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# Phylogenetic Relationships of Species within the Gobiid Genus *Gobiosoma sensu* Böhlke and Robins (1968) with comments on their relationships to other genera in the tribe Gobiosomini

by

James L. Van Tassell

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

**1998**

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# Abstract

## Phylogenetic Relationships of Species within the Gobiid Genus *Gobiosoma sensu* Böhlke and Robins (1968) with comments on their relationships to other genera in the tribe Gobiosomini

by

James L. Van Tassell

Advisor: Dr. C. Lavett Smith

The tribe Gobiosomini contains 24 of the 29 New World genera. The most speciose genus *Gobiosoma* has been divided into numerous subgenera by Ginsburg, Böhlke and Robins, and Hoese. Ginsburg erected numerous subgenera as temporary holding areas until additional information became available to ascertain relationships. Böhlke and Robins investigated the Atlantic species with comments on Pacific relatives, and Hoese studied the Pacific species. This study presents a phylogenetic analysis of all species in the Atlantic and Pacific with comments on the tribe Gobiosomini and genera related to *Gobiosoma.*

Fourty-five characters were incorporated into the study, including characters used to separate the subgenera by the previous authors and new characters from cheek myology, sensory papillae, pelvic fin ray structure, and the arrangement of upper jaw teeth. Species previously placed in *Gobiosoma* can now be assigned to four genera with no subgenera. The subgenera *Austrogobius*, *Garmannia*, and *Gobiosoma* are divided into the monophyletic genus *Gobiosoma* and a paraphyletic genus *Gobiolepis*. The subgenera

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*Tigrigobius* and *Elacatinus* are elevated to genera and the monophyly of *Elacatinus* is established.

The restricted definition of the tribe Gobiosomini is supported with additional characters from sensory papillae patterns and cheek myology. Genera included in the tribe are *Aboma*, *Aruma*, *Barbulifer*, *Chriolepis*, *Elacatinus*, *Eleotrica*, *Enypnias*, *Evermannichthys*, *Ginsburgellus*, *Gobiolepis*, *Gobiosoma*, *Gobulus*, *Gymneleotris*, *Nes*, *Pariah*, *Psilotris*, *Pycnomma*, *Risor*, *Robinsichthys*, *Tigrigobius*, and *Varicus*.

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## Acknowledgments

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# Introduction

Two classifications of the gobiid genus *Gobiosoma* Girard have been proposed since Ginsburg (1933a, 1933b, 1938a, 1938b, 1939a,b, 1942, 1944, 1953) first reviewed the group. Böhlke and Robins (1968) reviewed the western Atlantic seven-spined gobies (*Gobiosoma* and nine related genera), describing ten new species and commenting on the relationships of Pacific relatives. Their work remains the only published review of the group. Hoese's Ph.D. thesis (1971) reviewed the Pacific species of *Gobiosoma* with descriptions of three new species and comments on relationships of the subgenera. Hoese's work, unfortunately, remains unpublished; however, Hoese's arrangement of genera and subgenera has been used by authors such as Bussing (1981, 1990) and Sazima *et al.* (1997) when describing new species, creating additional confusion of the existing nomenclature. Each of these classifications has relied to one extent or another on the distribution of scales on the body and the presence or absence of cephalic lateral line pores, characters which tend to be homoplastic. The dependence on one or the other of these characters results in a variety of arrangements for *Gobiosoma*, including a plethora of subgenera.

The current study was undertaken to 1) search for new characters to help clarify the relationships among the species of *Gobiosoma*; 2) incorporate all species of *Gobiosoma* from both the Atlantic and Pacific oceans into one study; 3) incorporate all characters previously used in defining genera, subgenera, and species along with new informative characters into a phylogenetic analysis of *Gobiosoma* and related genera; 4) investigate the relationships among the species of *Gobiosoma* and comment on characters

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forming species associations; 5) search for a sister group to *Gobiosoma*; and 6) comment on the tribe Gobiosomini.

Most of the species within the group are found in the Caribbean region, an area with a complex geologic history (Rosen, 1975, Hedges, 1982, Pindell and Barrett, 1990, Page and Lydeard, 1994, Hedges, 1996). Past studies by Birdsong *et al.* (1988) along with findings in this study support a Mediterranean and eastern Atlantic origin for the group. If the ancestors of *Gobiosoma* came from the eastern Atlantic and Mediterranean regions, they would have either traveled with the North and South American plates when the Atlantic was forming or reached the continents through larval dispersal. Either scenario presents problems. If they traveled with the continents, gobiids would have had to evolve and be present in the Tethys Sea at least 120 million years ago. Current estimates from fossils range from 45 - 65 million years for Mediterranean gobiids (Patterson, 1993). If they dispersed by larval transport to the Americas, they would require planktonic larval stages lasting several weeks to make the trip across the Atlantic. Present members of *Gobiosoma* and related genera have larvae that are planktonic for only five to seven days. The only known exception is *Tigrigobius puncticulatum* (a Pacific species), with a planktonic larval stage of 51 days.

With the most primitive member of the 'Gobiosoma Group' (*Aboma*) restricted to the Pacific coast of Mexico, the original taxa would have to arrived before the closing of the Pacific and Atlantic oceans. One would expect their past evolutionary history in the Americas to be influenced by a number of vicariant events such as 1) the movement of the Caribbean plate eastward into the Atlantic; 2) the formation of the Caribbean island

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systems; 3) the closing of Central America; and 4) perhaps the biolide impact near the present Yucatan peninsula 65 million years ago (Hedged, 1996).

The separation of the Pacific and Atlantic oceans with the formation of Central America (Hedges, 1982), the resultant changes in oceanic circulation patterns, and the formation of coral reefs in the Caribbean (Pinndell and Barrett, 1990) would have further divided the species and provided additional niches for rapid evolution of species. Rapid evolution of species is particularly evident among the coral reef species in the *Elacatinus* complex. The 13 species within this genus (as defined in this study) all exhibit very similar color patterns, and many readily hybridize in the aquarium (although all hybrids currently produced at the New Jersey State Aquarium by Alex Vagelli are sterile).

New informative characters were found in the myology of the suspensorium, papillae patterns, dentition patterns of the upper jaw, and the structure of the fifth pelvic ray. The changes in the insertion patterns of the suspensorium muscles added the greatest number of new characters. Other areas were investigated but yielded no additional informative characters. These include 1) vertebral foramen patterns, particularly in the caudal region; 2) dorsal rib attachment patterns; 3) gill arches; 4) urohyal shapes; and 5) the pelvic girdle.

The search for the sister group to *Gobiosoma* produced several likely candidates but was hampered by the current lack of specimens for several groups in museum collections. *Microgobius*, *Bollmannia*, and *Parrella*, included in the tribe Gobiosomini by Birdsong (1975), proved to be the least likely candidates for the sister group. The only

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characters they share in common with the rest of the tribe are seven spines in the first dorsal fin and a pterygiophore pattern of 3(221110). Patterns observed in their cheek myology and sensory papillae patterns would not place them close to the remaining *Gobiosoma* or the other related genera. The best candidates appear to be *Corcyrogobius* and *Odondebuenia*, but they were unavailable in sufficient numbers to dissect or clear and stain and therefore could not be incorporated into the complete data matrix. Each of the phylogenetic analyses conducted with the various proposed sister groups, however, resulted in placing the genus *Aboma* as the sister group to *Gobiosoma* and the related genera.

While this study does clarify some of the relationships and presents additional informative characters for the groups, it faces the inevitable problems inherent in gobioid systematics, namely the lack of sufficient specimens and a well-corroborated phylogeny for the suborder Gobioidei.

## Diversity Within the Suborder Gobioidei

The suborder Gobioidei is one of the most diverse of the Percomorphs, with approximately 2121 species in 268 genera (Nelson, 1994). They represent 5-10% of all teleosts, with species occurring in marine, fresh, and brackish water environments. Both the smallest extant vertebrate, *Trimmatom nanus* (Winterbottom and Emery, 1981), with a length of 8.0 mm SL for gravid females, and the lightest weight vertebrate, *Schindleria praematura* (Schindler, 1930), with a maximum weight of 8 mg (Bruun, 1940), belong to the suborder. Some gobioids are amphidromous, returning to their freshwater streams by

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traversing the face of 130 m waterfalls (Fitzsimons and Nishimoto, 1990). Gobioids occupy a diverse variety of marine habitats including open water, sandy or rocky biotopes, tidepools, caves, sponges, and mudflats. They are found at depths ranging from 0 to 500 meters and in temperatures ranging from 7$^0$C for *Leucopsarion petersi* Hilgendorf (Matsui, 1986) to 40$^0$C for *Chlamydogobius eremius* (Zietz, 1896), (Glover, 1973).

Nelson (1994) divides the suborder Gobioidei into eight families, employing the six families recognized by Hoese (1984) and adding the Odontobutidae for genera split off from the eleotrids (Hoese and Gill, 1993) and the Schindleriidae (Johnson and Brothers, 1993). The eight families recognized by Nelson include Rhyacichthyidae (loach gobies), Odontobutidae, Eleotridae (sleepers), Gobiidae (gobies), Kraemeriidae (sandfishes), Xenisthmidae, Microdesmidae (wormfishes) and Schindleriidae. Pezold (1993) subdivided the Gobiidae of Hoese (1984) into five subfamilies, removing 56 genera from the subfamily Gobiinae and placing them in the Gobionellinae. The genus *Gobiosoma* is in the Gobiinae as defined by Pezold (1993).

## History of Gobioid Classification

In 1758, Linnaeus recognized one genus (*Gobius*) with seven species. This was increased to seven genera in 1800 by Lacepède, eleven genera in 1801 by Bloch and Schneider, twenty-three genera by Günther in 1861b, and ninety-nine genera by Bleeker in 1874. Günther (1861b), Bleeker (1874), and Jordan (1885-1923) proposed the earliest classification systems for gobioid interrelationships. These systems were based primarily

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on the structure of the fins, but also utilized numbers and type of scales (ctenoid *vs.* cycloid), teeth, and placement of eyes.

Günther (1861b) recognized four groups of gobioids: the Gobiinae, containing species currently recognized as gobiids, eleotrids, and periophthalmids; the Amblyopina, containing the genus *Amblyopus*; the Trypauchenina, containing *Trypauchen* and *Trypauchenichthys*; and the Callionymina with three genera: *Platyptera*, *Callionymus*, and *Vulsus*. In 1874 Bleeker diagnosed four subfamilies: Eleotriformes, Gobiiformes, Amblyopodiformes (Amblyopina and Trypauchena of Günther), and Luciogobiiformes (gobioids without a first dorsal fin).

The first classification based largely on osteology, *e.g.* bones of the cranium and pectoral girdle and number of vertebrae, was by Regan (1911). He recognized three families: the Eleotridae, Gobiidae, and Psammichthyidae. The Eleotridae were separated from the Gobiidae on the basis of the shape of the palatine and the greater development of the mesopterygoid and scapula in the eleotrids. Based on these characteristics, the genus *Rhyacichthys* was also placed within the eleotrids. The family Gobiidae was divided into two subfamilies, Gobiinae and Periophthalminae, with the taenioids included within the Gobiinae. Regan established the family Psammichthyidae (=Kraemeriidae according to Maugé 1986 in Eschmeyer, 1990) and provisionally placed it within the Gobioidei.

Sanzo (1911) was the first to study the gobioid lateralis system. This system of external neuromast organs (so-called 'sensory papillae') forms distinct patterns on the head region. Neuromast patterns can be divided into two basic groupings, one where the neuromasts are primarily in longitudinal rows (fig. 1) and the other with neuromasts in

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transverse rows (fig. 2). These patterns have been shown to be useful in defining genera and species (Hoese 1971, 1983; Gill *et al.*, 1992) and have been used extensively by Miller (1963, 1973, 1992b, to cite a few) in defining taxa and arranging systems of classification.

Jordan (1923) produced an extensive treatment of the group. He divided the order Gobioidei into eight families (Rhyacichthyidae, Eleotridae, Gobiidae, Periophthalmidae, Gobioididae, Trypauchenidae, Doliichthyidae, and Psammichthyidae) but gave no diagnoses for these families. Duncker (1928) recognized four families (Eleotridae, Gobioididae, Periophthalmidae, and Gobiidae), based on the work of others. Berg (1940) separated the group into two superfamilies (Eleotrioidae and Gobioidae) comprising three families in total for the groups. The superfamilies separated the eleotrids and *Rhyacichthys* from all other gobioids. His three families were the Eleotridae, the Gobiidae (including taeniodids), and the Periophthalmidae (including kraemeriids).

Ginsburg (1933a) and Koumans (1953) both pointed out the inadequacies of the classification system of gobioids, but it was not until 1955 that Gosline made the next major osteological study. Gosline gave evidence for the placement of the microdesmids and kraemeriids among the gobioids and demonstrated that the shape of the palatine and the presence or absence of the scapula did not adequately separate the Eleotridae and the Gobiidae. He based his separation of these two families on the presence of six branchiostegal rays in eleotrids and five in gobiids. In 1960, Takagi made an extensive study of the cephalic sensory canal systems of gobies from Japan. A portion of the study was published in 1967 and the complete work published in 1988. Takagi examined 82

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species of 54 genera from Japanese waters and amended the terminology of the cephalic sensory canals, head pores, and sensory papillae patterns. He divided the gobioids into two groups, those possessing both cephalic sensory canals and sensory papillae, which he considered as the plesiomorphic condition, and those possessing only sensory papillae, the derived condition. Akihito (1963, 1967) conducted an extensive study on the scapula of gobioids, noting that the scapula is well-developed in the primitive genera. Later, in 1969, Akihito produced a detailed study of the higher classification of gobioid fishes based on the osteology of 85 species in 71 genera.

Miller (1963) briefly outlined the major differences between gobiids and eleotrids, commenting that the position of separate pelvic fins was not sufficient to separate eleotrids from gobiids. He produced a considerably different classification based largely on osteological characters. The characters he included are the number of epurals, hypural connection, the presence or absence of the endopterygoid, the number of branchiostegal rays, development of the scapula, the number of pectoral radials, presence or absence of the postcleithrum, a metapterygoid bridge to the quadrate, a preoperculum-symplectic bridge, and the extent of development of the oculoscapular and preopercular canals. Miller (1973) divided the suborder Gobioidei into two families: Rhyacichthyidae, with only one species, and Gobiidae, with close to 2000 species. Rhyacichthyidae was recognized by two plesiomorphies, the presence of three epurals and a well-developed cephalic lateralis system. Miller's Gobiidae shared the derived character states of one or two epurals and a reduced cephalic lateralis system. Miller (1973) further divided the Gobiidae into seven subfamilies: Eleotrinae, Pirskeninae, Xenisthminae, Gobionellinae,

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Tridentigerinae, Gobiinae, and Kraemeriinae and included the Pholidichthyidae within the Gobiinae. Springer (1983) strengthened Miller's classification of the Gobioidei by incorporating additional synapomorphies. He removed the Pholidichthyidae because it did not share any of the synapomorphies that he considered diagnostic for the gobioids.

Conflicting phylogenetic schemes based on synapomorphies in skeletal and sensory papillae systems were discussed by Miller *et al.* in 1980. Using electrophoretic techniques to differentiate hemoglobin polymorphisms, they attempted to resolve the conflicting hypotheses, but no close relationship to either of the phylogenetic schemes was apparent from the study. Springer (1983) studied the Gobioidei cladistically and proposed the four following synapomorphies for all gobioids: parietals absent, pelvic intercleithral cartilage present, dorsal end of interhyal fails to meet the dorsal end of the symplectic, and basibranchial 1 cartilaginous. To this list Miller (1992a) added the presence of a sperm duct gland. Subsequently, others have provided a partial resolution of groups within the Eleotridae (Hoese & Gill, 1993), or given evidence for monophyly within the Gobiidae: sicydiines (Hoese, 1984; Harrison, 1989, 1993; Parenti and Maciolek, 1993); oxudercines (Murdy, 1989); Amblyopinae and Gobiinae (Pezold, 1993).

Some resolution to the phylogenetic problems within the lower members of the Gobioidei was presented by Hoese and Gill (1993). They were able to define three families (Rhyacichthyidae, Odontobutidae, Gobiidae) and divide the Gobiidae into the subfamilies Butinae, Eleotridinae, and Gobiinae based on sixteen characters. The Gobiidae were diagnosed according to the following synapomorphies: (1) no autogenous middle radial in the first pterygiophore of the second dorsal fin; (2) upper proximal radial

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of the pectoral fin usually in contact with the cleithrum and extending well above the scapula; (3) anterior elongation of the procurrent caudal cartilage; and (4) scales without transforming ctenii.

Pezold (1993) divided Hoese's (1984) Gobiinae into a monophyletic Gobiinae and a smaller group, the subfamily Gobionellinae, for which monophyly could not be established. Pezold's Gobiinae is diagnosed by the presence of a single anterior interorbital pore, a single posterior pair of nasal pores, the interorbital portion of the oculoscapular canal fused, one epural, most species with 3-22110 first dorsal fin pterygiophore formula, 26 or 27 vertebrae, and two prehemal pterygiophores in most species.

The family Rhyacichthyidae is generally accepted as the sister group to all other gobioids. Monophyly of the remaining gobioids is supported by three synapomorphies (Springer, 1983): (1) lateral line canal not extending onto the body; (2) ventral process of the hyomandibula broad with the dorsal tips of the interhyal and symplectic widely separated from each other; and (3) mandibula sensory canal absent. To this list Hoese and Gill (1993) added (4) change in the position of the penultimate branchiostegal ray; and (5) reduction of head canals with the separation of the preopercular canal from the oculoscapular canal and possibly the reduction in the number of pores.

## The Tribe Gobiosomini

There are about 100 genera in the Gobiinae worldwide with 29 genera in the New World, 26 of which are restricted to the New World (Birdsong and Robins, 1995).

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The New World goby fauna is dominated by the tribe Gobiosomini (Birdsong, 1975) in the Gobiinae (*sensu* Pezold, 1993). The Gobiosomini contains 24 of the 26 New World genera and thus, according to Birdsong and Robins (1995), represent 40% of the New World gobioid genera.

The Gobiosomini, as originally proposed by Birdsong (1975) and later revised by Birdsong *et al.* (1988), unite what was commonly called the American seven-spined gobies and several closely allied genera, all endemic to the New World. Additional genera were added to the tribe by Hoese (1976) and Birdsong & Robins (1995). Genera currently included in the tribe are *Akko* Birdsong and Robins, 1995*;* *Aruma* Ginsburg, 1933; *Barbulifer* Eigenmann & Eigenmann, 1888; *Bollmannia* Jordan in Jordan and Bollmann, 1890; *Chriolepis* Gilbert, 1892; *Eleotrica* Ginsburg, 1933a; *Enypnias* Jordan & Evermann, 1898; *Evermannichthys* Metzelaar, 1920; *Ginsburgellus* Böhlke & Robins, 1968; *Gobiosoma* Girard, 1858 (including *Aboma* Jordan and Starks, 1895 and *Elacatinus* Jordan, 1904); *Gobulus* Ginsburg, 1933; *Gymneleotris* Bleeker, 1874; *Microgobius* Poey, 1876; *Nes* Ginsburg, 1933;, *Ophiogobius* Gill, 1863; *Palatogobius* Gilbert, 1971; *Pariah* Böhlke, 1969; *Parrella* Ginsburg, 1938; *Psilotris* Ginsburg, 1953; *Pycnomma* Rutter, 1904; *Risor* Ginsburg, 1933; *Robinsichthys* Birdsong, 1988; and *Varicus* Robins & Böhlke, 1961. Böhlke and Robins (1968) defined the genus *Gobiosoma* to include the subgenera *Austrogobius* de Buen, 1950,; *Elacatinus* Jordan, 1904; *Garmannia* Jordan and Evermann in Jordan, 1895; *Gobiosoma* Girard, 1858; and *Tigrigobius* Fowler, 1931. While the tribe may not be monophyletic, later work by Birdsong *et al.* (1988) inferred a subset of the group, known as the '*Gobiosoma* Group' (all genera except *Bollmannia*,

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*Microgobius*, *Palatogobius*, *Akko*, and *Parrella*) to be monophyletic.

Many of the genera within the tribe are monotypic. They include *Aboma*, *Akko*, *Aruma*, *Eleotrica*, *Ginsburgellus*, *Gymneleotris*, *Nes*, *Ophiogobius*, *Palatogobius*, *Pariah*, *Risor*, and *Robinsichthys*. Several contain only a few species (*Pycnomma*, 2 spp.; *Enypnias*, 2 spp.; *Psilotris*, 3 spp.; *Gobulus*, 4 spp.; *Evermannichthys*, 4 spp.; *Parrella*, 5 spp.) and are rather distinctive. The most speciose genera, other than *Gobiosoma* (37 spp.), are *Microgobius* (14 spp.) and *Bollmannia* (13 spp.).

Characters used to unite the Gobiosomini are a dorsal fin pterygiophore formula of 3-221110 ( in all genera except *Evermannichthys*, *Pariah*, and *Risor*), a vertebral count of 11+16-17 (in all but *Evermannichthys*, and *Pariah*), and the fusion of hypurals 1+2 with 3+4 (in all genera except *Aboma*, *Akko*, *Bollmannia*, *Microgobius*, *Palatogobius*, and *Parrella*) (Birdsong, 1975).

The largest genus, *Gobiosoma*, has been divided into as few as four or as many as seven subgenera (Ginsburg, 1933b, 1944; Böhlke and Robins, 1968; Hoese, 1971) based on squamation, cephalic pore patterns, or sensory papillae patterns. The characters used to define the genus and to separate the subgenera phenetically include (1) the number of pores and the extent of development of the head lateral line canal system, (2) elongation of dorsal fin spines, (3) precaudal and caudal vertebral numbers, (4) the shape of the 'tongue', (5) the extent of squamation on the body and (6) the presence or absence of basicaudal scales. While the species within *Gobiosoma* are, in general, well-defined, their phylogenetic relationships have not been investigated cladistically. Previous authors agree little on the arrangement of the species within the subgenera or which subgenera to

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include within the genus *Gobiosoma*.

The species of *Gobiosoma sensu* (Böhlke and Robins, 1968) were first studied by Isaac Ginsburg in a series of papers from 1933 to 1953. He recognized three genera (*Aboma, Gobiosoma, Garmannia*) based on the extent of squamation: *Aboma* (monotypic), completely scaled; *Garmannia,* scaled at least on the posterior half of the trunk and possessing four transverse scales on the caudal peduncle; and *Gobiosoma,* either completely naked or possessing only two modified basicaudal scales. *Gobiosoma* and *Garmannia* were divided into numerous subgenera: *Gobiosoma* into the subgenera *Elacatinus*, *Nes*, *Gobiosoma*, *Aruma*, *Dilepidion* Ginsburg, 1933, *Gerhardinus* Meek & Hildebrand, 1928, and *Garmannia* into the subgenera *Tigrigobius*, *Gobicula,* Ginsburg 1944, *Gobiolepis* Ginsburg, 1944, *Garmannia*, *Gobiohelpis* Ginsburg, 1944, *Gobiculina* Ginsburg, 1944, and *Risor*, again based on the extent of squamation. Ginsburg erected the subgenera as temporary holding areas for the species until he could obtain sufficient data on each species to change the arrangement. In his final published papers, he alluded to sensory papillae patterns as a character that could be used to rearrange the species. His later work on this subject, however, was never published.

Böhlke and Robins reviewed the Atlantic species of *Gobiosoma* and closely related genera in 1968 and included nominal Pacific species of *Gobiosoma* in discussing general relationships. The genera included in their study were *Gobiosoma*, *Risor*, *Ginsburgellus*, *Nes*, *Aruma*, *Enypnias*, *Barbulifer*, *Eleotrica*, *Gymneleotris*, and *Pycnomma*. Ten new species and one new genus were described. They elevated Ginsburg's subgenera *Nes* and *Aruma* to genera and made *Garmannia* a subgenus of

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*Gobiosoma.* Their classification was based on the presence or absence of oculoscapular and preopercular canal pores and numbers of vertebrae rather than on scale patterns as adopted by Ginsburg. According to Böhlke and Robins, *Gobiosoma* was composed of five subgenera (*Elacatinus, Gobiosoma, Austrogobius, Tigrigobius, Garmannia*).

Hoese (1971) revised the eastern Pacific species of *Gobiosoma* in his doctoral dissertation. The nine Pacific species, three of which were new, are separated by color pattern, extent of squamation, presence or absence of head barbels, cephalic lateral line pore patterns, fin ray counts, sensory papillae patterns, vertebral counts, elongation of the sphenotic, and changes in the length to width ratio of the skull. He included the genus *Aboma* as a subgenus of *Gobiosoma* and commented on the type species, *Aboma etheostoma*, as perhaps the most primitive member of *Gobiosoma*. Several new species were described and the subgenus *Gobiolepis* (Ginsburg 1944) was resurrected. However, the new species described in his thesis still remain unpublished.

For the purposes of this study, the genus *Gobiosoma* refers to the classification of Böhlke and Robins (1968). A synopsis of the genera and subgenera proposed in the classifications of Ginsburg, Böhlke and Robins, Hoese, and the classification proposed herein are given in Table 1.

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# Methods

## Phylogenetic Methodology

The phylogenetic relationships presented are based on examination of osteological, meristic, and myological features. A total of 45 characters is defined or described in detail in the section 'Characters and Discussions' and are summarized in Table 2.

Parsimony was employed to find the best phylogenetic hypothesis supported by the data set. The Wagner or strict parsimony method was used, in which character reversals and convergences are permitted and counted equally (Swofford & Maddison, 1987). Parsimony analyses were performed using the HENNIG86 computer program, version 1.5 (by J.S. Farris). Successive weighting was used as a means of basing groupings on more reliable characters without making prior decisions about the importance or weight of the characters. This technique has been found to reduce the ambiguity of the data set. Justification and discussions of successive weighting are provided in Farris (1969), Carpenter (1988), Naylor (1992), and Goloboff (1993). Tree diagnostics and character state distributions on the trees were done with the aid of the CLADOS computer program version 1.5 (by K. Nixon).

Outgroup comparison was used to determine the plesiomorphic state and polarization for the characters. The primary outgroup used to polarize characters was the genus *Gobius* with secondary outgroups of *Vanneaugobius*, *Odondebuenia*, and

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*Corcyrogobius* used when data was available. A detailed discussion of the outgroups is given in the section on outgroup selection. Binary character states were employed whenever possible. All multistate characters were run unordered in the analyses. Missing entries in the data matrix, represented by "?", were incorporated when the character state was not present in the taxon.

The search for characters began with a survey of the literature. A database was produced incorporating all characters incorporated in the original description of each of the species in the study. All species were then re-examined for characters not provided in the original description and the new information incorporated in the database. An evaluation of the characters was conducted to determine the validity of each character and its possible use for analysis of generic position as opposed to species level differences. A broad spectrum of systems was scanned in order to incorporate as many new or diverse characters as possible. Characters were chosen regardless of their apparent homoplasy (*e.g.*, scale distribution patterns and presence or absence of cephalic lateral line pores), since many components of relationships may be supported partly or totally by homoplastic characters.

