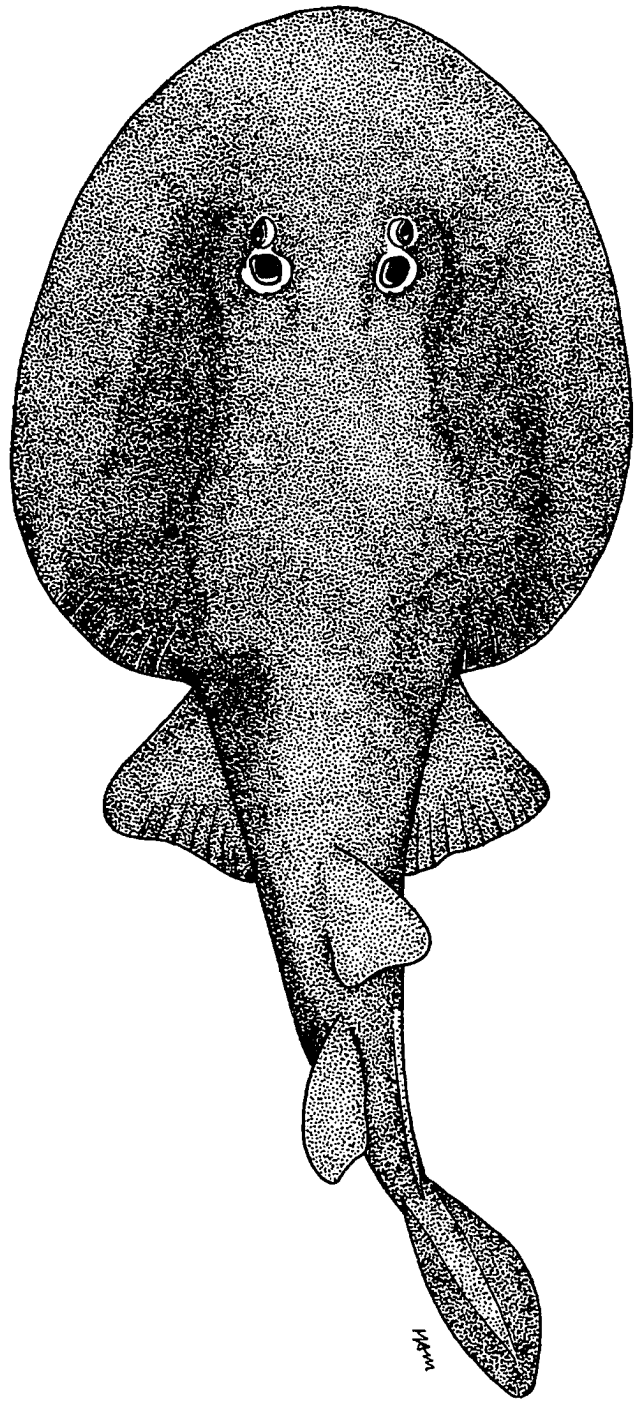
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Figure 64. Illustration of N. timlei (based on paralectotype BMNH 1909.7.12.10). Copyright FAO (Rome), reproduced from Carvalho et al. (in press) with permission.

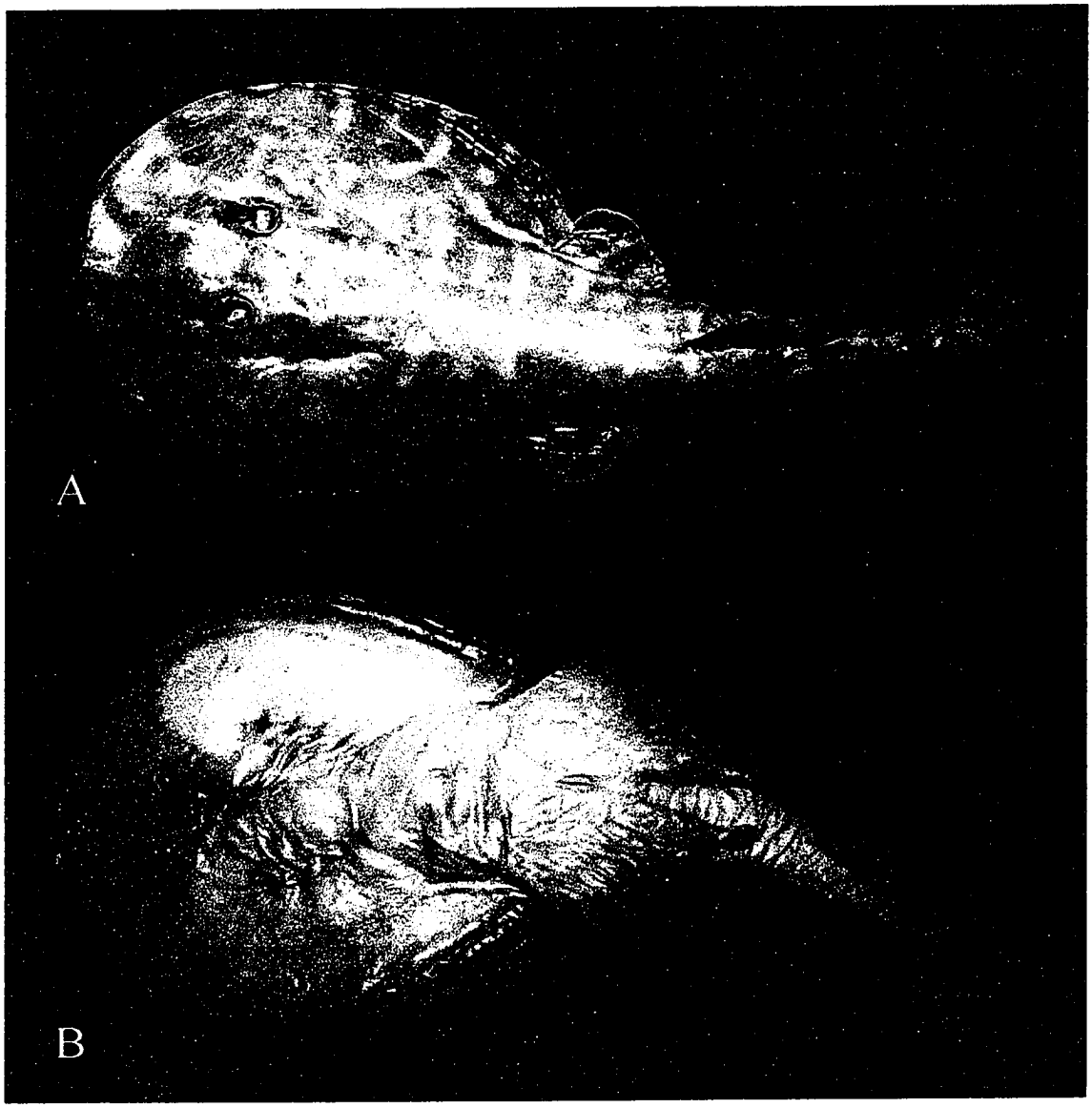
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Figure 65. Holotype of Narcine vermiculatus Breder, 1928 (YPM 1143, 204 mm TL; Chiapas coast, Mexico) in dorsal (A) and ventral (B) views.

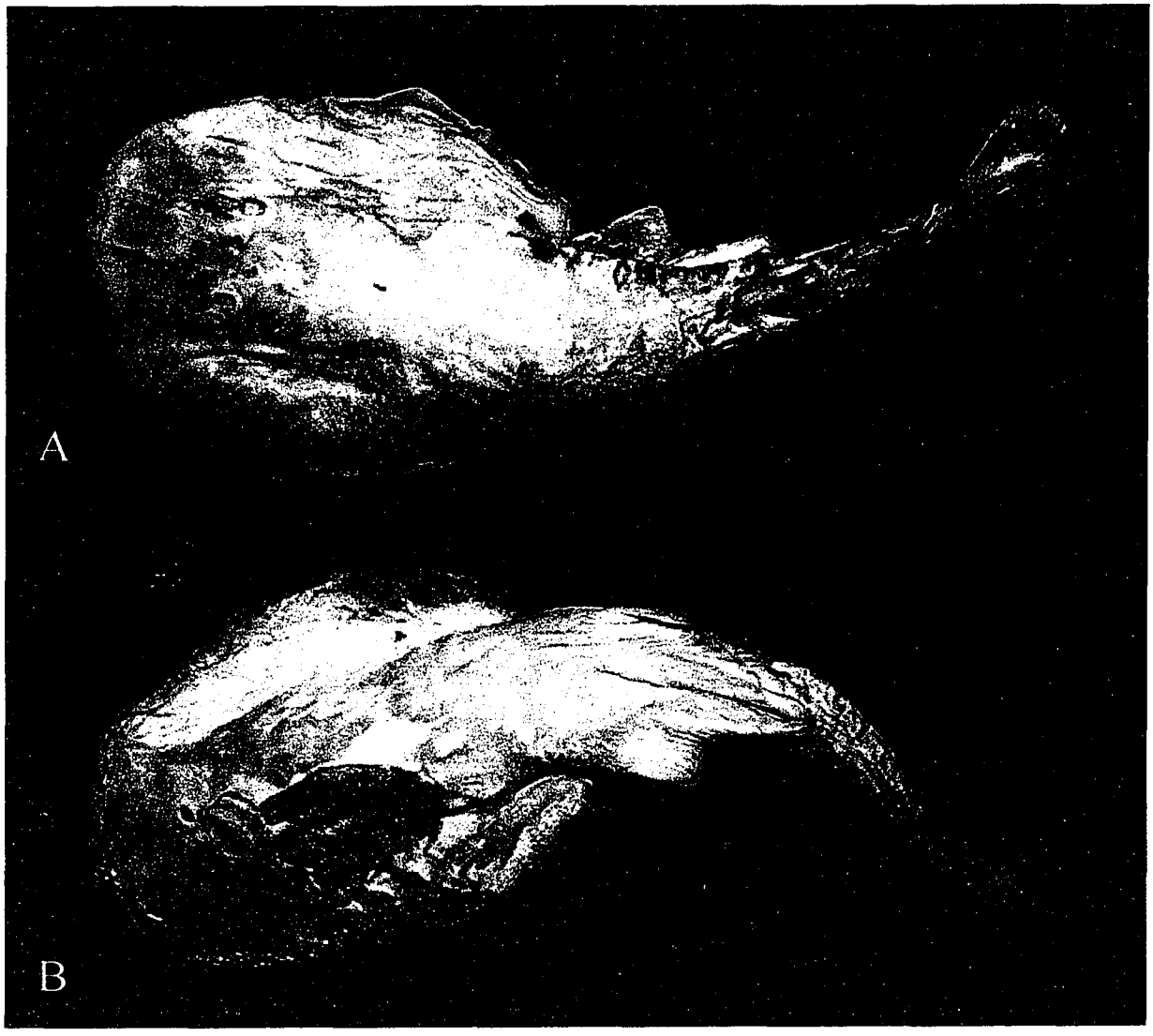
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Figure 66. Holotype of Narcine schmitti Hildebrand, 1948 (USNM 94044, 220 mm TL; "White Friars Island," Mexico) in dorsal (A) and ventral (B) views.

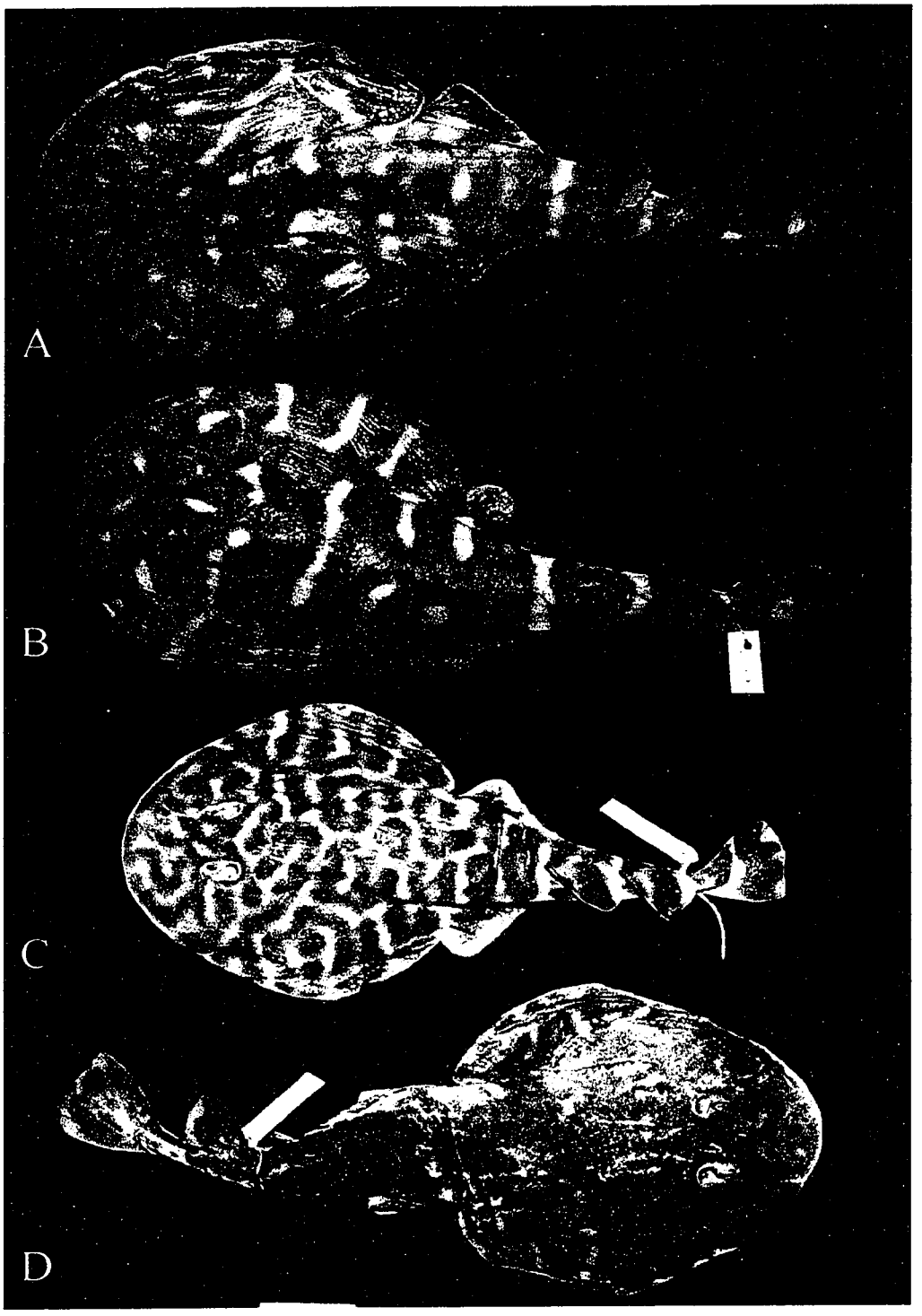
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Figure 67. Representative specimens of N. vermiculatus. A) FMNH 62372 (208 mm TL; Sinaloa coast, Mexico); B) CAS 54014 (173 mm TL; Nayarit, Mexico); C and D) CAS 49094 (223 and 195 mm TL; Nayarit, Mexico).

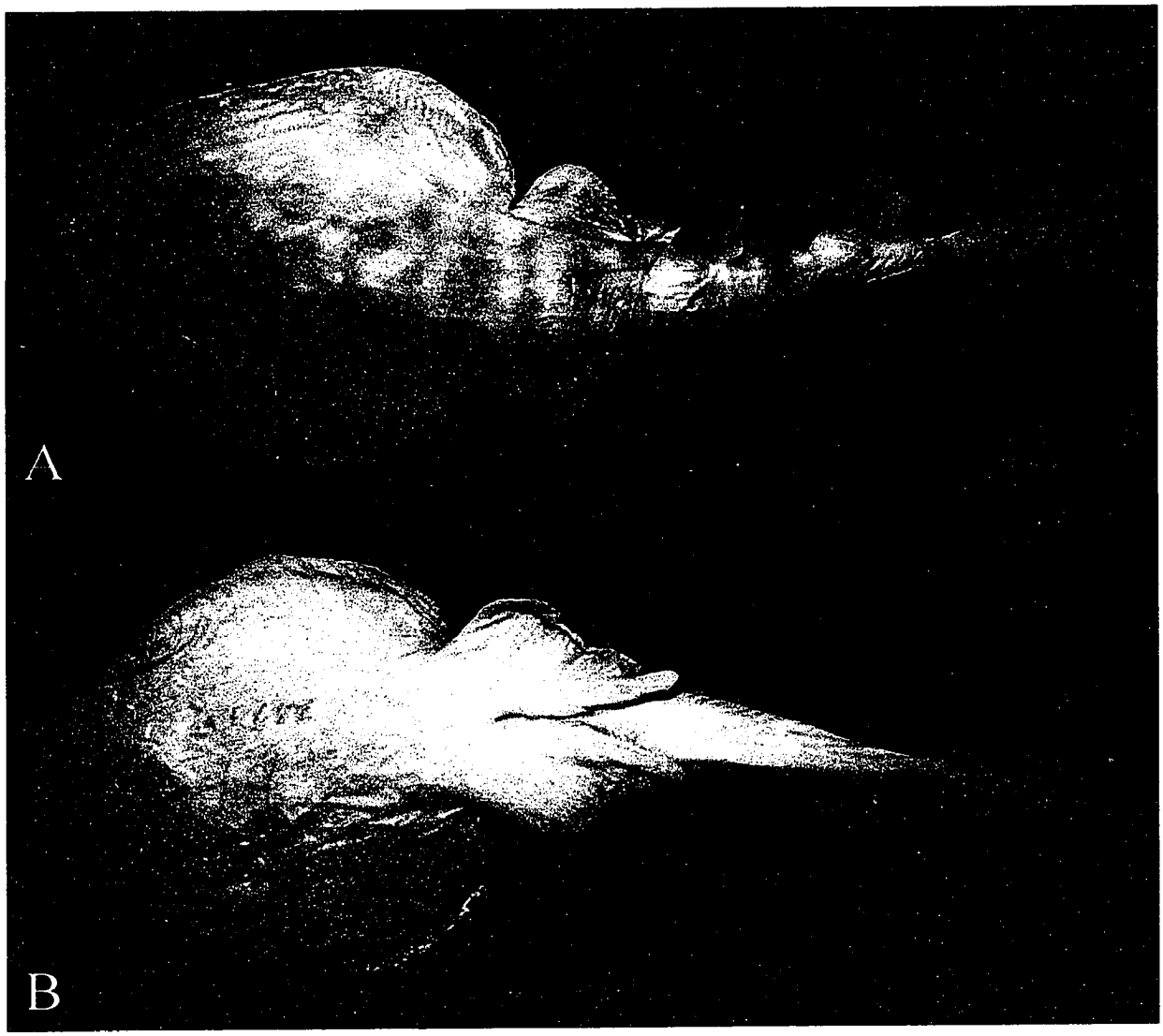
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Figure 68. Dorsal (A) and ventral (B) views of holotype of Narcine westraliensis McKay, 1966 (WAM P6963, 211 mm TL; Shark Bay, Western Australia).

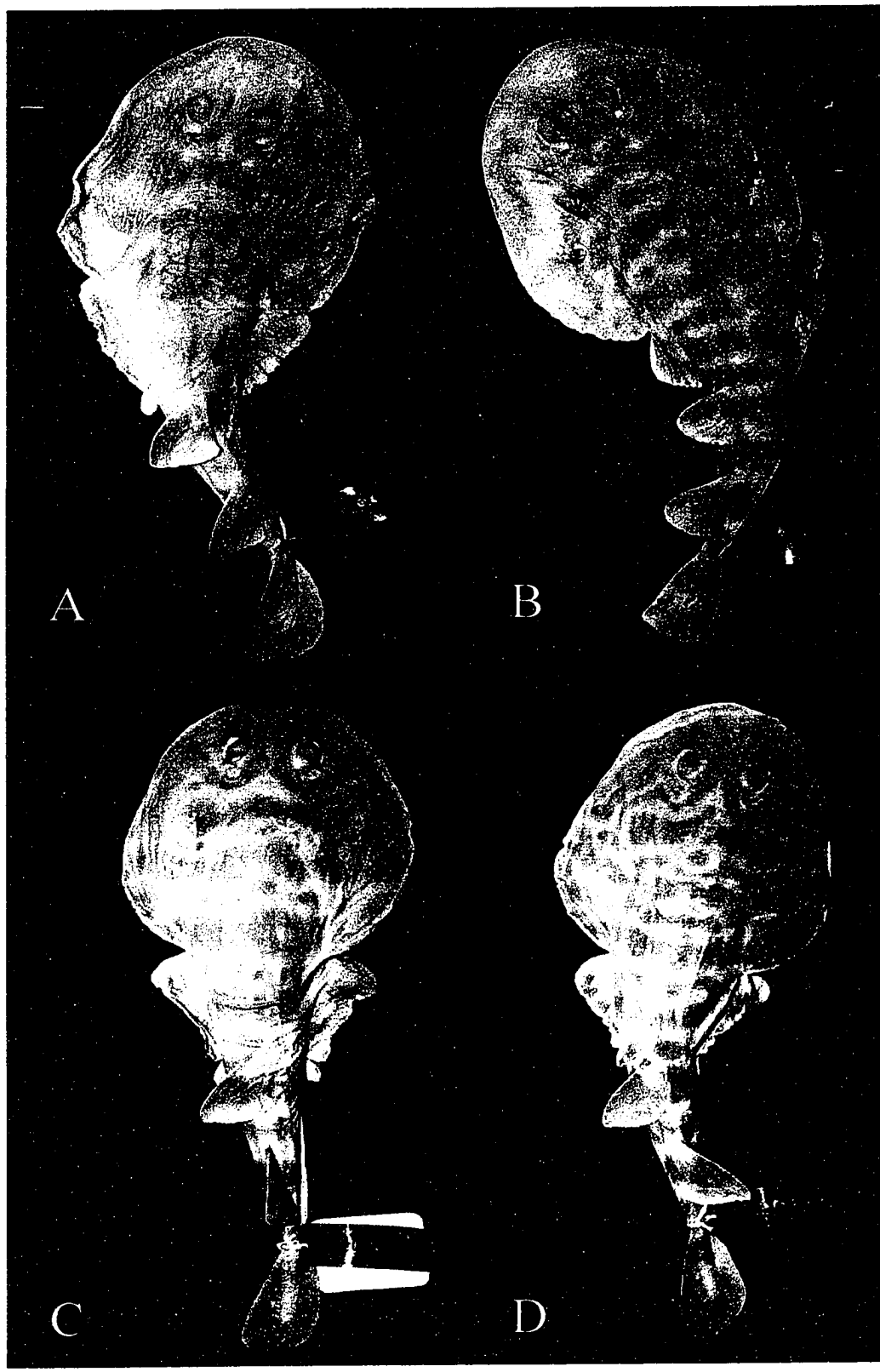
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Figure 69. Dorsal views of selected paratypes of N. westraliensis, all from Shark Bay (Western Australia). A) WAM P6997 (200 mm TL); B) WAM P 7033 (195 mm TL); C) WAM P6946 (214 mm TL); D) WAM P6959 (202 mm TL).