## Osteological Observations

Observations were made on cleared and stained specimens, prepared following the method of Dingerkus and Uhler (1977), where ossified bone is stained with Alizarin Red and the cartilage counter-stained with Alcian Blue. The number of specimens examined is given in the appendix. A minimum of two specimens per species was cleared and

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stained, one male and one female. Where collection size permitted, additional specimens and size ranges were included for most of the species included in the study. Some specimens examined had been prepared some time prior to this study as part of museum collections and were stained for bone only. Several species (*Gobiosoma bosc*, *G. robustum*, *Elacatinus oceanops*, *E. figaro*) were bred at the New Jersey State Aquarium and provided ontogenetic series.

## Myological Observations

Muscles of the upper jaw and suspensorium were examined by dissection of alcohol-preserved specimens. The overlying integument was removed by making an incision along the dorsal region of the cranium and carefully pulling the skin forward and away from the muscles. Extraneous connective tissue was removed with the use of forceps. Allowing the specimen to desiccate slightly facilitated the separation and differentiation of the muscles. The small size (e.g. 3 - 8 mm head lengths in many cases) of the species complicated the dissections of the deeper muscles. However, it was found that the A3 muscle could be readily separated by locating its tendon to the coronomeckelian bone under the anteroventral edge of the A2 and using a small probe to carefully separate the A3 from the A1 and A2 complex.

## Measurements

All measurements were taken to the nearest 0.01mm with Fowler needle-point digital calipers following the procedures used by Böhlke and Robins (1968).

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## Drawings

Initial drawings of cranial muscles, cephalic sensory papillae, and osteology were made with the use of a camera lucida attached to a Nikon binocular dissecting microscope model MSZ-10. The drawings were then scanned and the resultant bitmap images converted to vector drawings using the computer program Micrographics Designer 7.0.

## Meristics

Scales in the lateral line series were counted from the mid-posterior margin of the pectoral fin base, along the midline. Scales extending over the caudal fin origin were included.

Scales in the transverse series were counted from the origin of the anal fin obliquely upwards and rearwards to the base of the second dorsal fin.

Extent of scale distribution: Scale distribution is divided into three body sections: the anterior trunk, from the pectoral fin to the origin of the second dorsal fin; the posterior trunk, from the origin of the second dorsal fin to the anal fin terminus; and the caudal peduncle, from the anal fin terminus to the caudal fin base. Scale patterns are recorded as present and covering the entire section; reduced, not covering the entire section; absent from the section.

Dorsal pterygiophore formula, *e.g.* 3-221110: The first digit indicates the interneural space into which the first pterygiophore of the spinous dorsal fin inserts, with the first interneural space occurring between the first and second vertebrae. The digits following the hyphen each represent an interneural space, beginning with the one into

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which the first pterygiophore inserts. The number represents the number of pterygiophores inserting at that location (Birdsong *et al.*, 1988).

Anal pterygiophores: The number of anal fin pterygiophores in advance of the first haemal spine. Pterygiophores directly under the haemal spine are counted as if they were in advance of the spine.

Precaudal vertebrae: The number of vertebrae without a closed haemal arch, determined from cleared and stained specimens.

Caudal vertebrae: The number of vertebrae with a closed haemal arch, including the urostyle, as determined from cleared and stained specimens.

## Sensory Papillae

The terminology used follows Miller (1986) based on Sanzo (1911) (figs. 1,2). The patterns incorporated in this study involve horizontal row b; the vertical rows under row b, rows 5i and 6i; the vertical row above row b, row 5s; and the vertical rows anterior to row b, rows 1, 2, 3, 4 (fig. 2).

## Cephalic Lateral Line Pore System

The terminology used is based on Akihito *et al.* (1984). The following pores are present in the material examined: anterior oculoscapular canal with pores B, C(S), D(S), E, F, G, and H; posterior oculoscapular canal with pores K and L; and the preopercular canal with pores M, N, and O present. Pores are paired, with representatives on each side of the head unless marked by (S) indicating a single pore (fig. 3).

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## Myology

A summary of the muscles examined and the variation in their points of origin and insertion is given below. A detailed discussion of the adopted terminology and its justification is given in the section on myology of the suspensorium.

**Adductor mandibulae 1** - originates on the preopercle and pterotic and inserts on the primordial ligament (maxillo-dentary ligament of Winterbottom, 1974a).

**Adductor mandibulae 1α** - originates on the preopercle, pterotic, and generally also on the sphenotic and inserts on the coronoid process of the anguloarticular.

**Adductor mandibulae 1 β** - originates on the metapterygoid, lateral part of the LAP, and preopercle and inserts on the maxilla. It is generally combined with the A1α at its origin but may be completely separate from the A1α when originating at the anterior of the LAP.

**Adductor mandibulae 1γ** - originates on the anterior process of the sphenotic and inserts on the maxilla.

**Adductor mandibulae 2** - originates on the preopercle, metapterygoid, and quadrate and inserts on the coronoid process of the anguloarticular.

**Adductor mandibulae 2γ** - originates on the quadrate's anterio-ventrolateral edge and inserts along the primordial ligament up to or joining with the maxilla.

**Adductor mandibulae 3** - originates on the metapterygoid and inserts by an elongate strong tendon onto the medial surface of the dentary.

**Adductor mandibulae ω** - originates on the medial surface of the dentary or articular and inserts on the tendon of the A3.

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**Levator arcus palatini** - Originates along the ventrolateral edge of the sphenotic and inserts on the metapterygoid and hyomandibula.

## Abbreviations Used:

### Institutional:

| | |
|---|---|
| AMNH | American Museum of Natural History, New York |
| ANSP | Academy of Natural Sciences of Philadelphia |
| BMNH | Natural History Museum, London |
| CAS | California Academy of Sciences, San Francisco |
| FMNH | Field Museum of Natural History, Chicago |
| FMRI | Florida Dept. of Environmental Protection, Florida Marine Research Institute. |
| GCRL | Gulf Coast Research Laboratory Museum, Mississippi |
| LACM | Natural History Museum of Los Angeles County |
| MCZ | Museum of Comparative Zoology, Harvard |
| SIO | Scripps Institute of Oceanography, La Jolla, California |
| SU | Stanford University, California |
| UF | Florida Museum of Natural History, Gainesville, Florida |
| USNM | National Museum of Natural History, Washington, D.C. |

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# Anatomical:

## Myology:

| | |
|---|---|
| A1 | adductor mandibulae 1 |
| A1β | adductor mandibulae 1β |
| A1γ | adductor mandibulae 1γ |
| A2 | adductor mandibulae 2 |
| A2γ | adductor mandibulae 2γ |
| A3 | adductor mandibulae 3 |
| Aω | adductor mandibulae ω |
| LAP | levator arcus palatini |
| TS | tendinous sheath |
| rm5 | *ramus mandibularis* V |

## Osteology and morphology:

| | |
|---|---|
| AN | anterior nostril |
| APM | anterior pelvic membrane |
| ART | anguloarticular |
| BAR | barbel |
| COR | coronoid process |
| DEN | dentary |
| ECT | ectopterygoid |

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| | |
|---|---|
| EPI | epiotic |
| EPU | epural |
| EXOC | exoccipital |
| FR | frontal |
| HYO | hyomandibula |
| HYP | hypural |
| LEPS | lateral edge of the pterotic and sphenotic |
| MAX | maxilla |
| MTP | metapterygoid |
| PAL | palatine |
| PL | primordial ligament |
| PN | posterior nostril |
| PMAX | premaxilla |
| POP | preoperculum |
| POPB | preopercle bridge |
| PTE | pterotic |
| QUA | quadrate |
| SPH | sphenotic |
| SPP1 | sphenotic process 1 |
| SPP2 | sphenotic process 2 |
| SOC | supraoccipital |
| SYM | symplectic |

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## Outgroup Selection

The polarization of characters within the Gobioidei, as a whole, remains a problem due to the lack of a well-corroborated sister group for the suborder (Winterbottom, 1993). In any phylogenetic study, a well-corroborated sister group is helpful, if not necessary, for the polarization of characters within the ingroup. While several outgroups for *Gobiosoma* have been proposed, none have been subjected to any phylogenetic analysis. The genera hypothesized by Miller and Tortonese (1969), Miller (1972, 1978, 1988), and Birdsong *et al.* (1988) as possible outgroups were incorporated in this study, and genera which might prove useful as possible outgroups were surveyed from the Atlantic, eastern Pacific, and Mediterranean. Within each of these regions, there are genera which can be grouped according to similarities in dorsal fin pterygiophore patterns, vertebral numbers, and anal fin pterygiophores (Birdsong *et al.*, 1988). Three groups of genera (*Microgobius* group, *Vanneaugobius* group, *Gobius* group) and a hypothetical outgroup were used in the preliminary analysis, separately and in combination, to ascertain their effect on ingroup relationships.

**The *Microgobius* Group**: This group contains the genera *Microgobius*, *Bollmannia*, and *Parrella*. These genera were originally placed in the tribe Gobiosomini by Birdsong (1975), but later studies (Miller, 1978; Birdsong *et al.*, 1988) cast doubts on the monophyly of the tribe with their inclusion. The '*Gobiosoma* Group' was proposed as a possible monophyletic subunit of the tribe by Birdsong *et al.* (1988), based on the fusion of hypurals 1 + 2 with hypurals 3 + 4 in the genera of that group. The fusion of

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hypurals 1-4 with the terminal element is found in other gobioid fishes, such as *Odondebuenia*, that are not placed in the Gobiosomini group based on other characters. This putative synapomorphy for the '*Gobiosoma* group' according to Birdsong *et al.* (1988) is not shared by *Microgobius*, *Bollmannia*, and *Parrella*. The '*Gobiosoma* Group' includes the following genera: *Aboma*, *Aruma*, *Barbulifer*, *Chriolepis*, *Eleotrica*, *Enypnias*, *Evermannichthys*, *Ginsburgellus*, *Gobiosoma* (including *Elacatinus*), *Gobulus*, *Gymneleotris*, *Nes*, *Palatogobius*, *Pariah*, *Pycnomma*, *Ophiogobius*, *Risor*, and *Varicus*. The present study has shown that all of the above genera except *Aboma* possess hypural fusion.

Since the *Microgobius* group shares with the '*Gobiosoma* Group' the possession of seven spines in the first dorsal fin with a pterygiophore pattern of 3-221110, a vertebral count of 11 precaudal and 16 caudal vertebrae, and they are found in the eastern Pacific and western Atlantic (Regions 1 and 5 of Birdsong *et al.*, 1988), they are included as a probable outgroup.

The *Microgobius* group differs, however, from the genera in the '*Gobiosoma* Group' in the general arrangement of cheek sensory papillae, lack of hypural fusion (fig. 4A), and the myology of the upper jaw and suspensorium. *Microgobius* possesses a forward extension of sensory papillae row b which ends anterior to vertical row 4 and an increased number of transverse sensory papillae rows under the eye (Fig. 5A). The genera in the '*Gobiosoma* Group' have a more reduced sensory papillae row b which does not extend anterior to the last complete transverse papillae row (termed row 4 by others), and a reduction in the number of transverse papillae rows under the eye from four in *Gobius*

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(fig. 6) to three in *Gobiosoma* (fig. 7). When one or more of the anterior papillae rows is lost, what to call the remaining rows becomes difficult. Homology has not been established for each of the anterior rows, and hence it is impossible to determine which row was lost. (See the Characters and Discussion section for a detailed explanation of this character.) Differences in the cheek myology will be discussed in the section on myology.

**The *Vanneaugobius* Group**: This genus of small gobies found in the warm-temperate eastern Atlantic-Mediterranean region contains the species *V. pruvoti* (Fage 1907), *V. dollfusi* Brownell 1978, and *V. cannariensis* Van Tassell, Miller & Brito 1988. *Vanneaugobius* shares the following characters with the '*Gobiosoma* Group': a short row b not extending anterior to row 5s (fig. 8A); and the presence of modified basicaudal scales (fig. 9).

Two additional genera from the Mediterranean region which show similarities with the '*Gobiosoma* Group' are *Odondebuenia* and *Corcyrogobius*. *Odondebuenia* possesses fusion of hypurals 1 + 2 with hypurals 3 + 4 (fig. 4B), a character common to all members of the '*Gobiosoma* Group' except *Aboma*, a reduced number of anterior transverse papillae rows (fig. 8B), and basicaudal scales (fig. 9). *Corcyrogobius* (fig. 10), according to Miller (1972), exhibits a papillae pattern closely resembling that of *Elacatinus* (fig. 11) and *Tigrigobius* (fig. 12) and was hypothesized by Miller (1972) as forming a possible link to those genera. Miller bases this 'close' relationship on the three genera sharing a reduced row b, a loss of one anterior transverse row under the eye, and a

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reduced number of papillae in each of the transverse row (as compared to species of *Gobius*) [See Miller (1986) for detailed drawings of papillae patterns in *Gobius*.]. The limited availability of specimens of *Corcyrogobius* and *Odondebuenia* meant that cheek myology and osteological characters could not be obtained for these genera. Their inclusion as a possible outgroup to the '*Gobiosoma* Group' will have to await additional collections of specimens.

**The *Gobius* Group**: *Gobius* was chosen since it exhibits more plesiomorphic characters than the ingroup. It differs from the '*Gobiosoma* Group' in possessing additional anterior and posterior oculoscapular pores G, K, and L (fig. 6); four transverse sensory papillae rows under the eye; an anterior nostril with a process on the rim in most species; and predorsal scales. The '*Gobiosoma* Group' lacks all these characters except for the retention of pores K and L in some species. The *Gobius* group exhibits more plesiomorphic characters than the other outgroups and might therefore aid in polarizing characters.

**Hypothetical Outgroup**: The use of a hypothetical outgroup was proposed by Nixon and Carpenter (1993) to aid in polarizing characters when there is no well-corroborated sister group. It was therefore used alone and in combination with the other hypothesized outgroups.

Miller (1978) proposed *Gorogobius* as a close relative to *Elacatinus* and *Tigrigobius*, two of the subgenera of *Gobiosoma sensu* (Böhlke and Robins,1968). He

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suggested this affinity on the basis of agreement in sensory papillae patterns in all three genera and further supported the relationship by the close association of Caribbean fishes with fishes in the region of West Africa, where *Gorogobius* is found. Miller further suggested that the tropical West African region may have acted as a refuge for fishes from the Tethys region during periods of temperature reduction and sea level changes. While biogeographic history and sensory papillae patterns might link *Gorogobius* to the *Gobiosoma* subgenera, there are other anatomical features which dispute this. *Gorogobius* has a vertebral count of 10 precaudal and 17 caudal vertebrae and 2-3 anal pterygiophores anterior to the first haemal spine, while *Elacatinus* and *Tigrigobius* have 11 precaudal vertebrae and 2 anal pterygiophores (Birdsong *et al.* 1988). Birdsong *et al.* (1988) included *Gorogobius* in their *Bathygobius* group, although they commented that this group was united only on the basis of phenetic similarity. Due to the differences listed above and the scarcity of specimens, *Gorogobius* could not be included in this study.

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## Results of the Outgroup Analysis

The analysis was performed using Hennig 86 (Farris, 1988). Consecutive weighting was used to help eliminate the effects of homoplasy (Naylor, 1992). First, several trees are constructed by a single pass through the matrix and branch-swapping applied to each of the initial trees, retaining no more than one tree for each initial tree (the mh* program option). Extended branch swapping was then applied to each of the trees, and all available space was used to store the trees generated (the bb* program option). Successive weighting (the xs w program option) was employed. This option calculates weights as the product of the character consistency and character retention indices and then scales them to lie within the range of 0 - 10. The above options are repeated until the character weights remain the same. All multistate characters were run unordered. Ten consensus cladograms were produced (figs. 13-22) and their statistics are summarized in Table 4.

The cladograms exhibit similarities in topology and species relationships for all combinations of outgroups except those analyses that include *Microgobius* as one of the outgroups. In those instances, the resultant cladograms produced large numbers of equally parsimonious trees (up to 625 trees with lengths of 299-308) with low consistency indices (ci= 57, 58, 54). When *Microgobius* or *Microgobius* and a hypothetical ancestor were incorporated in the outgroup, species within the *Gobiosoma* subgenera *Garmannia*, *Austrogobius*, and *Gobiosoma* are disbursed between the genera *Aboma*, *Aruma*, *Barbulifer*, and *Enypnias*. The distribution of species can be seen in figure 18 from node 68 on. All other outgroup combinations formed groups of species within *Gobiosoma* that

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were not divided by other monophyletic genera (figs. 13-17).

There is little difference in the topologies of those trees which do not include *Microgobius* in the analysis. All the trees demonstrate the monophyly of a species complex consisting of *Gobiosoma sp. nov.* H, *G. ginsburgi*, *G. longipala*, *G. bosc*, *G. paradoxum*, and *G. robustum*. *Gobiosoma parri* is included in this clade in all analyses except when *Vanneaugobius* is used as the outgroup. This species association is here referred to the genus *Gobiosoma*. Another monophyletic clade, containing all of the species in the subgenera *Tigrigobius* and *Elacatinus*, is also formed in all of the analyses and a paraphyletic assemblage of *Gobiosoma spilotum*, *G. grosvenori*, *G. chiquita*, *G. spes*, *G. schultzi*, *G. hildebrandi*, *G. sp. nov.* B and *G. homochroma* is produced. This paraphyletic group is here referred to the genus *Gobiolepis*.

Regardless of the outgroup chosen, *Aboma etheostoma* appears as the sister group to the remaining species and genera. The cladograms produced with a hypothetical ancestor and *Gobius* as outgroups resulted in trees with the highest consistency indices (ci= 64), highest retention indices (ri = 89), and the lowest number of equally parsimonious trees (36 trees). Since both cladograms result in the same tree, the one with the hypothetical ancestor will be used for purposes of discussion in this study, with comments on the others where appropriate.

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## Myology of the Suspensorium

The use of myological characters to elucidate phylogenetic relationships has received recent attention in several groups (Tetraodontiformes, Winterbottom,1974b; Lutjanidae, Johnson,1980; Cichlidae, Stiassny,1981; Branchiostegidae, Marino and Dooley, 1982; Gadiformes, Howes, 1988; Mugilidae, Harrison & Howes, 1991, Stiassny, 1993). While observed variations have helped to elucidate relationships within the families, homology between the various muscle subdivisions remains uncertain between families. Winterbottom (1974a) helped by clarifying and synonymizing many of the names in use prior to 1974 in his monograph of the striated muscles of the Teleostei. The basic conclusions drawn from previous studies indicate that while the homology of the adductor mandibulae between major taxa is not in question, the homology of the subdivisions is difficult if not impossible to establish between families (Winterbottom, 1974a; Gosline 1986, 1993). These studies indicate that evolution of muscles occurs by the subdivision of existing muscles, the reduction and/or loss of muscles, or changes in fiber direction. All of these alterations have functional significance and therefore show possible evolutionary changes and relationships.

Myology of the Gobioidei has, with few exceptions, received little attention in the literature. Hoese and Gill (1993) used the insertion point of the A1β tendon relative to the primordial ligament to elucidate eleotrid relationships. Birdsong and Robins (1995) included drawings of the cheek myology in their description of *Akko dionea* but did not comment on relationships. Winterbottom (1974a) and Gosline (1993) included several of the 200+ genera of gobies in their studies, using some of the larger, less specialized

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forms from which to draw conclusions.

The tribe Gobiosomini contains some of the more derived members of the Gobiidae and exhibits modifications in the adductor mandibulae complex not observed in other studies. Changes in the origin and insertion of the adductor mandibulae complex occur within the group, as well as the development and separation of two new muscles of the complex. These new muscles arise from subdivisions in the A1α/A1β complex and the A2. These changes add further complexity to defining the A1α and A2 muscles of fishes in general. A summary of the muscles present in the suspensorium of Gobioidei examined in this study is given in Tables 5 and 6. The origins and insertions of the muscles in the suspensorium are given in Tables 7 and 8.

Winterbottom (1974a) defined the A1 section of the adductor complex by its dorsal position and insertion on the maxilla. Winterbottom (1974a) cited other possible insertions such as from the lachrymal to the articular (Allis, 1903), articular only (Alexander, 1964) or the posterodorsal face of the premaxilla. When the A1 insertion shifts to a point other than the maxilla, the problem of differentiating it from the A2 arises. Kesteven (1943) used the position of the *ramus mandibularis* V to separate the A1 and A2. Winterbottom (1974a) commented on the position of this nerve as an unreliable character based on studies by Edgeworth (1935). More recent studies by Gosline (1986) and Howes (1988), however, indicate that the course of the *ramus mandibularis* V appears to be nearly constant, and that the visibility of the nerve on the external surface of the adductor mandibulae 2 may be the result of changes in the course of the musculature's occluding the nerve and not changes in the position of the nerve. In

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the gobioid genera examined in this study, the *ramus mandibularis* V was always visible on the external surface between the A1 and A2 complexes and was used to differentiate the two muscles even when changes in the A1 insertion occurred.

In *Gobionellus oceanicus* and the plesiomorphic genera examined in this study (*Eleotris potamophila*, *Eleotris pisonis*), and those reported by Hoese and Gill (1993) for *Rhyacichthys*, Butinae, and Eleotridinae, the A1 inserts on the maxilla and/or the primordial ligament. In the Gobiosomini (excluding *Microgobius*, *Bollmannia*, *Parrella*) the A1 generally inserts on the coronoid process of the anguloarticular. Since the origin and insertions of the A1β and A2 remain the same and the *ramus mandibularis* V is present between the A1/A2 division, it is assumed that the insertion of the A1 must have switched from the maxilla and primordial ligament to the coronoid process of the anguloarticular.

## Cheek Myology in the Gobioidei - Terminology

**Adductor mandibulae 1 (A1)**: When the A1 is not divided into separate sections, the origin is on the posterior preopercle from the midpoint of the preopercle dorsally. The posterior margin of the A1 runs along the anterior edge of the preopercular canal and then dorsally on to the ventroposterior pterotic. The origin generally does not extend anteriorly to the sphenotic. Most of the dorsal edge of the A1 is located well below the ventral edge of the oculoscapular canal. The A1 inserts along the primordial ligament with the dorsal-most fibers inserting on the maxilla (fig. 23).

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**Adductor mandibulae 1α (A1α)**: The A1α can originate in several locations. These include (1) the preopercle at the anterolateral edge of the preopercular canal, dorsal to the A2 and dorsoanteriorly along the lateral edge of the pterotic (fig. 24); (2) the preopercle at the anterolateral edge of the preopercular canal from the dorsaoventral midpoint then dorsally to the lateral edge of the pterotic, and anteriorly along the lateral edge of the sphenotic (fig. 25); and (3) only on the pterotic, sphenotic, and frontal, extending dorsomedially to the suture between the frontals (fig. 26). The A1α insertions include (1) the coronoid process of the anguloarticular inserting with the A2 via a tendon or tendonous sheath (fig. 27B) and (2) inserting with two heads, one on the primordial ligament up to the maxilla and the other via a tendon onto the coronoid process (fig. 28A).

**Adductor mandibulae 1β (A1β):** The A1β originates from one of the following positions: (1) on the lateral surface of the metapterygoid starting at the posteroventral edge of the LAP and continuing along the metapterygoid ventral to the terminus of the LAP (fig. 29B); (2) lateral to the LAP originating on the lateral surface of the metapterygoid, the anterior edge of the preopercle at the preopercular canal and dorsally on the lateral edge of the pterotic, with an anterior extension occasionally reaching the sphenotic (fig. 30); and (3) on the lateral surface of the metapterygoid at the anterior end of the insertion of the LAP (fig. 31). The A1β insertion is always on the maxilla either directly, via a tendon, or along the dorsal end of the primordial ligament to the maxilla.

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**Adductor mandibulae 1γ (A1γ):** The A1γ is described here for the first time. Homology with muscles of the same name in other families is not assumed. The A1γ originates on the anterolateral process of the sphenotic, then extends ventrally along the anterior edge of the A1α, inserting directly on the maxilla, lateral to the insertion of the A1β (fig. 29A).

**Adductor mandibulae 2 (A2)**: The A2 originates from the mid-preopercle along the anterior edge of the sensory canal and runs ventrally to the ventrolateral edge of the quadrate and anteriorly along the ventrolateral edge of the quadrate. The origin of the A2 may extend anteriorly to the midpoint of the quadrate (fig. 32A) or continue anteriorly to the quadrate's condyle (fig. 30). Insertion points for the A2 include (1) an insertion on the coronoid process of the anguloarticular via a tendon or tendinous sheath (fig. 32A); or (2) two heads, one inserting on the coronoid process and the other running along the primordial ligament, towards or joining with the maxilla (fig. 30A). When the section along the maxilla-mandibula ligament to the maxilla becomes large, it separates from the remainder of the A2 and forms a separate muscle, here called the A2γ.

**Adductor Mandibulae 2γ (A2γ):** Originates along the anteroventral edge of the quadrate and inserts, along the primordial ligament, onto the maxilla and may join with the A1γ, when present (fig. 29A).

**Adductor mandibulae 3 (A3)**: The adductor mandibulae 3 exhibits almost no variation in origin and insertion within the species examined. The origin is consistently on the lateral surface of the metapterygoid, ventral to the insertion of the levator arcus palatini and the insertion is, via a tendon, onto the medial surface of the dentary and the

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medial surface of the coronomeckelian bone (figs. 23-33). The only exception occurs in *Chriolepis minutilis* (fig. 34), in which two subdivisions of A3 occur. One originates on the lateral face of the metapterygoid and a second originates on the dorsal surface of the sphenotic; both insert via the same tendon to the coronomeckelian bone.

**Adductor mandibulae ω (Aω)**: This muscle has been observed on larger specimens inserting in the fossa of the anguloarticular and originating on the tendon from the A3. Most adult gobiids examined were too small to determine if this muscle was present.

**Levator arcus palatine (LAP)**: The LAP originates along the lateral edge of the sphenotic, ventral to the oculoscapular canal and inserts on the lateral surface of the metapterygoid, anterior margin of the preopercle, and ventral part of the hyomandibula (figs. 27-29).

## Changes in Suspensorial Myology

The suspensorium in *Gobiosoma* and related genera ('*Gobiosoma* Group' of Birdsong *et al.*, 1988) exhibits changes in the origin, insertion, and number of subdivisions of the adductor mandibulae complex not previously reported in other studies. Additionally, two new muscles evolve from sections of the A1/A1β complex and the A2, here defined as the A1γ and A2γ. These derived characters have proven useful in resolving some relationships within the Gobiosomini and gobioid relationships in general.