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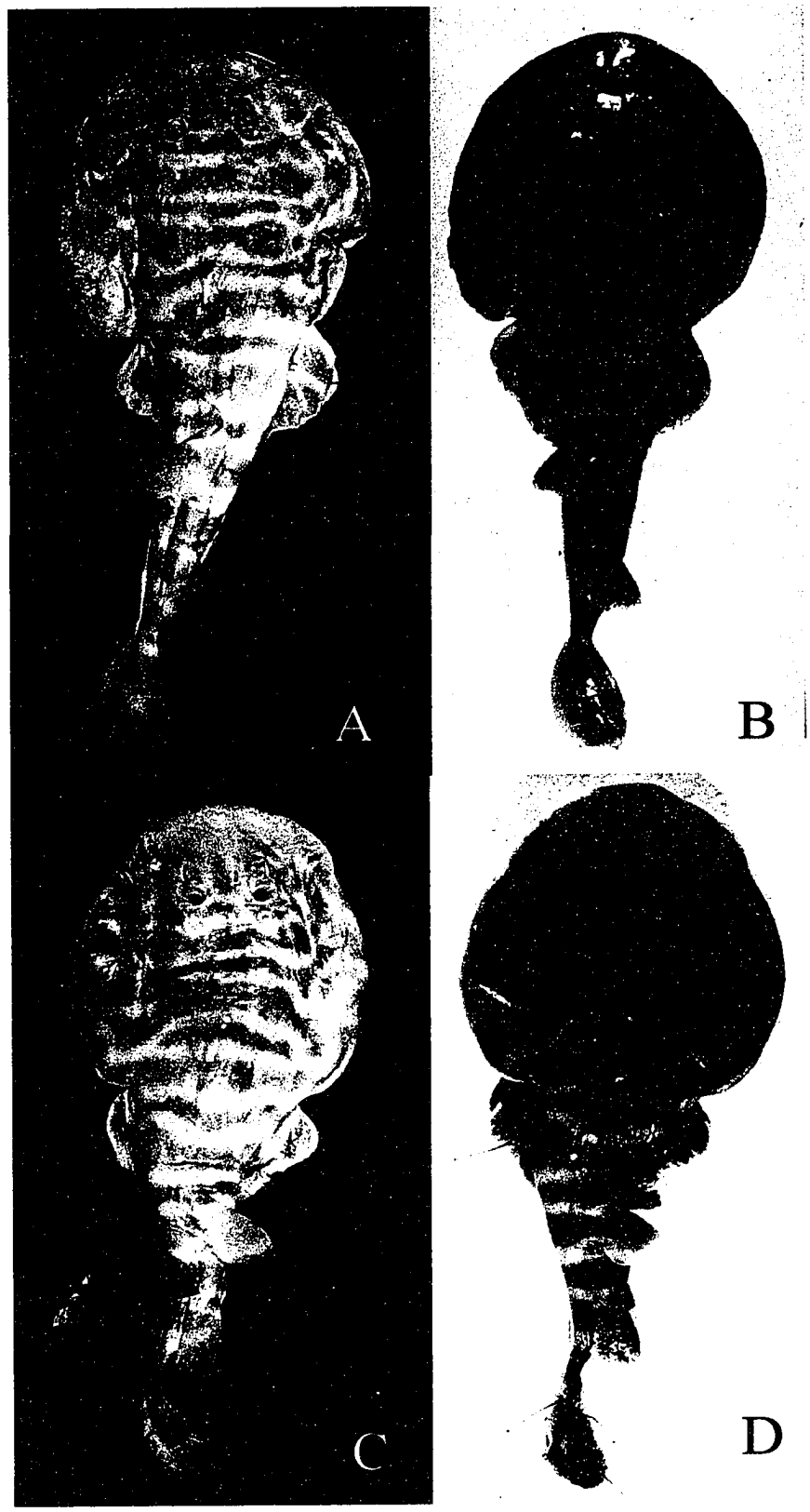


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Figure 70. Dorsal views of representative specimens of N. westraliensis. A and B) Comparison of preserved and freshly collected specimen CSIRO H1038-01 (211 mm TL; NW of Port Hedland, Western Australia); C and D) Comparison of preserved and freshly collected specimen CSIRO CA4220 (225 mm TL; NW of Port Hedland, Western Australia). B and D courtesy of CSIRO.

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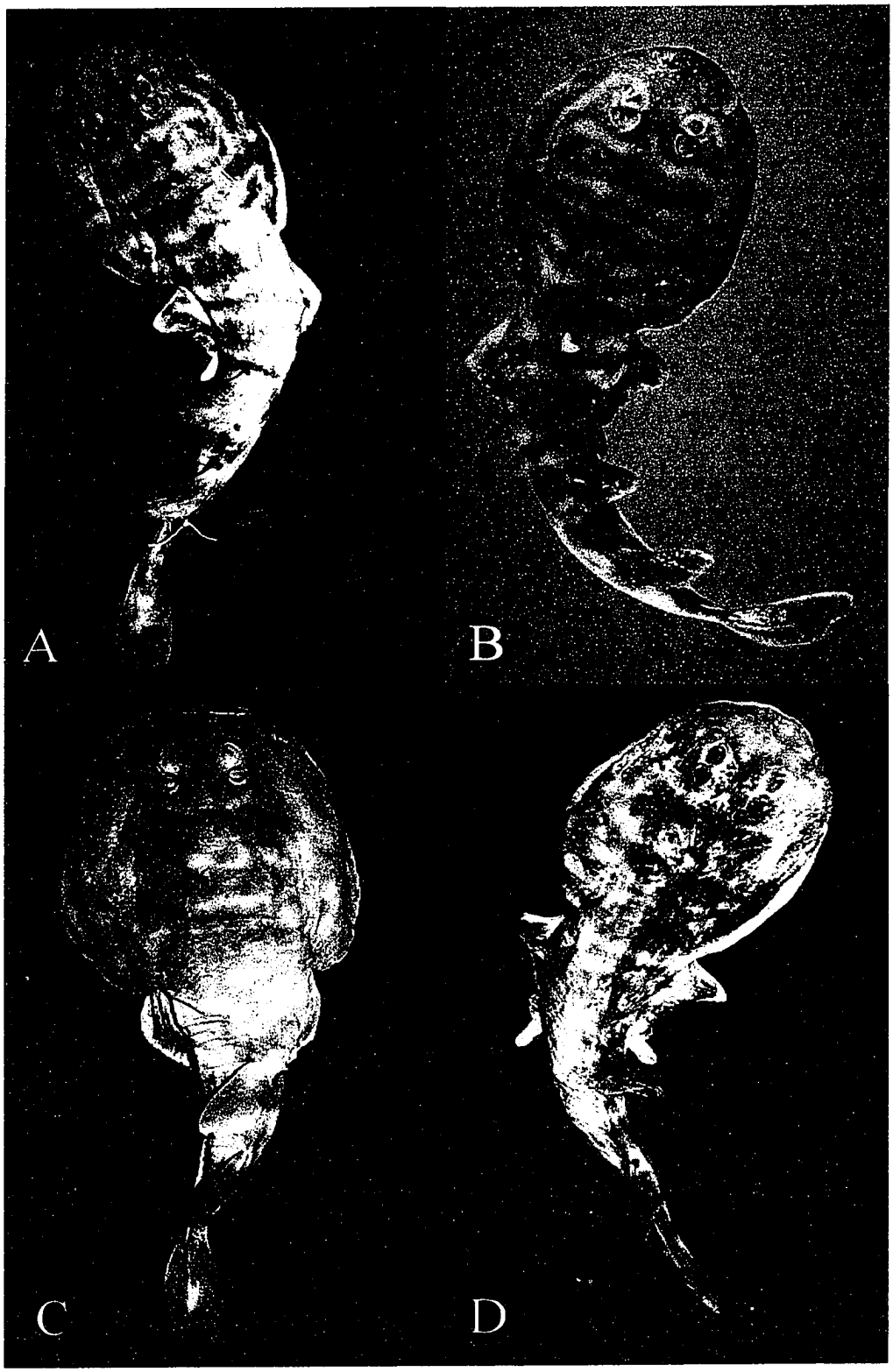


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Figure 71. Representative specimens of N. westraliensis in dorsal view. A and B) Comparison of preserved and freshly collected specimen CSIRO CA4221 (241 mm TL; NW of Port Hedland, Western Australia); C) WAM P23837.001 (200 mm TL; Exmouth Gulf, Western Australia); D) WAM P29334.011 (246 mm TL; Ningaloo Marine Park, Western Australia). B courtesy of CSIRO.

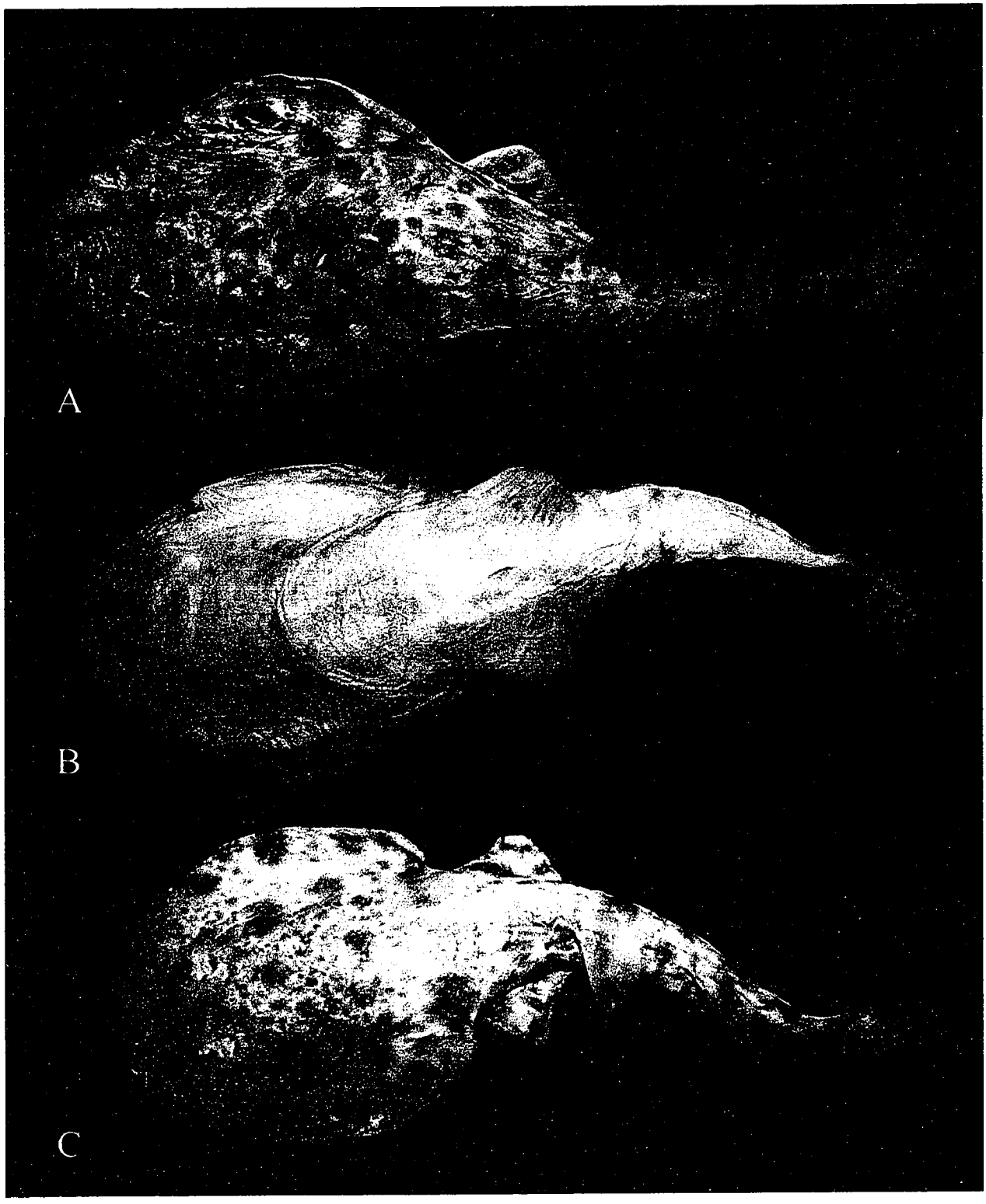
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Figure 72. Representative specimens of Narcine sp. nov. A. A and B) dorsal and ventral views of QM I.23187 (241 mm TL, Gulf of Carpentaria); C) QM I.28005 (223 mm TL; Gulf of Carpentaria).

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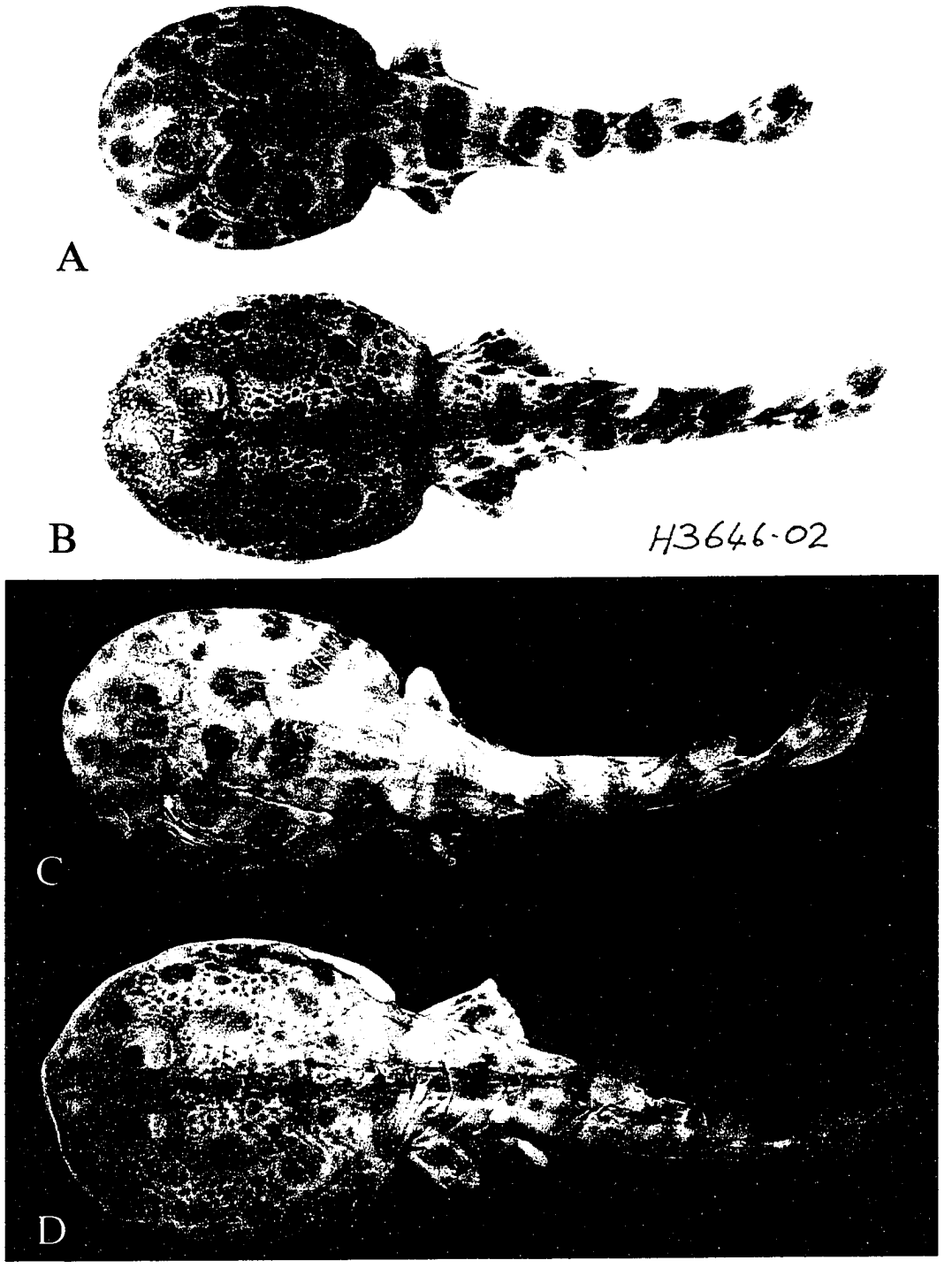


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Figure 73. Representative specimens of Narcine sp. nov. A in dorsal view. A and B) Freshly collected specimens CSIRO H3646-02 (169 and 186 mm TL; Gulf of Carpentaria); C and D) preserved specimens CSIRO H3646-02. A and B courtesy of CSIRO.

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Figure 74. Specimens of Narcine sp. nov. A in dorsal view. A and B) Preserved and freshly collected CSIRO CA2273 (194 mm TL; Arafura Sea); C) NTM 13329-001 (173 mm TL; Timor Sea); D) NTM 12262-003 (177 mm TL; Northern Territory). B courtesy of CSIRO.

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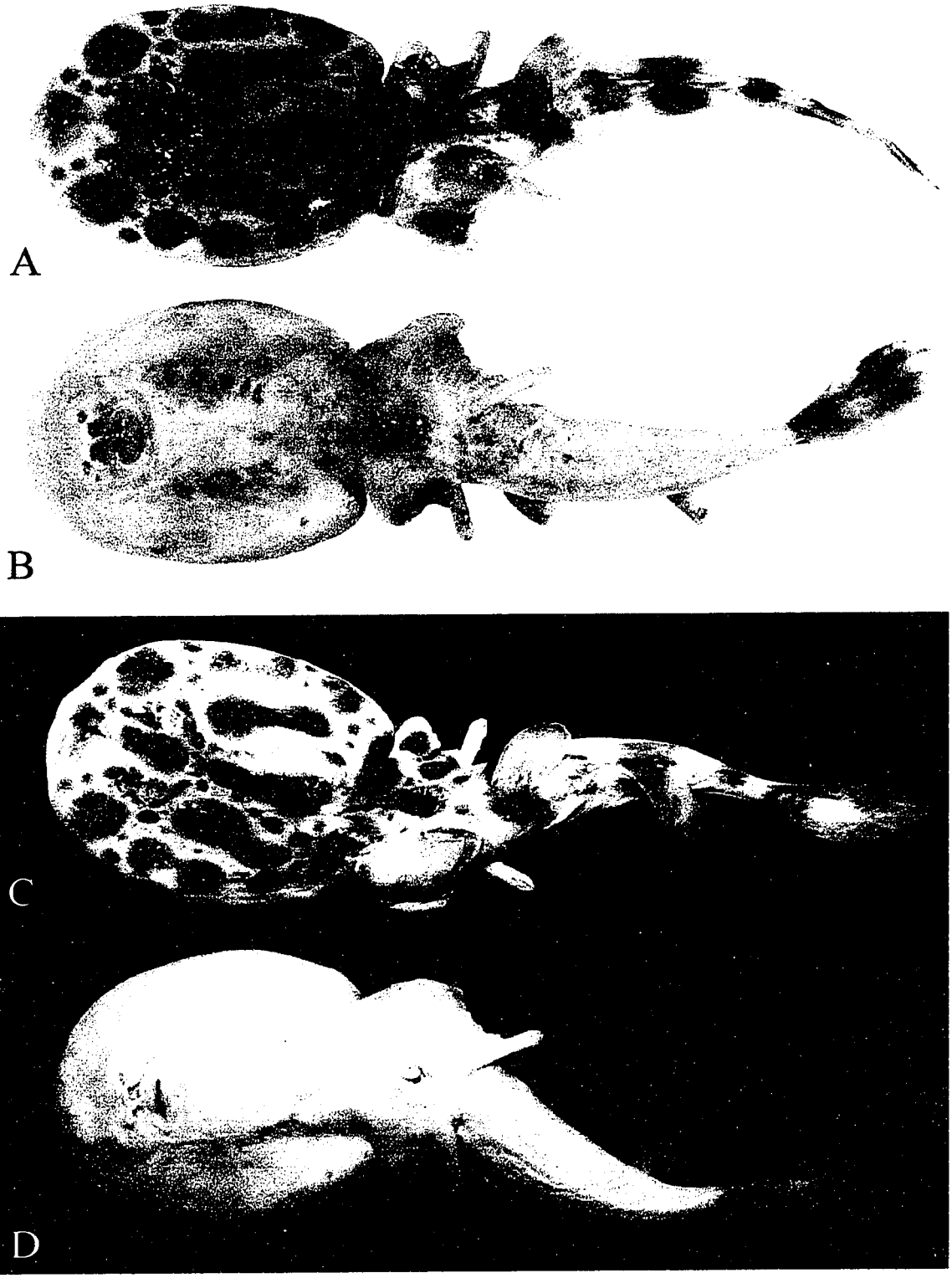


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Figure 75. Narcine sp. nov. A. Freshly collected (A and B) and preserved (C and D) CSIRO H773-01 (166 mm TL; Arafura Sea), in dorsal and ventral views. A and B courtesy of CSIRO.

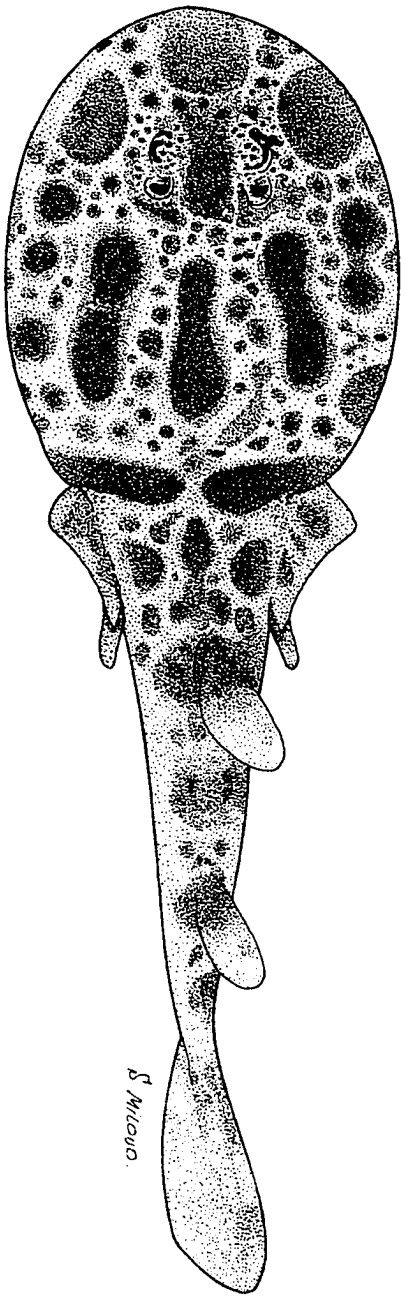
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Figure 76. Illustration of Narcine sp. nov. A, based on CSIRO H773-01. Reproduced from Carvalho et al. (in press), with permission from FAO (Rome).

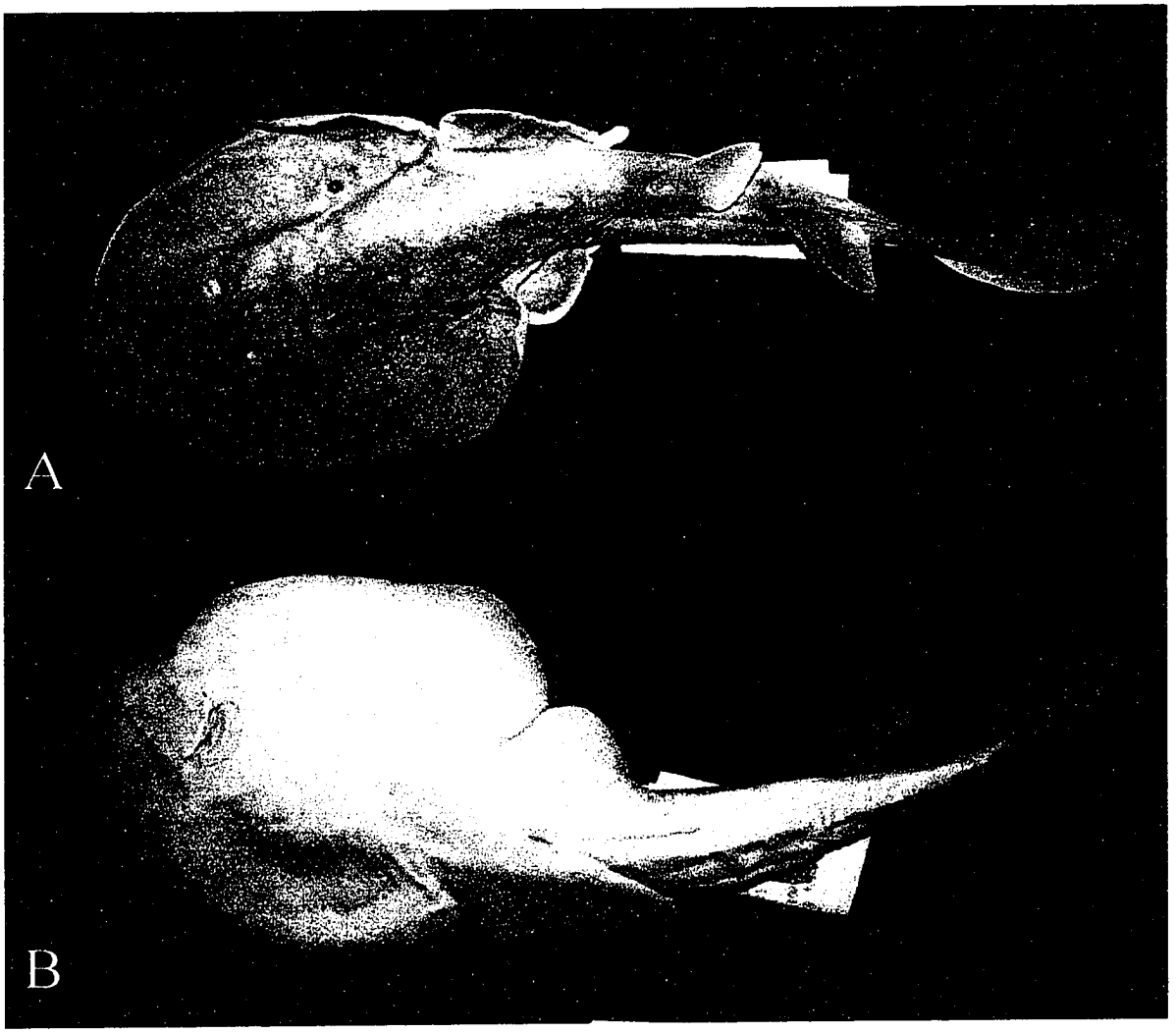
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Figure 77. Narcine sp. nov. B (CSIRO H2597-09, 302 mm TL; W of Green Head, Western Australia), in dorsal (A) and ventral (B) views.

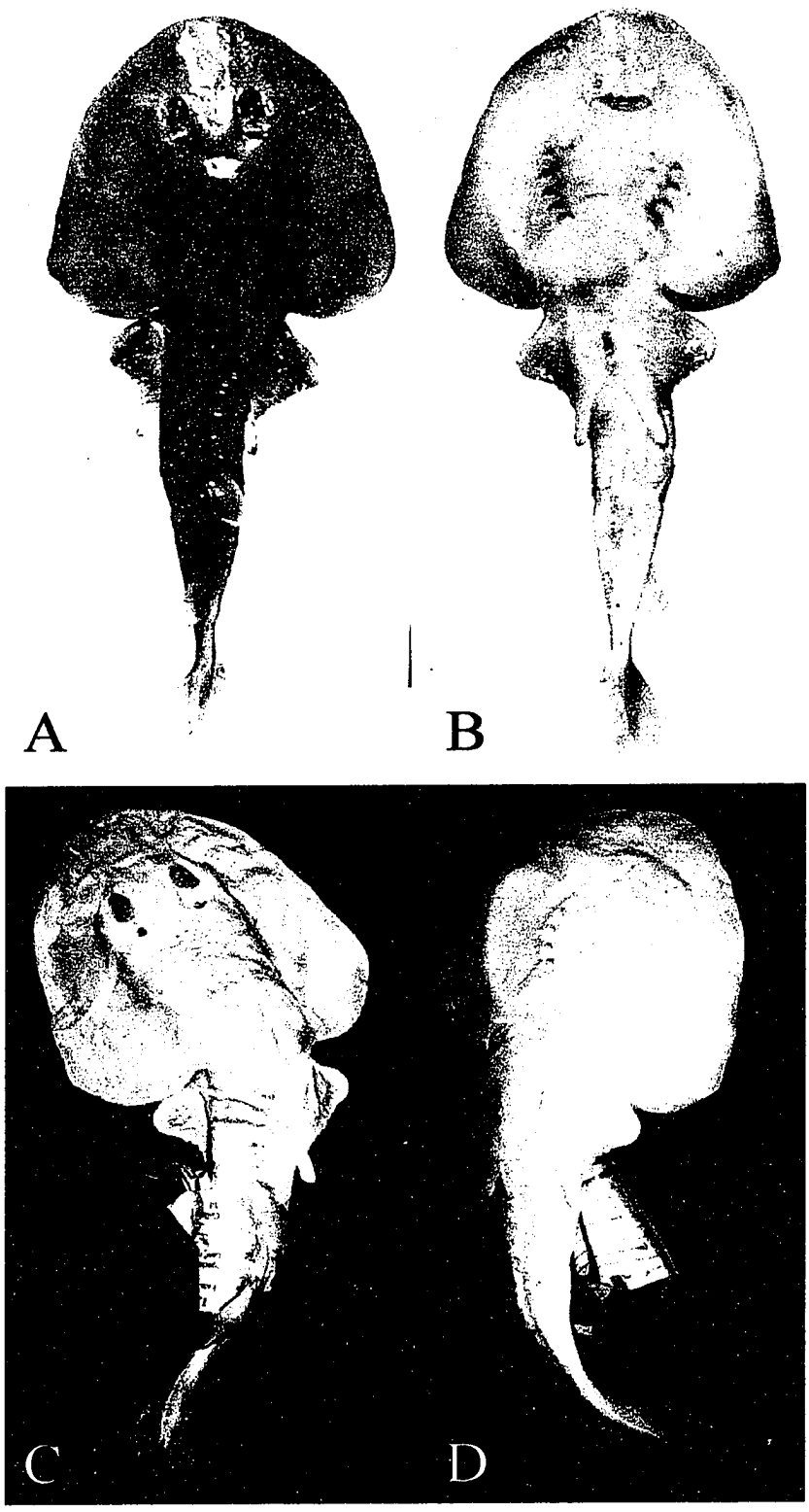
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Figure 78. Representative specimens of Narcine sp. nov. B. A and B) Freshly collected CSIRO H1035-03 (272 mm TL; N of Dampier Archipelago, Western Australia) in dorsal and ventral view; C and D) CSIRO H1035-03 in preservative, dorsal and ventral. A and B courtesy of CSIRO.

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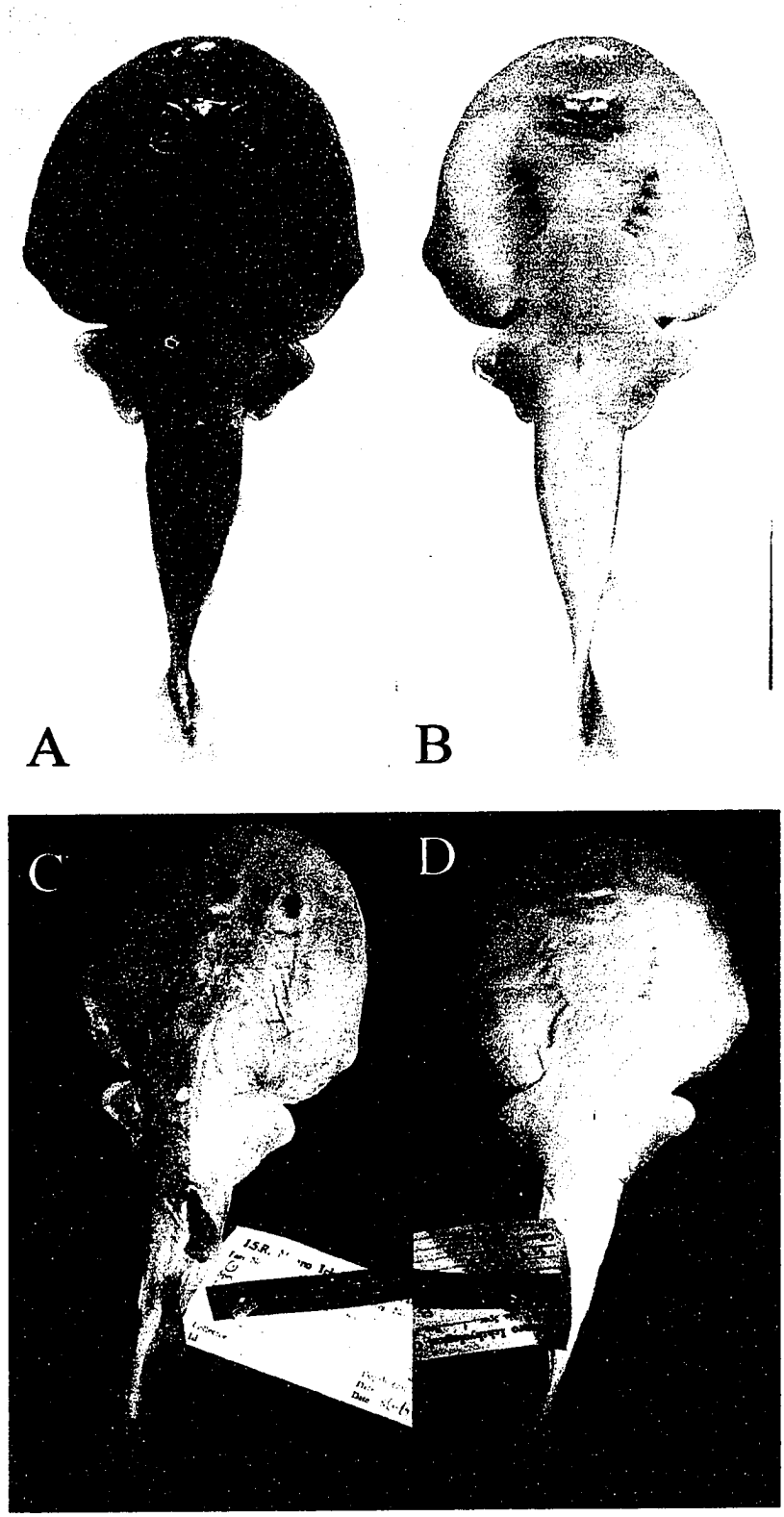


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Figure 79. Specimens of Narcine sp. nov. B in dorsal and ventral views. A and B) Freshly collected CSIRO H4070-07 (244 mm TL; NW of Port Hedland, Western Australia); C and D) CSIRO H4070-07 in preservative. A and B courtesy of CSIRO.

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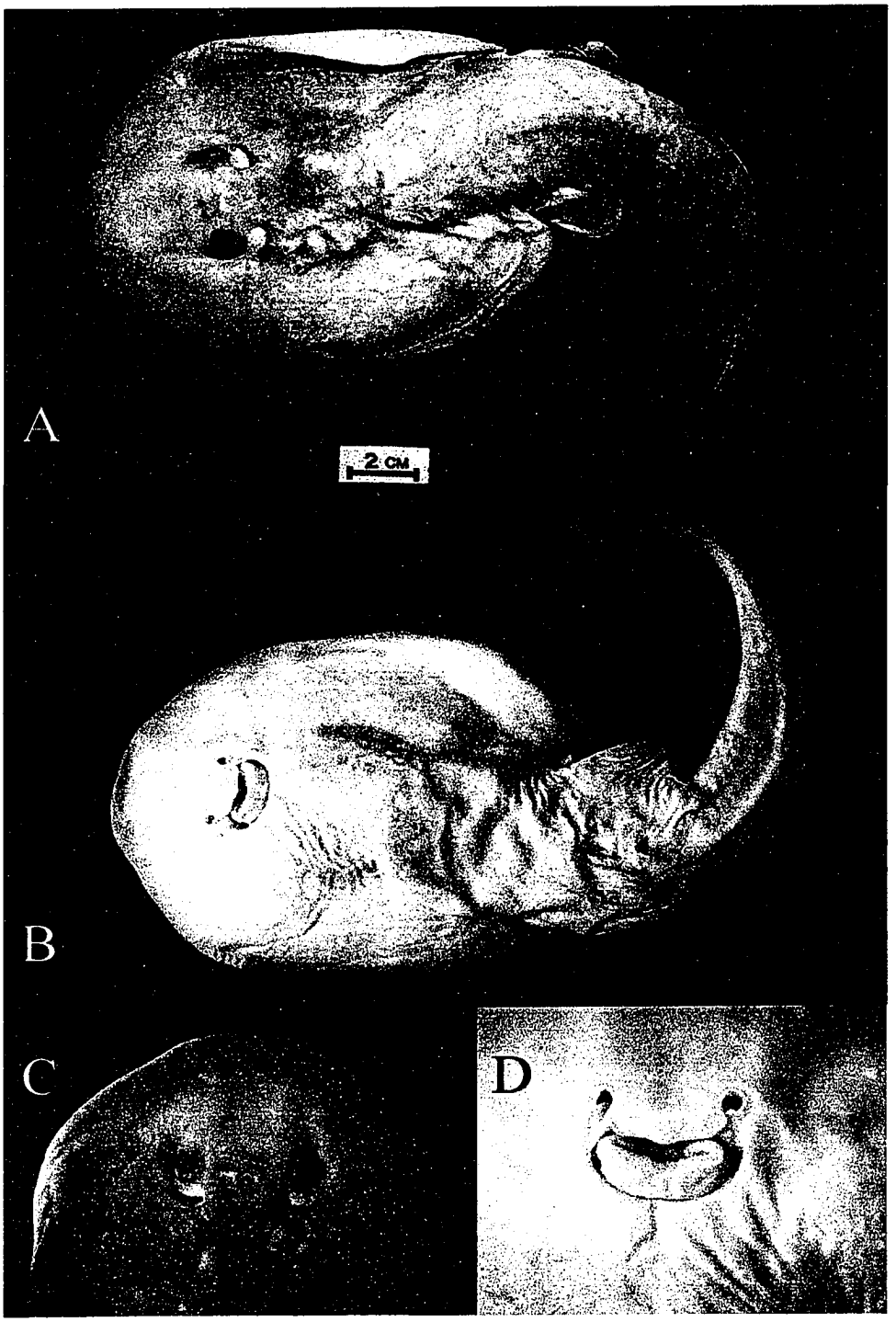


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Figure 80. Narcine sp. nov. B (MNHN 1996-1556, 302 mm TL; Arafura Sea). A) dorsal; B) ventral; C) dorsal snout area; D) nasoral region.

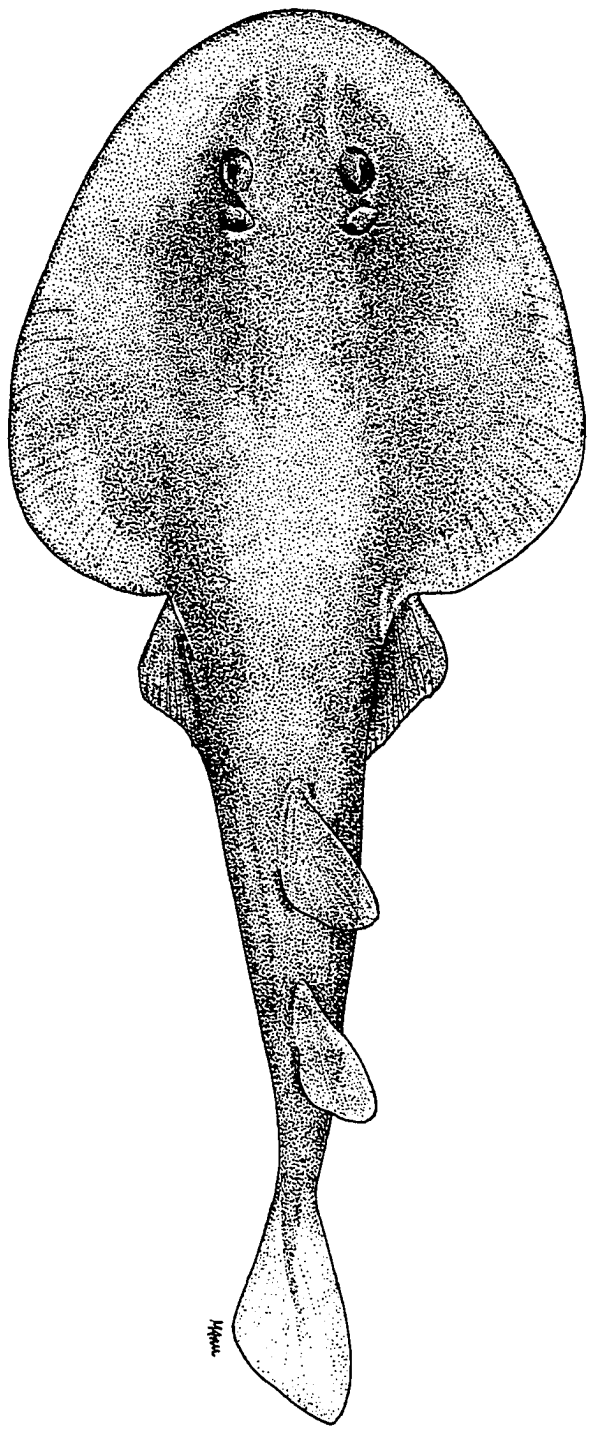
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Figure 81. Illustration of Narcine sp. nov. B from Carvalho et al. (in press). Reproduced with permission from FAO (Rome).

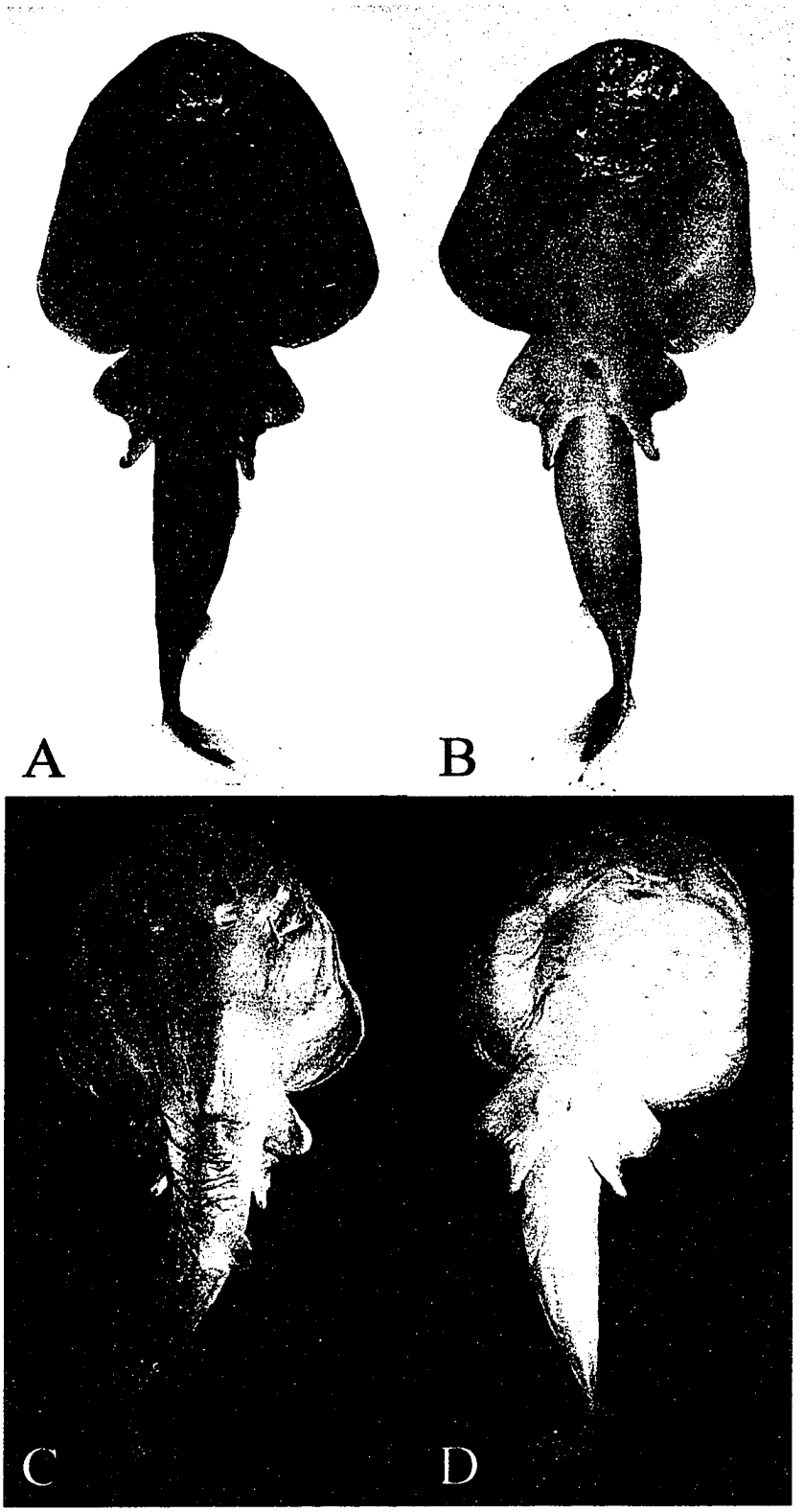
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Figure 82. Representative specimens of Narcine sp. nov. C in dorsal and ventral views. A and B) Freshly collected CSIRO H719-06 (260 mm TL; Queensland); C and D) CSIRO H719-06 in preservative. A and B courtesy of CSIRO.