The A1β exhibits two separate and distinct origins in the Gobioidei with no intermediate stages observed in specimens examined. It either originates only on the

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metapterygoid at the anterior edge of the LAP, directly under the eye and forming part of the base for the eye socket (fig. 31B), or the A1β originates on the preopercle at the posterior edge of the LAP. When originating on the preopercle, the origin is along the anterior edge of the preopercular canal and then either ventrally along the metapterygoid near the ventral insertion of the LAP (fig. 35) or dorsally onto the pterotic, occasionally reaching as far forward as the sphenotic. A separate A1β with an origin at the anterior of the LAP has been observed in several Eleotridinae examined in this study, and in the Butinae and Odontobutidae according to Hoese and Gill (1993). They commented that the A1β is not separate from the A1 in Eleotridinae and most other gobioids and that a separate A1β may define the Butinae plus the Odontobutidae. Having examined several of the same species and additional Eleotridinae, I find an A1β present, separate, and originating anterior to the LAP in some Eleotridinae (*Eleotris pisonis*, *Dormatator latifrons*). Therefore the presence of a separate A1β would not define the Butinae and Odontobutidae as proposed by Hoese and Gill (1993) but would also include a subset of their Eleotridinae. Springer (1983) noted the presence of an intraorbital bone in several eleotrids, and Akihito (1986) included it in his figures of specimens of *Bostrychus* and *Oxyeleotris*. [See Winterbottom (1993) for comments on the use of the term intraorbital *versus* infraorbital.] The occurrence of a separate A1β and an infraorbital within the same genera might represent additional synapomorphies linking a subset of the Eleotridinae to the Butinae and Odontobutidae. However, additional species will need to be examined before conclusions can be drawn.

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The A1β exhibits a series of changes in its origin within the Gobiidae when originating posterior to the LAP. In primitive gobiids, the origin is along the ventral insertion of the LAP and dorsally along the anterior margin of the preopercle canal, ending below the lateral edge of the pterotic (fig. 33B). There is a shift in the origins of both the A1α and A1β anteriorly along the lateral edge of the pterotic and anteriorly onto the sphenotic, reaching the anterior of the sphenotic in some species. Associated with this more dorsoanterior origin of the A1β, there is also a change in the point of insertion. The anteromedial fibers tend to be more dorsolaterally located on the lateral face of the adductor mandibulae 1β and insert on the maxilla (figs. 33B, 38B). In *Gobiosoma,* A1β is divided into two subsections at its origin, while the point of insertion remains unchanged. The two distinct points of origin are (1) on the metapterygoid along the ventral insertion of LAP and, to a small extent, on the anterior part of the preopercle; and (2) only on the anterolateral process of the sphenotic. I refer to the type 1 origin as the A1β (fig. 29) and the type 2 origin as the A1γ (fig. 36). The A1γ has been observed in the Gobioidei only in *Gobiosoma* and is present in all species examined. Only *Gobiosoma hemigymnum* and an undescribed species from the Pacific could not be examined due to insufficient specimens. It is, therefore, considered a synapomorphy uniting all four subgenera of *Gobiosoma* as defined by Böhlke and Robins (1968).

Within the Gobiosomini, the A1α inserts on the coronoid process of the anguloarticular by a strong tendon or tendinous sheath with few exceptions. The exceptions are *Gobiosoma homochroma*, *G. parri*, and *Pariah scotus* where a second insertion occurs on the primordial ligament; and in *Aruma histrio*, *Chriolepis minutillus*,

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and *Nes longus* where a second insertion occurs on the tendon of the adductor mandibulae 3. In *Bollmannia chlamydes*, where there is no separate A1β, the A1 inserts along the primordial ligament from the maxilla to the dentary (fig. 37). The origin of the A1 in the more primitive members of the Gobioidei extends from the mid-preopercle dorsally up to the pterotic, with the dorsal edge being located well below the lateral edge of the pterotic and sphenotic (figs. 31, 33, 35). In the Gobiosomini, the A1α expands dorsoanteriorly along the pterotic and onto the sphenotic, reaching the anteriolateral process of the sphenotic in some species. In the more derived members of the Gobiosomini (*Elacatinus, Eleotrica, Gobulus, Nes, Tigrigobius*) the origin moves dorsally over the lateral edge of the pterotic and sphenotic and onto the cranial roof (fig. 38). *Evermannichthys spongicola* exhibits the most derived condition; the A1α originates only on the dorsal pterotic, sphenotic, and frontals. No origin exists from the suspensorium (fig. 26).

Changes in the origin and insertion of the A2 have also been observed in the Gobiidae. The primitive condition for the A2 is to originate on the midsection of the preopercle along the anterior margin of the preopercle canal and along the ventral margin of the preopercle to the ventrolateral edge of the posterior part of the quadrate. When this occurs, the insertion is on the coronoid process of the anguloarticular by a tendon or tendinous sheath. In some members of *Gobius*, *Sufflogobius* (fig. 33), *Zebrus* (fig. 30), and *Padogobius,* the origin is shifted anteriorly along the quadrate, and some of the anterior muscle fibers insert along the primordial ligament but do not reach the maxilla. In *Aruma*, *Chriolepis*, *Elacatinus*, *Eleotrica*, *Evermannichthys*, *Gobiolepis*, *Gobiosoma*, *Gobulus*, *Gymneleotris*, *Nes*, *Pariah*, *Pycnomma*, and *Tigrigobius,* a greater portion of the

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anterior fibers moves along the primordial ligament and inserts on the maxilla at the ventral terminus of the A1β insertion (figs. 24, 25, 29, 36). When this condition occurs, the muscle is generally separate from the remainder of the A2. This new division of the A2 is named the adductor mandibulae 2γ. The A2γ is found in all species of *Gobiosoma* and related genera except *Aboma.* It has not been found in other members of the Gobioidei except *Zebrus zebrus* and *Gobius paganellus,* where it occurs in a very reduced state and is not considered a separate and distinct muscle.

The adductor mandibulae 3 is present in all species examined but shows little if any variation in the origin and insertion patterns. It always originates on the lateral surface of the metapterygoid and hyomandibula ventral to the levator arcus palatini and inserts via a strong tendon into the dentary on the coronomeckelian bone.

The levator arcus palatini is also present in all species examined. It, too, shows little if any variation. The origin is always along the ventrolateral edge of the sphenotic and the insertion on the lateral surface of the metapterygoid and hyomandibula.

## Characters and Discussion

Many of the characters used in this study exhibit relatively high levels of homoplasy. But homoplastic characters do not necessarily equate to "bad" data per se (Goloboff, 1991) as long as homoplasy is minimized. As long as there is resolution then the high levels of homoplasy are just that and not necessarily an indication of "bad" data. Carvalho (1996), in his study on elasmobranch phylogeny, has shown that homoplastic data may in fact be good data if careful character coding and additional congruent

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characters are incorporated. His resultant single most parsimonious tree is supported by characters, almost half of which are homoplastic. Almost every node contains characters that occur homoplastically elsewhere on the tree and some nodes are supported by only homoplastic characters. His study and others (Carvalho and Maisey, 1996, Shirai, 1992) have shown that discarding homoplastic characters a priori prohibits resolution within the elasmobranchs. The discovery of additional characters that are congruent with homoplastic features may change tree topology in their favor in which case, according to Carvalho (1996), the "homoplasy" becomes synapomorphy.

The suborder Gobioidei is particularly ramped with homoplastic characters making the group difficult to resolve. Add to that the lack of a well resolved sister-group to the Gobiosomini or '*Gobiosoma* Group' and character polarization becomes difficult. I have polarized characters based on their distribution within the ingroup and proposed outgroups. Finial resolution on character polarity can not occur until detailed information on the occurrence of these characters in the over 2,000 species in the subfamily Gobioidei is known.

### Character 1: Barbel on upper lip

A barbel, which is usually very small, is present on the upper lip near the anterior nostril in several species of *Gobiosoma* and in some related genera (fig. 39B). This character was first noted by Ginsburg (1933a) and was used by him in defining subgenera. Larger barbels at the same location are found in *Aruma* and *Barbulifer* (fig. 39A). Barbels are not present in any of the outgroups. The presence of a barbel is,

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therefore, considered a derived character and its presence is coded as 1.

### Character 2: Branching of the fifth pelvic fin ray

The fifth pelvic fin ray generally has several branches in gobiids. It is present as a single unbranched fin ray in *Chriolepis*, *Eleotrica*, and *Pycnomma*. The presence of the unbranched ray is considered derived and is coded as 1. This character appears only once on the tree at node 48 defining a monophyletic group of the aforementioned genera.

### Character 3: Pelvic disc

In eleotrids, the pelvic fins are separate; and in most gobiids they are united, forming a disc-like structure. The united disc (fig. 40A) is secondarily lost in some genera such as *Chriolepis*, *Eleotrica*, *Gymneleotris, Odondebuenia*, *Pycnomma*, and *Vanneaugobius* (fig. 40B), where only a small remnant of the anterior and posterior membranes remain. Many of the gobiids with separate pelvics were originally placed in the eleotridids until studies of the skeleton showed that the separate fins are a derived condition and not homologous to the eleotridid condition (Miller and Tortonese, 1969). When a hypothetical outgroup is used, the separate pelvic fin exhibits no homoplasy within the Gobiosomini and appears only at node 50, uniting *Gymneleotris*, *Chriolepis*, *Eleotrica*, and *Pycnomma*. If *Vanneaugobius* is included as the outgroup, the character exhibits homoplasy appearing in *Vanneaugobius* and again at node 50.

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## Character 4: Number of first dorsal fin spines

The number of first dorsal fin spines is relatively constant in gobiids, with six spines being the common condition. While common does not equate to primitive (Yeates, 1995), six spines are present in the outgroup. Therefore, a change in the number of spines would be derived, at least within *Gobiosoma* and related genera included in the ingroup. The character is coded as 0 for six spines present, 1 for seven spines. The seven spine condition is also found in *Rhyacichthys* from the Pacific, and *Gobiusculus* from the northeastern Atlantic.

The only exception to the number of D1 spines, within Gobiosomini, occurs in *Evermannichthys*. In the type species *Evermannichthys spongicola,* the dorsal fin ray count ranges from five to seven, modally 6. In *Evermannichthys metzelaari,* the number of dorsal rays range from three to seven, modally 5. *Evermannichthys* is a highly derived member of the tribe adapted to living within sponges and exhibits several unique adaptations, such as a very elongate narrow body and a row of modified ctenoid scales ventrally along the caudal peduncle. None of the other members of the Gobiosomini exhibit these characters. Since only *E. spongicola* is included in the analysis, the modal number of 6 spines is used.

The character state 0 is found only in the outgroup and *Evermannichthys*.

## Characters 5, 6, 7: Scales on the trunk

Variation in the extent of scales on the body was the primary character used by Ginsburg (1933b) in defining the subgenera. While the more primitive members of the

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Gobiosomini possess scales over most of the trunk, there is a tendency for loss of scales throughout the group, with the more derived species being completely scaleless. This general trend was noted by Böhlke and Robins (1968). Scale loss occurs first on the anterior trunk and progresses posteriorly. Several patterns of scale distribution occur. The most common types of changes are for the forward extent of scales to end in a vertical line or for one or more rows, generally at the midline, to extend forward from the scaled posterior section. Two other conditions may also occur in conjunction with the above: a small separate patch of scales may occur under the pectoral fin, or a loss of vertical scale rows may occur at the posterior end of the trunk. The latter condition occurs only in *Gobiosoma spes*, *G. schultzi*, and *G. yucatanum*.

The scale patterns are divided into three multistate characters relating to the caudal peduncle (character 5), posterior trunk (character 6), and anterior trunk (character 7). Each of the characters is coded as 0 when completely scaled in that region, 1 when partly scaled, and 2 when no scales are present. The character was run unordered in the analysis.

## Character 8: Scales on predorsal region

Scales present on the predorsal region are a primitive character found only in the outgroup genera *Bollmannia* and *Gobius*. All species within the ingroup lack predorsal scales. The character is coded 0 for presence of scales and 1 for absence of predorsal scales.

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## Character 9: Modified basicaudal scales.

Modified basicaudal scales are ctenoid scales which are located on the terminus of the caudal peduncle and bear elongate ctenii (fig. 9). There may be as many as six scales present, as in *Gobiosoma homochroma* and *Gobiosoma chiquita*, but most species have only two on each side, occupying the dorsal- and ventral-most positions in the last scale row. Modified basicaudal scales are present in 22 of the 40 species included within the ingroup and in several cases are the only scales present. The scales are also present in the outgroup genera *Vanneaugobius*, *Odondebuenia*, and *Wheelerigobius*. These scales have not been observed in other species of Gobioidei. The value of the character in establishing relationships within the ingroup is diminished by the apparent loss of the scales in a number of species. Their presence is considered derived and is coded as 1 in the matrix.

## Characters 10-15: Oculoscapular head pores

The Gobioidei possess an oculoscapular canal with pores A-L present in Rhyacichthyidae and the more primitive members of the Gobiidae (Akihito *et al.*, 1984). In the Gobiinae, there is a loss of a section of the canal containing pores I and J. This separates the canal into the anterior oculoscapular canal with pores A-H and the posterior oculoscapular canal with pores K and L. Further pore reductions occur in the subfamily Gobiinae. The anterior canal terminates with pore B, located near the posterior nasal opening, and the canal unites near the anterior of the eye forming a single median pore C(S) (Pezold, 1993). Further pore losses occur within the Gobiosomini. The posterior

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oculoscapular canal is absent in most of the species and complete loss of all oculoscapular canal pores occurs in *Gobulus*, *Chriolepis*, *Nes*, *Psilotris*, and *Varicus*.

Anterior oculoscapular canal pores C-H are coded as present (state 0) or absent (state 1). The presence or absence of pore B directly correlates with pore C in *Gobiosoma* and would have resulted in redundant coding if included. The posterior oculoscapular canal is either present, with pores K and L (state 0), or absent (state 1).

Pore C (character 10) is lost at node 53 and secondarily derived at node 46. It is present in all species of *Gobiosoma*, *Gobiolepis*, *Tigrigobius*, *Elacatinus*, *Evermannichthys*, and *Ginsburgellus*. The presence of pore C is variable in *Risor* and is one of the characters originally used to separate *Risor* into three species. Pore D (character 11) is present in *Aboma*, *Enypnias*, all species of *Gobiosoma*, *Gobiolepis*, *Tigrigobius*, and *Elacatinus*. It exhibits homoplasy from node 53 to 44 with losses occurring at node 52 and in the genera *Barbulifer*, *Chriolepis*, and *Risor*; and secondarily gained at nodes 48 and 46. Pore D is generally absent from specimens of *Risor*, but this condition is variable even between specimens collected on the same sponge. In this analysis, pore D is coded as absent (state 1) in *Risor*.

Pore E (character 12) is present at node 68 (plesiomorphic at this level), lost at node 53 and regained at node 45. It is present in all species of *Gobiosoma*, *Gobiolepis* (except *G. homochroma* where its presence is variable), *Tigrigobius*, and *Elacatinus*.

Pore F (character 13) is plesiomorphic (state 0), being found at node 68. It is lost (state 1) at node 49 and in the genera *Enypnias* and *Chriolepis*; it is regained at node 44. Pore F is found in all species of *Gobiosoma*, *Gobiolepis*, *Tigrigobius*, and *Elacatinus*.

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Pore G (character 14) is present at node 68 (state 0) and lost (state 1) at node 67. Hence, it is present only in *Aboma etheostoma* and absent in all species within the ingroup.

The presence or absence of the posterior oculoscapular pores K and L, while generally lost within the ingroup, can be highly variable. *Gobiosoma bosc* and *G. robustum* are very similar and at times difficult to separate in collections. However, *Gobiosoma robustum* was placed in a separate subgenus, *Garmannia*, due to the absence of pores K and L, which *G. bosc* possesses (Böhlke and Robins, 1968). This character turns out to be variable in both species. The phylogeny presented here eliminates the subgenus *Garmannia* and places *Garmannia robustum* in the genus *Gobiosoma* along with *Gobiosoma bosc*. Pores K and L are present (state 0) at node 68 and lost in the genus *Gobiosoma* at node 58 and again in the genus *Gobiolepis* at node 61.

### Character 16: Preopercle canal pores

In the Gobioidei, the preopercular canal is separate from the oculoscapular canal and may contain as many as five pores labeled M through Q, according to Akihito *et al.* (1984). Within the Gobiinae, there is a trend towards reduction in the number of pores, with most species having three or less pores. In the Gobiosomini, there is a further reduction to two pores or the loss of all pores. Members of the outgroups all have three pores (M, N, O). This was coded as a multistate character with the following states state 0 for three pores M, N, and O present; state 1 for two pores present; and state 2 for no pores present. The character was run unordered in the analysis.

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The outgroup, *Aboma*, and all species of *Gobiosoma* have three pores (state 0). *Gobiolepis* species possesses three or two pores with the change to two pores occurring at node 59. Character state 2 (no pores) occurs at node 52 and a reversal to two pores occurs at node 44. All members of *Tigrigobius* and *Elacatinus* have two preopercular pores.

### Character 17: Total vertebral number

Total vertebral number consists of the precaudal vertebrae plus the caudal vertebrae (including the urostyle). To show the variation taking place between the outgroups and members of the ingroup, total vertebral number was incorporated rather than recording both precaudal and caudal counts separately. Changes in caudal and precaudal number can occur in the outgroups without a change in the total vertebral number. Since an increase in caudal vertebrae number occurs within the ingroup as well as an increase in total vertebral numbers, only the total and caudal vertebral numbers were incorporated in this study.

### Character 18: Caudal vertebral number

Caudal vertebrae include those which have a closed haemal arch. All counts were made from cleared and stained specimens so counts are unequivocal. Caudal vertebral number in the outgroup is 16. There is an increase to 17 in *Tigrigobius* and *Elacatinus*, one of the characters used by Böhlke and Robins (1968) to define their subgenera. A multistate character with three states is used in the analysis. State 0 (16 caudal vertebrae)

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occurs in the outgroups. State 1 (17 caudal vertebrae) is considered derived, since it occurs only near the terminus of the tree. State 2 (18 caudal vertebrae) occurs only in *Evermannichthys* and since it is apomorphic for that genus adds little information to the analysis. The character was run unordered in the analysis.

State 0 (16 vertebrae) occurs at node 68 and state 1 (17 vertebrae) at node 47. State 2 (18 vertebrae) occurs only in *Evermannichthys* and is apomorphic for that genus. The genera *Gobiosoma* and *Gobiolepis* all have 16 caudal vertebrae and the genera *Tigrigobius* and *Elacatinus* all have 17 caudal vertebrae.

## Character 19: Dorsal pterygiophore formula

Dorsal pterygiophore formulae were used by Birdsong *et al.* (1988) along with numbers of vertebrae, epurals, and anal pterygiophores to divide the Gobioidei phenetically into 32 groups. While at least 15 to 20 pterygiophore patterns exist, only two patterns occur in the species included in this study. The outgroups have a 3-22110 pattern and all members of the ingroup (except *Evermannichthys* which exhibits variation in dorsal spine counts) have a 3-221110 pattern.

The polarity of this character was discussed by Bianco and Miller (1990) based on Miller (1987). They concluded that the starting sequence of 2211 was generalized since it is present in more species, and the less frequently present state of 12210 was apomorphic. Since their study, Birdsong *et al.* (1988) and Hoese & Gill (1993) have concluded that the polarity for this character can not be determined. With additional starting sequences possible and the commonality rule no longer accepted (Yeates, 1993), I would agree with

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the later authors.

### Character 20: Fusion of hypurals 1&2 with 3&4

Within the tribe Gobiosomini, hypurals 1&2 fuse with hypurals 3&4 forming a solid hypural plate (fig. 4B). The fusion varies from one quarter of the distance from the urostyle to the posterior end of the hypural plate to complete fusion of the plates. Hypural fusion is rarely found in gobiids, with the exception of the Gobiosomini, in which most species exhibit the character. Other genera with similar hypural fusion include the Mediterranean six-spined genus *Odondebuenia* and the Indo-Pacific six-spined genera *Eviota*, *Gobiodon*, *Gobiopterus*, *Kelloggella*, *Monishia*, and *Trimmatom* (Birdsong, 1988). Fusion of the plates is therefore considered derived and its presence is coded as state 1. This character is found in all members of the Gobiosomini except *Microgobius*, *Bollmannia*, *Parrella*, and *Aboma*. Its absence in *Microgobius*, *Bollmannia*, and *Parrella* lends support to their exclusion from the tribe and places *Aboma* as the sister group to the remaining members.

Hypural fusion does not exhibit homoplasy; state 0 occurs at node 68 and state 1 only at node 67.

### Character 21: Fifth pelvic ray with an elongate dorsal process at the articulation with the pelvic girdle

The pelvic rays articulate on the pelvic girdle with a u-shaped bracket. On the dorsal side of this u-shaped bracket there is a process, the site of attachment of the

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adductor profundus pelvicus muscle. An elongate expansion of this process on the fifth pelvic ray (fig. 41A) occurs in a variety of unrelated genera according to A. Gill (pers. comm.). Species that are less benthic and hence spend extended periods in the water column tend to possess longer dorsomedial processes, at least within the Gobiosomini. Members of *Ginsburgellus*, *Tigrigobius*, and *Elacatinus* exhibit this dorsomedial process, with species of *Elacatinus* generally having longer processes. Members of *Elacatinus* spend extended periods of time swimming above the substrate while feeding or cleaning other fishes (personal observation).

The possession of this dorsal process (state 1) is found in *Ginsburgellus* and most species of *Tigrigobius* and *Elacatinus*. State 1 occurs at node 44 and is lost in two members of *Tigrigobius* (*T. gemmatum* and *T. pallens*) at node 42.

### Character 22: Supraoccipital with elongate lateral wings

All of the outgroups possess a supraoccipital with elongate lateral wings (fig. 42). The lateral wings insert between the anterodorsal margin of the pterotic and the posterior margin of the frontals. This condition is also present in most of the species in the *Gobiosoma* group. The derived condition is for the lateral wings to be reduced (fig. 43). This state occurs in *Evermannichthys*, *Risor*, *Ginsburgellus*, *Tigrigobius*, and *Elacatinus* and is associated with the lateral compression of the skull which also occurs within those genera. The loss of lateral wings is synapomorphic for the aforementioned genera and occurs at node 46 of the consensus tree. State 1 also occurs in *Gobiolepis chiquita* but is considered secondarily derived for that genus.

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## Character 23: Maxillary process

The maxillary process occurs on the middorsoposterior edge of the maxilla and is the site of attachment for the tendon of the adductor mandibulae 1. This process is present in the outgroup genera *Vanneaugobius*, *Parrella*, *Microgobius*, *Bollmannia*, and in the ingroup genera *Aboma*, *Barbulifer*, and *Risor*. The loss of this process is considered derived and is coded as state 1 in the analysis. Its presence lends support to *Aboma* as the sister group for all other genera within the *Gobiosoma* group (Birdsong *et al.*, 1988). The absence of the maxillary process is a synapomorphy at node 67 with its presence occurring homoplastically as autapomorphies in *Barbulifer* and *Risor*.

## Character 24: Metapterygoid shape

The metapterygoid articulates with the hyomandibula posterodorsally, symplectic ventrally, and may or may not articulate with the quadrate anteroventrally. Within the outgroups of *Vanneaugobius*, *Gobius*, *Parrella*, *Microgobius*, and *Bollmannia*, the metapterygoid is not expanded dorsally but is instead rather narrow. This character has been discussed by Miller (1973), and reduction of the metapterygoid has been noted in the eleotridine *Tyson* (Springer, 1983) and illustrated for various genera by Harrison (1989). Extensive variation in shape exists within the Gobioidei and polarization for the group as a whole is not possible. While homoplasy exists within the ingroup (eight reversals in terminal taxa), the character does define node 43 (*Tigrigobius* and *Elacatinus*) and no reversals occur within those genera.

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## Character 25: Articulation of the metapterygoid with the quadrate

The metapterygoid may overlap the quadrate (fig. 44B) or the two bones may be distinctly separate (fig. 44A). In percoids and some eleotrids, the metapterygoid broadly attaches to the quadrate (Miller, 1973; Harrison, 1989). The more primitive gobioid condition is for the anteroventral end of the metapterygoid to overlap the quadrate, leaving a non-ossified space between the quadrate, metapterygoid, and symplectic (Miller, 1973). Within the outgroups, in the present study, the metapterygoid overlaps the quadrate only in *Vanneaugobius*. All other outgroups lack this condition, as do many gobiids. Overlapping the quadrate is therefore considered a secondarily derived condition within the ingroup and is coded as a binary character with the derived state (1) for presence of an overlapping metapterygoid.

State 0 appears in the outgroup and at node 52 uniting *Gymneleotris*, *Chriolepis*, *Pycnomma*, *Gobulus*, and *Nes*. State 1 (overlapping metapterygoid) is present in *Aboma*, *Barbulifer*, *Aruma*, *Eleotrica*, *Evermannichthys*, *Risor*, *Ginsburgellus*, all species of *Gobiosoma* and *Gobiolepis*, and all species of *Tigrigobius* and *Elacatinus* except *Tigrigobius macrodon* and *Elacatinus oceanops*.

## Character 26: Preopercular process

The non-ossified space between the symplectic and preopercle is a diagnostic character for gobioids (Regan, 1911; Gosline, 1968). In percoids the metapterygoid is in close contact with the symplectic, or only a small space exists between them. In *Bostrychus*, *Oxyeleotris*, and *Gobius niger*, well-developed processes are present between

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the symplectic and preopercle at the hyomandibula junction (fig. 44). The process may result from an extension of the symplectic, extension of the preopercle, or an extension of both processes. Only the elongate process from the preopercle is considered in this study.

The presence of an elongate preopercular process is considered plesiomorphic. It is present in *Parrella*, *Microgobius*, and eleotrids. This character is not informative when the *Microgobius* group is not included as an outgroup. This character was not included in the cladogram discussed here. The preopercle process is absent for all species within the ingroup except *Gobiolepis chiquita* and *Evermannichthys* and is not informative when the hypothetical outgroup and *Aboma* are used as the outgroup.

## Sensory papillae patterns - Characters 27-34

The validity and homology of sensory papillae patterns has been debated for years with no solid resolution for either side of the argument. I believe that there are some basic patterns that are informative, at least, at the species and genus levels within the groups in this study and have incorporated those patterns into characters 27 through 34. After surveying all species in the Mediterranean, eastern Atlantic, and western Atlantic with transverse papillae patterns several basic patterns emerge. Refer to Miller (1986) for figures of Mediterranean and north-eastern Atlantic species and my figure 2 for the generalized transverse papillae pattern.

In the generalized gobiid (fig. 2) there are four transverse rows anterior to horizontal row b (1, 2, 3, 4) and three transverse rows above row b (rows 5s, 6s, and 7).

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Note that the transverse rows 1-4 are continuous rows and are never divided into a superior (s) and inferior (i) section whereas rows 5 and 6 are divided into a separate superior and inferior section. Rows 5 and 6 are generally divided by the presence of row b. When row b is reduced at the anterior end, as in *Corcyrogobius* (fig. ) the row still exists as two separate sections. I use the term 'transverse rows under the eye' to refer to those rows that are never divided, rows 1-4 in figure 2 and refer to the remaining transverse rows as 5s, 6s, and 7 (for those that occur above the level of row b) and 5i and 6i (for those rows that occur below the level of row b).

The changes that occur involve the loss of one of the anterior transverse rows (rows 1-4), the change in position of rows 5i and 6i, and the combining of row 5s with both the anterior of row b and row 5i/6i. Justification for each of the characters is discussed below.

## Character 27: Horizontal sensory papillae row b with a long anterior extension

The generalized pattern found in most gobiids is for horizontal row b to terminate anteriorly just posterior to transverse row 4 (Miller and Wongrat, 1979). In *Microgobius* and *Bollmannia,* row b extends forward through row 4, the derived condition according to Miller and Wongrat (1979) (fig. 5). *Barbulifer* possesses a row somewhat similar to this condition; however, the horizontal row is divided by the transverse rows and it does not form a single continuous row as in *Microgobius* and *Bollmannia.* The condition found in *Barbulifer* (fig. 39A) is therefore not considered homologous.

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The sensory papillae patters of *Microgobius* and *Bollmannia* were discussed by Miller and Wongrat (1979). They concluded that those genera did not belong in the tribe Gobiosomini based on the forward extension of row b, the posterior extension of row d, and row 5i/6i's not extending below row d. Synapomorphies in papillae patterns would place *Bollmannia* closer to *Cryptocentrus* and *Microgobius* closer to *Callogobius*, *Psilogobius*, and *Egglestonichthys* (Miller and Wongrat, 1979). The inclusion of *Microgobius*, *Bollmannia*, and *Parrella* in the Gobiosomini was more recently questioned by Birdsong *et al.* (1988). Their inclusion in the current matrix only adds additional length to the trees and does not resolve the species of *Gobiosoma sensu* (Böhlke and Robins, 1968) into monophyletic groupings. *Microgobius*, *Bollmannia*, and *Parrella* lack apomorphic characters shared by the other members of the tribe, such as hypural fusion, reduction in cephalic pores, and reduction in scales. Their sensory papillae patterns are not similar to the other members of the tribe, making statements of homology difficult, if not impossible. Possession of seven spines in the first dorsal fin alone hardly warrants their inclusion in Gobiosomini.

The character (anterior extension of row b) is coded as present (1) or absent (0). It is used only in the analysis which includes the *Microgobius* group.

### Character 28: Sensory papillae row 5i/6i in relation to anterior of horizontal row b

A single transverse sensory papillae row posterior to the orbit and present in relation to horizontal row b has been termed row 5i/6i by Miller (1972, 1981) and the evolution of the character discussed and figured in Van Tassell *et al.* (1988). According

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to Miller (1972, 1981), the plesiomorphic condition is the possession of two transverse rows under row b, row 5i and 6i. The assumption is made that row 6i shortens dorsally and moves anteriorly under row 5i, forming a longer row 5i/6i which is located near the anterior of row b and extends ventrally below the limit of row d. Homology for this condition remains to be tested, but intermediate conditions for this character can be seen in *Wheelerigobius malzani* (Miller, 1981) and *Vanneaugobius canariensis* (Van Tassell *et al.*, 1988). The term 5i/6i is retained here for convenience and to avoid additional confusion by inventing new terminology. Regardless of terminology, there is only one row present in relation to row b within the ingroup, and three states exist. The row is either present anterior to and separate from row b (state 0), it is present anterior to row b but attached to it (state 1), or it is located under the middle of row b (state 2). The character is run unordered in the analysis.

The hypothetical outgroup is coded as state 0 based on row 5i/6i's being anterior to row b in *Corcyrogobius, Odondebuenia,* and *Vanneaugobius.* (Their relationship to the ingroup is discussed in the section Outgroup Selection.) Distribution of these character states across the ingroup indicates state 2 (row 5i/6i under the middle of row b) is found in a paraphyletic group containing the two monotypic genera *Aboma* and *Enypnias* along with the genus *Gobiosoma.* The remaining genera, which form a monophyletic group according to the consensus tree, share state 1 (5i/6i attached to the anterior of row b), except for *Evermannichthys* and, at node 57, *Gobiolepis schultzi* and *G. spes.* *Evermannichthys* possesses row 5i/6i in front of row b; however, this genus has highly reduced papillae patterns and row 5i/6i's appearing in front of row b is most likely due to

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reduction in the forward extension of row b. In *Gobiolepis schultzi* and *G. spes,* row 5i/6i is in the middle of b. The position of both *G. schultzi* and *G. spes* within *Gobiolepis* is problematic. Their current placement within *Gobiolepis* is based on the reversal of this character and scale character 6, which would have placed them in the genus *Gobiosoma.* It is being retained here in the genus *Gobiolepis* until additional characters can be found to resolve its placement.

### Character 29: Sensory papillae row 5i/6i in relation to horizontal row d

Sensory papillae row 5i/6i extends ventrally below the level of row d in the outgroups *Corcyrogobius* (fig. 10), *Odondebuenia* (fig. 8B), *Vanneaugobius* (fig. 8A) and many of the Old World gobiids with transverse papillae patterns (Miller, 1986). Extension of row 5i/6i below row d is therefore considered plesiomorphic (state 0) and its reduction to termination dorsal to row d is derived (state 1). Within the ingroup, state 1 occurs only at node 47 and unites the genera *Nes*, *Evermannichthys*, *Risor*, *Ginsburgellus*, *Tigrigobius*, and *Elacatinus*. Within *Gobiosoma*, the species *G. parri* exhibits a reduced row 5i/6i (state 1). The placement of *G. parri* within *Gobiosoma*, while occurring with most of the outgroups, does not occur when *Vanneaugobius* is used as the outgroup. In the latter case, *G. parri* forms a monotypic genus (fig. 16). *Gobiosoma parri* is retained in *Gobiosoma* until additional characters are found to warrant its placement elsewhere.

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### Character 30: Sensory papillae row 5s connected to row 5i/6i forming a continuous row

Sensory papillae row 5 is generally divided into a superior section located above row b, termed row 5s, and inferior row below row b termed 5i (fig. 8). Within the ingroup, many species have row 5s combined with 5i, forming a continuous row (fig. 45). This is a derived condition and is coded as state 1.

The hypothetical outgroup, *Aboma*, *Enypnias*, and *Gobiosoma,* exhibit state 0 (row 5s not connected). Node 65 possesses state 1; this state is reversed at node 52 and returns to state 1 again at node 45. The genera *Tigrigobius* and *Elacatinus* possess a continuous row (state 1) and *Gobiosoma* a separate row 5s (state 0). The genus *Gobiolepis* shows a transition of this character (figs. 45, 46, 47)

### Character 31: Transverse sensory papillae row 2 in relation to row d

In members of the outgroups and most other gobiids, transverse papillae row 2 ends at or dorsal to horizontal row d. In a few genera, row 2 extends ventrally past the level of row d. Since this occurs in *Aboma*, *Enypnias*, *Aruma*, and *Barbulifer* (fig. 39), the character was included in the analysis. On the strict consensus tree, only *Aruma* and *Barbulifer* are linked by this character (node 51).

### Character 32: Transverse sensory papillae row 3 in relation to row d

In members of the outgroups and most other gobiids, transverse papillae row 3 also ends at or above the level of horizontal row d. Four taxa possess an elongate row 3:

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*Enypnias*, *Gobiolepis grosvenori*, *Aruma*, and *Barbulifer*. The character was included and coded as derived when present. It appears on the cladogram at node 51, uniting *Aruma* and *Barbulifer*.

### Character 33: Number of sensory papillae rows in front of transverse row 5

The plesiomorphic condition for number of transverse rows of papillae is four rows in front of row b (fig. 6). This condition is seen in many Old World genera such as *Gobius*, *Chromogobius*, *Didogobius*, and others. The loss of one of these rows is considered derived (Miller, 1972) and is coded as state 1 in the analysis. All members of the ingroup have lost one transverse row (figs. 48, 49). The derived state is present in all members of the '*Gobiosoma* Group' and in *Odondebuenia* and *Corcyrogobius*.

### Characters 34: Number of transverse sensory papillae rows under horizontal row b

The plesiomorphic condition is the presence of two vertical papillae rows under row b (fig. 6). This state is found in *Gobius*, *Mesogobius*, *Maulogobius*, and *Neogobius* from the eastern Atlantic and Mediterranean Sea. The loss of one row, generally assumed to be the dorsal section of row 6i, is considered derived (Van Tassell *et al.*, 1988). All members of the ingroup have lost one of the rows under row b.

### Character 35: Sphenotic to pterotic length ratio

Anteroposterior elongation of the sphenotic in *Gobiosoma sensu* (Böhlke and

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Robins, 1968) and related genera was noted by Hoese (1971) and Birdsong (1975). This elongation results in the posterior displacement of the hyomandibula as noted by Hoese (1971). The relative lengths of the sphenotic and pterotic were determined by observation of cleared and stained specimens using a dissecting microscope. Length is defined as the distance along the lateral edge of the bones and was recorded as a ratio of sphenotic length to pterotic length to the nearest 0.1. Ratios of less than 0.5:1 were considered as not being elongate and ratios of 0.9:1 elongate.

All outgroups, including the *Microgobius* group, possess a ratio of less than 0.5:1, hence that is defined as the primitive condition (state 0). The elongate condition is a synapomorphy for all species within the ingroup.

### Character 36: Brain case length to width ratio

The shape of the brain case was used by Birdsong (1975) in his discussion of relationships between *Microgobius*, *Bollmannia*, *Parrella*, *Palatogobius*, and *Gobiosoma* as defined by Böhlke and Robins (1968). He referred to the braincase of *Gobiosoma* as being elongate, but did not explain the methods used in defining his term 'elongate.' While *Gobiosoma's* brain case is not as broad as the other genera he discussed, it does not appear elongate. In this study, digital calipers were used to measure the length and width of the cranium to the nearest 0.01 mm, and those measurements were used to determined the ratios. There is no distinct difference between 'elongate' and 'non-elongate,' but I have chosen the ratio of 1.2:1 to represent the elongate condition. All members of the outgroups possess ratios of less than 0.9:1 (state 0).

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The consensus tree (fig. 54) shows that elongation of the brain case occurs at node 43, defining *Tigrigobius* and *Elacatinus*. While several members of *Tigrigobius* are coded as state 0, they have ratios of 1.1:1 and are close to the cutoff point of 1.2:1. Other species that possess elongate brain cases are *Enypnias seminudus*, *Gobiosoma ginsburgi*, *Eleotrica cableae*, and *Evermannichthys spongicola*. However, the character does not unite those genera in the consensus tree.

### Character 37: Sphenotic with a connection to the lateral wings of the supraoccipital

Within the ingroup, a connection may exist between the lateral wing of the supraoccipital and the sphenotic (fig. 50). This connection occurs when the posteromedial part of the sphenotic forms an elongate strut that extends towards the dorsomedial section of the neurocranium, just posterior to the frontals. This extension meets the lateral wing of the supraoccipital, forming, in many cases, a strong connection with the latter. The sphenotic is not elongate in the outgroups and makes no connection with the sphenotic. In these groups the lateral wing of the supraoccipital articulates with the pterotic and frontal. The presence of this connection is considered derived and is coded as state 1 in the analysis.

The derived condition is found in *Aboma*, and at node 67 including the following taxa: *Enypnias*, *Gobiosoma* (in part), *Gobiolepis*(in part), *Aruma*, *Barbulifer*, *Gymneleotris*, *Chriolepis*, *Eleotrica*, *Gobulus*, and *Nes*. This condition is lost (fig. 43) at node 46 due to the loss of elongate lateral wings of the supraoccipital in the following

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genera: *Evermannichthys*, *Risor*, *Ginsburgellus*, *Tigrigobius*, and *Elacatinus*.

### Character 38: Number of lateral projections from the anterior of the sphenotic

The sphenotic in most gobiids is a relatively short bone along the anteroposterior axis. The anterior end of the sphenotic possesses a lateral process which forms a part of the posterior orbit. Within the ingroup, elongation of the sphenotic in some taxa (character 35) creates a concomitant elongation of its process (fig. 50), which in more extreme conditions divides into two separate processes (fig. 51). Observations of ontogenetic development of *Elacatinus figaro*, raised at the New Jersey State Aquarium, show that this process develops as a single process initially with two ventral struts. A foramen then develops between the struts and widens, dividing the process into two distinct and separate processes.

The possession of two lateral processes is considered derived and is coded as state 1 in the analysis. This state occurs at node 46 and is synapomorphic uniting *Evermannichthys*, *Risor*, *Ginsburgellus*, *Tigrigobius*, and *Elacatinus*.

### Character 39: Teeth in the upper jaw with the outer row enlarged

Tooth characters are generally sexually dimorphic (Birdsong, 1975). The presence or absence of canines in the jaws of gobiids varies with sex and age of the specimen. While number of tooth rows, relative size of each of the rows, and number and position of canines were recorded, the only character that showed consistent variation was

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the development of tooth length in the outer row of the upper jaw. The presence of a reduced length in the outer row of teeth occurs in the genus *Elacatinus* and is most likely an adaptation for cleaning behavior, which all members of this genus practice. This reduction in size can result in a complete loss of the outer row, as occurs in *Elacatinus oceanops*. The presence of a reduced outer row is coded as derived (state 1).

The derived state occurs at node 41 and is a synapomorphy for the genus *Elacatinus*. While some species in the genus *Tigrigobius* exhibit cleaning behavior, they do not possess a reduced outer row of teeth. The derived state is also present in *Ginsburgellus*, but may not be homologous with that occurring in *Elacatinus*. The teeth of the outer row in *Ginsburgellus* are chisel-shaped, while the other species possess conical teeth. *Ginsburgellus* also possesses a series of teeth in the upper jaw with a morphology not observed in other gobiids examined. There is a row of elongate teeth on the inner dorsal surface of the premaxilla which point back into the mouth and slightly towards the midline. These teeth are replaced from above, according to Böhlke and Robins (1968).

### Character 40: Upper tooth row with the outer row of teeth extending to the end of the premaxilla

Hoese (1971) noted that the outer row of teeth in some species did not extend to the end of the premaxilla and used this to define his genus *Elacatinus*, including the subgenus *Tigrigobius*. All members of the outgroup possess a complete outer row of teeth. This character is coded as state 1 for the presence of a reduced or incomplete outer

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row of teeth.

This character exhibits no homoplasy; it occurs only at node 43, being a synapomorphy uniting the genera *Tigrigobius* and *Elacatinus*, as defined in this study.

### Character 41: Dorsal extension of the origin of the adductor mandibulae muscle, A1α

The dorsal extension of the A1α was discussed in the section on myology. In the outgroups and most other gobiids and eleotrids, the adductor mandibulae does not extend over the lateral edge of the sphenotic onto the dorsal cranium. Extension of A1α over the lateral edge of the sphenotic is considered the derived state and is coded as state 1 in the analysis.

While state 1 occurs in *Eleotrica*, *Gobulus*, and *Nes,* it is not a synapomorphy for those genera in the consensus tree. State 1 occurs at node 43 which includes the genera *Tigrigobius* and *Elacatinus*. While some species of *Tigrigobius* show a reversal in the state, none of the species of *Elacatinus* exhibit a reversal.

### Character 42: Insertion of the adductor mandibulae muscle A2γ along the primordial ligament

In members of the outgroup, the adductor mandibulae 2 inserts on the coronoid process of the anguloarticular. A second state occurs in which the A2 has two insertions: one on the coronoid process and a second along the primordial ligament to the maxilla. This second state is considered the derived state and is coded as state 1 in the analysis.

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See the myology section for a detailed discussion of this character.

State 1 occurs at node 67, just above *Aboma* and is possessed by all species except *Gobulus*.

## Character 43: Insertion of the adductor mandibulae muscle A2$\gamma$ on the maxilla with the A1$\gamma$

When the A1$\gamma$ and A2$\gamma$ are both present, they tend to join together at the insertion points. This condition is not found in members of the outgroup or in other gobiids or eleotrids examined in this study. The combined insertion of these muscles is therefore considered derived and is coded as state 1 in the analysis. See the section on myology for a detailed description of this character.

While this character exhibits some homoplasy within the genera *Gobiosoma* and *Gobiolepis*, the derived state is always present in *Tigrigobius* and *Elacatinus*. State 0 occurs at node 68 and 54 and state 1 at nodes 60, 63, and 43. This character is absent from *Gobiosoma parri*, *G. ginsburgi*, *G. longipala*, *Gobiolepis spilotum*, and *G. homochroma*. While they all possess both an A1$\gamma$ and an A2$\gamma$, the muscles do not unite with each other at their insertion point on the maxilla. The absence of this character in the genera *Aruma*, *Barbulifer*, *Gymneleotris*, *Chriolepis*, *Eleotrica*, *Pycnomma*, *Gobulus*, *Nes*, *Risor*, and *Ginsburgellus* is due to their lack of an A1$\gamma$.

## Character 44: Adductor mandibulae muscle A2$\gamma$ inserts with the A1$\beta$

When the A1$\gamma$ is absent and the A2$\gamma$ present, the latter may insert on the maxilla

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below the insertion point of the A1β or insert at the same point as the A1β. The A2γ inserts at the level of the A1β in all species except *Aboma*, *Gobiosoma parri*, and *Evermannichthys spongicola*. It is the possession of state 0 in *Gobiosoma parri* that causes this species to form its own monotypic genus when *Vanneaugobius* is used as the outgroup in the analysis. Its placement in *Gobiosoma* is problematic; while the other members of *Gobiosoma* are restricted to Baja California and North America, *G. parri* is found only in Uruguay. However, since few specimens of *G. parri* were available for this study, it is being retained in the genus *Gobiosoma*.

### Character 45: Adductor mandibulae muscle A1γ present

The adductor mandibulae 1γ is present in species of *Enypnias*, *Gobiosoma*, *Gobiolepis*, *Tigrigobius*, *Elacatinus*, and *Risor*. Since it is not present in any members of the outgroup or other gobiids and eleotrids examined, its presence is considered derived and is coded a state 1 in the analysis. State 1 occurs at node 67 and 43 and reverts to state 0 at node 53 and in *Risor*.

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# Phylogenetic Results

Analysis of *Gobiosoma sensu* Böhlke & Robins (1968) and related genera, using a hypothetical outgroup with multistate characters left unordered and successive weighting employed, resulted in 36 equally most parsimonious cladograms (289 steps; CI= 64; RI= 89). A strict consensus tree was produced and is shown in figures 52, 53, 54 (161 steps; CI = 31; RI = 70) and a character analysis given in Table 9. This cladogram will form the basis of the discussion; comparisons to the other cladograms using different outgroups will be discussed later. Only the characters found at the nodes are informative in the consensus tree since they are found at those nodes on all 36 trees. Characters at the terminals, while possible synapomorphies for nodes on some of the 36 trees, are not informative on the strict consensus tree presented.

The consensus tree shows that changes between species are gradual, and this renders the delimitation of genera problematic. Similar generic problems occur with the haplochromine cichlids of Lake Victoria (van Oijen, 1996) and the carcharhiniform sharks (Naylor, 1992). One is faced with producing either a complete cladistic resolution of the group, creating large numbers of monotypic genera, or creating a few paraphyletic genera to form the basis of future discussions. I have opted for the latter, defining two monophyletic genera (*Gobiosoma* and *Elacatinus*) and two paraphyletic genera (*Gobiolepis* and *Tigrigobius*). Additional studies on molecular genetics, behavior, developmental osteology, reproductive biology, and embryology need to be completed before a more complete resolution is proposed. Several studies currently underway in the

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areas of reproductive biology and embryology at the New Jersey State Aquarium and mtDNA studies at the Museo Nacional de Ciencias Naturales in Madrid, Spain support the classification presented here and are mentioned in the next section.

The generic and subgeneric names proposed by Böhlke and Robins (1968) are presented in Table 1 and the new proposed classification is given in the section on Classification. Comparisons between the two cladograms indicate that several of the subgenera proposed by Böhlke and Robins (1968) do not form monophyletic groups. The subgenera of *Gobiosoma*, *Garmannia*, and *Austrogobius* (fig.15) are distributed between the proposed genera of *Gobiosoma* and *Gobiolepis*. The subgenus *Elacatinus sensu* (Böhlke and Robins, 1968) forms a monophyletic clade and is here elevated to generic status, and the subgenus *Tigrigobius sensu* Böhlke and Robins (1968) is here designated as a paraphyletic genus. The topology of the consensus tree is highly dependent on three characters: scale distribution, oculoscapular pores, and preopercular pores. Each of these shows reversals within each of the clades. Eliminating any one or all of these characters produces no resolution and results in an overflow number of equally parsimonious trees being produced (over 2277 trees), even when successive weighting is employed.

A monophyletic ingroup (node 67) is defined by seven characters (1, 14, 20, 23, 42, 44, and 45). Two of these characters represent unique synapomorphies for this clade. They are 1) the loss of cephalic head pore G and 2) the presence of hypurals 1+2 fused with 3+4 (characters 14 and 20). The presence of a barbel on the upper lip (character 1, state 1), while possessed by *Enypnias* and all members of *Gobiosoma* occurs in two

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species of *Gobiolepis* (*G. spilotum* and *G. homochroma*), and the genera *Aruma*, and *Barbulifer*. The barbel is lost in all other species. The absence of a process on the maxilla (character 23, state 1) occurs in all genera and species except *Barbulifer* and *Risor,* where it is present (state 0). The presence of an insertion of the A2 on the primordial ligament (character 42, state 1) occurs in all species of *Gobiosoma*, *Gobiolepis*, *Tigrigobius*, *Elacatinus*, and related genera except *Gobulus*. Adductor mandibulae 2γ is present and inserts along with A1β in all genera and species except *Gobiosoma parri* and *Evermannichthys*. Adductor mandibulae 1γ is present in *Enypnias*, *Gobiosoma*, *Gobiolepis*, *Tigrigobius*, *Elacatinus*, and *Risor*. It is completely absent from all of the related genera.

Three monophyletic clades exist at the next level. The monotypic genus *Enypnias*, a monophyletic *Gobiosoma*, and a monophyletic clade containing *Gobiolepis*, all related genera, *Tigrigobius*, and *Elacatinus*. *Enypnias* is defined by five characters, none of which are unique to the node. They include 1) the absence of basicaudal scales (character 9); 2) the absence of cephalic head pore F (character 13); 3) sensory papillae row 2's extending below the level of row d (character 31); 4) sensory papillae row 3's extending below the level of row d (character 32); and 5) and possession of an elongate brain case (character 36).

***Gobiosoma***: The monophyly of *Gobiosoma* is based on two multistate scale characters: the presence of some scales on the caudal peduncle (character 5, state 1) and the absence of scales on the posterior trunk (character 6, state 2). While both of those characters exhibit state changes within this clade and the clade comprised of *Gobiolepis*

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plus all other related genera, *Tigrigobius,* and *Elacatinus; Gobiosoma* remains a separate clade based on its retention of a sensory papillae pattern character which it shares with *Aboma* and *Enypnias,* sensory papillae row 5i/6i's being located under the middle of row b (character 28, state 2). In all other genera and species of the ingroup, row 5i/6i occurs either attached to the front of row b or is located just anterior of row b.

Changes in character states occur within the *Gobiosoma* clade. Anterior trunk scales (character 7), caudal peduncle scales (character 5), and modified basicaudal scales (character 9) are lost in most of the species. The general trend is for loss of all scales, including the modified basicaudal scales, in the more derived members of this clade.

***Gobiolepis*:** The *Gobiolepis* grade is defined by the possession of sensory papillae row 5i/6i's being attached to the anterior of row b (character 28, state 1). This single character is responsible for the major division of the ingroup. The shift of sensory papillae row 5i/6i to the anterior of row b separates species above this level from all others in which the row 5i/6i is located under the middle of row b. Only two exceptions occur. Row 5i/6i reverts to the middle of row b (node 57) when it unites *Gobiolepis spes* and *G. schultzi* and changes to state 0 (row 5i/6i in front of row b and not attached) in *Evermannichthys*. As discussed above, the placement of *Gobiolepis spes* and *G. schultzi* within the *Gobiolepis* grade is very tentative and is based on the reversal of characters that would have placed them in the *Gobiosoma* clade. *Evermannichthys* exhibits extensive reduction in sensory papillae numbers within each row. Having row 5i/6i in front of row b is due in this case to the loss of papillae from the anterior of row b and not the movement of row 5i/6i in front of row b. Comments on character 28 state changes

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were previously discussed in the character and discussion section above.

*Gobiolepis* is a paraphyletic assemblage with six of the seven nodes giving rise to terminal taxa, each with one or two characters per node. The general tree topology from the beginning of the *Gobiolepis* grade up is the result of: 1) the movement of sensory papillae row 5i/6i to the anterior of row b; 2) the trend for loss of head cephalic pores; and 3) the loss of body scales. Of the 36 trees produced in the analysis, the species composition and arrangement of the taxa within Gobiolepis remains unchanged. The only variation in the 36 equally parsimonious trees occurs in *Tigrigobius*.

The genus as defined here starts with *Gobiolepis spilotum* at node 65 and ends at node 54 with *Gobiolepis homochroma*. The species included in *Gobiolepis* are *Gobiolepis spilotum*, *G. grosvenori*, *G. chiquita*, *G. hildebrandi*, *G. sp. nov.* B, and *G. homochroma*. In addition, *Gobiosoma spes* and *G. schultzi* are placed in this grade based on the reduction of preopercle pores from 3 in *Gobiosoma* to 2 in *Gobiolepis*. A greater emphasis on papillae patterns places both of the species back in the *Gobiosoma* clade.

The following is a description of the characters that define each of the nodes within *Gobiolepis*. Node 63 is defined by two characters: the absence of a barbel on the upper lip (character 1, state 0) and the cheek muscle adductor mandibulae 2γ's inserting with adductor mandibulae 1γ on the maxilla (character 43, state 1). The absence of a barbel on the upper lip occurs in only two of the members of this genus, *Gobiolepis spilotum*, *G. homochroma*, and in all members of *Gobiosoma*. The insertion of adductor mandibulae 2 γ on the maxilla and also on adductor mandibulae 1γ occurs in all species in *Gobiolepis* except *G. spilotum* and *G. homochroma*. The occurrence of this character

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is less common in *Gobiosoma* but always occurs in *Tigrigobius* and *Elacatinus*. Since this character is unambiguous for all other genera, it is likely that interspecific transformations are taking place within *Gobiosoma* and *Gobiolepis*.

At node 61 the posterior oculoscapular pores K & L are absent (character 15, state 1). This state change remains for all other genera above this node. Node 59 possesses two characters: the absence of basicaudal scales and the presence of only two preopercle pores. Basicaudal scales exhibit extensive homoplasy within the ingroup. The number of preopercle pores is homoplastic within *Gobiolepis*. In all other genera, the number of pores is not variable and within the ingroup show a general decrease from 3 pores in *Gobiosoma* to two pores in *Tigrigobius* and *Elacatinus* and to no pores in most of the related genera.