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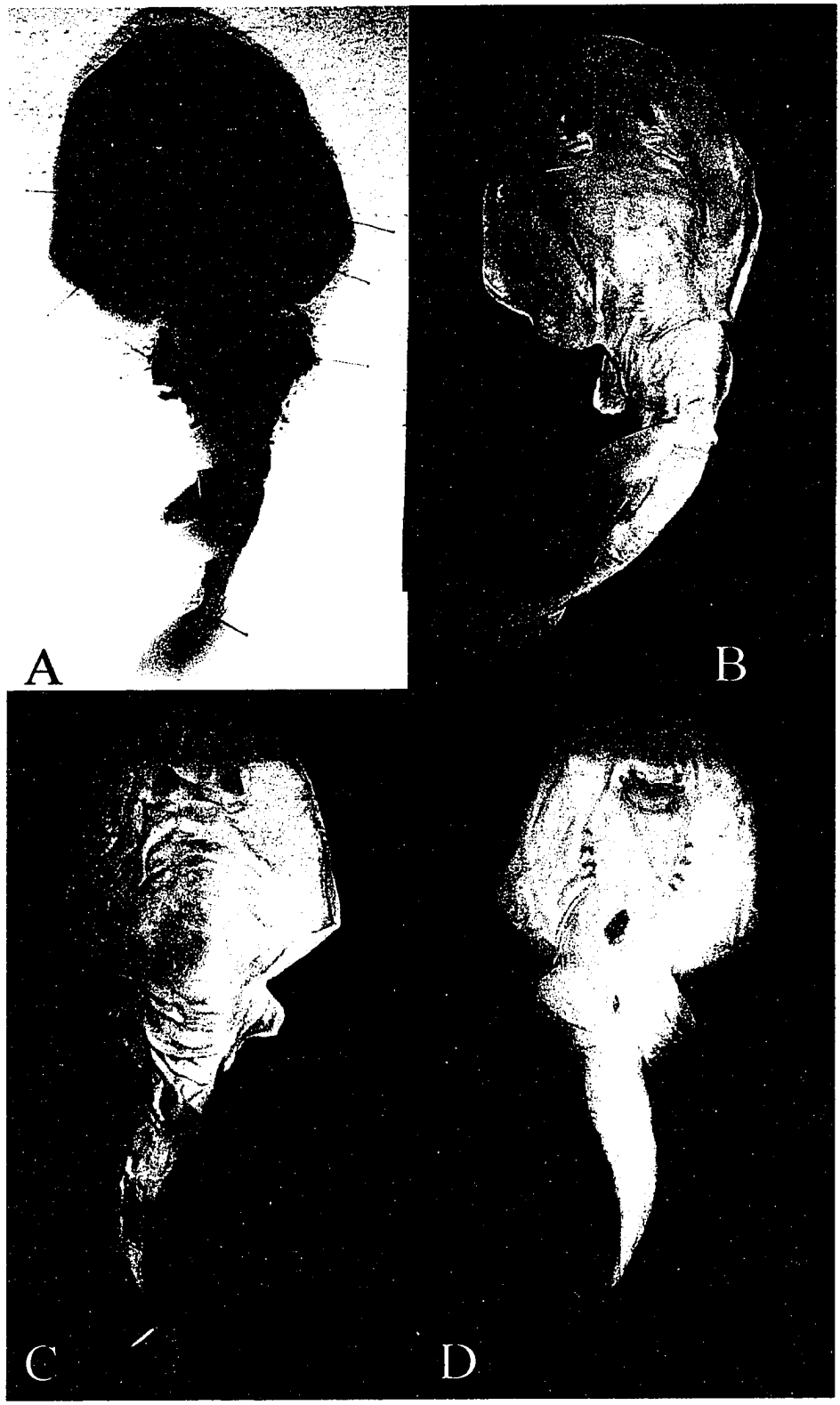


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Figure 83. Narcine sp. nov. C. A and B) Freshly collected and preserved CSIRO H719-01 (295 mm TL; Queensland) in dorsal view; C and D) Dorsal and ventral views of NTM 11750-010 (220 mm TL; Queensland). A courtesy of CSIRO.

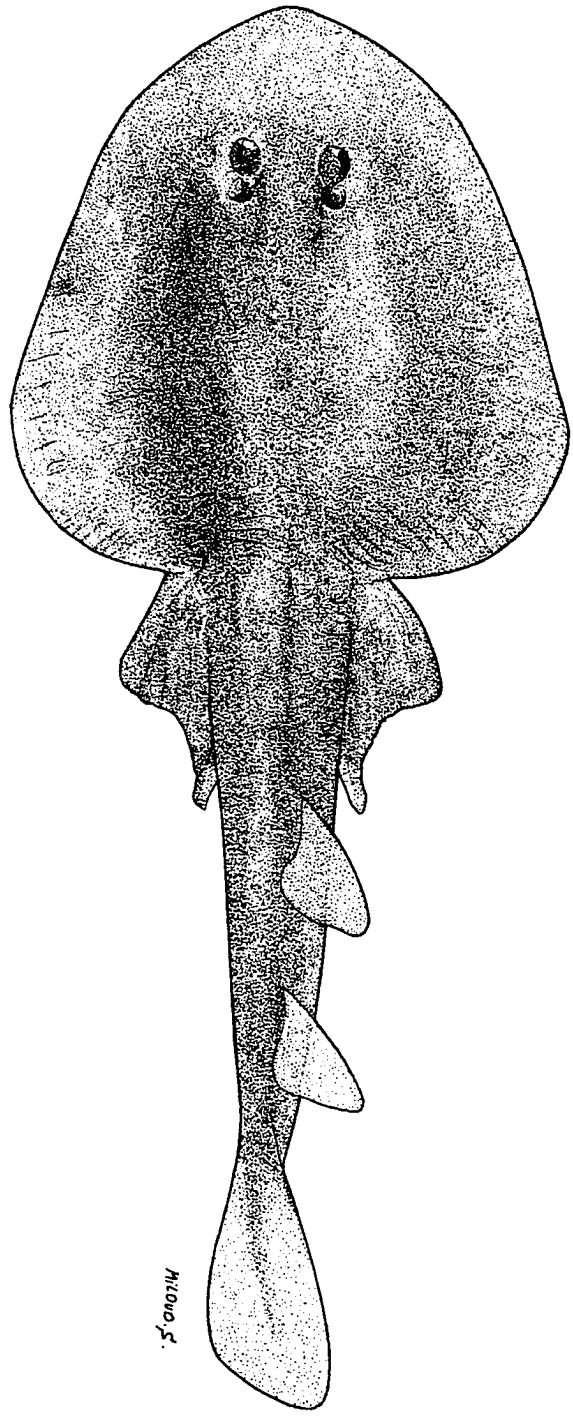
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Figure 84. Illustration of Narcine sp. nov. C, reproduced from Carvalho et al. (in press), with permnission from FAO (Rome).

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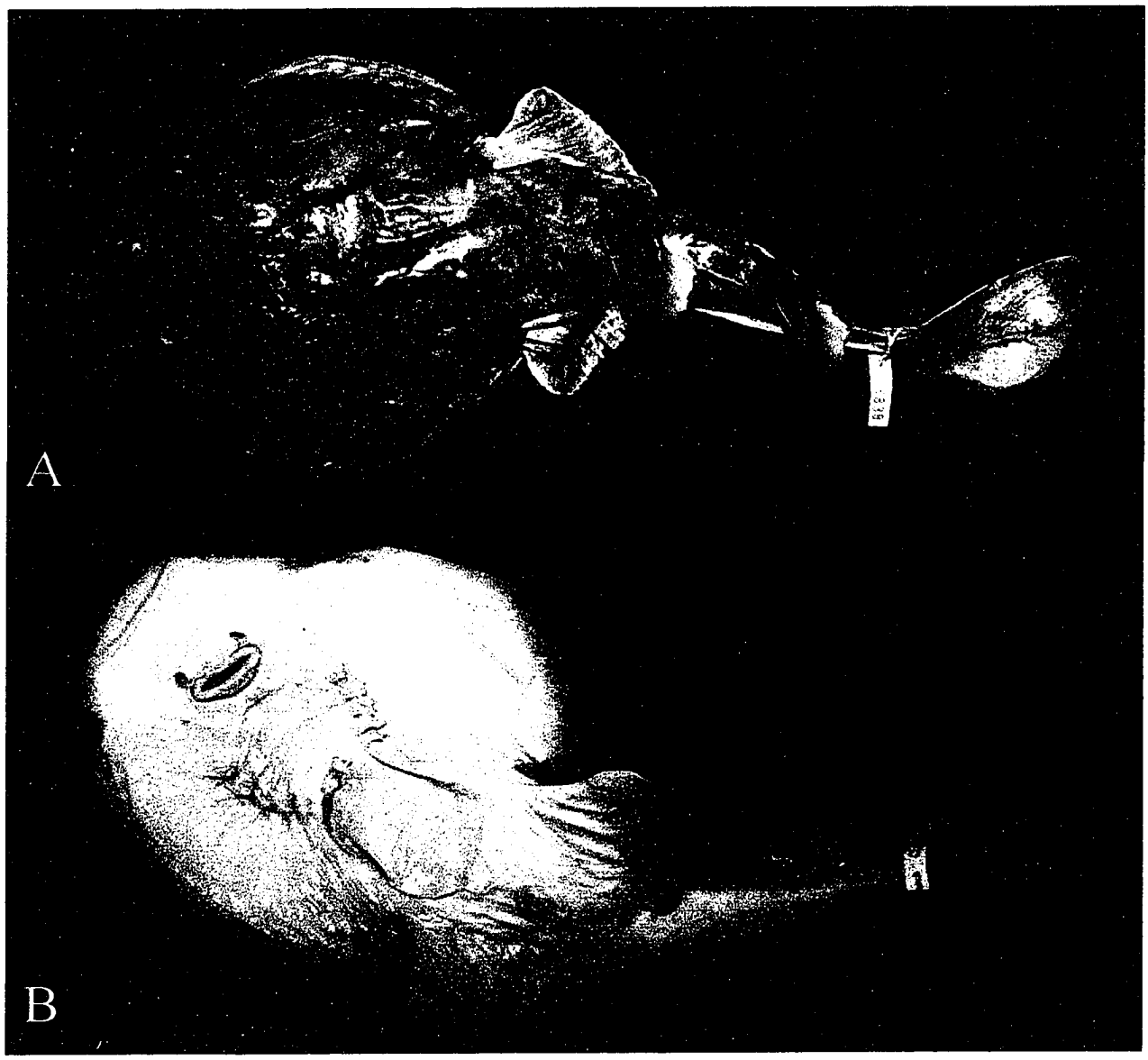


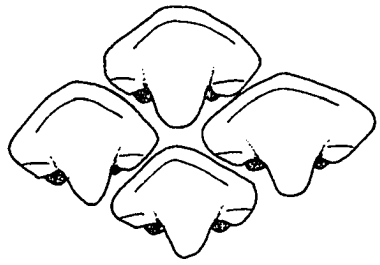
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Figure 85. Narcine sp. nov. D in dorsal (A) and ventral (B) views (CAS 66838, 325 mm TL; Gulf of Oman); C) teeth from tooth rows inside mouth of CAS 66838.

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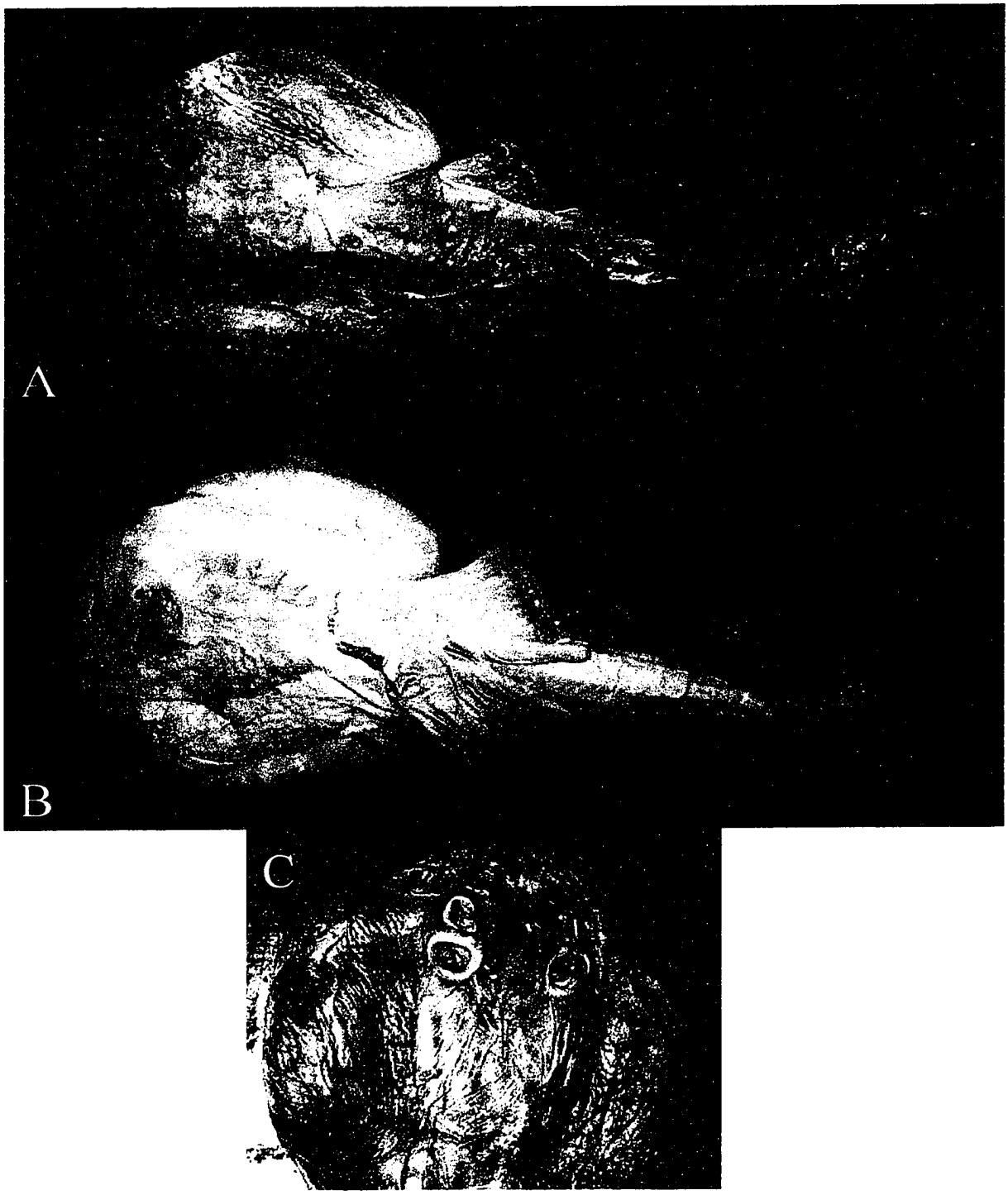


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Figure 86. Narcine sp. nov. D in dorsal (A) and ventral (B) views (CAS 58368, 240 mm TL; Gulf of Oman); C) dorsal disc of BMNH 1939.5.24.15 (291 mm TL; Gulf of Aden).

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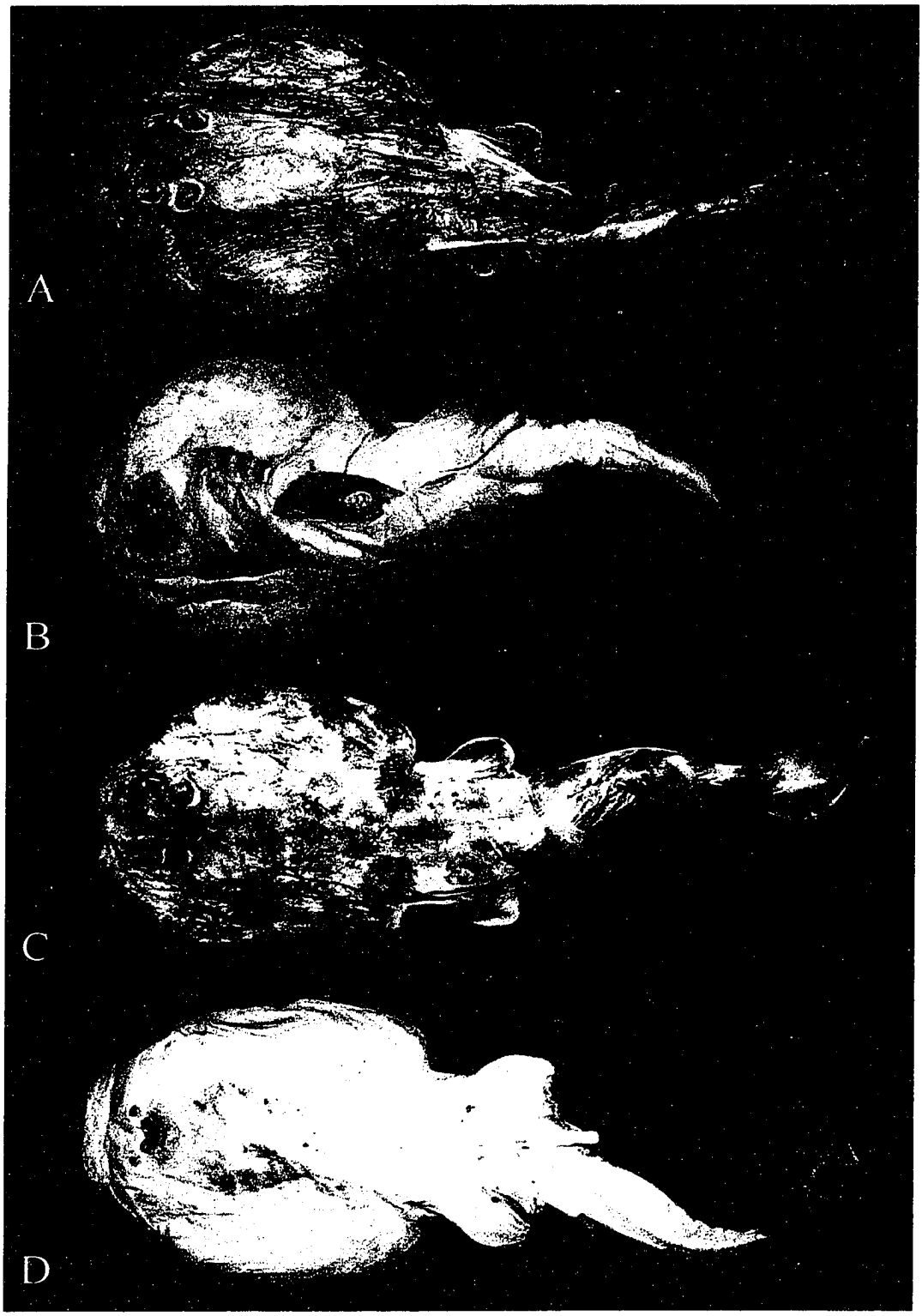


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Figure 87. Narcine sp. nov. D. A and B) Dorsal and ventral views of BMNH 1939.5.24.15 (291 mm TL; Gulf of Aden); C and D) Dorsal and ventral views of TCWC 8863.01 (350 mm TL; Gulf of Aden).

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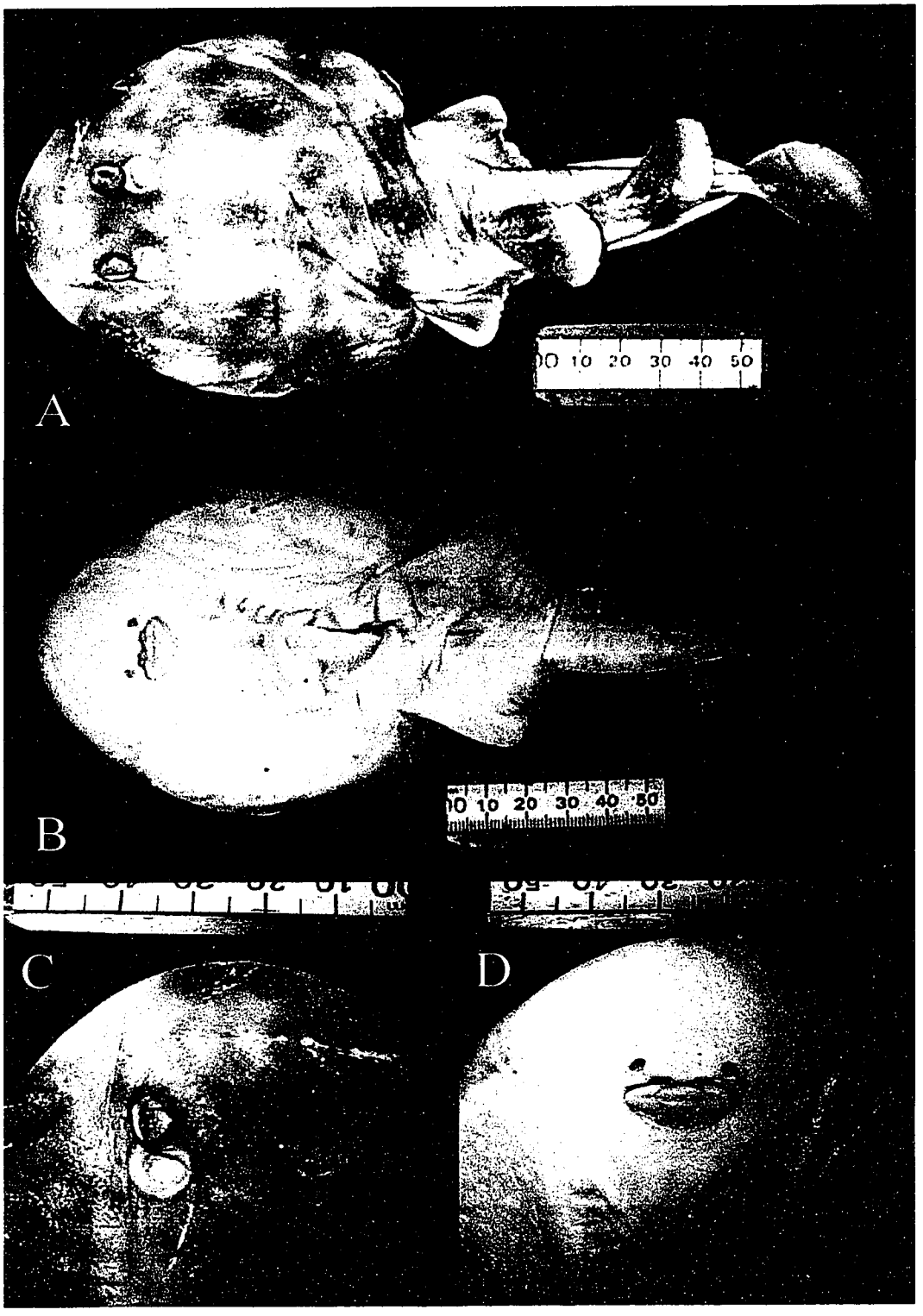


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Figure 88. Freshly collected specimen of Narcine sp. nov. E (Mozambique channel). A and B) Dorsal and ventral views; C and D) dorsal and ventral snout regions. Courtesy of L. J. V. Compagno.

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Figure 89. Narcine sp. nov. E. A and B) MNHN 1996-1554 (265 mm TL; Madagascar); C and D) MNHN 1996-1555 (356 mm TL; Madagascar).