Node 57 (characters 6, 28, and 30) supports the clade containing *Gobiolepis spes*, *G. schultzi*. The placement of this clade within *Gobiolepis* is questionable. Its placement is dependent on the reversal of the characters that define the *Gobiosoma* clade. Multistate character 6 (scales on posterior trunk) is state 1 at this node and is also found in some species of *Gobiosoma*. Character 28 (sensory papillae row 5i/6i in relation to row b), also multistate, is state 2 at this node, representing a secondary reversal to the state found in *Aboma*, *Enypnias*, and all species of *Gobiosoma*. Character 30 (row 5s connected to row 5i/6i) is present (state 1) at node 56 . There appears to be a transition of this character within *Gobiolepis*. While 5i/6i has moved towards the anterior end of row b, row 5s does not form the single papillae line that is present in *Gobiolepis hildebrandi*, *G. sp. nov.* b and *G. homochroma*, all members of *Tigrigobius* and *Elacatinus*. Figures 46, 47, and 7

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show the changes in the papillae pattern that occur within the group. Note the pattern forms in *Gobiolepis spilotum*, *G. grosvenori*, *G. chiquita* and the final pattern present in the remaining species shown in figure 45.

The coding for all characters in the matrix is the same for *G. spes* and *G. schultzi.* It is likely that *G. schultzi* should be synonomized with *G. spes*. The description of *G. schultzi* is based on 19 specimens collected from Lake Maracaibo in Venezuela and 17 additional specimens from nearby localities. All of the specimens are under 22 mm SL and the trait that separates the two species from each other (elongate first dorsal fin rays) may not develop until they attain a larger size (Böhlke and Robins, 1968). They are being retained within *Gobiolepis* until additional information is obtained to resolve their placement.

Node 55 (*Gobiolepis sp. nov.* B) is supported by the symplesiomorphic state for character 7, the presence of a completely scaled anterior trunk. In the *Gobiolepis,* grade species are either completely or partly scaled on the anterior trunk, whereas *Gobiosoma* species are either partly scaled or posses no scales on the anterior trunk.

Node 54 (*Gobiolepis homochroma*) possesses character 43 state 0 (adductor mandibulae A2γ does not insert on A1γ and the maxilla). As shown above, this character is only variable in *Gobiolepis* and *Gobiosoma.*

The related genera, those not included in the subgenera of *Gobiosoma* according to Böhlke and Robins (1968), occur from node 53 to 43. Four characters define this node. They are 1) no scales present on the posterior trunk (character 6), 2) no scales present on anterior trunk (character 7), 3) cephalic head pore C absent (character 10), and

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4) adductor mandibulae 1γ absent (character 45). None of these characters are unique at this level. The absence of scales on the posterior and anterior trunk does not reverse at a node above this point but does occur in several of the terminal taxa. Cephalic pore C is lost (character 10, state 1) at this node and regained (state 0) in *Evermannichthys* and remains present for the rest of the tree. Only *Risor* is variable, with the pore C's being either present or absent.

Adductor mandibulae A1γ is distinctly absent from most genera at this node, but reappears in *Risor* and at node 43 all *Tigrigobius* and *Elacatinus*. It is absent from *Aboma,* the hypothetical outgroup, and all other outgroup genera examined in this study.

*Barbulifer* and *Aruma* form a monophyletic clade based on four characters. Presence of a barbel on the lip (character 1 state 1), no scales on caudal peduncle (character 5 state 2), sensory papillae rows 2 and 3 extending ventrally below row d (characters 31 and 32, state 1) define this monophyletic group. None of these characters are unique. *Enypnias* possesses all of the above except that it is scaled on the posterior trunk; both *Aruma* and *Barbulifer* are completely scaleless.

Node 52 defines two monophyletic clades: the *Gymneleotris*, *Chriolepis*, *Eleotrica*, and *Pycnomma* clade and the *Gobulus* 'plus all other species' clade. The node is supported by four characters: cephalic pore D absent (character 11, state 1), no preopercular pores present (character 16, state 2), metapterygoid's not overlapping the quadrate (character 25, state 0), and sensory papillae row 5s not connected to papillae row 5i/6i (character 30, state 0).

Node 50, which includes Gymneleotris and the clade containing Chriolepis,

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Eleotrica, and Pycnomma is defined by possessing pelvic fins that do not form a complete disc (character 3, state 1). This character is unique within the ingroup and present only at this node.

The *Chriolepis* clade (node 48) is defined by the unique possession of an unbranched fifth pelvic ray (character 2 state 1), basicaudal scales present (character 9 state 1), and the presence of cephalic pore D (character 11, state 0) in *Eleotrica* and *Pycnomma*.

Node 47, which contains *Nes*, *Evermannichthys*, *Risor*, *Ginsburgellus*, *Tigrigobius*, and *Elacatinus*, is defined by three characters: 1) the presence of an increase in total vertebrae to 28 (character 17 state 1), 2) an increase in caudal vertebrae to 17 (character 18 state 1), and 3) sensory papillae row 5i/6i's not extending below row d (character 29 state 1). With the exception of *Evermannichthys*, none of these characters exhibit changes in state at nodes above this point.

The next two nodes contain the monotypic sponge-dwelling genera *Evermannichthys* and *Risor*. At this level, the supraoccipital lacks the elongate lateral wings (character 22 state 1), and there are two lateral projections from the sphenotic (character 38, state 1). These characters are unique and are synapomorphies linking the remaining species.

Node 44 defines *Ginsburgellus* and the large clade of *Tigrigobius* and *Elacatinus*. Böhlke and Robins (1968) proposed a close relationship between *Ginsburgellus* and both their subgenera of *Tigrigobius* and *Elacatinus*. Here *Ginsburgellus* forms the sister group to the *Tigrigobius* and *Elacatinus* clade. This node possesses three characters, one of

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which is unique to all but two species of *Tigrigobius*: the elongation of the fifth pelvic process (character 21, state 1).

Node 43 defines a monophyletic clade comprising the genera *Tigrigobius* and *Elacatinus*. This clade contains all the coral reef species and is defined by seven characters, one of which (character 40) is unique to the clade. The characters defining node 43 include the presence of basicaudal scales (character 9 state 1), a metapterygoid with an expanded dorsal extension (character 24 state 1), an elongate brain case (character 36 state 1), the outer row of teeth in the upper jaw's not extending to the end of the premaxilla (character 40 state 1), the dorsal origin of the adductor mandibulae A1α's extending over the lateral edge of the sphenotic (character 41 state 1, in most species), the adductor mandibulae A2γ's inserting with the adductor mandibulae A1γ and the maxilla (character 43 state 1), and adductor mandibulae A2γ present in all species (character 45 state 1).

The genus *Tigrigobius* as defined here is paraphyletic due to the inclusion of *Elacatinus*. The monophyletic clade of *Elacatinus* is represented by three species in this analysis. There are, however, ten additional species that belong in the clade. All are exceedingly similar in osteology, meristics, external appearance, and behavior. Their similarities are so close that many species readily hybridize in the aquarium. The *Elacatinus* clade is defined by two characters at node 41: the absence of basicaudal scales (character 9 state 0) and teeth in upper jaw not enlarged (character 39 state 1). The lack of enlarged teeth in the upper jaw is most likely related to cleaning behavior, which most species within the group have been observed to practice (Van Tassell *et al.*, 1994) .

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To have a better understanding of which nodes and clades are supported by the characters, the more homoplastic characters were removed individually and in groups to ascertain their effect on tree topology. In the *Gobiosoma* clade, *Gobiosoma parri* is the only species that appears outside the clade, forming a separate monophyletic genus between *Aboma* and *Enypnias*. The same pattern is observed when *Vanneaugobius* is used as the outgroup (fig. 16). Within the *Gobiolepis* grade, *Gobiolepis spilotum*, *G. grosvenori*, and *G. chiquita* form their own monophyletic clade when scale characters are removed. The character that unites them under these conditions is character 30 (row 5s not connected to 5i/6i). The change in this character is discussed above.

The species that show changes in clades are all associated with the genera *Gobiosoma* and *Gobiolepis*. Both of these proposed genera exhibit changes in scale characters and posterior oculoscapular pores K and L. The species within *Gobiosoma* and *Gobiolepis* are distributed from New York to Uruguay in the Atlantic and from Baja California to northern Peru in the Pacific (figs. 55,56). They occupy habitats in coastal and estuarine water. The *Tigrigobius* and *Elacatinus* clades do not exhibit the magnitude of changes in these characters seen in *Gobiosoma* and *Gobiolepis*. Both *Tigrigobius* and *Elacatinus* are restricted to more tropical waters, generally inhabiting coral reef environments (fig. 57,58).

## Characters defining the genera

This section includes comments on the character distribution within the genera *Aboma*, *Enypnias*, *Gobiosoma*, *Gobiolepis*, *Tigrigobius*, and *Elacatinus* with only

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occasional reference to the 'related genera'.

All of the above genera possess ventral fins which are united into a complete pelvic disk, all pelvic fin rays branched, seven spines in the first dorsal fin, a pterygiophore formula of 3-221110, the lack of a preopercle process, and an elongate sphenotic. The elongate sphenotic is the only character unique to those genera. A complete pelvic disk with all branched rays is found in most gobies. The lack of a complete disk is found within the ingroup only in *Gymneleotris*, *Chriolepis*, *Eleotrica*, and *Pycnomma*, where the disk is assumed to be secondarily lost. Within those genera the loss of a branched fifth pelvic ray also occurs uniting *Chriolepis*, *Eleotrica*, and *Pycnomma*. Seven spines in the first dorsal is not uncommon in other gobiids but that in combination with the pterygiopore formula of 3-221110 is found, according to Birdsong (1988), only in the Philippine genus *Tukugobius*.

Vertebral number exhibits no homoplasy within the above genera. The total vertebral number is 27 in *Aboma*, *Enypnias*, *Gobiosoma*, and *Gobiolepis*. This increases to 28 in *Tigrigobius* and *Elacatinus*. The increase is due to a change in the caudal vertebral number from 16 in *Aboma*, *Enypnias*, *Gobiosoma*, and *Gobiolepis* to 17 in *Tigrigobius* and *Elacatinus*. The increase in caudal vertebrae occurs at the level of *Nes* in the cladogram. This character plus additional characters in myology place *Nes*, *Risor*, *Evermannichthys*, and *Ginsburgellus* all as close contenders for the sister-group to the *Tigrigobius* and *Elacatinus* complex. The large number if apomorphic character exhibited by each of the genera prevent a clear resolution given the present set of characters employed.

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There are two sensory papillae pattern characters that are unchanged within the ingroup. One is the reduction in the number of transverse row under the eye from four in most of the outgroups to three. The second change is the number of rows under row b being reduced from two rows to only one.

Within the myology character the A1$\gamma$ is present in all of the above genera except *Aboma*. The dorsal extent of the A1 over the oculoscapular canal is relatively consistent in its distribution. It does not extend over the canal in *Aboma*, *Enypnias*, *Gobiosoma*, and *Gobiolepis*. It does extend over the canal in all species of *Elacatinus* examined but remains variable with in the genus *Tigrigobius*.

The last character that exhibits little homoplasy is the connection between the supraoccipital and the sphenotic. The connection exists in *Aboma*, *Enypnias*, *Gobiosoma* (except *G. parri*), and *Gobiolepis* (except *G. grosvenori* and *G. chiquita*). Both the *Gobiosoma parri* and *Gobiolepis grosvenori* specimens are very small and this might result in the connection not developing. In *Gobiolepis chiquita* the specimens are large enough and the sphenotic and supraoccipital close to connecting, but the actual connection does not develop. This connection does not occur in any of the outgroups examined or in any of the other gobiids examined in the course of this study. Within *Tigrigobius* and *Elacatinus* there is no connection, except for *Tigrigobius zebrella* in which there is a slight connection.

### ***Aboma***

The genus *Aboma* forms the sister-group to the remaining '*Gobiosoma* Group'

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based on: 1) the lack of hypural fusion, 2) cephalic head pore G present, 3) the adductor mandibulae 2 not inserting along the primordial ligament, and 4) the absence of the adductor mandibulae 1γ. *Aboma* also is more completely scaled than other species in the ingroup. The scales extend forward to the first or second dorsal spine. The upper naked area extends from the upper pectoral fin base to the first of second dorsal origin and the lower naked area extends from the lower margin of the pectoral fin base to the anus. *Aboma* shares the following sensory papillae patterns with *Enypnias* and *Gobiosoma*: 1) row 5i/6i located under the middle of row b, 2) row 5i/6i extending below the level of row d and 3) papillae row 5s is not connected to row 5i/6i. *Aboma* also possess the apomorphic character of transverse row 2 extending below the level of row d. *Enypnias* possess a similar papillae pattern but it's row 3 also extends below the level of row d.

### *Enypnias*

The position of *Enypnias* is not resolved. It shares sensory papillae patterns with *Aboma* and *Gobiosoma* such as row 5i/6i under the middle of row b, row 5i/6i extending below row d, and row 5s not connected with row 5i/6i that place it close to those genera. It also shares with *Aboma* a similar scale distribution pattern, the presence of cephalic head pores K and L, and papillae row 2 extending below the level of row d. The presence of a large barbel on the upper lip and papillae rows 2 and 3 extending below the level of row d would place it close to *Aruma* and *Barbulifer*, but those characters tend to be more homoplastic and are given less weight in the current analysis which places *Enypnias* closer to *Gobiosoma*.

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## *Gobiosoma*

The species of *Gobiosoma* share several papillae patterns with *Aboma* and *Enypnias*, as mentioned above, which removes them from the rest of the ingroup, especially *Gobiolepis*. With the exception of differences in papillae patterns both *Gobiosoma* and *Gobiolepis* are very similar. The other characters they possess, which have been used by previous authors to form subgenera, are all homoplastic within the genera *Gobiosoma* and *Gobiolepis* (as defined in this study). The monophyly of the *Gobiosoma* clade is based on two scale characters (5,6) which are homoplastic within the clade and the remaining genera of the ingroup. However, *Gobiosoma* is less scaled than *Aboma*, *Enypnias* and *Gobiolepis*, with four of the seven species being scaleless. None of the species of *Gobiolepis* are scaleless. All species of Gobiosoma also possess a small barbel on the upper lip. A similar barbel is possessed by only two of the eight species in *Gobiolepis*.

## *Gobiolepis*

The genus *Gobiolepis* is more heavily scaled then *Gobiosoma*. All of the species are completely scaled on the caudal peduncle and five of the eight have scales on the posterior and anterior trunk. No species in the genus are without scales. The scale characters plus the forward shift in papillae row 5i/6i to the anterior of row b separate these species from those placed in *Gobiosoma*. This genus remains a very paraphyletic assemblage with very weak support for all of the nodes. Additional studies are certainly necessary to resolve the species of *Gobiolepis* and *Gobiosoma*.

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### *Tigrigobius* and *Elacatinus*

The *Tigrigobius* and *Elacatinus* clade is well separated from *Gobiosoma* and *Gobiolepis*. The possession of two separate lateral projection from the sphenotic, the lack of lateral wings on the supraoccipital, and the outer row of teeth in the upper jaw not extending to the posterior end of the premaxilla is found in all of the species. Both genera also possess a wide metapterygoid which overlaps the quadrate in all species except *T. macrodon* and *E. oceanops*. While both of these characters are variable in the other genera and certainly highly variable in the subfamily (see Harrison, 1989 for comments on variability and polarization of this character) it is consistent within these genera.

*Elacatinus* is separated from *Tigrigobius* by two characters in this analysis; the lack of basicaudal scales (a very homoplastic character of little value) and the outer row of teeth in the upper jaw being reduced in size. This tooth character is found only in *Ginsburgellus* where it is assumed to have evolved independently. While the teeth of *Ginsburgellus* are reduced their shape is different and were most likely evolved for its specialized life living in association with sea urchins.

## Additional Support

Additional support for the tree presented comes from data being collected as part of the captive breeding program at the New Jersey State Aquarium at Camden. Eight species within the ingroup were bred and information on egg, larval, and breeding behavior noted. To date two species of *Gobiosoma* (*G. bosc*, *G. robustum*), two species

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of *Tigrigobius* (*T. puncticulatum, T. macrodon*) and five species of *Elacatinus* (*E. oceanops*, *E. genie*, *E. figaro*, *E. randalli*, *E. evelynae*) have been bred. The eggs of *Tigrigobius* and *Elacatinus* possess an extra internal membrane, are highly elliptical, and possess 4 to 6 protruberances at the distal end; those of *Gobiosoma* are only slightly elliptical with no protruberances or extra internal membrane. Differences between *Elacatinus* and *Tigrigobius* occur in spawning position and the care of their eggs. *Tigrigobius* deposit the eggs on the inside bottom of rock caves and only the male guards the eggs, leaving for only a second or two to feed. In *Elacatinus* the eggs are deposited inside caves at the top; both parents participate in brooding the eggs; and both parents may leave the eggs unguarded, remaining on top of the rock caves rather than on the inside with the eggs. The mtDNA studies are very preliminary at this time, but they also show a very close link between members of *Elacatinus* and indicate that the separation of *Tigrigobius* from *Elacatinus* may be warranted.

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## Classification

Species are listed alphabetically by genera according to the proposed classification. For the genera *Gobiosoma*, *Gobiolepis*, *Tigrigobius*, and *Elacatinus*, an asterisk before the species name indicates a species that was not included in the study but is assumed to be in that genus based on external characters. Related genera, with all included species, are listed following the aforementioned genera. Species synonymies are compiled primarily from the literature.

### ***Gobiosoma* Girard, 1858**

Type species: *Gobiosoma molestum* Girard, 1858 = *Gobiosoma bosc* Lacepède, 1800, by subsequent designation by Bleeker, 1874: 310.

*Austrogobius* de Buen, 1950: 122 (name introduced); 1951: 64-68; Type species: *Gobiosoma parri* Ginsburg, 1933b, by monotypy.

*Dilepidion* Ginsburg, 1933a: 17; Type species: *Gobiosoma ginsburgi* Hildebrand and Schroeder, 1928, by original designation.

*Garmannia* Jordan and Evermann, in Jordan *et al.* 1895: 497; Type species: *Gobius paradoxus* Günther, 1861a:372, by original designation.

### ***Gobiosoma bosc* (Lacepède, 1798)**

*Gobius bosc* Lacepède, 1800:555 (from a manuscript by Bosc; as restricted by Hildebrand and Schroeder.)

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*Gobius alepidotus* Bloch and Schneider, 1801 (Apparently based on Lacepède's account)(Ginsburg, 1933b)

*Gobius viridipallidus* Mitchil, 1815 (New York; as restricted by Cuvier and Valenciennes)(Ginsburg, 1933b)

*Gobiosoma molestum* Girard, 1858 (Ginsburg, 1933b)

*Gobiosoma alepidota* Uhler and Lugger; 1876 (Ginsburg, 1933b)

**_Gobiosoma ginsburgi_ Hildebrand and Schroeder, 1928**

*Gobiosoma ginsburgi* Hildebrand and Schroeder, 1928:324; Holotype USNM 87655; Type locality: Chesapeake Bay.

***Gobiosoma sp. nov H***

*Gobiosoma heterolepidotum* (manuscript name)Hoese, 1971 :76 (unpublished thesis); Manuscript type SIO 67-274 (formerly UA 65-33); Type locality: Punta Peñasco, Sonora, Mexico. Conglomerate reef, midtidal pool.

**_Gobiosoma longipala_ Ginsburg, 1933a**

*Gobiosoma longipala* Ginsburg, 1933a:18; Holotype USNM 86158; Type locality: Boca Grande, Florida, 2 April 1917.

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**_Gobiosoma nudum_ (Meek and Hildebrand, 1928)**

*Gobiosoma nudum* (Meek and Hildebrand, 1928): 889, pl. 88; Type locality: tidepools, Panama City, Pacific coast of Panama.

**_Gobiosoma parri_ Ginsburg, 1933b**

*Gobiosoma parri* Ginsburg, 1933b: 44-46; Holotype: USNM 93177; Type locality: Pocitos, Uruguay.

**_Gobiosoma paradoxum_ (Günther, 1861a)**

*Gobius paradoxus* Günther, 1861a: 372; Holotype not listed in original publication; Type locality: western coast of Central America; dorsal spines erroneously listed as six; 1861b: 549-550 (description).

**_Gobiosoma robustum_ Ginsburg, 1933a**

*Gobiosoma robustum* Ginsburg, 1933a:15-16; Holotype USNM 92802; Type locality: Laguna Madre, near Corpus Pass, Texas.

**_Gobiolepis_ Ginsburg, 1944**

*Gobiolepis* Ginsburg, 1944: 379; Type species: *Garmannia hildebrandi* Ginsburg, 1939a, by original designation.

*Gobiohelpis* Ginsburg, 1944: 380; Type species: *Garmannia spes* Ginsburg, 1939a:69, by original designation.

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*Gobiculina* Ginsburg, 1944: 380; Type species: *Garmannia homochroma* Ginsburg, 1939:62, by original designation.

***Gobiolepis chiquita*** **(Jenkins and Evermann, 1889)**

*Gobius chiquita* Jenkins and Evermann, 1889: 146; Holotype USNM 39634; Type locality: Guaymas, Mexico; spines erroneously listed as six.

***Gobiolepis grosvenori*** **(Robins, 1964)**

*Garmannia grosvenori* (Robins), 1964:399-402; Holotype ANSP 101166; Paratypes UMML 14380; Type locality: Boca Chita Pass, Dade Co., FL.

***Gobiolepis hildebrandi*** **(Ginsburg, 1939a)**

*Garmannia hildebrandi* Ginsburg, 1939a: 61-62; Holotype USNM 107297; Type locality: Gatun Locks, upper lock, Atlantic side of Panama Canal; also from Pedro Miguel Locks, Pacific side.

***Gobiolepis homochroma*** **(Ginsburg, 1939a)**

*Garmannia homochroma* Ginsburg, 1939a: 62-63; Holotype USNM 107296; Type locality: Pedro Miguel Locks, Pacific slope of Panama.

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***Gobiolepis schultzi* (Ginsburg, 1944)**

*Garmannia schultzi* Ginsburg, 1944: 375-378; Holotype USNM 121546; paratypes (6) USNM 121547; Type locality: Venezuela, Lake Maracaibo, 7 km S of Maracaibo City.

***Gobiolepis spes* (Ginsburg, 1939a)**

*Garmannia spes* Ginsburg, 1939a: 62; Holotype USNM 107299; Type locality: Canal Zone, dry dock, Mt. Hope.

***Gobiolepis spilotum* (Ginsburg, 1939a)**

*Garmannia spilota* Ginsburg, 1939a: 62; Holotype USNM 81828; Type locality: Colon, Panama, in tidepools.

****Gobiolepis yucatanum* (Dawson, 1971)**

*Gobiosoma yucatanum* Dawson, 1971: 433-437; Holotype USNM 205368; Type locality: Mexico, Quintana Roo, south side of harbor of Cd. Chetumal.

***Tigrigobius* Fowler, 1931**

*Tigrigobius* Fowler, 1931: 401 Type species: *Gobiosoma macrodon* Beebe and Tee-Van 1928, by original designation.

*Gobicula* Ginsburg, 1944: 379. Type species: *Garmannia gemmata* Ginsburg 1939b, by original designation.

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***Tigrigobius diqueti* Pellegrin, 1901**

*Tigrigobius digueti* Pellegrin, 1901

*Gobiosoma brocki* Ginsburg, 1938a: 58-59; Holotype CAS-SU 32970; Type locality: Los Frailes near Cape San Lucas, Baja CA.

***Tigrigobius dilepis* (Robins & Böhlke, 1964)**

*Garmannia (Tigrigobius) dilepis* Robins and Böhlke, 1964: 3-6, fig. 2; Holotype ANSP 100815; Type locality: Sta. 589, coral head off large bay at NW end of Conception Island, Bahamas, 25 ft..

***Tigrigobius gemmatum* (Ginsburg, 1939a)**

*Garmannia gemmata* Ginsburg, 1939a:3-5, fig. 2; Holotype USNM 107291; Type locality: Old Providence Island, Caribbean Sea.

****Tigrigobius inornatus* (Bussing, 1990)**

*Elacatinus inornatus* Bussing, 1990:109-110; Holotype LACM 32493-43; Type locality: Isla Cocinero, Islas Murcielagos, Costa Rica (10051'N, 85054'W) depth 9 meters.

***Tigrigobius janssi* (Bussing, 1981)**

*Elacatinus janssi* Bussing, 1981: 251-256, fig. 1; Holotype LACM 32524-45; Type locality: Bahia Herradura just south of the Gulf of Nicoya (9$^{0}$38'45"N, 84$^{0}$40'55"W), Pacific coast of Costa Rica.

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******Tigrigobius limbaughi*** **(Hoese, 1984)**

*Elacatinus limbaughi* Hoese: Species pictured with description in Burgess & Axelrod, 1984. Species was never described by Hoese. No type exists. This species may be a variation of *T. digueti* and not a valid species.

***Tigrigobius macrodon*** **(Beebe & Tee-Van, 1928)**

*Gobiosoma macrodon* Beebe & Tee-Van, 1928:226; Holotype originally no. 7462 in the Tropical Research Collection of the New York Zoological Society now at USNM 170896; Type locality: Port-au-Prince Bay, Haiti.

***Tigrigobius multifasciatum*** **(Steindachner, 1876)**

*Gobiosoma multifasciatum* Steindachner, 1876:Sitzbar. k. k. Ak. Wiss. Wien 74 (abt.1): 231 and 238 (Ichthyol. Beit. 5: 183 and 190); Type locality: St. Thomas; Barbados and Bartholomew, Lesser Antilles.

******Tigrigobius nesiotus*** **(Bussing, 1990)**

*Elacatinus nesiotus* Bussing, 1990:110-112; Holotype LACM 44821-3; Type locality: East side of Isla del Coco, 300m SW of Cabo Descubierto; depth 20 meters.

***Tigrigobius pallens*** **(Ginsburg, 1939a)**

*Garmannia pallens* Ginsburg, 1939a:63; Holotype USNM 107327; Type locality: Barahona Harbor, Santo Domingo, 2-4 ft.

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***Tigrigobius puncticulatum*** **(Ginsburg, 1938)**

*Gobiosoma punticulatum* Ginsburg,1938: 57-58; Holotype CAS-SU 32963; Type locality: Los Frailes, near Cape San Lucas, Baja California.

*Gobiosoma rubrifrons* Fowler, 1944: 282, 383, fig. 237, Type locality: Saboga, Perlas Islands, Gulf of Panama.

***Tigrigobius saucrum*** **(Robins, 1960)**

*Garmannia saucra* Robins, 1960: 281-285, 1 fig.; Holotype ANSP 92985; Type locality: South Cay, Jamaica, 3 miles south of Port Royal, north side of cay in 3-5 ft. of water.

***Tigrigobius zebrella*** **(Robins, 1958)**

*Garmannia zebrella* Robins, 1958:192-194; Holotype ANSP 53387; Type locality: Monos Island, Trinidad.

***Elacatinus*** **Jordan, 1904**

*Elacatinus* Jordan, 1904: 542; Type species: *Gobiosoma oceanops* Jordan, 1904, by original designation and by monotypy. This subgenus frequently has been misspelled in the literature, *Elecatinus* and *Lactinius* being the most common misspellings.