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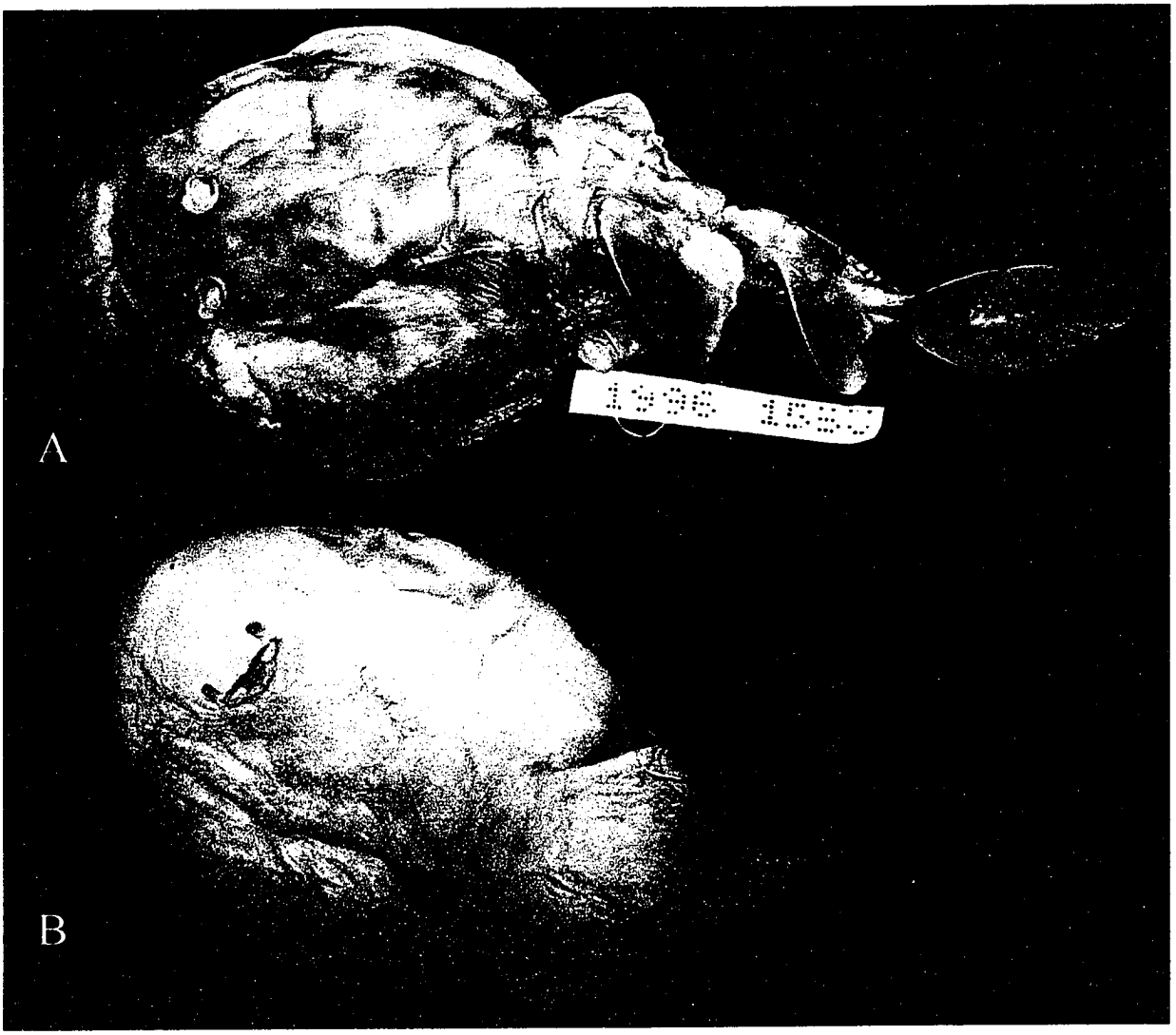


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Figure 90. Narcine sp. nov. E. A and B) MNHN 1996-1553 (257 mm TL; Madagascar) in dorsal and ventral views

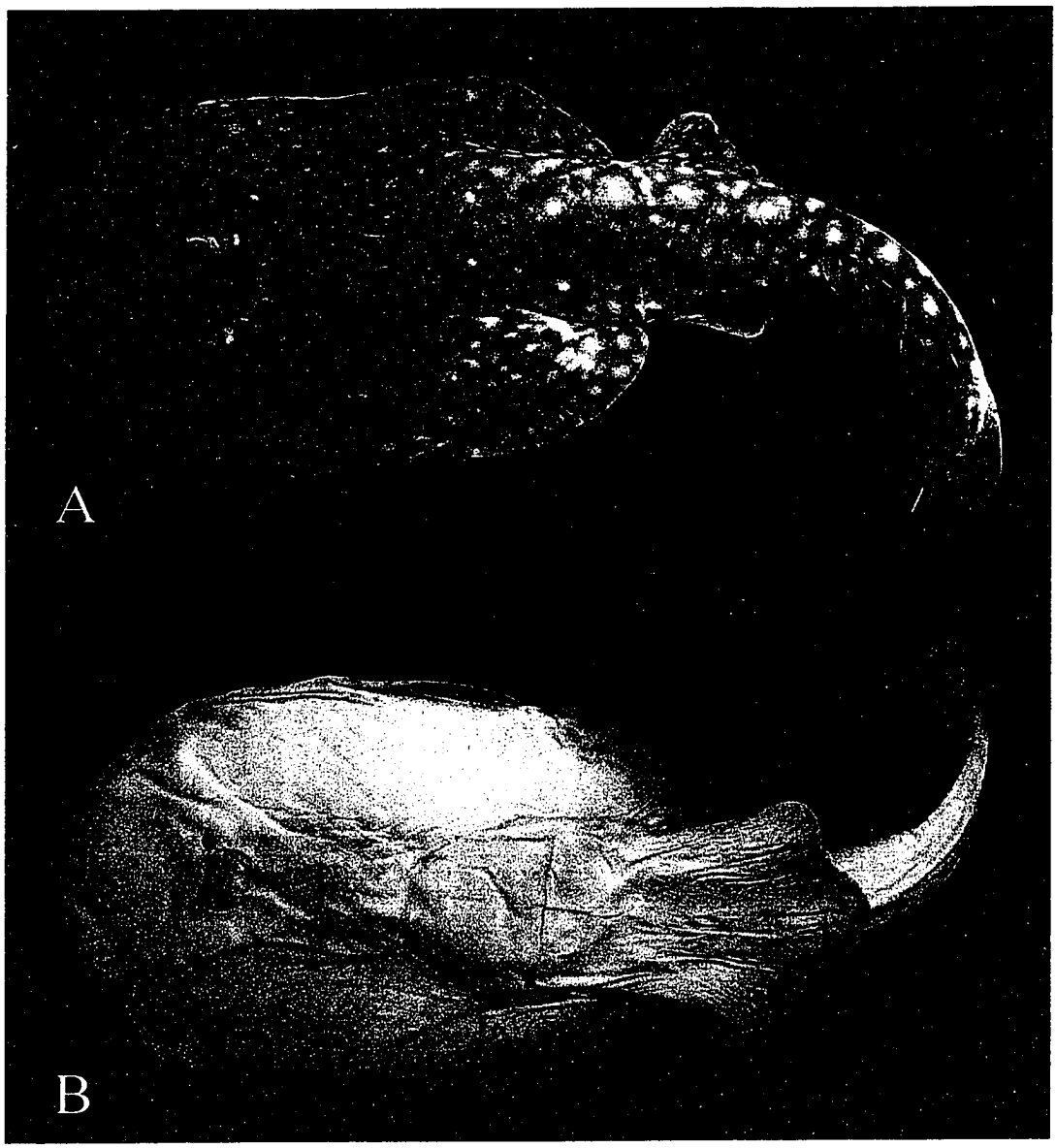
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Figure 91. Narcine sp. nov. F (USNM 222200, 277 mm TL; S of Buenaventura, Colombia) in dorsal (A) and ventral (B) views.

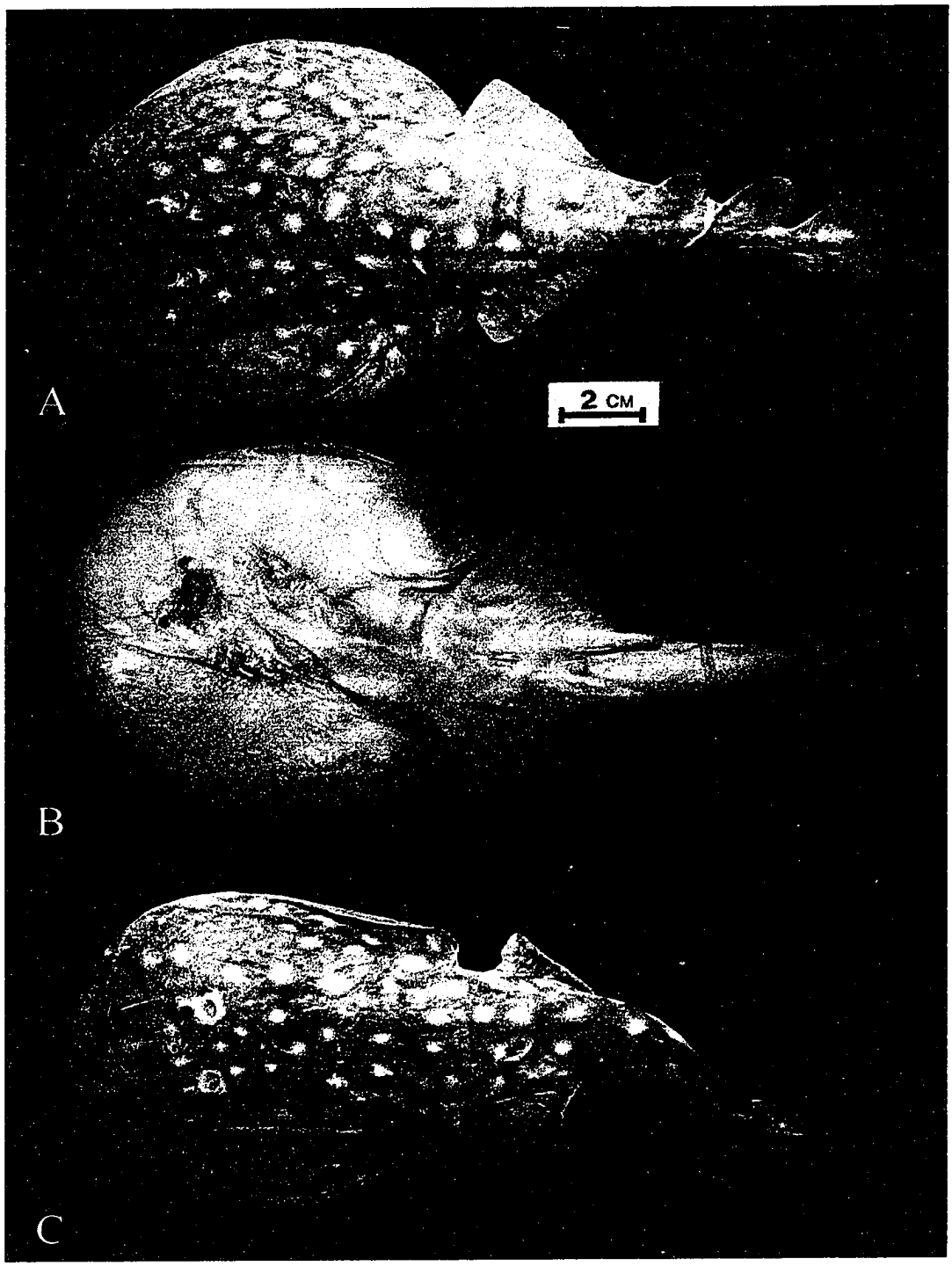
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Figure 92. Narcine sp. nov. F. A and B) Dorsal and ventral views of USNM 235919 (206 mm TL; Cabo Manglares, Colombia); C) USNM 222198 (174 mm TL; S of Buenaventura, Colombia).

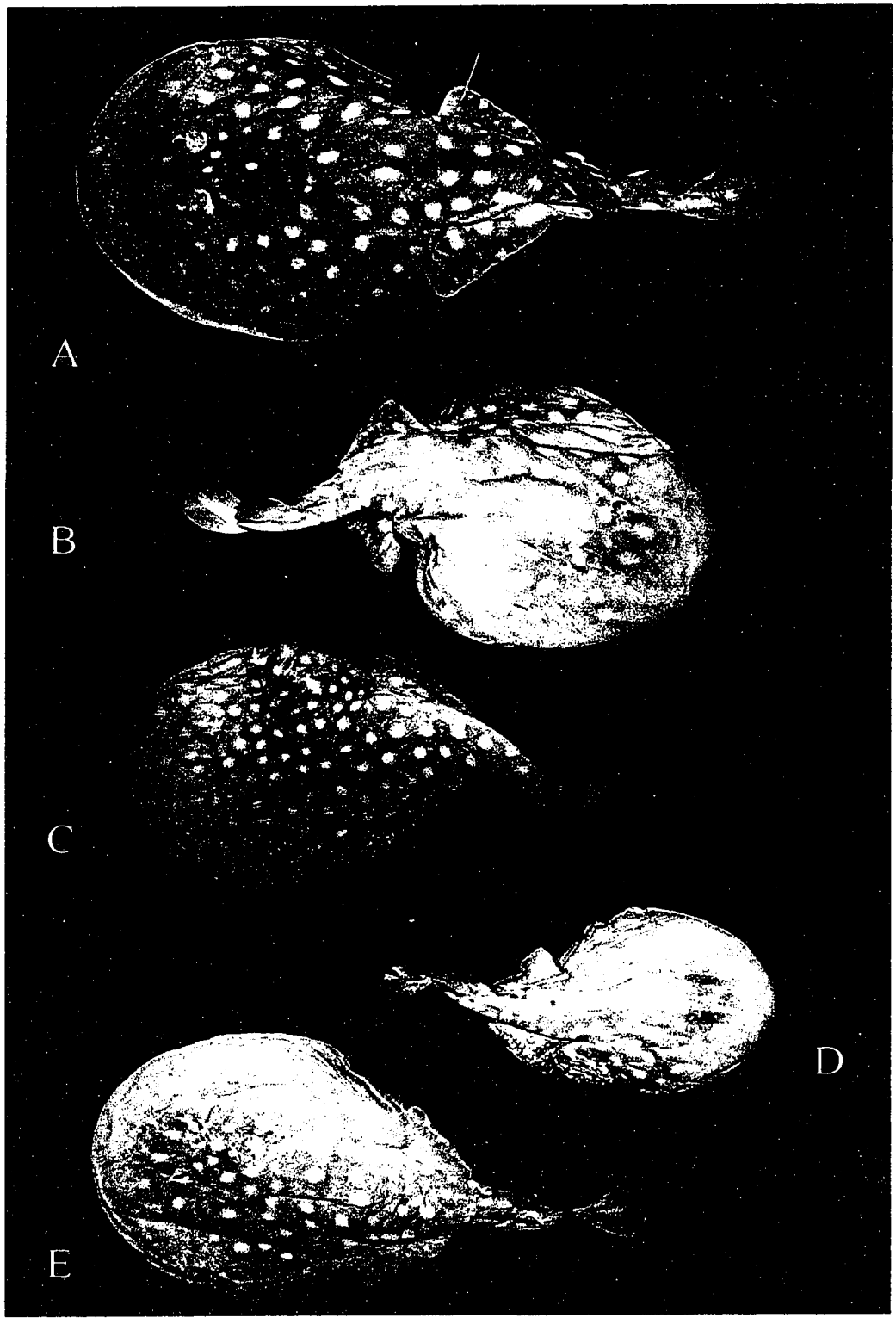
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Figure 93. Narcine sp. nov. F. A) USNM 222198 (174 mm TL; S of Buenaventura, Colombia); B) USNM 222199 (130 mm TL; Cabo Manglares, Colombia); C) USNM 222199 (146 mm TL); D) USNM 222199 (86 mm TL); E) USNM 222199 (127 mm TL).

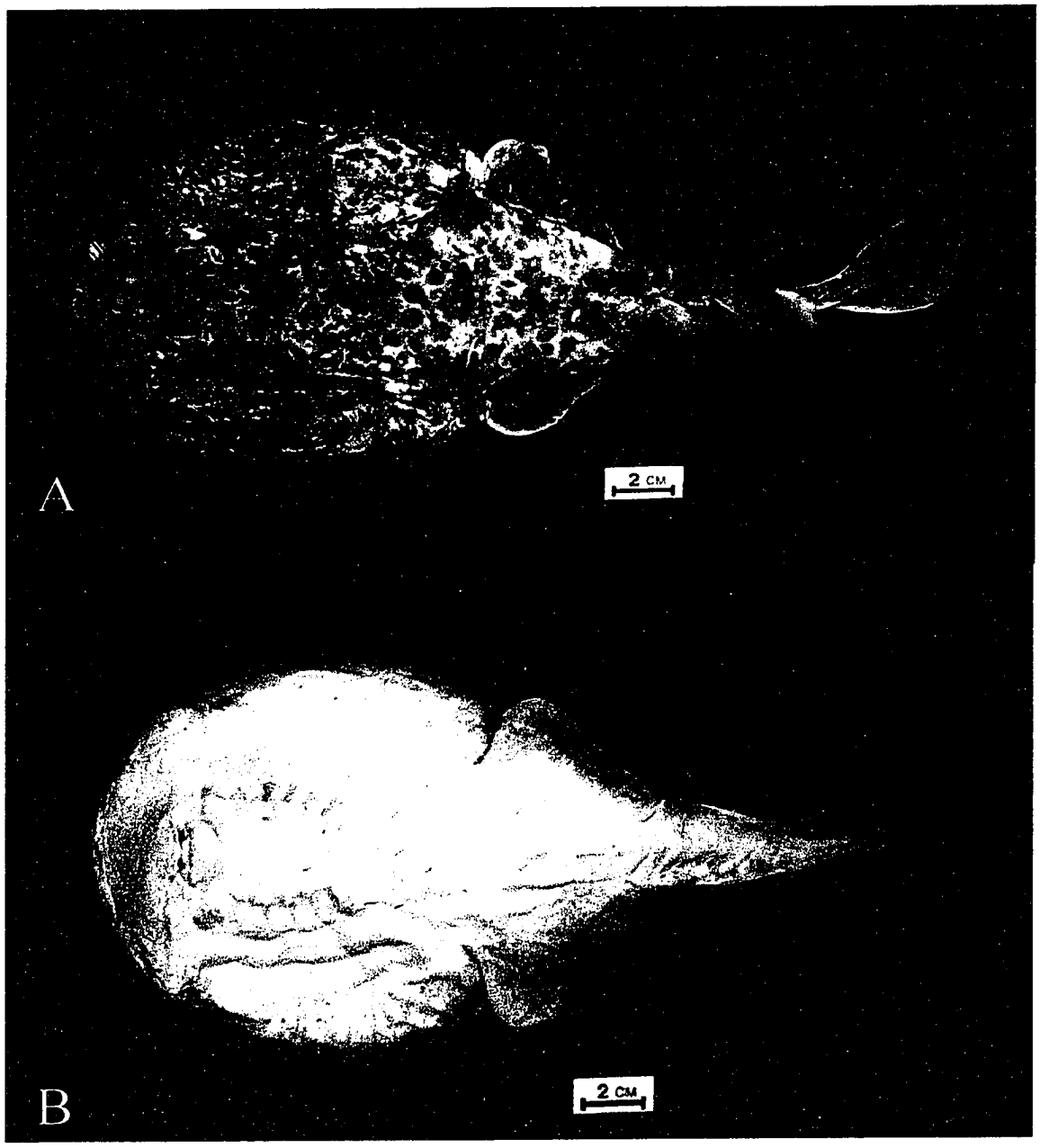
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Figure 94. Narcine sp. nov. G in dorsal (A) and ventral (B) views (BMNH 1984.4.11.2, 306 mm total length; Indonesia).

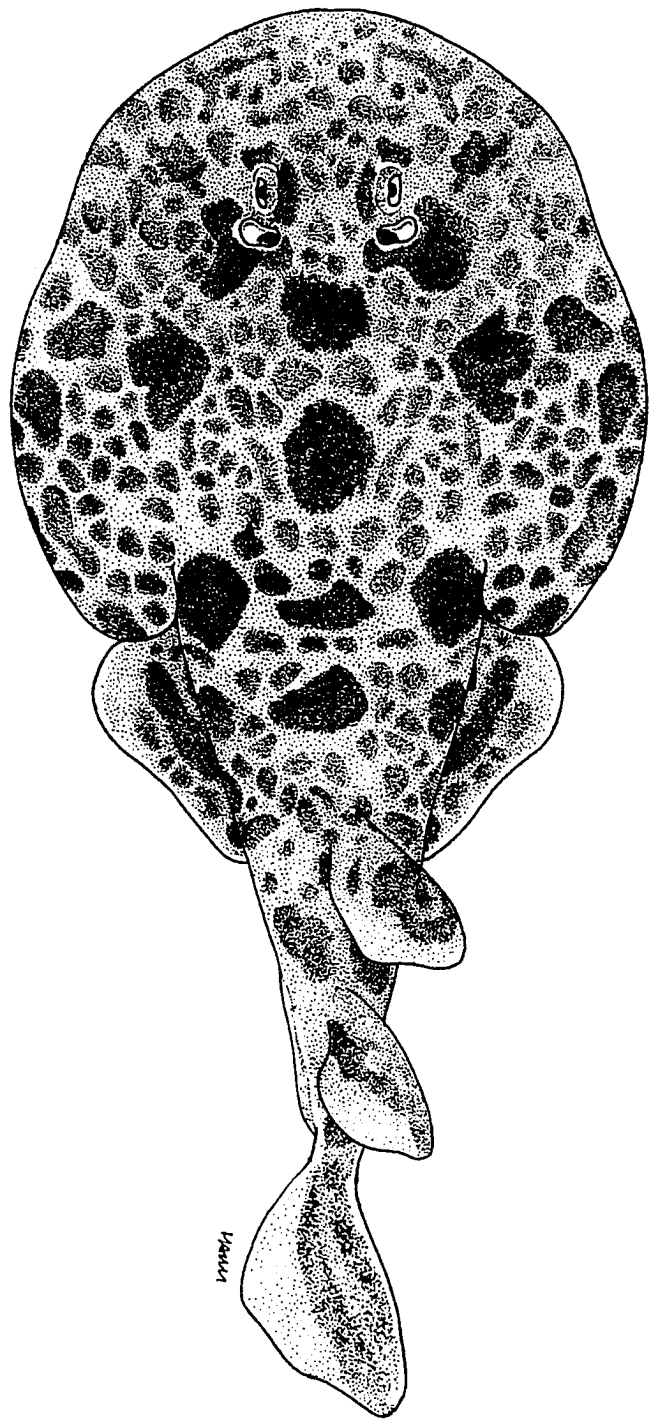
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Figure 95. Illustration of Narcine sp. nov. G. Reproduced from Carvalho et al. (in press) with permission of FAO (Rome).

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Figure 96. Narcine sp. nov. H. A and B) Dorsal and ventral views of USNM 263402 (233 mm TL; Visayan Sea, Philippines); C and D) USNM 263400 (257 mm TL; Philippines).

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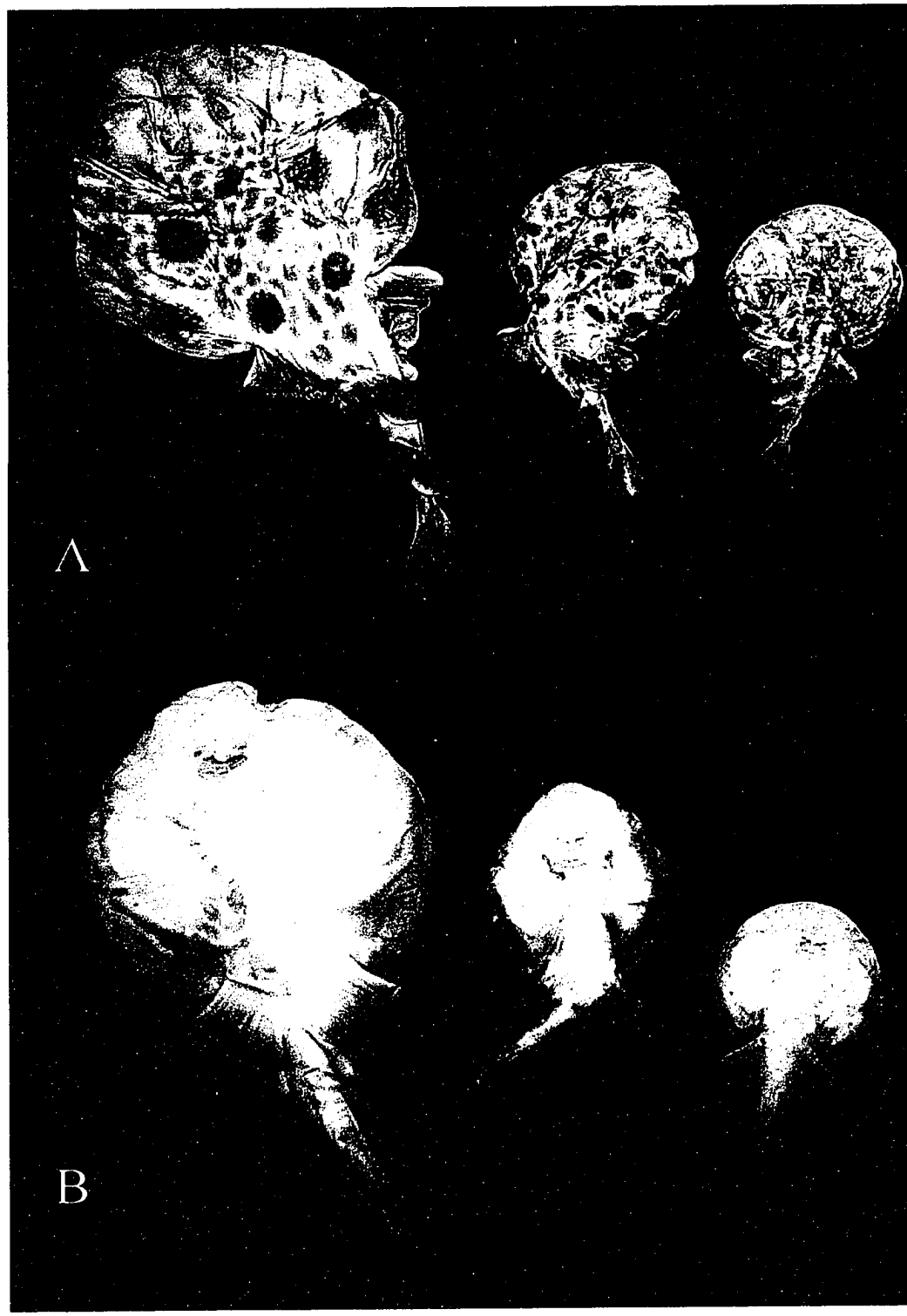


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Figure 97. Narcine sp. nov. H. A) Dorsal view, from left to right, of USNM 263401 (233 mm TL; Visayan Sea, Philippines), USNM 263398 (141 mm TL; Philippines) and USNM 263399 (103 mm TL; Philippines); B) Ventral view of same.