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******Elacatinus atronasum* **(Böhlke & Robins, 1968)**

*Gobiosoma (Elacatinus) astronasum* Böhlke and Robins, 1968: 88-90, fig. 6; Holotype: UF 15427; Type locality: Bahama Islands, at the eastern edge of the Great Bahama Bank.

******Elacatinus chancei* **(Beebe & Hollister, 1933)**

*Gobiosoma chancei* Beebe and Hollister, 1933: 87-88, fig. 17; Holotype USNM 170955; Type locality: Grenada, British West Indies, St. George's Bay.

******Elacatinus evelynae* **(Böhlke & Robins, 1968)**

*Gobiosoma (Elacatinus) evelynae* Böhlke and Robins, 1968: 103-109, fig. 10; Holotype ANSP 110559; Type locality: sta. 496, Bahamas, Great Bahama Bank, Nassau vicinity, Green Cay (N of Rose Island), ca. 1/4 mi. NNW of Cay; ca. 50 ft.

***** ***Elacatinus figaro*** **Sazima, Moura, and Rosa, 1996**

*Elacatinus figaro* Sazima, Moura, and Rosa, 1996: 33-38, figs. 1-6; Holotype MZUSP 50859; Type locality: Pedra do Navio, Ilha Anchieta, Ubatuba, São Paulo, Brazil, depth 5 m, 02 May 1996.

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***Elacatinus genie* (Böhlke & Robins, 1968)**

*Gobiosoma (Elacatinus) genie* Böhlke & Robins, 1968: 109-114, fig. 11; Holotype ANSP 110574; Type locality: sta. 243, Bahamas, Great Bahama Bank, Nassau vicinity, between North Cay and the small cay just off Long Cay; 6-13 ft.

***Elacatinus horsti* (Metzelaar, 1922)**

*Gobiosoma horsti* Metzelaar, 1922: 139, fig. 2; Lectotype: Zool. Mus. Amsterdam 446; Type locality: Caracasbay, SW part of Curacao, from sponge.

***Elactinus illecebrosum* (Böhlke & Robins, 1968)**

*Gobiosoma (Elacatinus) illecebrosum* Böhlke & Robins, 1968: 114-116, fig. 12; Holotype ANSP 110693; Type locality: sta. WAS-CARIB-8, Yucatan, Banco Chinchorro, around Cay Norte; 15-20 ft.

***Elacatinus louisae* (Böhlke & Robins, 1968)**

*Gobiosoma (Elecatinus) louisae* Böhlke and Robins, 1968: 90-94, fig.7; Holotype ANSP 110691; Type locality: sta. 14 (G64-43), W side of Grand Cayman Island at dropoff, offshore from N side of Georgetown; 100-115 ft.

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***Elacatinus oceanops* Jordan, 1904**

*Elacatinus oceanops* Jordan, 1904: 542, pl.2, fig.3; Holotype CAS-SU 8365, cotype CAS-SU 2757; Type locality: Garden Key, Tortugas, Florida; habitat on coral heads at depths of 3-8 ft.

***Elacatinus prochilos* (Böhlke & Robins, 1968)**

*Gobiosoma (Elacatinus) prochilos* Böhlke and Robins, 1968: 97-100, fig.9; Holotype ANSP 110628; Type locality: sta. TE-57, St. Barthelemy, Port de Gustavia, off the rocky cliffs just S of Anse Galet; 40-45 ft.

***Elacatinus randalli* (Böhlke & Robins, 1968)**

*Gobiosoma (Elacatinus) randalli* Böhlke and Robins, 1968: 94-97, fig. 8; Holotype ANSP 110672; Type locality: sta TE-25, Grenadines, St. Vincent Island, N end of Anse Mahaut, just S of Cumberland Bay; 20-25 ft.

***Elacatinus tenox* (Böhlke & Robins, 1968)**

*Gobiosoma (Elacatinus) tenox* Böhlke and Robins, 1968: 83-85, fig. 4; Holotype ANSP 110688; Type locality: sta. TE-42, Dominica, Prince Rupert Bay, Portsmouth; 50ft.

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***Elacatinus xanthiprora* (Böhlke & Robins, 1968)**

*Gobiosoma (Elacatinus) xanthiprora* Böhlke and Robins 1968: 85-87, fig.5; Holotype ANSP 110898; Type locality: Florida, Monroe Co., 1/4 mi. SE of Alligator Reef Light; about 75 ft.

## Related Genera

***Aboma* Jordan and Starks, 1895**

*Aboma* Jordan and Starks 1895: Type species *Aboma etheostoma* Jordan and Starks; Fishes of Sinaola, Proc. Calif. Acad. Sci 2d ser., 1895: 497.

***Aboma etheostoma* Jordan and Starks, 1895**

*Aboma etheostoma* Jordan and Starks; Fishes of Sinaola, Proc. Calif. Acad. Sci 2d ser., 1895: 497. locality: Mazatlan, Mexico.

***Akko* Birdsong and Robins, 1995**

Type species *Akko dioaea* by monotypy.

****Akko dioaea* Birdsong and Robins, 1995**

*Akko dioaea* Birdsong and Robins, 1995; Holotype USNM 329524; Type locality: Brazil, Amapa Province east of Ilha de Maracá, 02°32'N, 49°57'W in 20 m, Oregon II Sta. 19951, 25 May 1976.

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***Aruma* Ginsburg, 1933a**

Type species: *Gobiosoma occidentale* Ginsburg 1933:16-17, by original designation; erected as a subgenus of *Gobiosoma.*

***Aruma histrio* (Jordan, 1884)**

*Gobiosoma histrio* Jordan 1884:260; Holotype USNM 35147; Type locality: Guaymas, Mexico.

*Gobiosoma occidentale* Ginsburg 1933a; Holotype USNM 92801; Type locality: La Paz Harbor, Mexico.( Hoese, 1976)

***Barbulifer* Eigenmann and Eigenmann 1888(1889)**

Type species: *Barbulifer papillosus* Eigenmenn and Eigenmann 1888(1889): 70 [= *Gobiosoma ceuthoecum* Jordan and Gilbert 1884] by original designation,

***Barbulifer ceuthoecus* (Jordan and Gilbert, 1884)**

*Gobiosoma ceuthoecum* Jordan and Gilbert 1884: 29; Holotype USNM 34970; Type locality: Key West, Florida, from the cavity of a sponge.

****Barbulifer pantherinus* (Pellegrin, 1901)**

*Gobiosoma pantherinum* Pellegrin, 1901: 165; syntypes MNHN 01-295; Type locality: Sargassum floating in the Gulf of California.

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*Gobiosoma spiriti-sancti* Wade, 1946: 219, pl. 30; Holotype LACM 21556; type locality: Espiritu Santo Island, Gulf of California, Mexico). (Böhlke and Robins, 1968)

****Barbulifer antennatus* Böhlke and Robins, 1968**

*Barbulifer antennatus* Böhlke and Robins, 1968: 126; Holotype ANSP 110642; Type locality: sta. 410, Bahamas, Grand Bahamas Bank, Exuma Cays, baylet on SE side of Warderick Wells Cay; to ca. 6 ft.

****Barbulifer mexicanus* Hoese, 1985**

*Barbulifer mexicanus* Hoese 1985: 337-338; Holotype SIO 61-248; Type locality: Los Frailes, Baja California, Gulf of Mexico.

***Chriolepis* Gilbert, 1892**

Type species *Chriolepis minutillus* Gilbert, 1892:558 by original designation.

***Chriolepis minutillus Gilbert, 1892***

*Chriolepis minutillus Gilbert 1892: 558;* Holotype USNM 48261; Type locality: Albatross Exp. Sta. 2825, Gulf of California.

****Chriolepis cuneata* Bussing, 1990**

*Chriolepis cuneata* Bussing 1990:113-115; Holotype LACM 4428-1; Type locality: Isla San Jose, Islas Murcielagos, Costa Rica depth 10-14 meters.

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***Chriolepis dialepta* Bussing, 1990**

*Chriolepis dialepta* Bussing 1990:115-117; Holotype LACM 44821-4; Type locality: East side Isla del Coco, 300 m SW Cabo Desubierta, in 20 meters depth;

*Chriolepis walkeri*, Findley 1983. (Bussing 1990)

***Chriolepis imswe* Greenfield 1981**

*Chriolepis imswe* Greenfield 1981: 269-271; Holotype FMNH 83894; Type locality: Carrie-Bow Cay, Belize, at the barrier-reef dropoff east of cay, depth 21-25 m.

***Chriolepis lepidotus* Findley, 1975**

*Chriolepis lepidotus* Findley 1975: 94-97; Holotype USNM 211456; Type locality: Malpelo Island, Colombia, east side of island, depth ca. 10 meters, above the coral zone, cobble bottom with some calcareous sand and boulders, very sparse algae growth.

***Chriolepis tagus* Ginsburg, 1953**

*Chriolepis tagus* Ginsburg, 1953 :21-22; Holotype USNM 123232; Type locality: Tagus Cove, Albemarle Island, Galapagos Archipelago, 10-18 fathoms.

***Chriolepis zebra* Ginsburg, 1938**

*Chriolepis zebra* Ginsburg, 1938: 109-111; Holotype in Hancock Coll.; Type locality: San Gabriel Bay, Espiritu Santo Island, Gulf of California, shore collection.

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***Eleotrica* Ginsburg, 1933a**

Type species: *Eleotrica cableae* Ginsburg 1933, by original designation.

*Alepidoeleotris* Herre 1935:413; synonym of *Eleotrica (*Birdsong and Robins 1995:682)

***Eleotrica cableae* Ginsburg, 1933a**

*Eleotrica cableae* Ginsburg 1933a:11-12; Holotype USNM 65517; Type locality: Chatham Island, Galapagos Archipelago

*Alepidoeleotris tigris* Herre (1935:413) synonomized Birdsong and Robins (1995:682).

***Enypnias* Jordan and Evermann, 1898**

Type species: *Gobius seminudus* Günther, 1861, by original designation; proposed as a subgenus of *Garmannia.*

***Enypnias seminudus* (Günther, 1861a)**

*Gobius seminudus* Günther 1861:a 372; Type number and location of specimen not listed in original publication; Type locality: west coast of Central America. 1861b: 554 (description).

****Enypnias aceras* Ginsburg, 1939a**

*Enypnias aceras* Ginsburg, 1939a: 61; Holotype USNM 107298; Type locality: Miraflores Locks, lower chamber, Pacific slope, Panama Canal.

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***Evermannichthys* Metzelaar, 1919**

Type species: *Evermannichthys spongicola* Metzelaar 1919, by original designation [= *Evermannichthys metzelaari* Hubbs, 1923]

*Radcliffella* Hubbs, 1921: 2; Type species *Garmannia spongicola* Radcliffe, 1917, by original designation. (Böhlke and Robins, 1969)

***Evermannichthys spongicola* (Radcliffe, 1917)**

*Garmannia spongicola* Radcliffe, 1917: 423-425, fig. (unnumbered); Holotype USNM 77501; Type locality: North Carolina, 1 mile SE of fishing buoy, 34°19'N, 76°48' W in 14¾ fms., from sponge.

****Evermannichthys silus* Böhlke and Robins, 1969**

*Evermannichthys silus* Böhlke and Robins 1969: 10-11,fig. 1; by original designation; Holotype ANSP 111865; Type locality: sta. TS-71, Bahamas, Samana (Atwood) Cay, E of the Graet Bahama Bank, middle of W half of S side of cay; 90 ft. 27 Jan. 1968.

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******Evermannichthys metzelaari*** **Hubbs 1923**

*Evermannichthys spongicola* Metzelaar, 1919: 139-140, figs. 39-40; Holotype not listed; Type locality; Curacao;

*Evermannichthys metzelaari* Hubbs, 1923:1-2 (substitute name for *E. spongicola*, preoccupied as result of referral to *Evermannichthys* of *Garmannia spongicola* Radcliffe).

******Evermannichthys convictor*** **Böhlke and Robins, 1969**

*Evermannichthys convictor* Böhlke and Robins, 1969: 11-13, fig. 2;by original designation; Holotype ANSP 111862; Type locality: sta. TS-7, Bahamas, Graet Bahama Bank, Green Cay (E of southern Andors ISland), W side of cay, 100 yards S of sand spit at far NW end; 45 ft.; 10 Jan. 1968.

***Ginsburgellus*** **Böhlke and Robins, 1968**

Type species *Gobiosoma novemlineatum* Fowler, 1950 = *Ginsburgellus novemlineatus*, the only species in the genus.

***Ginsburgellus novemlineatus*** **(Fowler, 1950)**

*Gobiosoma novemlineatum* Fowler 1950: 89, figs. 44-46; Holotype ANSP 71778; Type locality: Caribbean Sea, San Andres [St. Andrews Island] off coast of Nicaragua. Erdman 1956: 335 (Puerto Rico; color; association with sea urchin, *Echinometra).*

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***Gobulus* Ginsburg, 1933a**

Type species: *Gobulus crescentalis* (Gilbert) = *Gobiosoma cresentalis* Gilbert, 1892.

***Gobulus crescentalis* (Gilbert, 1892)**

*Gobiosoma cresentalis* Gilbert, 1892:557; Holotype not listed; Type locality: Albatross Exp. Sta. number 2825; Gulf of California, lat. 24°22'15"N., long. 110°19'15"W., 7 fathoms.

****Gobulus hancocki* Ginsburg, 1938**

*Gobulus hancocki* Ginsburg 1938: 118-119; Holotype in USNM; Type locality: Secus Island, Panama; shore, coral tide flat.

****Gobulus myersi* Ginsburg, 1939a**

*Gobulus myersi* Ginsburg ,1939a:63; Holotype USNM 107283; Type locality: Gulf of Mexico, off Cape Sable; Albatross station 2374, lat. 29°11'30", long. 85°29', 26 fathoms. Note: according to Hastings 1983 the type locality is the extreme northeastern Gulf of Mexico. Ginsburg had the correct latitude and longitude but listed the wrong location for those marks. (Hastings, 1983).

***Gymneleotris* Bleeker, 1874**

Type species: *Eleotris seminudus* Günther 1864, by original designation.

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***Gymneleotris seminudus* (Günther, 1864)**

*Eleotris seminudus* Günther 1864:24 pl. 4, figs. 2, 2a; Holotype not listed. Type locality: Pacific coast of Panama.

***Nes* Ginsburg, 1933a**

Type species: *Gobiosoma longum* Nichols 1914 by original designation; described as a subgenus of *Gobiosoma*.

***Nes longus* (Nichols, 1914)**

*Gobiosoma longum* Nichols 1914: 143, fig. 1; Holotype AMNH 5068; Type locality: Florida Keys near Key West.

*Gobiosoma lividiris* Fowler 1944: 140-141, 383, 472; Holotype not listed; Type locality: Old Providence Island, Caribbean Sea; description based on five small juveniles, characters erroneously recorded. (Böhlke and Robins, 1968)

***Palatogobius* Gilbert, 1971**

Type species *Palatogobius paradoxus* Gilbert 1971 by original designation.

***Palatogobius paradoxus* Gilbert, 1971**

*Palatogobius paradoxus* Gilbert, 1971: 31-34, figs. 1,2,3a,4a; Holotype ANSP 109182; Type locality: St. John, Virgin Islands.

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**_Pariah_ Böhlke, 1969**

Type species: *Pariah scotius* Böhlke 1969, by original designation.

***_Pariah scotius_ Böhlke, 1969**

Pariah scotius Böhlke 1969: 3-4, fig. 1; Holotype ANSP 111855; Type locality: sta. TS-52a, Bahamas, Mayaguana Island, SE end of island, 1/2 mi. NW of Southeast Point; 85 ft. 22 Jan. 1968.

**Psilotris Ginsburg, 1953**

Type species *Psilotris alepis*, by original designation and monotypy

***_Psilotris alepis_ Ginsburg, 1953**

*Psilotris alepis* Ginsburg 1953: 22; Holotype USNM 197515; Type locality: St. Croix Island, Virgin Islands, on reef, 8 Apr. 1937. Note: Holotype listed by Ginsburg as USNM 123231.

***_Psilotris batrachodes_ Böhlke, 1963**

*Psilotris batrachodes* Böhlke, 1963: 6-7; Holotype ANSP 98416; Type locality: sta. 304, Bahamas, Sandy Cay (Nassau vicinity), N of the E end, eroded limestone covered with algae, sea-fans, corals, etc., to 20 ft., 17 May 1956.

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****Psilotris boehlkei* Greenfield, 1993**

*Psilotris boehlkei* Greenfield, 1993: 771-773; Holotype ANSP 106059 male; Type locality: St. Barthelemy, Les Saintes, Port de Gustavia, southwest of Les Saintes (17°55'N, 62°53'W), 18.3-19.8m, from low coral and sponges on white sand bottom.

****Psilotris celsus* Böhlke, 1963**

*Psilotris celsus* Böhlke, 1963: 7-9; Holotype ANSP 98427; Type locality: sta. 414, coral head N of Green Cay (N of Rose Id.), Nassau vicinity, Bahamas, to 45 ft., 21 July 1957.

****Psilotris kaufmani* Greenfield *et. al.,* 1993**

*Psilotris kaufmani* Greenfield *et. al.,* 1993:183-185; Holotype LACM 8939-29, male 32.2mm SL; Type locality: Jamaica, Montego Bay, 0.8 km off Chatham Hotel, 15.2 m, in or around rocks.

***Pycnomma* Rutter, 1904**

Type species: *Pycnomma semisquamatum* Rutter, 1904, by monotypy; *Dichomma* used on plates but corrected in explanation of plates, p. 254.

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***Pycnomma semisquamatum* Rutter, 1904**

*Pycnomma semisquamatum* Rutter, 1904: 252; Holotype Dept. of Ichthyology, California Acadamy of Science No. 1478; Type locality: San Jose Island, Gulf of California.

***Pycnomma roosevelti* Ginsburg, 1939b**

*Pycnomma roosevelti* Ginsburg, 1939b: 1-3, fig. 1; Holotype USNM 108139; Type locality: Old Providence Island.

**Risor Ginsburg, 1933b**

Type species: *Garmannia binghami* Parr 1930, by original designation [=*Garmannia rubra* Rosen 1911]

***Risor ruber* (Rosen, 1911)**

*Garmannia rubra* Rosen 1911: 63, fig. 1 Holotype not listed in publication; Type locality: among sponges, corals etc. near the shore at Mastic Point, Andros, Bahamas.

*Risor mirus* Ginsburg 1939a: 60; Holotype Bingham Oceanographic Coll. 1691; Type locality: Siguanea Bay, Isle of Pines, Cuba. (Böhlke and Robins, 1968)

?*Microgobius spec.*: Metzelaar 1919: 138 (a specimen from Bay of Asiento, Curacao was placed in the synonymy of *mirus* by Longley and Hildebrand (1941: 228)). (Böhlke and Robins, 1968)

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### ***Robinsichthys* Birdsong, 1988**

Type species *R. arrowsmithensis* Birdsong 1988, by original designation.

### ***Robinsichthys arrowsmithensis* Birdsong, 1988**

Robinsichthys arrowsmithensis Birdsong, 1988: 439-441, figs. 1-3, tables 1-3; Holotype USNM 290207; Type locality: 21$^0$02'N, 86$^0$26'W, R/V Gerda sta 952, beginning depth 586 m, ending depth 92 m, 28 Jan. 1968.

### ***Varicus* Robins and Böhlke, 1961**

Type species: *Varicus bucca* Robins and Böhlke 1961:47 by original designation.

### ***Varicus bucca* Robins and Böhlke, 1961**

*Varicus bucca* Robins and Böhlke, 1961: 47-49; Holotype ANSP 93083; Type locality: Saba Bank between St. Kitts, British West Indies and St. Croix, Virgin Islands, Lat 17033'N., Long. 63035'W., 125-132 fathoms, M/V *Oregon*, Station 2356.

### ***Varicus marilynae* Gilmore, 1979**

*Varicus marilynae* Gilmore 1979: 126-128; Holotype USNM 218406; Type locality: Atlantic Ocean off Sebastian Inlet, Brevard and Indian River counties, Florida; 27$^0$50.3'N, 79$^0$57.0'W; 61-79 m.

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### **Varicus benthonis* (Ginsburg, 1953)

*Chriolepis benthonis* Ginsburg, 1953:22; Holotype USNM 47641; Type locality: *Blake* Expedition, station CCXLI, Alexander Agassiz, off Progresso, Yucatan, Mexico, lat. 23$^{0}$13'N., long. 89$^{0}$10'W., 84 fathoms.

### **Varicus vespa* (Hastings & Bortone, 1981)

*Chriolepis vespa* (Hastings & Bortone) 1981: 428-432; Holotype USNM 221523; Type locality: northeastern Gulf of Mexico, 28$^{0}$24'N, 85$^{0}$15'W, R/V Bellows (cruise Bureau of Land Management, BLM 15, station III-C, 183 m, 26 July 1975.

### **Varicus fisheri* (Herre, 1942)

*Chriolepis fisheri* Herre, 1942: 297; Holotype not listed in publication; type locality: Barbados, depth 45 fathoms.

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# Tables and Illustrations

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**Table 1.** Past arrangements of genera and subgenera of the *Gobiosoma* complex as proposed by Ginsburg 1933-1944, Böhlke & Robins 1968, and Hoese 1971. The new arrangement proposed herein is given in the last column.

| Ginsburg | Böhlke & Robins | Hoese | Proposed |
|---|---|---|---|
| ***Aboma*** | ***Aboma*** | ***Gobiosoma***<br>(*Gobiosoma*)<br>(*Gobiolepis*)<br>(*Aboma*) | ***Aboma*** |
| ***Gobiosoma***<br>(*Gobiosoma*)<br>(*Gerhardinus*)<br>(*Dilepidion*)<br>(*Elacatinus*)<br>(*Aruma*)<br>(*Nes*) | ***Nes*** | | ***Gobiosoma*** |
| ***Garmannia***<br>(*Garmannia*)<br>(*Gobiolepis*)<br>(*Gobiculina*)<br>(*Gobiohelpis*)<br>(*Tigrigobius*)<br>(*Risor*) | ***Gobiosoma***<br>(Gobiosoma)<br>(Austrogobius)<br>(Tigrigobius)<br>(Garmannia)<br>(Elacatinus) | | ***Gobiolepis*** |
| | ***Risor*** | | ***Elacatinus*** |
| | ***Aruma*** | | ***Tigrigobius*** |
| | | | ***Risor*** |
| | | | ***Aruma*** |
| | | | ***Nes*** |

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**Table 2. List of characters used in the analysis**: The following character list is a summary of each character and the states present in the matrix. A detailed description and discussion of each character is given in the text. All multistate characters were coded as unordered in the analysis.

1. Barbel on the upper lip near the anterior nostril
    0 - barbel absent
    1 - barbel present
2. Fifth pelvic fin ray
    0 - fifth ray is branched
    1 - fifth ray is composed of only a single unbranched ray
3. Pelvic disc
    0 - pelvic disc united forming a complete disk
    1 - pelvic disc not united, fins separated
4. First dorsal fin spines
    0 - six spines
    1 - seven spines
    2 - more than seven spines
5. Scales on the caudal peduncle
    0 - completely scaled
    1 - some scales present
    2 - no scales present
6. Scales on the posterior section of the trunk
    0 - completely scaled
    1 - some scales present
    2 - no scales present
7. Scales on the anterior of the trunk
    0 - completely scaled
    1 - some scales present
    2 - no scales present

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**Table 2.** (cont)

8. Scales on the predorsal region
    - 0 - some scales present
    - 1 - no scales present
9. Basicaudal scales
    - 0 - absent
    - 1 - present
10. Cephalic head pore C
    - 0 - present
    - 1 - absent
11. Cephalic head pore D
    - 0 - present
    - 1 - absent
12. Cephalic head pore E
    - 0 - present
    - 1 - absent
13. Oculoscapular canal pore F
    - 0 - present
    - 1 - absent
14. Oculoscapular canal pore G
    - 0 - present
    - 1 - absent
15. Posterior oculoscapular canal pores K and L
    - 0 - present
    - 1 - absent
16. Preopercle canal
    - 0 - three pores present
    - 1 - two pores present
    - 2 - no pores present

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**Table 2.** (cont)

17. Total vertebral number
    - 0 - 27 vertebrae present
    - 1 - 28 vertebrae present
    - 2 - more than 29 vertebrae present
18. Caudal vertebral number
    - 0 - 16
    - 1 - 17
    - 2 - 18
19. Pterygiophore pattern
    - 0 - 3-22110
    - 1 - 3-221110
20. Hypural fusion
    - 0 - hypurals not fused
    - 1 - hypurals fused
21. Fifth pelvic ray with an elongate dorsal process at the articulation of the spine with the pelvic girdle
    - 0 - elongate process not present
    - 1 - elongate process present
22. Supraoccipital with elongate lateral wings
    - 0 - present
    - 1 - absent
23. Maxillary process: A process that extends posteriorly from the maxilla. The process originates from the lower half of the maxilla.
    - 0 - present
    - 1 - absent
24. Metapterygoid shape
    - 0 - narrow with no dorsal projecting extension
    - 1 - wide with an expanded dorsal projecting extension

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**Table 2.** (cont)

25. Metapterygoid and quadrate articulation
    - 0 - metapterygoid does not overlap the quadrate
    - 1 - metapterygoid overlaps the quadrate
26. Preopercular process
    - 0 - present
    - 1 - absent
27. Sensory papillae row b with a long anterior extension
    - 0 - absent
    - 1 - present
28. Sensory papillae row 5i/6i in relation to anterior of horizontal row b
    - 0 - In front of the anterior of row b
    - 1 - At the front of row b and attached to it
    - 2 - In the middle of row b
29. Sensory papillae row 5i/6i in relation to horizontal row d
    - 0 - extending below the level of row d
    - 1 - not extending below the level of row d
30. Sensory papillae row 5s connected to row 5i/6i forming a continuous row
    - 0 - absent
    - 1 - present
31. Sensory papillae transverse row 2
    - 0 - not extending ventrally below the level of papillae horizontal row d
    - 1- row 2 extending ventrally below the level of row d
32. Sensory papillae transverse row 3
    - 0 - not extending ventrally below the level of row d
    - 1 - extending ventrally below the level of row d
33. Number of transverse sensory papillae rows in front of row 5
    - 0 - four rows in front of row 5
    - 1 - three rows in front of row 5

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**Table 2.** (cont)

34. Number of transverse sensory papillae rows under horizontal row b
    - 0 - two rows under row b
    - 1 - one row under row b
35. Sphenotic to pterotic length ratio
    - 0 - ratio of less than 0.5:1 - sphenotic not elongate
    - 1 - ratio of more than 0.9:1 - sphenotic elongate
36. Braincase length to width ratio
    - 0 - not elongate
    - 1 - elongate
37. Sphenotic connected to the lateral wings of the supraoccipital
    - 0 - absent
    - 1 - present
38. Number of lateral projections from the sphenotic
    - 0 - one projection at the anterior end forming the posterior of the orbit
    - 1 - two projections present, an anterior projection forming the posterior of the orbit and a more posterior projection with the hyomandibula attached
39. Teeth in upper jaw with the outer teeth enlarged
    - 0 - outer row of teeth enlarged
    - 1 - outer row of teeth not enlarged
40. Upper tooth row with the outer row complete, extending to the end of the maxilla
    - 0 - outer tooth row complete
    - 1 - outer tooth row not complete, ending before the end of the maxilla
41. Dorsal extension of the A1$\alpha$ muscle
    - 0 - muscle not extending over the ocula-scapular canal
    - 1 - muscle extending over the ocula-scapular canal on the frontals
42. A2 or A2$\gamma$ if present inserts along the primordial ligament to the maxilla
    - 0 - does not insert on the primordial ligament
    - 1 - inserts along the primordial ligament to the maxilla

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**Table 2.** (cont)

43. A2γ inserts on the maxilla and the A1γ
    - 0 - A2γ does not insert on the A1γ
    - 1 - A2γ inserts on the maxilla and the A1γ
44. A2 γ inserts with the A1β
    - 0 - not reaching the A1 β
    - 1- inserts at the A1β on the maxilla
45. A1 γ
    - 0 - absent
    - 1 - present

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**Table 3. Data Matrix**: The matrix shown contains all taxa and characters used in the study. Different subsets of this matrix were used in various parts of the study. A detailed description of taxa and characters used in each analysis is given in the text.

| **Character number** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** |
|---|---|---|---|---|---|---|---|---|---|---|
| Hypothetical Outgroup | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Vanneaugobius canariensis* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| *Gobius paganellus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Parrella maxillaris* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Microgobius signatus* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Bollmannia chlamydes* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Aboma etheostoma* | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| *Aruma histrio* | 1 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 1 |
| *Barbulifer ceuthoecus* | 1 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 1 |
| *Chriolepis minutillus* | 0 | 1 | 1 | 1 | 0 | 2 | 2 | 1 | 1 | 1 |
| *Elacatinus oceanops* | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 0 |
| *Elacatinus horsti* | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 0 |
| *Elacatinus janssi* | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 1 | 0 |
| *Elacatinus punticulatum* | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 1 | 0 |
| *Elacatinus xanthiprora* | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 0 |
| *Eleotrica cableae* | 0 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 1 |
| *Enypnias seminudus* | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Evermannichthys spongicola* | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 1 | 0 | 0 |
| *Gobiosoma chiquita* | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| *Gobiosoma hildebrandi* | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Gobiosoma homochroma* | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| *Gobiosoma paradoxum* | 1 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 0 |
| *Gobiosoma robustum* | 1 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 0 |
| *Gobiosoma schultzi* | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| *Gobiosoma spes* | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| *Ginsburgellus novemlineatus* | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 0 |
| *Gobiosoma grosvenori* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| *Gobiosoma parri* | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 |
| *Gobiosoma spilotum* | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| *Gobiosoma sp.* B | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Gobiosoma bosc* | 1 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 0 |
| *Gobiosoma ginsburgi* | 1 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 1 | 0 |
| *Gobiosoma sp.* H | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 0 |
| *Gobiosoma longipala* | 1 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 1 | 0 |
| *Gobiosoma dilepis* | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 1 | 0 |
| *Gobiosoma gemmatum* | 0 | 0 | 0 | 1 | 0 | 2 | 2 | 1 | 1 | 0 |
| *Gobiosoma macrodon* | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 0 |
| *Gobiosoma multifasciatum* | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 0 |
| *Gobiosoma pallens* | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 |
| *Gobiosoma saucrum* | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 0 |
| *Gobiosoma zebrella* | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 0 |
| *Gobulus crescentalis* | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 1 |
| *Gymneleotris seminudus* | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Nes longus* | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 1 |
| *Pycnomma semisquamatum* | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Risor ruber* | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 1 |

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**Table 3** (cont)

| **Character number** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** |
|---|---|---|---|---|---|---|---|---|---|---|
| Hypothetical Outgroup | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Vanneaugobius canariensis* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| *Gobius paganellus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Parrella maxillaris* | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 |
| *Microgobius signatus* | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Bollmannia chlamydes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Aboma etheostoma* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Aruma histrio* | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Barbulifer ceuthoecus* | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| *Chriolepis minutillus* | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 |
| *Elacatinus oceanops* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Elacatinus horsti* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Elacatinus janssi* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Elacatinus punticulatum* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Elacatinus xanthiprora* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Eleotrica cableae* | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 1 |
| *Enypnias seminudus* | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Evermannichthys spongicola* | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 |
| *Gobiosoma chiquita* | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Gobiosoma hildebrandi* | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| *Gobiosoma homochroma* | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| *Gobiosoma paradoxum* | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Gobiosoma robustum* | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Gobiosoma schultzi* | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| *Gobiosoma spes* | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| *Ginsburgellus novemlineatus* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Gobiosoma grosvenori* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Gobiosoma parri* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Gobiosoma spilotum* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Gobiosoma sp.* B | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| *Gobiosoma bosc* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Gobiosoma ginsburgi* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Gobiosoma sp.* H | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Gobiosoma longipala* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Gobiosoma dilepis* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Gobiosoma gemmatum* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Gobiosoma macrodon* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Gobiosoma multifasciatum* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Gobiosoma pallens* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Gobiosoma saucrum* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Gobiosoma zebrella* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Gobulus crescentalis* | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 |
| *Gymneleotris seminudus* | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 1 |
| *Nes longus* | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 |
| *Pycnomma semisquamatum* | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 1 |
| *Risor ruber* | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 |

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**Table 3** (cont)

| **Character number** | **21** | **22** | **23** | **24** | **25** | **26** | **27** | **28** | **29** | **30** |
|---|---|---|---|---|---|---|---|---|---|---|
| Hypothetical Outgroup | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Vanneaugobius canariensis* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Gobius paganellus* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | ? | ? | 0 |
| *Parrella maxillaris* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | ? | 1 | 0 |
| *Microgobius signatus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | ? | 1 | 0 |
| *Bollmannia chlamydes* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | ? | 1 | 0 |
| *Aboma etheostoma* | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 0 |
| *Aruma histrio* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Barbulifer ceuthoecus* | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Chriolepis minutillus* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Elacatinus oceanops* | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 |
| *Elacatinus horsti* | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Elacatinus janssi* | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Elacatinus punticulatum* | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Elacatinus xanthiprora* | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Eleotrica cableae* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Enypnias seminudus* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 |
| *Evermannichthys spongicola* | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Gobiosoma chiquita* | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Gobiosoma hildebrandi* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Gobiosoma homochroma* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Gobiosoma paradoxum* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 |
| *Gobiosoma robustum* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 |
| *Gobiosoma schultzi* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 |
| *Gobiosoma spes* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 |
| *Ginsburgellus novemlineatus* | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Gobiosoma grosvenori* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| *Gobiosoma parri* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 0 |
| *Gobiosoma spilotum* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 |
| *Gobiosoma sp.* B | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Gobiosoma bosc* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 |
| *Gobiosoma ginsburgi* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 |
| *Gobiosoma sp.* H | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 |
| *Gobiosoma longipala* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 |
| *Gobiosoma dilepis* | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Gobiosoma gemmatum* | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Gobiosoma macrodon* | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 |
| *Gobiosoma multifasciatum* | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Gobiosoma pallens* | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Gobiosoma saucrum* | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Gobiosoma zebrella* | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Gobulus crescentalis* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Gymneleotris seminudus* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Nes longus* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| *Pycnomma semisquamatum* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Risor ruber* | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 |

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**Table 3** (cont)

| **Character Number** | **31** | **32** | **33** | **34** | **35** | **36** | **37** | **38** | **39** | **40** |
|---|---|---|---|---|---|---|---|---|---|---|
| Hypothetical Outgroup | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Vanneaugobius canariensis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Gobius paganellus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Parrella maxillaris* | 0 | 0 | 2 | ? | 1 | 0 | 1 | 0 | 0 | 0 |
| *Microgobius signatus* | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bollmannia chlamydes* | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Aboma etheostoma* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Aruma histrio* | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Barbulifer ceuthoecus* | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Chriolepis minutillus* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Elacatinus oceanops* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Elacatinus horsti* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Elacatinus janssi* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Elacatinus punticulatum* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| *Elacatinus xanthiprora* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Eleotrica cableae* | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Enypnias seminudus* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Evermannichthys spongicola* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 |
| *Gobiosoma chiquita* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma hildebrandi* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma homochroma* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma paradoxum* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma robustum* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma schultzi* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma spes* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Ginsburgellus novemlineatus* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| *Gobiosoma grosvenori* | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Gobiosoma parri* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Gobiosoma spilotum* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma sp.* B | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma bosc* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma ginsburgi* | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Gobiosoma sp.* H | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma longipala* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma dilepis* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Gobiosoma gemmatum* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Gobiosoma macrodon* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| *Gobiosoma multifasciatum* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| *Gobiosoma pallens* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Gobiosoma saucrum* | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Gobiosoma zebrella* | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |
| *Gobulus crescentalis* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Gymneleotris seminudus* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Nes longus* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Pycnomma semisquamatum* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Risor ruber* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |

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**Table 3** (cont)

| **Character number** | **41** | **42** | **43** | **44** | **45** |
|---|---|---|---|---|---|
| Hypothetical Outgroup | 0 | 0 | 0 | 0 | 0 |
| *Vanneaugobius canariensis* | 0 | 0 | 0 | 0 | 0 |
| *Gobius paganellus* | 0 | 1 | 0 | 1 | 0 |
| *Parrella maxillaris* | 0 | 0 | 0 | 0 | 0 |
| *Microgobius signatus* | 0 | 0 | 0 | 0 | 0 |
| *Bollmannia chlamydes* | 0 | 1 | 0 | 0 | 0 |
| *Aboma etheostoma* | 0 | 0 | 0 | 0 | 0 |
| *Aruma histrio* | 0 | 1 | 0 | 1 | 0 |
| *Barbulifer ceuthoecus* | 0 | 1 | 0 | 1 | 0 |
| *Chriolepis minutillus* | 0 | 1 | 0 | 1 | 0 |
| *Elacatinus oceanops* | 1 | 1 | 1 | 1 | 1 |
| *Elacatinus horsti* | 1 | 1 | 1 | 1 | 1 |
| *Elacatinus janssi* | 0 | 1 | 1 | 1 | 1 |
| *Elacatinus punticulatum* | 1 | 1 | 1 | 1 | 1 |
| *Elacatinus xanthiprora* | 1 | 1 | 1 | 1 | 1 |
| *Eleotrica cableae* | 1 | 1 | 0 | 1 | 0 |
| *Enypnias seminudus* | 0 | 1 | 0 | 1 | 1 |
| *Evermannichthys spongicola* | 0 | 1 | 0 | 0 | 0 |
| *Gobiosoma chiquita* | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma hildebrandi* | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma homochroma* | 0 | 1 | 0 | 1 | 1 |
| *Gobiosoma paradoxum* | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma robustum* | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma schultzi* | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma spes* | 0 | 1 | 1 | 1 | 1 |
| *Ginsburgellus novemlineatus* | 0 | 1 | 0 | 1 | 0 |
| *Gobiosoma grosvenori* | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma parri* | 0 | 1 | 0 | 0 | 1 |
| *Gobiosoma spilotum* | 0 | 1 | 0 | 1 | 1 |
| *Gobiosoma* sp. B | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma bosc* | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma ginsburgi* | 0 | 1 | 0 | 1 | 1 |
| *Gobiosoma sp.* H | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma longipala* | 0 | 1 | 0 | 1 | 1 |
| *Gobiosoma dilepis* | 1 | 1 | 1 | 1 | 1 |
| *Gobiosoma gemmatum* | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma macrodon* | 1 | 1 | 1 | 1 | 1 |
| *Gobiosoma multifasciatum* | 1 | 1 | 1 | 1 | 1 |
| *Gobiosoma pallens* | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma saucrum* | 0 | 1 | 1 | 1 | 1 |
| *Gobiosoma zebrella* | 1 | 1 | 1 | 1 | 1 |
| *Gobulus crescentalis* | 1 | 0 | 0 | 1 | 0 |
| *Gymneleotris seminudus* | 0 | 1 | 0 | 1 | 0 |
| *Nes longus* | 1 | 1 | 0 | 1 | 0 |
| *Pycnomma semisquamatum* | 0 | 1 | 0 | 1 | 0 |
| *Risor ruber* | 0 | 1 | 0 | 1 | 1 |

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**Table 4. Summary statistics for all cladograms produced using the proposed outgroups.** Tree lengths, CI, RI, and number of equally most parsimonious trees for each consensus tree is shown. Trees were produced using successive weighting in Hennig86.

| OUTGROUP | Length | CI | RI | # Trees |
|---|---|---|---|---|
| Hypothetical and all others | 309 | 54 | 87 | 108 |
| *Aboma* only | 251 | 59 | 89 | 212 |
| Hypothetical only | 289 | 64 | 89 | 36 |
| Hypothetical, *Vanneaugobius*, *Gobius* | 307 | 57 | 88 | 72 |
| Hypothetical and *Gobius* | 305 | 60 | 88 | 72 |
| *Gobius* | 274 | 64 | 89 | 36 |
| Hypothetical and *Vanneaugobius* | 304 | 58 | 88 | 921 |
| *Vanneaugobius* | 270 | 60 | 88 | 12 |
| Hypothetical and *Microgobius* | 308 | 57 | 87 | 318 |
| *Microgobius* | 299 | 58 | 88 | 625 |

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**Table 5. Synopsis of muscles in the suspensorium of *Gobiolepis*, *Gobiosoma*, *Elacatinus*, and *Tigrigobius*.** **s** - muscle subdivided into two distinct sections either completely or at least distinctly separate near the insertion; **ns** - muscle not divided into sections; **?** - can not be determined either due to the condition of the specimen or the lack of a specimen to dissect; **p** - muscle present; **a** - muscle absent; **vec** - dorsal origin ending at the ventral margin of the lateralis canal on the sphenotic and pterotic; **bc** - dorsal origin ending below the ventral margin of the lateralis canal on the sphenotic and pterotic; **dec** - dorsal origin ending at the dorsal margin of the lateralis canal on the sphenotic and pterotic; **acf** - dorsal origin ending on the frontal but not extending to the midline suture between the two frontals; **acfc** - dorsal origin extending to the frontal crest

| ***Gobiolepis* Group** | **A1** | **A1 Origin** | **A1β** | **A1γ** | **A2γ** |
|---|---|---|---|---|---|
| *Gobiolepis chiquita* | s | vec | P | p | p |
| *Gobiolepis grosvenori* | s | vec | P | p | p |
| *Gobiolepis hildebrandi* | s | vec | P | p | p |
| *Gobiolepis homochroma* | *s* | vec | P | ? | P |
| *Gobiolepis sp b* | s | dec | P | p | p |
| *Gobiolepis sp h* | s | vec | P | p | p |
| *Gobiolepis spilotum* | s | vec | P | p | p |

| ***Gobiosoma* Group** | | | | | |
|---|---|---|---|---|---|
| *Gobiosoma bosc* | s | vec | P | p | p |
| *Gobiosoma ginsburgi* | s | dec | P | p | p |
| *Gobiosoma longipala* | s | vec | P | p | p |
| *Gobiosoma nudum* | s | acf | P | p | p |
| *Gobiosoma parri* | s | bc | P | p | p |
| *Gobiosoma robustum* | s | vec | P | p | p |
| *Gobiosoma schultzi* | s | dec | ? | P | p |
| *Gobiosoma spes* | s | dec | P | p | p |
| *Gobiosoma yucatana* | s | vec | P | P | p |

| ***Elacatinus* Group** | | | | | |
|---|---|---|---|---|---|
| *Elacatinus horsti* | s | acf | p | p | p |
| *Elacatinus oceanops* | s | acf | p | p | p |
| *Elacatinus xanthiprora* | s | acfc | p | p | p |

| ***Tigrigobius* Group** | | | | | |
|---|---|---|---|---|---|
| *Tigrigobius dilepis* | s | acfc | p | p | p |
| *Tigrigobius gemmatum* | s | dec | P | p | p |
| *Tigrigobius janssi* | s | dec | P | p | p |
| *Tigrigobius macrodon* | s | acfc | p | p | p |
| *Tigrigobius multifasciatum* | s | acf | P | p | p |
| *Tigrigobius pallens* | s | vec | P | p | p |
| *Tigrigobius puncticulatum* | s | dec | P | p | p |
| *Tigrigobius saucrum* | s | dec | P | p | p |
| *Tigrigobius zebrella* | s | acfc | p | p | p |

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**Table 6. Synopsis of muscles in the suspensorium of comparative material, outgroups, and related genera.** s - muscle subdivided into two distinct sections either completely or at least distinctly separate near the insertion; ns - muscle not divided into sections; ? - can not be determined either due to the condition of the specimen or the lack of a specimen to dissect; **p** - muscle present; **a** - muscle absent; **vec** - dorsal origin ending at the ventral margin of the lateralis canal on the sphenotic and pterotic; **bc** - dorsal origin ending below the ventral margin of the lateralis canal on the sphenotic and pterotic; **dec** - dorsal origin ending at the dorsal margin of the lateralis canal on the sphenotic and pterotic; **acf** - dorsal origin ending on the frontal but not extending to the midline suture between the two frontals; **acfc** - dorsal origin extending to the frontal crest

|  | **A1** | **A1 Origin** | **A1β** | **A1γ** | **A2γ** |
|---|---|---|---|---|---|
| **COMPARATIVE MATERIAL** |  |  |  |  |  |
| *Bunaka herwerdeni* | s | bc | p | a | a |
| *Chromogobius sp. nov.* | s | bc | p | a | a |
| *Coryphopterus eidolon* | s | bc | p | a | a |
| *Cryptocentrus sp.* | s | bc | p | a | a |
| *Dormitator latifrons* | s | bc | p | a | a |
| *Eleotris pisonis* | s | bc | p | a | a |
| *Eleotris potamophila* | ns | bc | a | a | a |
| *Gobionellus oceanicus* | ns | bc | a | a | a |
| *Padogobius martensii* | s | bc | p | a | a |
| *Sufflogobius bibarbatus* | s | bc | p | a | a |
| *Thorogobius ephippiatus* | s | bc | p | a | a |
| *Zebrus zebrus* | s | bc | p | a | p |
| **OUTGROUPS** |  |  |  |  |  |
| *Bollmannia chlamydes* | ns | bc | a | a | a |
| *Gobius niger* | s | bc | p | a | a |
| *Gobius paganellus* | s | bc | p | a | p |
| *Microgobius signatus* | s | bc | p | a | a |
| *Parrella ginsburgi* | s | bc | p | a | a |
| *Parrella macropteryx* | s | bc | p | a | a |
| *Parrella maxillaris* | s | bc | p | a | a |
| *Vanneaugobius canariensis* | s | bc | p | a | a |
| **RELATED GENERA** |  |  |  |  |  |
| *Aruma histrio* | s | bc | p | a | p |
| *Aboma etheostoma* | s | bc | p | a | a |
| *Chriolepis minutillus* | s | dec | p | a | p |
| *Evermannichthys spongicola* | s | dec | p | a | p |
| *Eleotrica cableae* | s | acf | p | a | p |
| *Ginsburgellus novemlineatus* | s | ve | p | p | p |
| *Gobulus hancocki* | s | acfc | p | a | p |
| *Gobulus cresentalis* | s | acfc | p | a | p |
| *Gymneleotris seminudus* | s | ve | p | a | p |
| *Nes longus* | s | acfc | p | a | p |
| *Pariah scotus* | s | ve | p | a | p |
| *Pycnomma semisquamatum* | s | ve | p | a | p |
| *Risor ruber* | s | ve | p | p | p |
| *Varicus vespa* | s | ve | p | a | a |

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**Table 7. Origins and insertions of suspensorium muscles in *Gobiolepis*, *Gobiosoma*, *Elacatinus*, and *Tigrigobius*.** **sph.** - sphenotic; **pte** - pterotic; **pre** - preopercle; **cor** - coronoid process; **met** - metapterygoid ; **max** - maxilla; **lap-l** - along the lateral surface of the lavator arcus palatini; **lap-p** - along the posterior edge of the lavator arcus palatine **pl** - primordial ligament.

| | **A1α** | | **A1β** | |
|---|---|---|---|---|
| | **Origin** | **Insertion** | **Origin** | **Insertion** |
| **Gobiolepis** | | | | |
| *Gobiolepis chiquita* | sph,pte,pre | cor | met | max |
| *Gobiolepis grosvenori* | sph,pte,pre | cor | lap-l | max |
| *Gobiolepis hildebrandi* | sph,pte,pre | cor | lap-l,met | max |
| *Gobiolepis homochroma* | sph,pte,pre | pl,cor | sph,lap-p | max |
| *Gobiolepis sp. b* | sph,pte,pre | cor | lap-l,met | max |
| *Gobiolepis sp. h* | sph,pte,pre | cor | lap-l,met | max |
| *Gobiolepis spilotum* | sph,pte,pre | cor | lap-l,met | max |
| **Gobiosoma** | | | | |
| *Gobiosoma bosc* | sph,pte,pre | cor | lap-l,met | max |
| *Gobiosoma ginsburgi* | sph,pte,pre | cor | lap-l,met | max |
| *Gobiosoma longipala* | sph,pte,pre | cor | lap-l,met | max |
| *Gobiosoma nudum* | sph,pte,pre | cor | lap-l,met | max |
| *Gobiosoma parri* | sph,pte,pre | pl,cor | lap-l,met | max |
| *Gobiosoma robustum* | sph,pte,pre | cor | lap-l,met | max |
| *Gobiosoma schultzi* | sph,pte,pre | cor | lap-l,met | max |
| *Gobiosoma spes* | sph,pte,pre | cor | lap-l,met | max |
| *Gobiosoma yucatana* | sph,pte,pre | cor | lap-l,met | max |
| **Elacatinus** | | | | |
| *Elacatinus horsti* | sph,pte,pre | cor | lap-l,met | max;pl |
| *Elacatinus oceanops* | sph,pte,pre | cor | lap-l,met | max |
| *Elacatinus xanthiprora* | sph,pte,pre | cor | lap-l,met | max |
| **Tigrigobius** | | | | |
| *Tigrigobius dilepis* | sph,pte,pre | cor | met | max |
| *Tigrigobius gemmatum* | sph,pte,pre | cor | lap-l,met | max |
| *Tigrigobius janssi* | sph,pte,pre | cor | lap-l,met | max |
| *Tigrigobius macrodon* | sph,pte,pre | cor | met | max |
| *Tigrigobius multifasciatum* | sph,pte,pre | cor | lap-l;met | max |
| *Tigrigobius pallens* | sph,pte,pre | cor | lap-l;met | max |
| *Tigrigobius puncticulatum* | sph,pte,pre | cor | lap-l;met | max |
| *Tigrigobius saucrum* | sph,pte,pre | cor | lap-l;met | max |
| *Tigrigobius zebrella* | sph,pte,pre | cor | lap-l;met | max |

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**Table 7** (cont)

| | A1γ | | A2 | | A2γ | |
|---|---|---|---|---|---|---|
| | **Origin** | **Insertion** | **Origin** | **Insertion** | **Origin** | **Insertion** |
| **Gobiolepis** | | | | | | |
| *Gobiolepis chiquita* | sph | max to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiolepis grosvenori* | sph | max to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiolepis hildebrandi* | sph | max to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiolepis homochroma* | ? | ? | pre, qu | cor | qua | max to A1β |
| *Gobiolepis sp. b* | sph | max to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiolepis sp. h* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiolepis spilotum* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| **Gobiosoma** | | | | | | |
| *Gobiosoma bosc* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiosoma ginsburgi* | sph | max | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiosoma longipala* | sph | max, pl | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiosoma nudum* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiosoma parri* | sph | max | pre, qu | cor | qua | pl, max |
| *Gobiosoma robustum* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiosoma schultzi* | sph | max to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiosoma spes* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Gobiosoma yucatana* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| **Elacatinus** | | | | | | |
| *Elacatinus horsti* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Elacatinus oceanops* | sph | pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Elacatinus xanthiprora* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| **Tigrigobius** | | | | | | |
| *Tigrigobius dilepis* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Tigrigobius gemmatum* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Tigrigobius janssi* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Tigrigobius macrodon* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Tigrigobius multifasciatum* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Tigrigobius pallens* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Tigrigobius puncticulatum* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Tigrigobius saucrum* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |
| *Tigrigobius zebrella* | sph | max, pl to A2γ | pre, qu | cor | qua | pl, max to A1γ |

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**Table 8. Origins and insertions of suspensorium muscles in related genera, outgroups, and comparative material.** **art** - articular; **sph.** - sphenotic; **pte** - pterotic; **pre** - preopercle; **cor** - coronoid process; **met** - metapterygoid ; **max** - maxilla; **lap-l** - along the lateral surface of the lavator arcus palatini; **lap-p** - along the posterior of the lavator arcus palatine **pl** - primordial ligament; **qua** - quadrate; ** = not present; **d** - dorsal; **v** - ventral; **a** - anterior; **p** - posterior; **den** - dentary; **ta3** - tendon of adductor mandibulae 3; **sym** - symplectic; **mA1** - medial surface of the adductor mandibulae 1

| | **A1** | | **A1β** | |
|---|---|---|---|---|
| | **origin** | **insertion** | **origin** | **insertion** |
| **COMPARATIVE MATERIAL** | | | | |
| *Eleotris potamophila* | d-pre, pte | max, pl | ** | ** |
| *Eleotris pisonis* | d-pre, pte | pl, cor | met, sym | max |
| *Dormitator latifrons* | m-pre | cor | a-lap, met | max, pl |
| *Gobionellus oceanicus* | pre, pte, sph | max, cor | ** | ** |
| *Cryptocentrus sp.* | d-pre, pte, sph | cor | a-spn, lap-l | max, pl |
| *Coryphopterus eidolon* | pre | pl, cor | p-lap | max, pl |
| *Padogobius martensii* | pre, pte, sph | pl, cor | pte, p-lap | max, pl |
| *Chromogobius sp.* | pre, pte, sph | pl, cor | pre, sph | max, pl |
| *Thorogobius ephippiatus* | pre, pte, sph | pl, cor | p-lap, met | max, pl |
| *Sufflogobius bibarbatus* | pre, hyo | cor | p-lap, met | max, pl |
| *Zebrus zebrus* | pre, pte, sph | cor | m-sph, p-lap | max, pl |
| *Bunaka herwerdeni* | pre, pte, sph | cor | a-lap, met | max, pl |
| **OUTGROUPS** | | | | |
| *Gobius niger* | pre, pte, sph | cor | m-sph, p-lap | max, pl |
| *Gobius paganellus* | pre, pte, sph | cor | m-sph, p-lap | max, pl |
| *Vanneaugobius canariensis* | pre, pte, sph | cor | mA1 | max, pl |
| *Microgobius signatus* | pre, pte,sph | cor | pre, met | max |
| *Bollmannia chlamydes* | pre, pte | max, pl | ** | ** |
| *Parrella ginsburgi* | pre, pte | cor, den | p-lap | max |
| *Parrella macropteryx* | pre, pte, sph | cor, max | p-lap | max |
| *Parrella maxillaris* | pre, pte, sph | cor | lap, pre | max |
| **RELATED GENERA** | | | | |
| *Aruma histrio* | pre, pte, sph | den, ta3 | l-lap, met | max |
| *Aboma etheostoma* | pre, pte, sph | cor | l-lap, met | max |
| *Chriolepis minutillus* | pre, pte, sph | cor, ta3 | l-lap, met | max, pl |
| *Evermannichthys spongicola* | d-sph, d-pte | cor | l-lap, met | max |
| *Eleotrica cableae* | pre, pte, sph | cor | l-lap, met | max |
| *Gobulus hancocki* | pre, pte, sph | cor | d-sph | max |
| *Gobulus cresentalis* | pre, pte, sph | cor | d-sph, p-lap, met | max |
| *Ginsburgellus novemlineatus* | pre, pte | cor | l-lap, met | max |
| *Chriolepis vespa* | pre, pte, sph | cor | l-lap, met | max |
| *Pycnomma semisquamatum* | pre, pte, sph | cor | l-lap, met | max, pl |
| *Nes longus* | pre, pte, sph | cor, pl | l-lap, met | max |
| *Risor ruber* | pre, pte, sph | cor | l-lap, met | max |
| *Gymneleotris seminudus* | pre, pte, sph | cor | l-lap, met | max |
| *Pariah scotus* | pre, pte, sph | cor, pl | l-lap, met | max |