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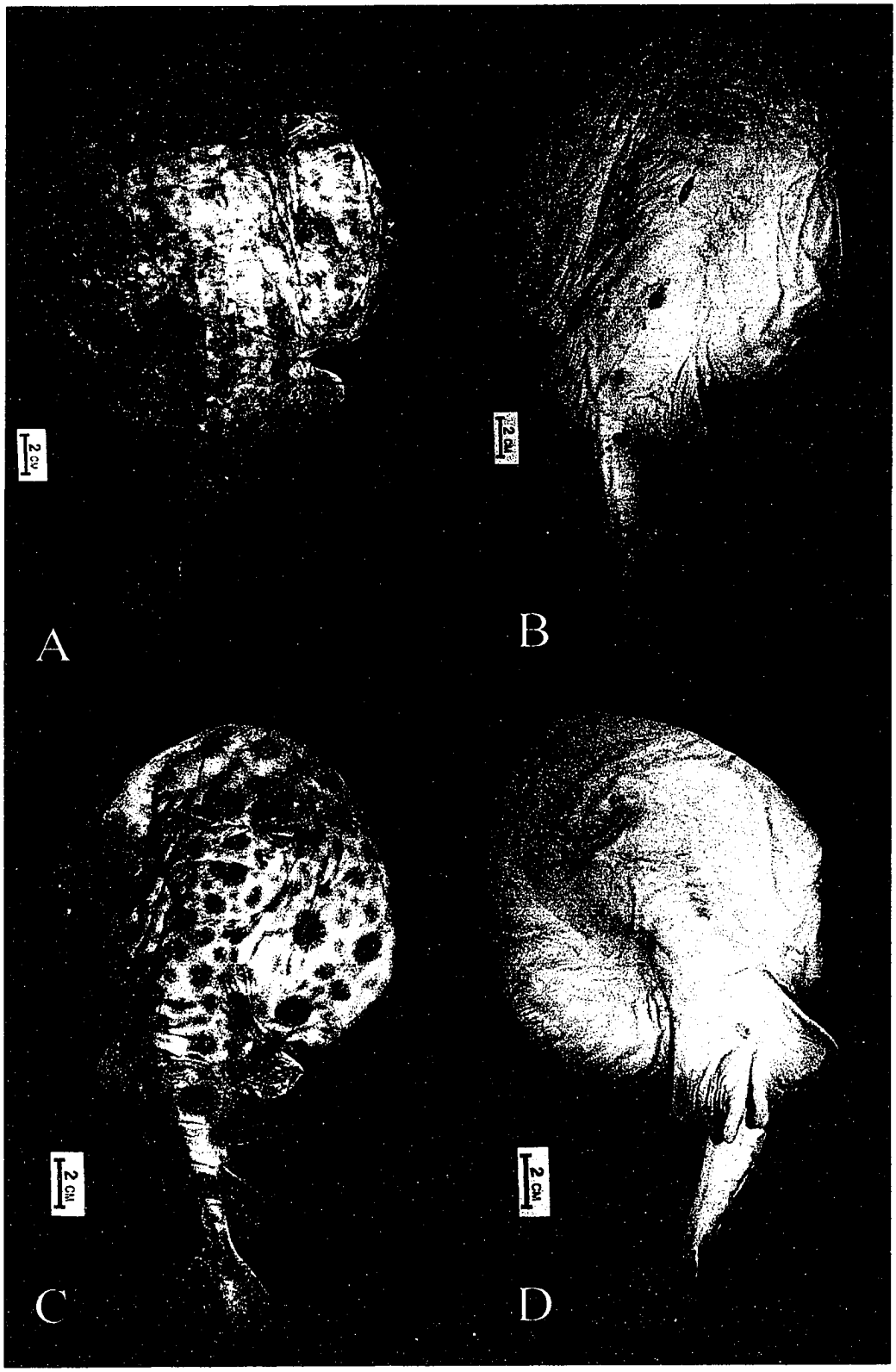


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Figure 98. Narcine sp. nov. H. A and B) Dorsal and ventral views of CAS 58358 (336 mm TL; Myanmar); C and D) Dorsal and ventral views of CAS 58358 (275 mm TL; Myanmar).

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Figure 99. Illustration of Narcine sp. nov. H. Reproduced from Carvalho et al. (in press), with permission from FAO (Rome).

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Figure 100. Narcine sp. nov. I (BPBM 21418, 312 mm TL; Gulf of Oman). Courtesy of J. Randall.

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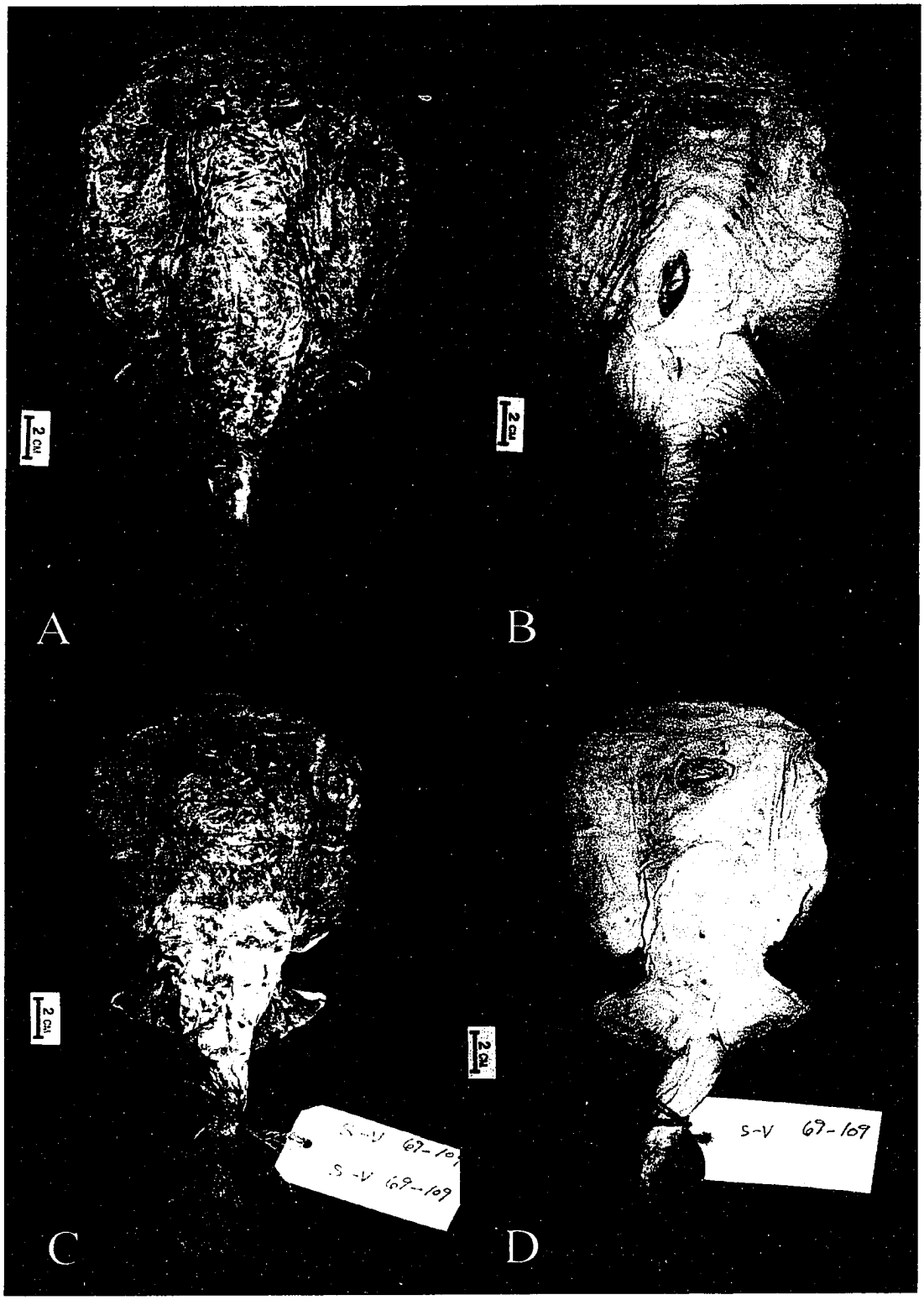


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Figure 101. Narcine sp. nov. I. A and B) Dorsal and ventral views of BPBM 21418, 312 mm TL; Gulf of Oman); C and D) CAS 58398 (298 mm TL; Sri Lanka).

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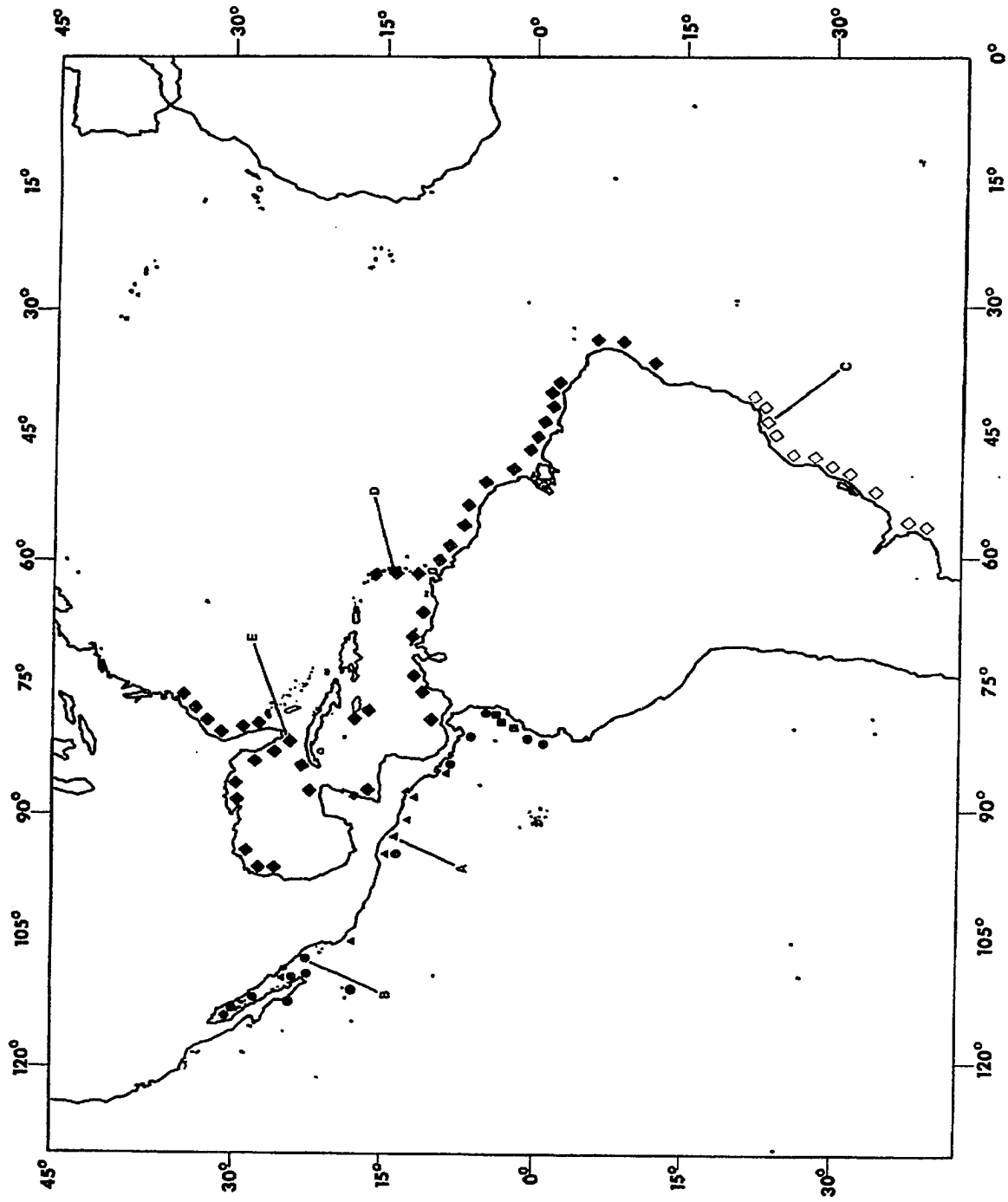


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Figure 102. Map depicting distribution of eastern Pacific and western Atlantic species of Narcine. Eastern Pacific species: N. entemedor (●); N. vermiculatus (▲); Narcine sp. nov. F (■). Western Atlantic: N. brasiliensis (◇); N. bancroftii (◆). A: type-locality of Narcine vermiculatus Breder, 1928 (off Chiapas, Mexico). B: type-locality of Narcine entemedor Jordan and Starks, 1895 (Mazatlán, Mexico). C: type-locality of Torpedo brasiliensis von Olfers, 1831 and Narcine brachypleura Miranda Ribeiro, 1923 (Rio de Janeiro). D: type-locality of Narcine punctata Garman, 1881 (St. Vincent). E: type-locality of Narcine corallina Garman, 1881 and Narcine umbrosa Jordan, 1884 (Key West, Florida). Symbols may indicate more than one lot.

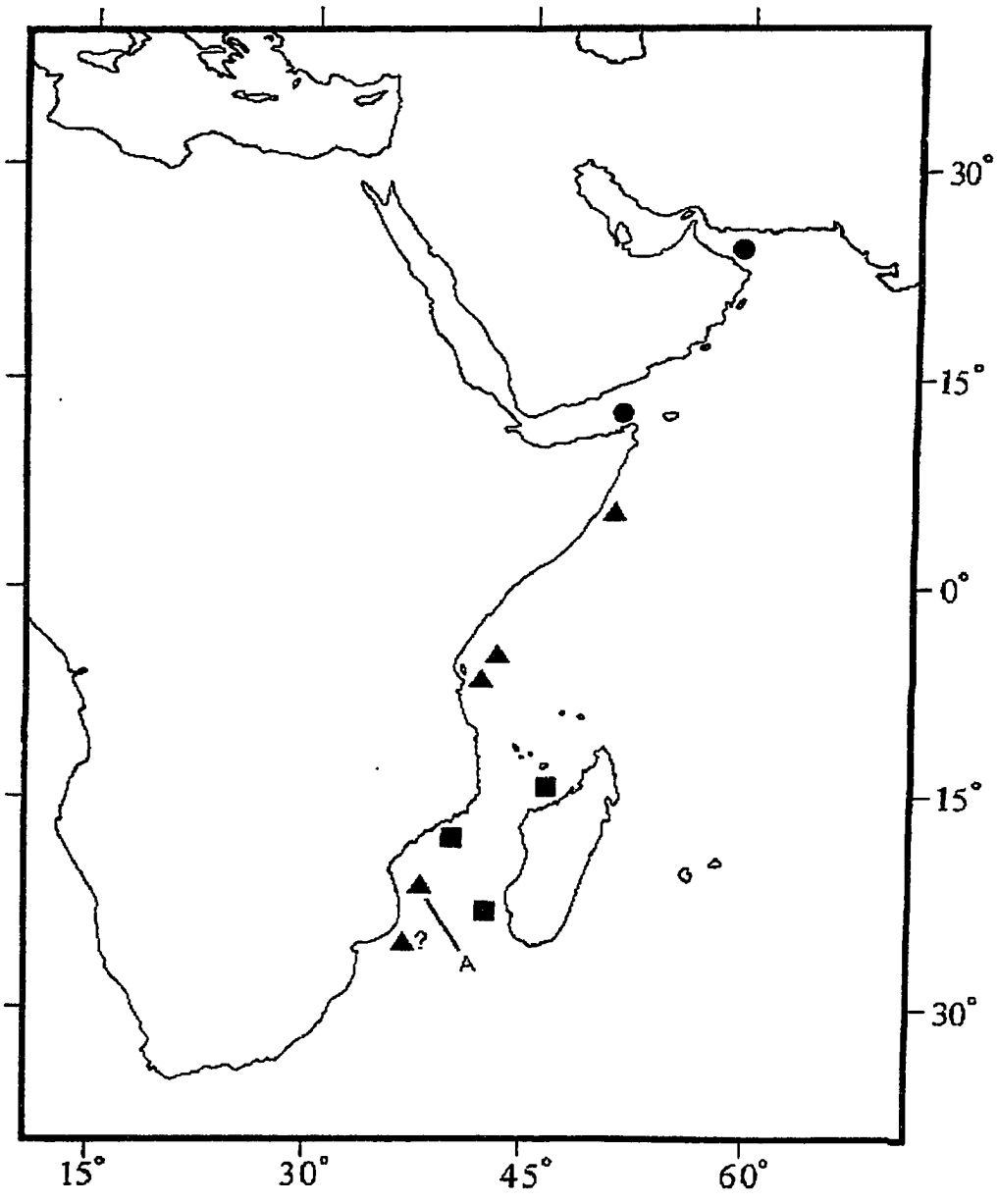
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Figure 103. Map depicting distribution of western Indian Ocean species of Narcine. N. rierai (▲); Narcine sp. nov. D (●); Narcine sp. nov. E (■). A: type-locality of Heteronarce rierai Lloris and Rucabado, 1991 (Mozambique). Symbols may indicate more than one lot.

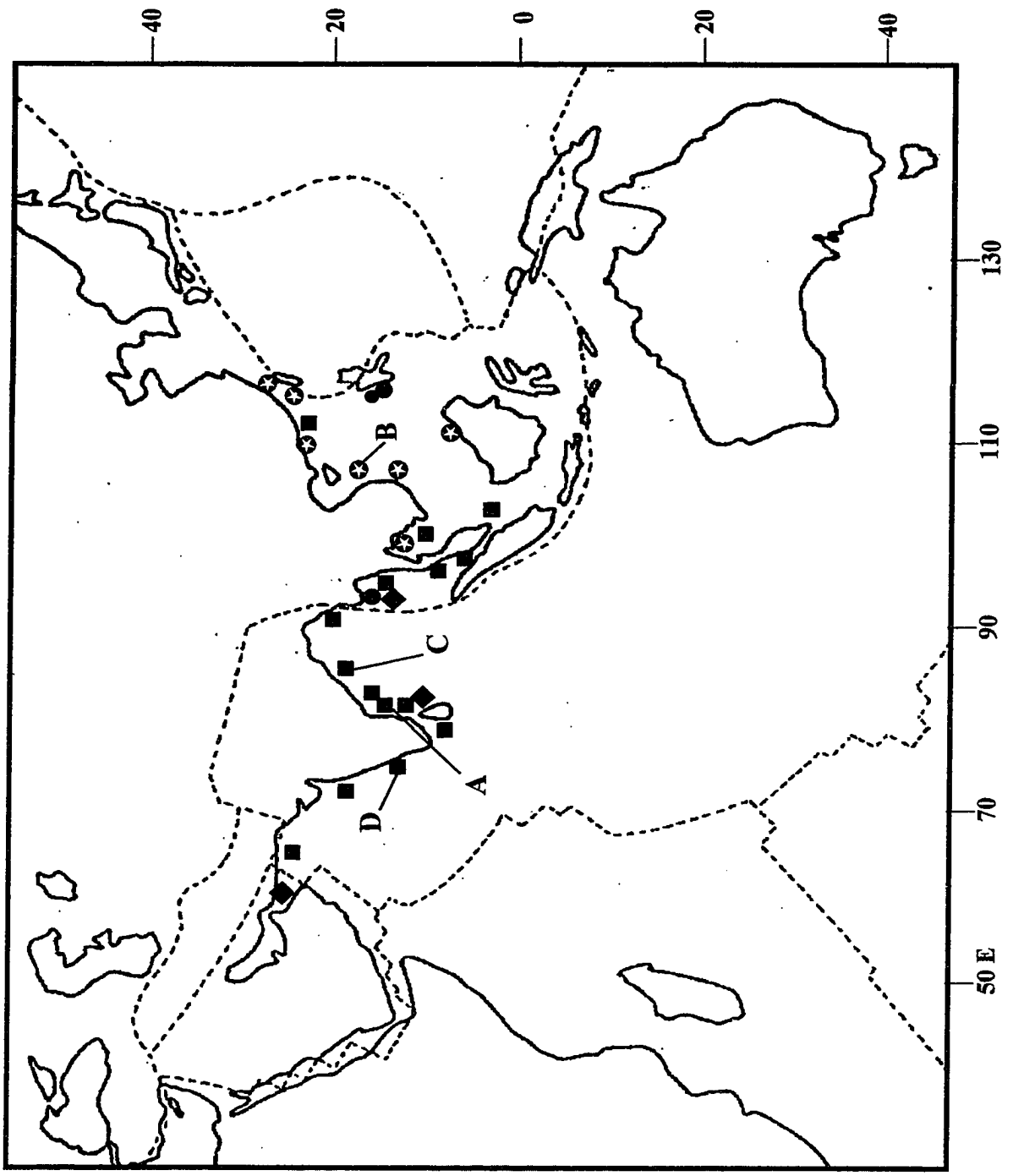
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Figure 104. Map indicating distribution of some Indo-Pacific species of Narcine. N. brevilabiata (✪); N. timlei (■); Narcine sp. nov. H (●); Narcine sp. nov. I (◆). A: type-locality of Raja timlei Bloch and Schneider, 1801 (Tranquebar, India). B: type-locality of Narcine brevilabiata Bessednov, 1966 (southern Gulf of Tonkin). C: type-locality of Narcine brunnea Annandale, 1909 (Orissa and Arrakan coasts, India). D: type-locality of Narcine microphthalma Valenciennes, 1852 (Malabar coast, India). Symbols may indicate more than one lot.

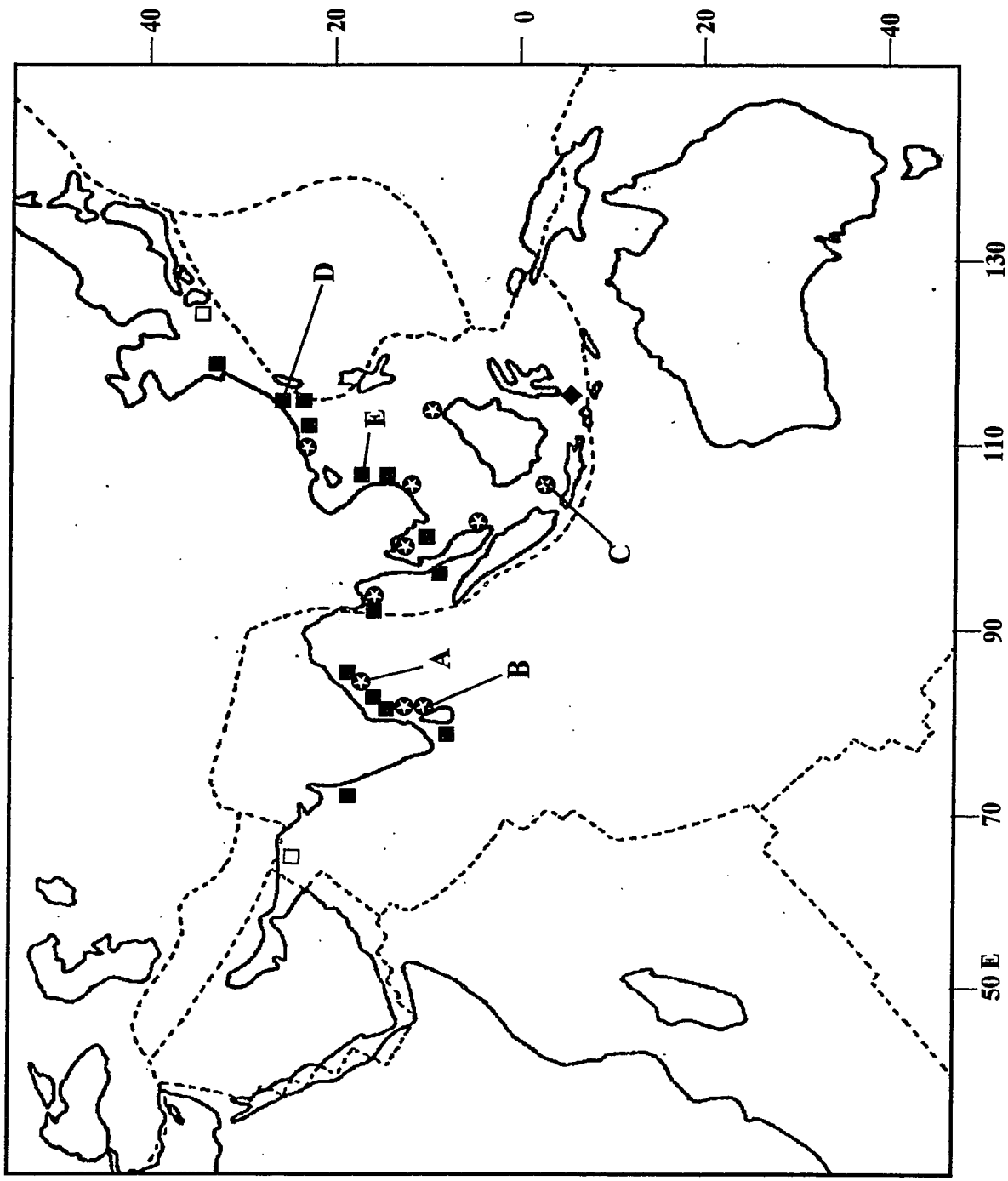
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Figure 105. Map indicating distribution of some Indo-Pacific species of Narcine. N. lingula (■); N. maculata (✪); Narcine sp. nov. G (◆). A: type-locality of Raja maculata Shaw, 1804 and Raja bicolor Shaw, 1804. B: type-locality of Narcine firma Garman, 1913. C: type-locality of Narcine maculata Duméril, 1852 (Java, Indonesia). D: type-locality of Narcine lingula Richardson, 1846 (Canton, China). E: type-locality of Narcine prodorsalis Bessednov, 1966 (southern Gulf of Tonkin). Open squares are literature records of N. lingula. Symbols may indicate more than one lot.

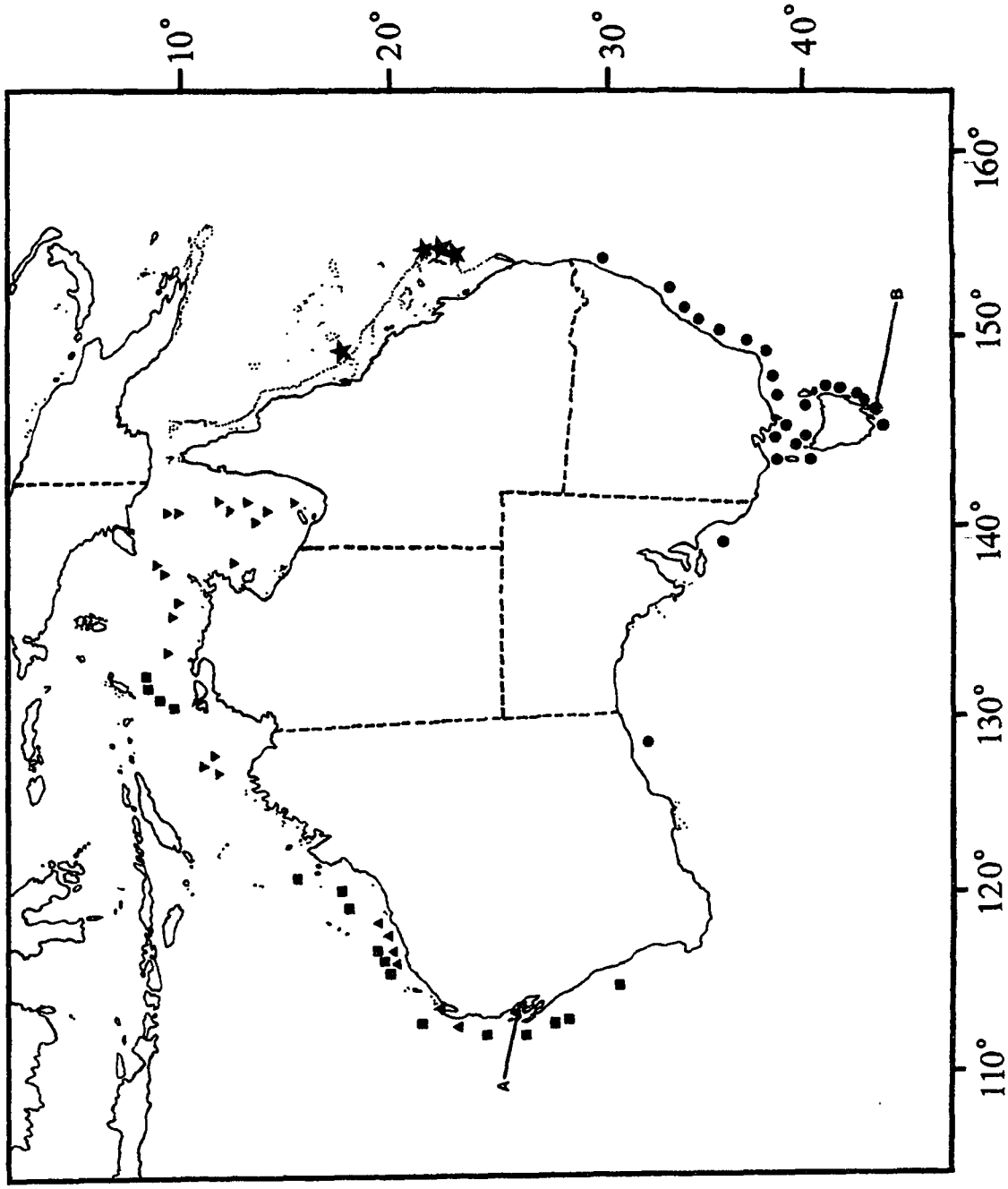
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Figure 106. Map indicating distribution of Australian species of Narcine. N. tasmaniensis (●); N. westraliensis (▲); Narcine sp. nov. A (▼); Narcine sp. nov. B (■); Narcine sp. nov. C (★). A: type-locality for Narcine westraliensis McKay, 1966. B: type-locality for Narcine tasmaniensis Richardson, 1841. Symbols may indicate more than one lot.

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Figure 107. Holotype of Narcine molini Jaekel, 1894 from Eocene of Monte Bolca, Italy (UP 26276, 915 mm TL) anterior to top (holotype in part and counter-part, but only one part shown).

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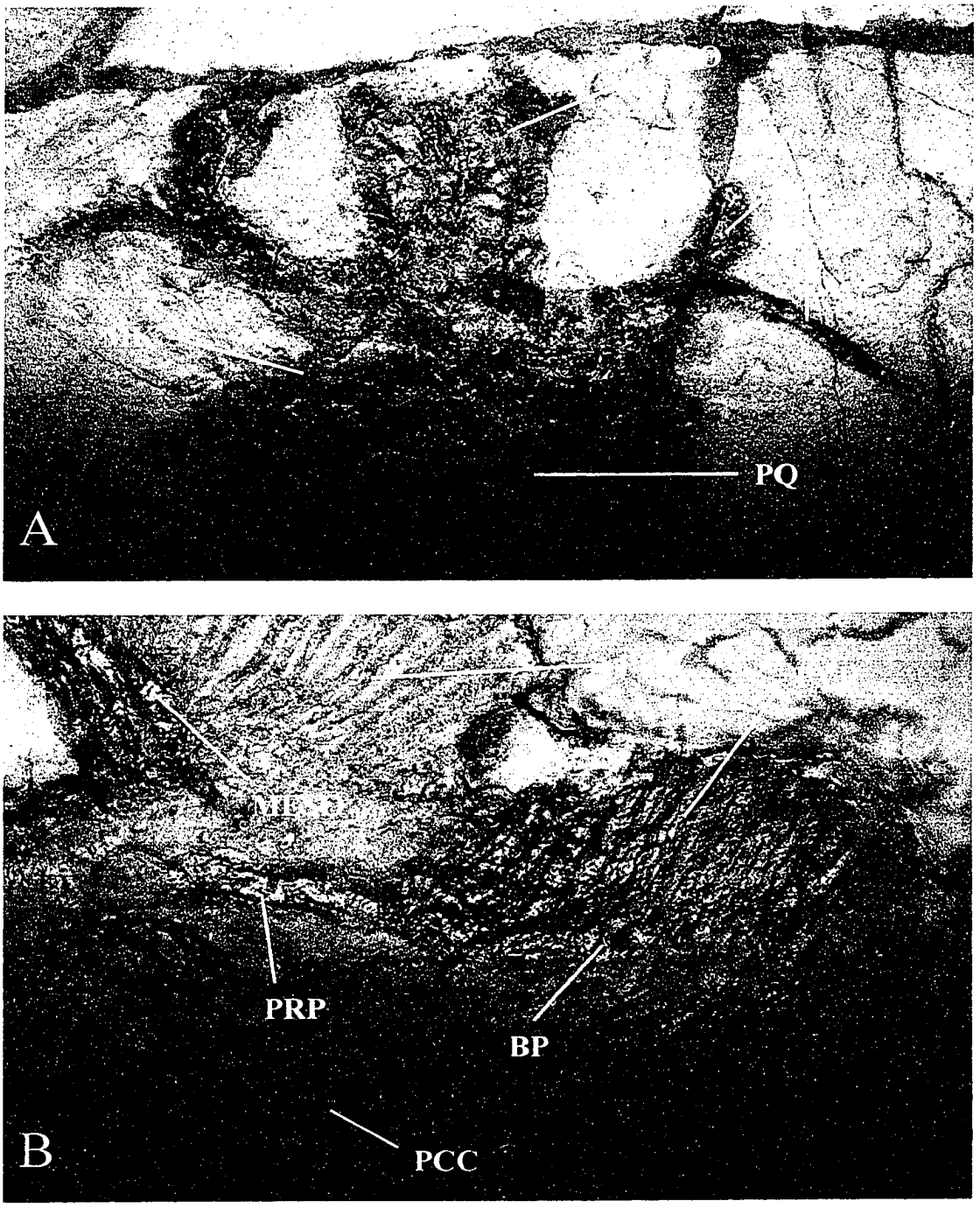


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Figure 108. Detail of head and jaws (A) and right pelvic area (B) of holotype of Narcine molini Jaekel, 1894 (UP 26276); anterior to left in B.

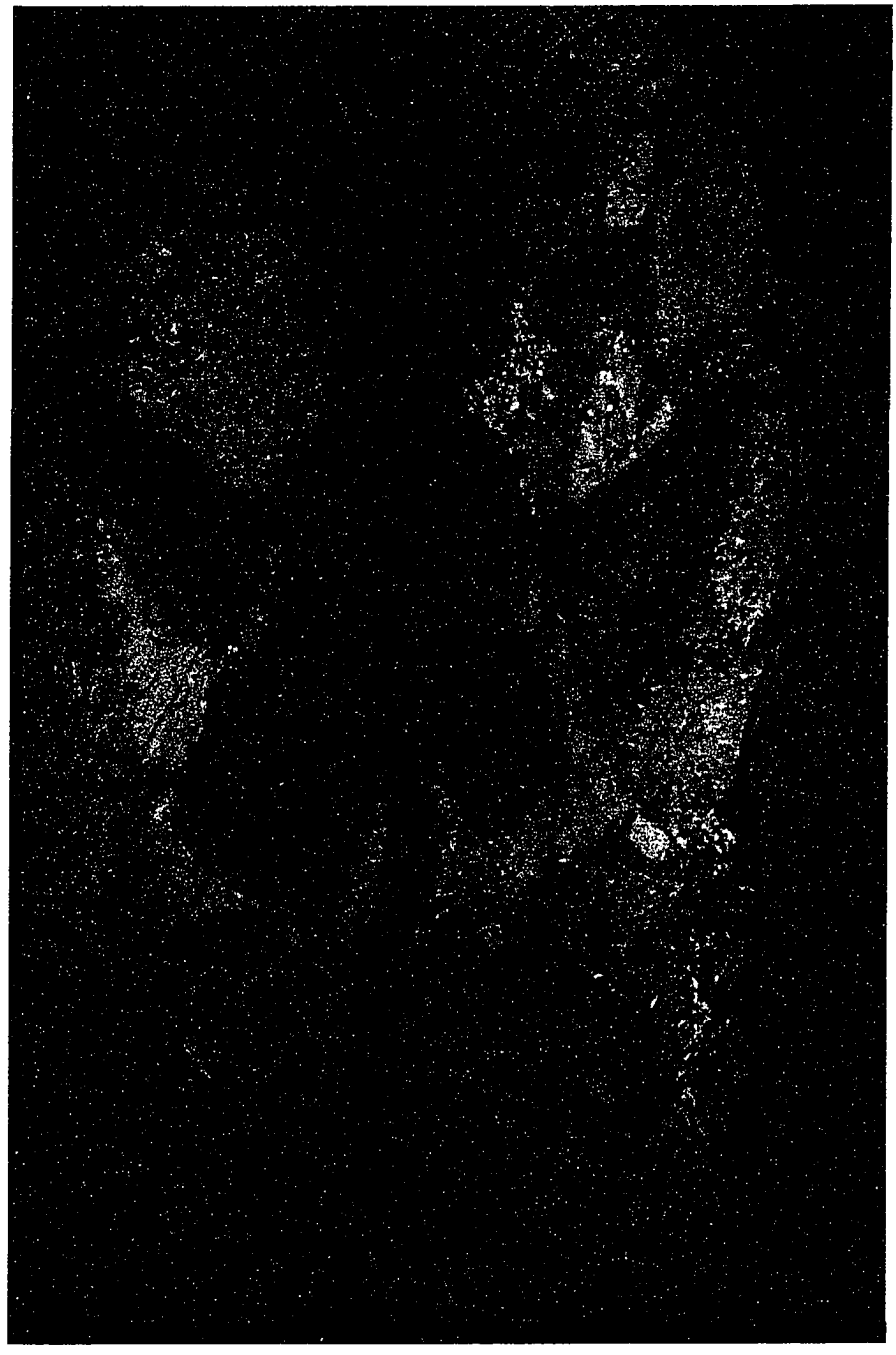
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Figure 109. "Narcine" molini (MCSN IG135576, 719 mm TL) from Eocene of Monte Bolca, Italy.

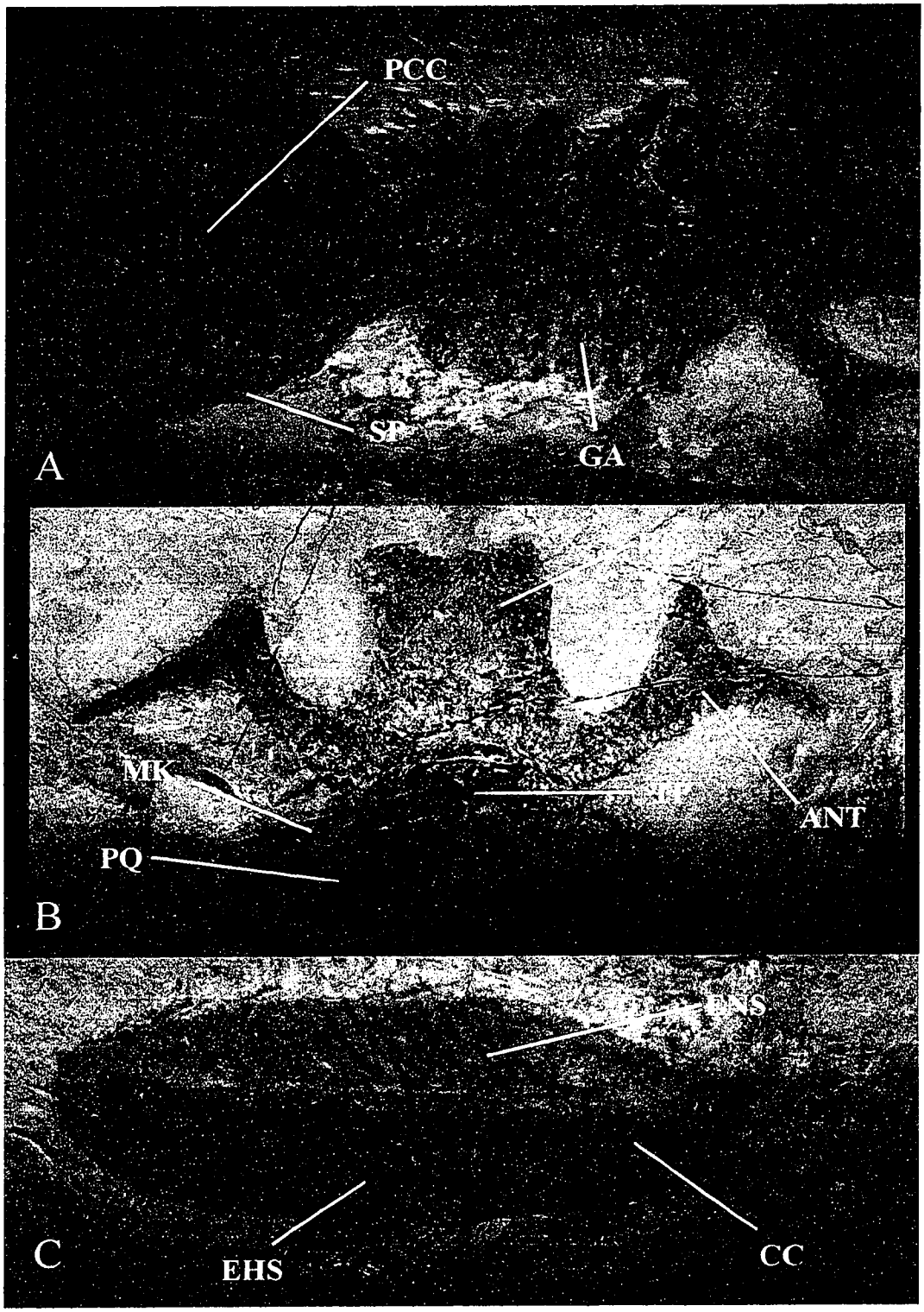
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Figure 110. Detail of gill arches and pectoral girdle (A), head and jaws (B) and caudal fin (C) of "Narcine" molini (MCSN 135576).

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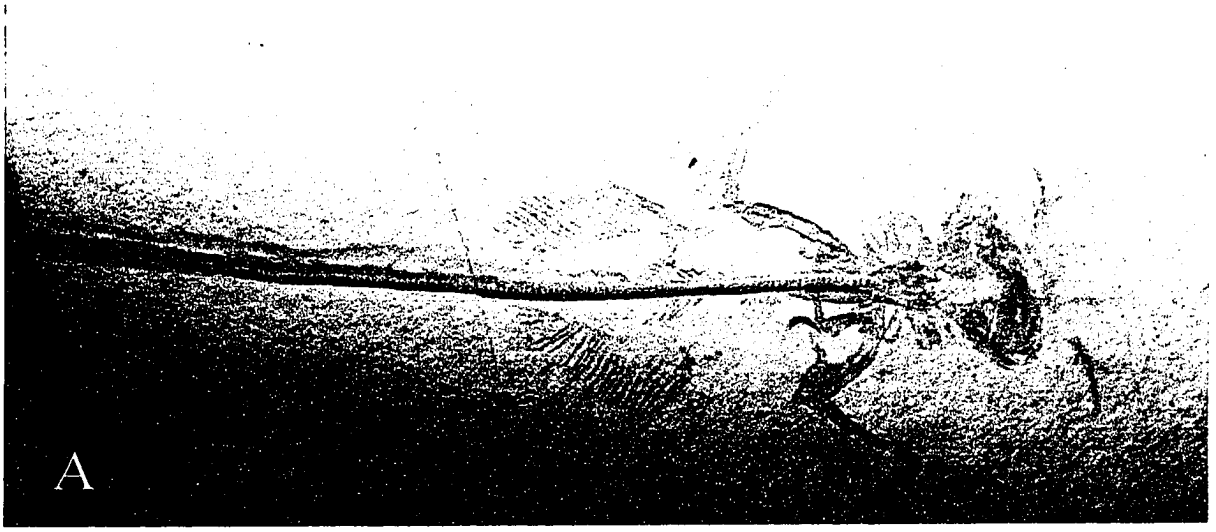


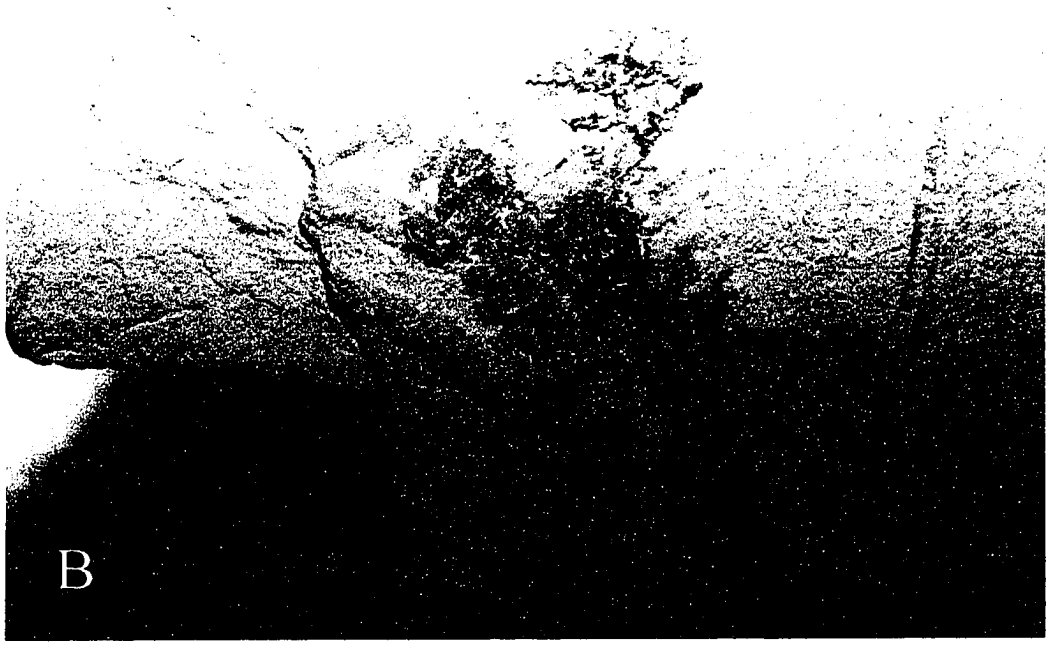
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Figure 111. Undetermined specimens of fossil Narcinidae from Eocene of Monte Bolca, Italy. A) MB uncat. (98 mm TL, Cerato collection), anterior to right; B) MB IG135581 (50 mm TL), anterior to top.

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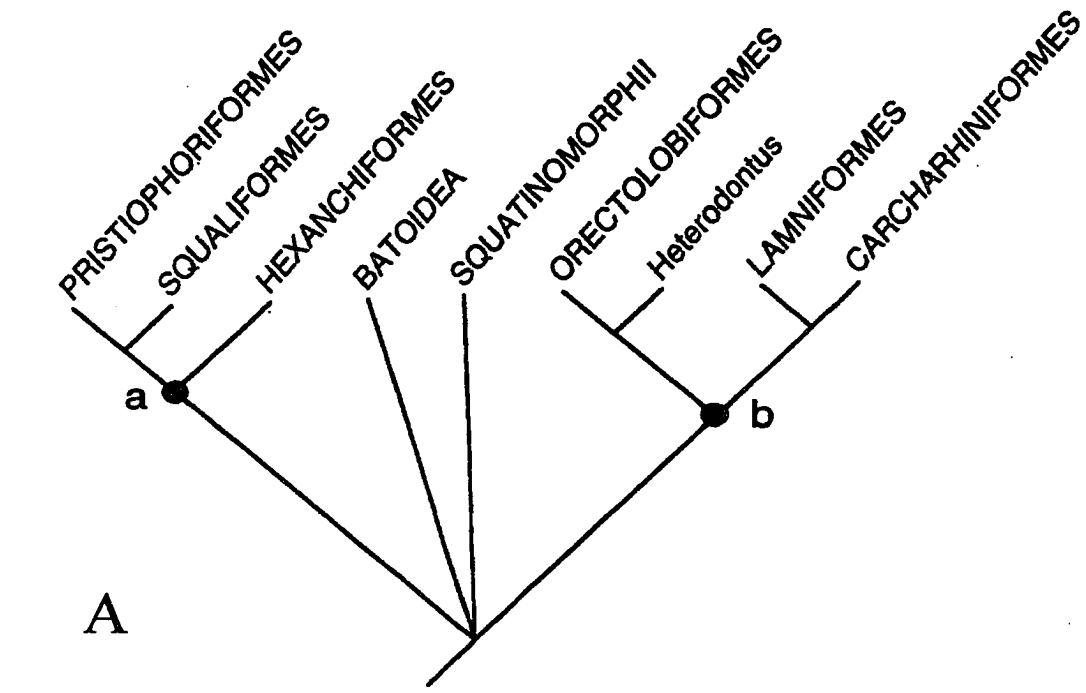
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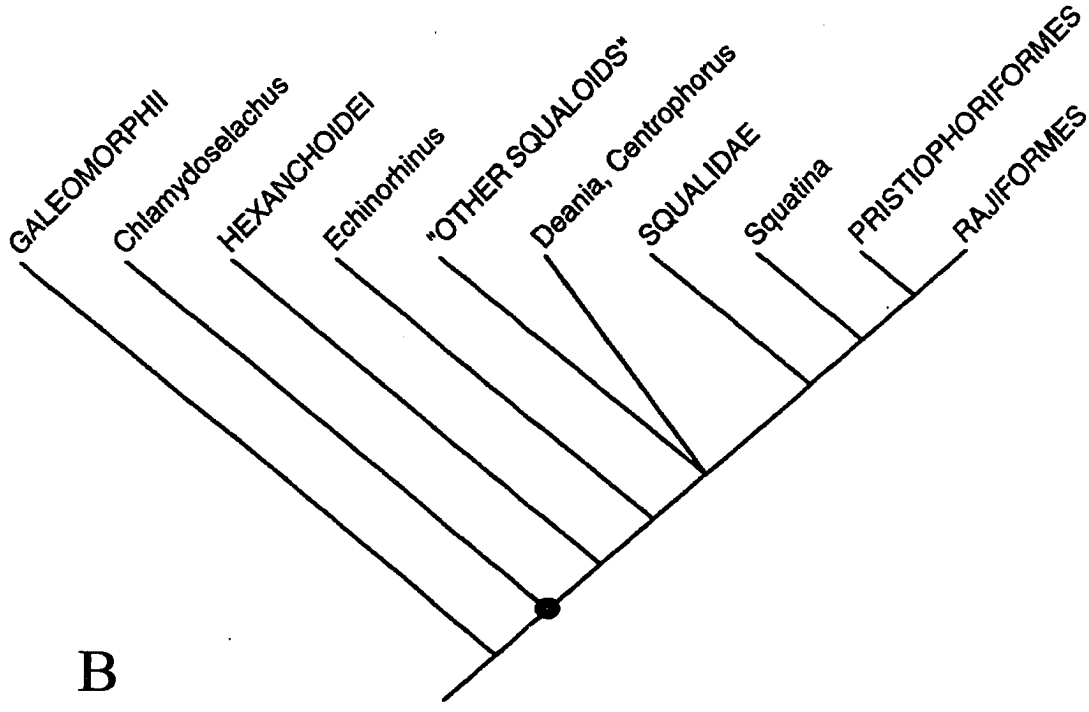
PART II

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Figure 112. A) The supraordinal elasmobranch groups of Compagno (1973, 1977). **a**, Squalomorphii; **b**, Galeomorphii. B) Phylogenetic relationships of Recent elasmobranchs advocated by Shirai (1992c). The marked node delimits Squalea. Note the paraphyly of Hexanchiformes and Squaliformes (as defined by Compagno, 1973, 1977, 1984).

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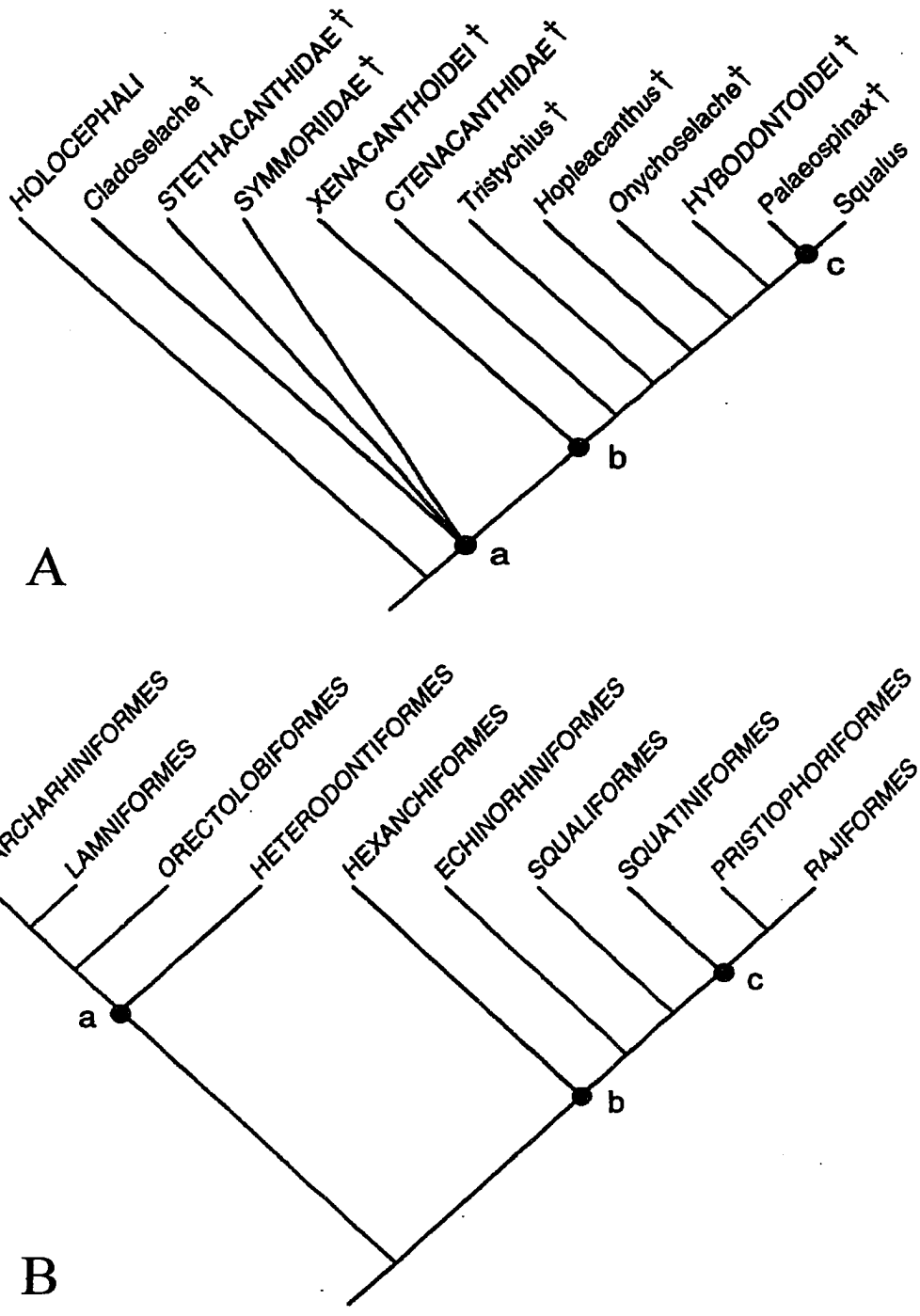




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Figure 113. A) Relationships among the major Paleozoic and Mesozoic elasmobranch groups, modified from Gaudin (1991), demonstrating the limits of the Euselachii and Neoselachii as adopted here (only a few representative taxa are included). Squalus represents all Recent elasmobranchs. **a**, Elasmobranchii; **b**, Euselachii; **c**, Neoselachii. Daggers indicate fossil taxa. The Hybodontoidei is delimited as in Maisey (1989a). The Neoselachii probably includes other taxa (such as Synechodus, orthacodontids and anacoracids). B) Ordinal relationships of the Recent Elasmobranchii. This tree is derived from the phylogenetic analysis conducted for the present paper (see Methods section of Part II for details). Characters optimized at the root are (numbers as in Tables 46 and 47, states of a multi-state series are in parentheses, and characters with more than one equally most-parsimonious optimization are indicated with an "!"): 19(1), 28!, 37! and 59!. **a**, Galeomorphii; **b**, Squalea; **c**, Hypnosqualea (characters for these nodes are listed in Fig. 114).

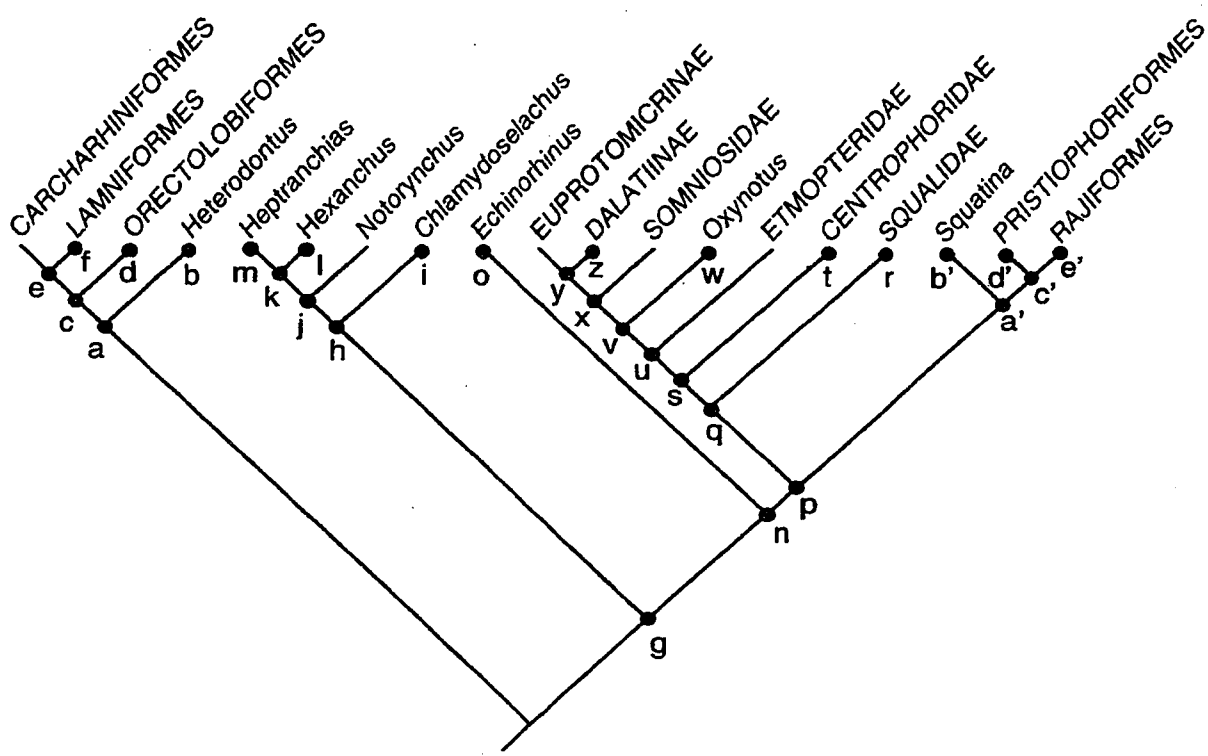
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Figure 114. Relationships within Recent elasmobranchs, depicting interrelationships within Hexanchiformes and Squaliformes. Character numbers are as in Tables 46 and 47. Refer to the text for a discussion of many characters listed here (cf. Shirai, 1992c). Characters at the root are listed in Fig. 113 (B). Characters for nodes are as follows (reversals contain a "-" before the character, independent occurrences are denoted with an asterisk, states of a multi-state series are indicated in parentheses, and characters with multiple equally most-parsimonious optimizations show an "!" after the character number): node **a** (Galeomorphii): 2*, 4!, 13, 26(5)!, 27(1)*!, 55*!, 67; node **b** (Heterodontea): 1(2), 57; node **c** (Galeoidea): 7, 24*, -28*!, 43, 49(2)*, 51*; node **d** (Orectolobiformes): 30*; node **e** ("higher galeoids": 1(1), -4!, 26(2)!, -27(0)!, -55!, -59*!; node **f** (Lamniformes): 64; node **g** (Squalea): 8(1)!, 9, 10, 11, 26(4)!, 32!, 44!, 47!, 49(1)*; node **h** (Hexanchiformes): 12(1)!, 20, -37, 40, 44(1)!, 45, 50, -59!; node **i** (Chlamydoselachoidea): -19(0), -28!, -32*!, - 47!, 49(2), 51*, 65*; node **j** (Hexanchoidea): 12(2)!, 17, 21!, 29(1), 31(1), 42, 58(1); node **k** (Hexanchidae): 2*, 5(1)*, 6*, 15; node **l**: -21!; node **m**: 65*; node **n** (Echinorhinoidea + Squaloidea + Hypnosqualea): 5(1)*, 19(2), 24, 56, 66; node **o** (Echinorhiniformes): 17*, 29(3), 39(3)*, 58(1)*; node **p** (Squaloidea + Hypnosqualea): 2*, -8(0)!, -26(0)!, -44!, 46(1)!, 48!, 60!, 63!; node **q** (Squaliformes): 6*, 31(2)*, -49(0), 58(2); node **r** (Squaloidei): 54(1), 62; node **s** (Dalatioidei): 26(1)!, -46(0)!, -48!, -63!; node **t**: 39(2); node **u** (unnamed): 35, 61; node **v** (unnamed): 23, 27(1)!, 39(1); node **w** (Oxynotidae): -6; node **x** (unnamed): 49(1)*; node **y** (Dalatiidae): 39(3)*; node **z**: 33*, 34*; node **a'** (Hypnosqualea): 5(2), 16, 38(1)!, 41!, 52, 53!, 54(2); node **b'** (Squatiniformes): 55*!, -60!; node **c'** (Pristiobatea): 3, 8(2)!, 14, 17*, 18, 22, 25, 27(2)!, 36, 38(2)!, 46(2)!; node **d'**: 31(2)*, - 41!, -53!; node **e'**: 8(3)!, -9, -10, -11, 29(2), 30*, -32*!, 33*, 34*.

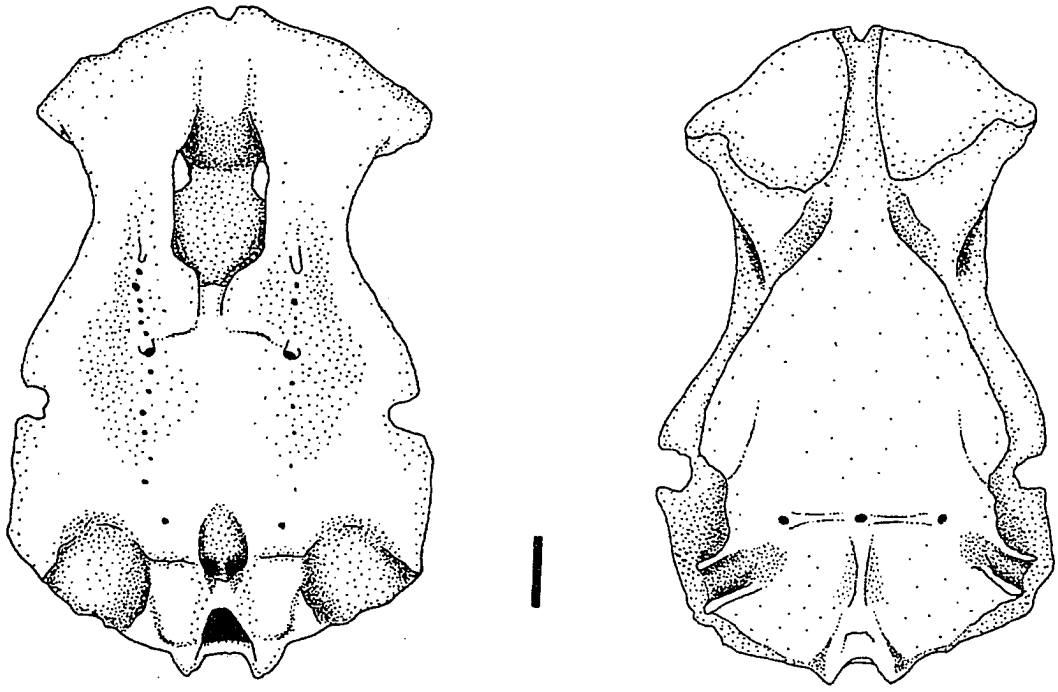
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Figure 115. Dorsal (A) and ventral (B) view of the neurocranium of Heterodontus francisci (AMNH 217862), anterior to top. Scale bar = 1cm.

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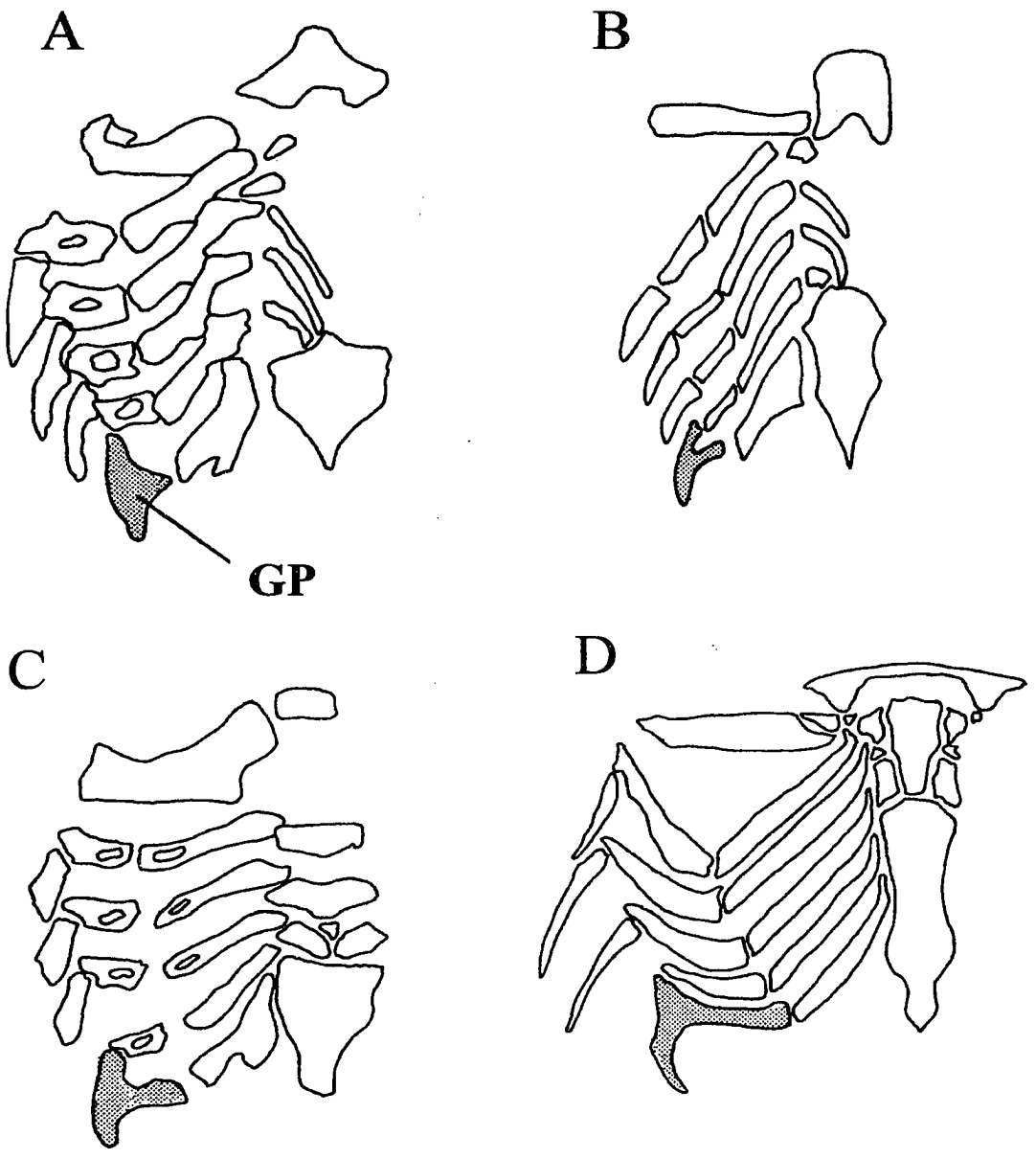


A B

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Figure 116. Dorsal view of gill and hyoid arches, depicting the gill pickax (GP) in representative galeomorph and squalean taxa (anterior to top). The hyomandibula is not shown. Dorsal elements pulled to left (right side not shown). The gill pickax is stippled. (A) Hemiscyllium ocellatum (AMNH 38151); (B) Pseudocarcharias kamoharai (AMNH 71984); (C) Dalatias licha (AMNH 19446); (D) Pristis pristis (AMNH 44011).

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