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**Table 8** (cont)

| | A2 | | A2γ | |
|---|---|---|---|---|
| | **origin** | **insertion** | **origin** | **insertion** |
| **COMPARATIVE MATERIAL** | | | | |
| *Bunaka herwerdeni* | m-pre, qua | cor | ** | ** |
| *Chromogobius sp.* | m-pre, qua | cor, pl | ** | ** |
| *Coryphopterus eidolon* | m-pre, qua | cor, pl | ** | ** |
| *Cryptocentrus sp.* | m-pre, qua | cor | ** | ** |
| *Dormitator latifrons* | m-pre, qua | cor, pl | ** | ** |
| *Eleotris pisonis* | pre, qua | cor, pl | ** | ** |
| *Eleotris potamophila* | ** | ** | ** | ** |
| *Gobionellus oceanicus* | pre, qua | cor | ** | ** |
| *Padogobius martensii* | m-pre, qua | cor, pl | ** | ** |
| *Sufflogobius bibarbatus* | m-pre, qua | cor, pl | ** | ** |
| *Thorogobius ephippiatus* | m-pre, qua | cor | ** | ** |
| *Zebrus zebrus* | m-pre, qua | cor, pl | ** | ** |
| **OUTGROUPS** | | | | |
| *Bollmannia chlamydes* | m-pre, qua | art, pl | ** | ** |
| *Gobius niger* | m-pre, qua | cor | ** | ** |
| *Gobius paganellus* | m-pre, qua | cor | ** | ** |
| *Microgobius signatus* | m-pre, qua | cor | ** | ** |
| *Parrella ginsburgi* | m-pre, qua | cor, den | ** | ** |
| *Parrella macropteryx* | m-pre, qua | cor | ** | ** |
| *Parrella maxillari* | m-pre, qua | cor | ** | ** |
| *Vanneaugobius canariensis* | m-pre, qua | cor | ** | ** |
| **RELATED GENERA** | | | | |
| *Aruma histrio* | m-pre, qua | cor | qua | pl, max to A1β |
| *Aboma etheostoma* | m-pre, qua | cor | ** | ** |
| *Chriolepis minutillus* | m-pre, qua | cor | qua | pl, max to A1β |
| *Evermannichthys spongicola* | pte, pre | cor | qua | pl, max to A1β |
| *Eleotrica cableae* | m-pre, qua | cor | qua | pl, max to A1β |
| Ginsburgellus novemlineatus | m-pre, qua | cor | qua | pl, max to A1β |
| *Gobulus hancocki* | d-pre, qua | cor | qua | pl, max to A1β |
| *Gobulus cresentalis* | d-pre, qua | cor | qua | pl, max to A1β |
| *Gymneleotris seminudus* | m-pre, qua | cor | qua | pl, max to A1β |
| *Nes longus* | m-pre, qua | cor | qua | pl, max to A1β |
| *Pariah scotus* | m-pre, qua | cor | qua | pl, max to A1β |
| *Pycnomma semisquamatum* | m-pre, qua | cor | qua | pl, max to A1β |
| *Risor ruber* | m-pre, qua | cor | qua | pl, max to A1β |
| *Varicus vespa* | m-pre, qua | cor | ** | ** |

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**Table 9. Character analysis for the cladogram presented in the discussion.** A hypothetical outgroup is used with all other proposed outgroups eliminated. Characters with # were not used in this analysis.

| Character number | Steps | CI | RI | Character number | Steps | CI | RI |
|---|---|---|---|---|---|---|---|
| 1 | 4 | 25 | 72 | 24 | 9 | 11 | 57 |
| 2 | 1 | 100 | 100 | 25 | 5 | 20 | 50 |
| 3 | 1 | 100 | 100 | 26 | 3 | 33 | 0 |
| 4 | 2 | 50 | 0 | 27 | # | # | # |
| 5 | 12 | 16 | 52 | 28 | 4 | 50 | 81 |
| 6 | 10 | 20 | 46 | 29 | 3 | 33 | 86 |
| 7 | 7 | 28 | 58 | 30 | 3 | 33 | 88 |
| 8 | 1 | 100 | 100 | 31 | 3 | 33 | 33 |
| 9 | 12 | 8 | 35 | 32 | 3 | 33 | 33 |
| 10 | 3 | 33 | 75 | 37 | # | # | # |
| 11 | 6 | 16 | 0 | 38 | # | # | # |
| 12 | 2 | 50 | 90 | 35 | # | # | # |
| 13 | 4 | 25 | 40 | 36 | 8 | 12 | 41 |
| 14 | 1 | 100 | 100 | 37 | 6 | 16 | 70 |
| 15 | 2 | 50 | 88 | 38 | 1 | 100 | 100 |
| 16 | 3 | 66 | 94 | 39 | 2 | 50 | 66 |
| 17 | 2 | 50 | 93 | 40 | 1 | 100 | 100 |
| 18 | 3 | 66 | 93 | 41 | 7 | 14 | 40 |
| 19 | # | # | # | 42 | 2 | 50 | 50 |
| 20 | 1 | 100 | 100 | 43 | 5 | 20 | 77 |
| 21 | 3 | 33 | 77 | 44 | 3 | 33 | 33 |
| 22 | 2 | 50 | 93 | 45 | 4 | 25 | 72 |
| 23 | 3 | 33 | 33 |  |  |  |  |

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**Figure 1.** Longitudinal pattern of sensory papillae (neuromasts). A typical longitudinal pattern of sensory papillae found in generalized gobiids.

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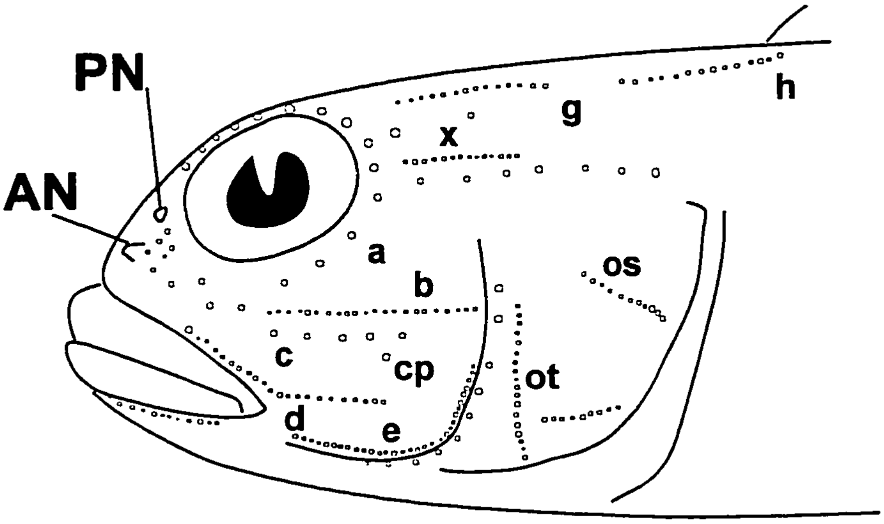

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**Figure 2.** Transverse pattern of sensory papillae. A typical transverse pattern of sensory papillae found in generalized gobiids.

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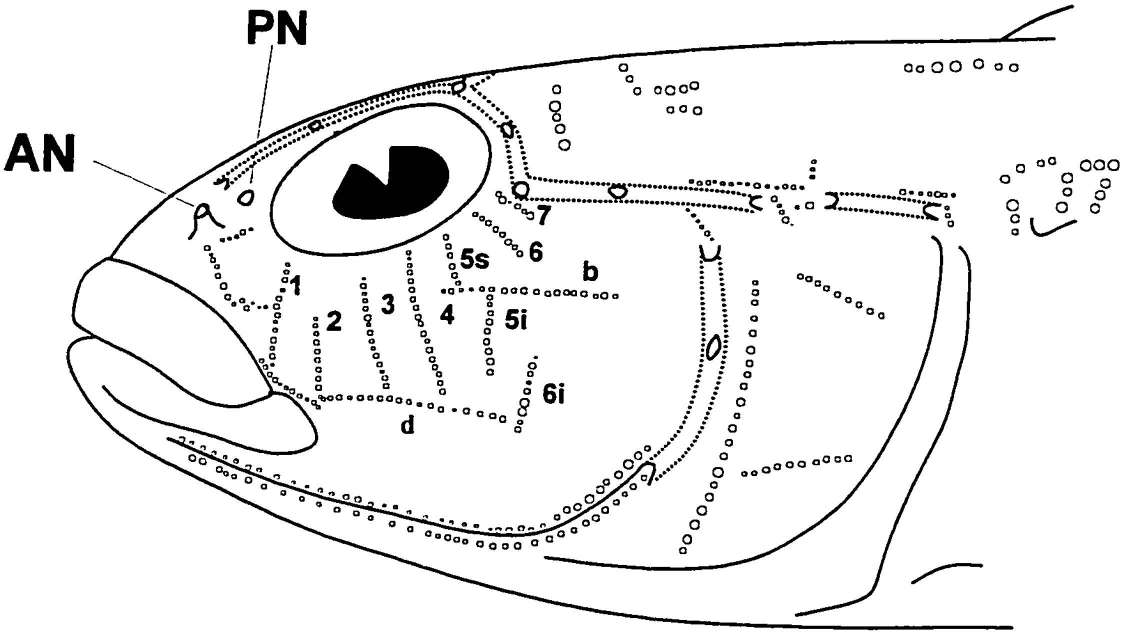

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**Figure 3.** Cephalic lateral line system. The distribution of pores presented uses terminology modified from Akihito *et. al.* (1984).

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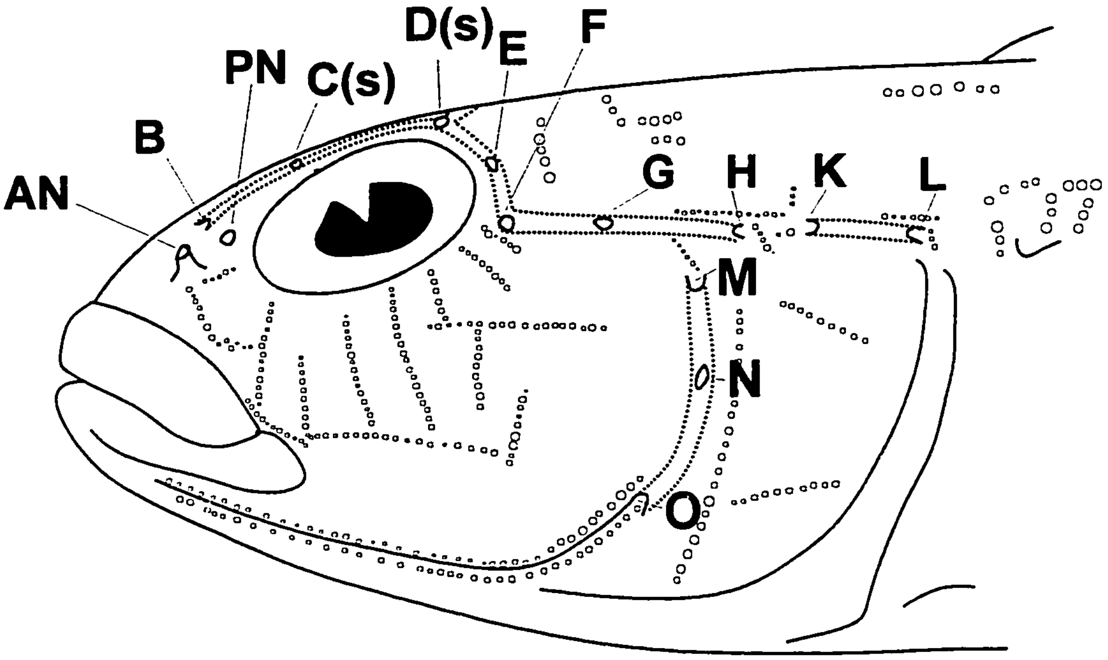

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**Figure 4.** Caudal osteology showing the typical gobiid condition in which hypurals 1+2 are not fused with hypurals 3+4 (A) and the condition found in *Gobiosoma* and related genera in which hypurals 1+2 are fused with 3+4 (B) .

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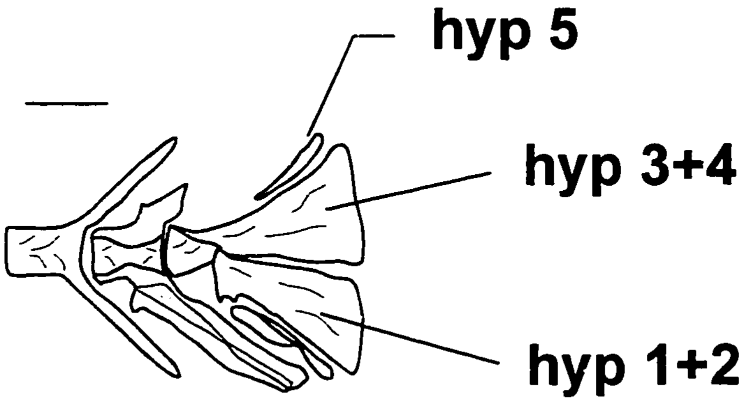
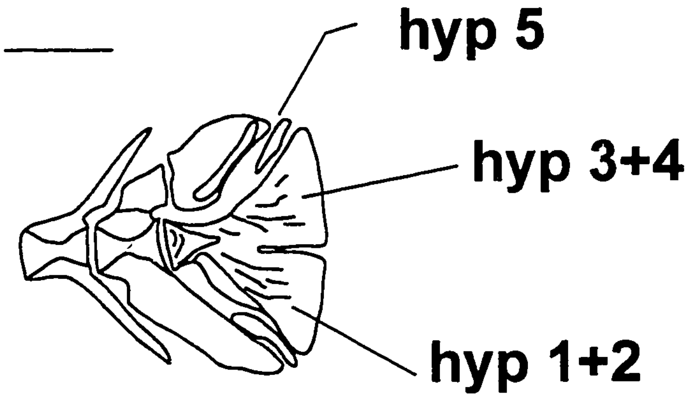


**A**



**B**

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**Figure 5.** Sensory papillae pattern of *Microgobius signatus* (A) and *Bollmannia chlamydes* (B).

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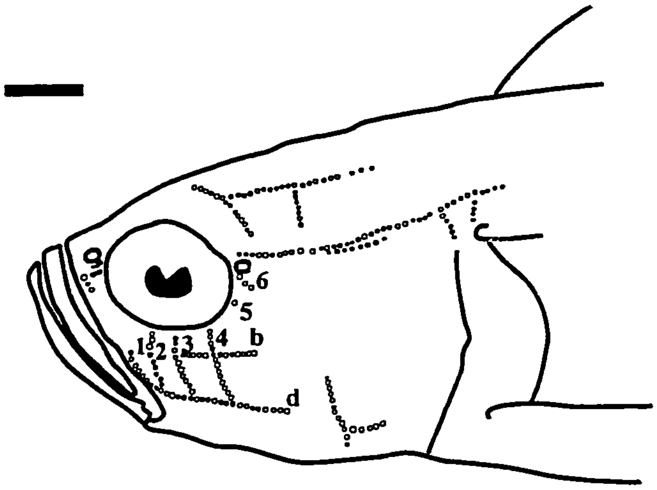
*Microgobius signatus*

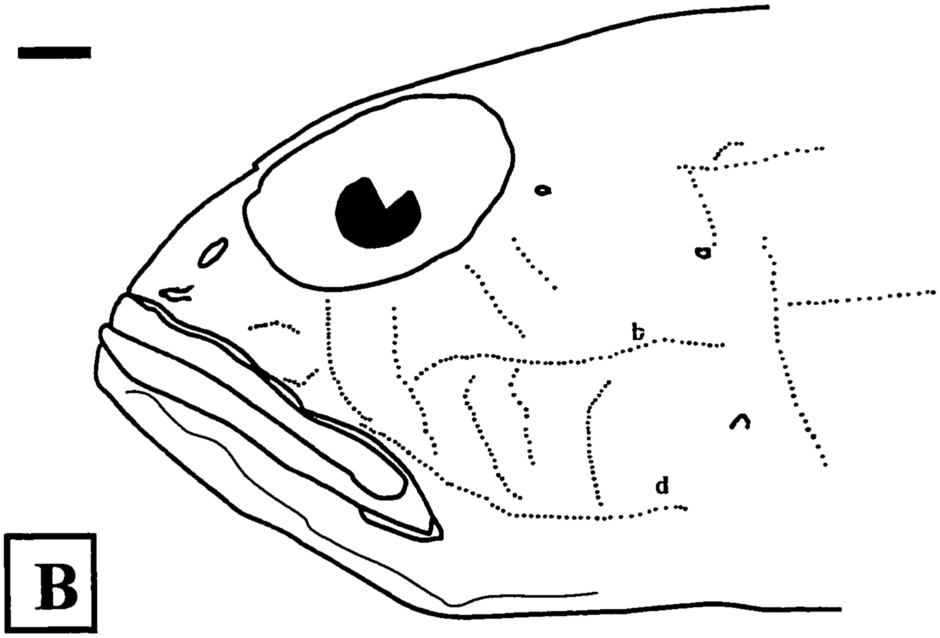
**ANSP 105209**



**A**

*Bollmannia chlamydes*

**CAS 42777**



**B**

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**Figure 6.** Sensory papillae pattern of typical species of *Gobius*. *Gobius couchi* (A) and *Gobius paganellus* (B).

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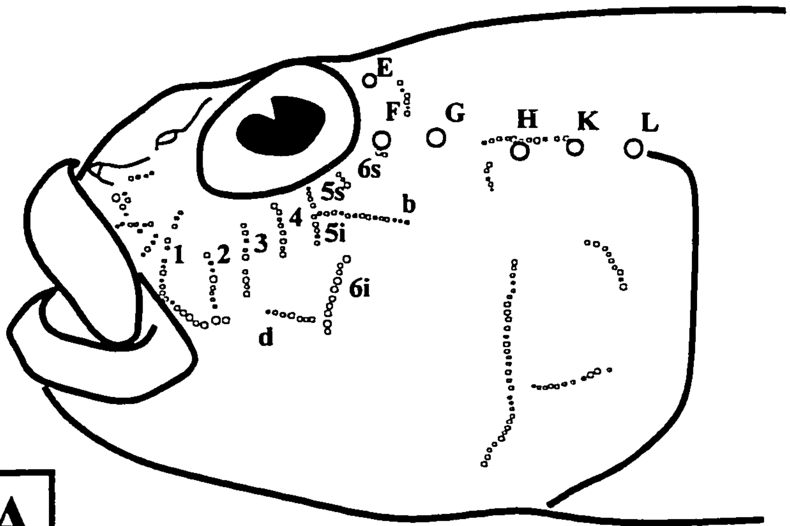
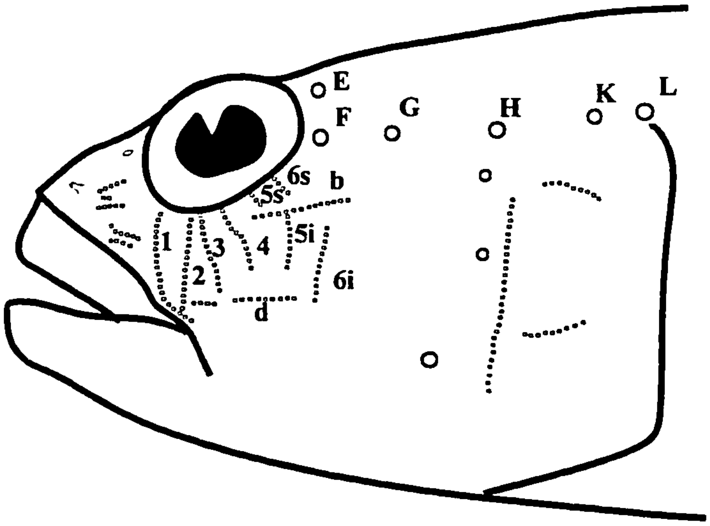
## *Gobius couchi*



**A**

## *Gobius paganellus*



**B**

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**Figure 7.** Sensory papillae pattern of *Gobiosoma chiquita*.

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*Gobiosoma chiquita*

**SU 66911**

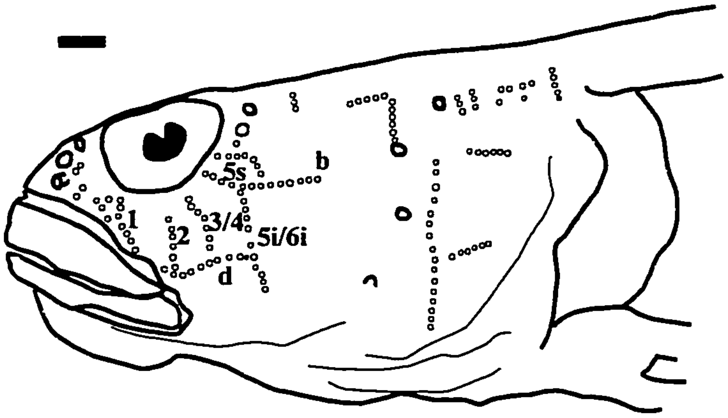

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**Figure 8.** Sensory papillae pattern of *Vanneaugobius pruvoti* (A) and *Odondebuenia balearica* (B).

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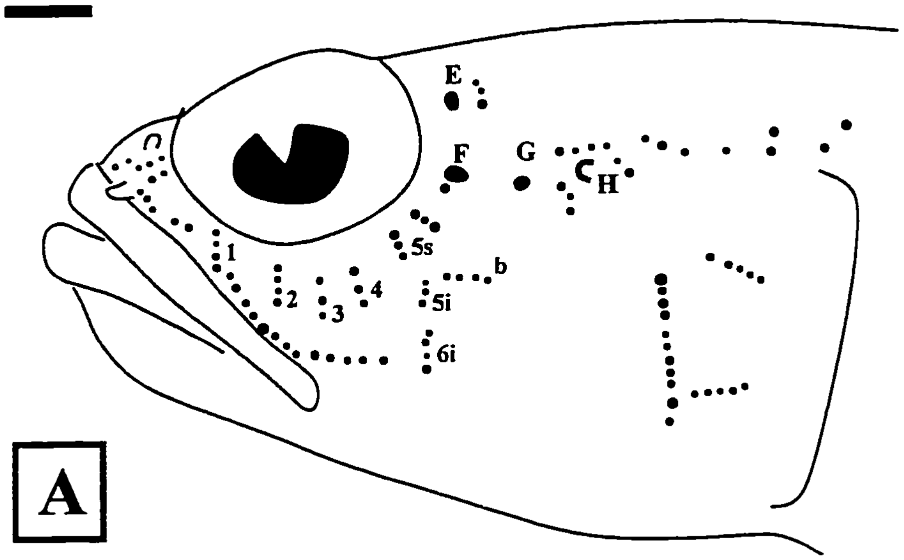
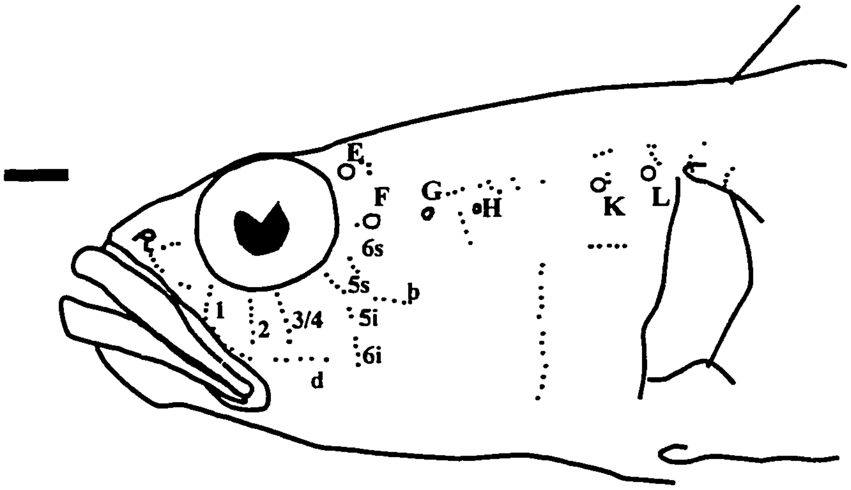
***Vanneaugobius pruvoti***



**A**

*Odondbuenia balearica*

**USNM 048411**



**B**

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**Figure 9.** Modified basicaudal scales. Scales with elongate ctenii found at the base of the caudal peduncle.

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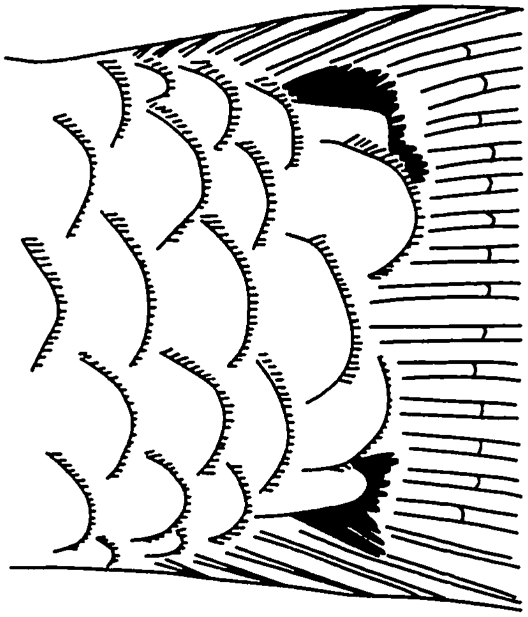
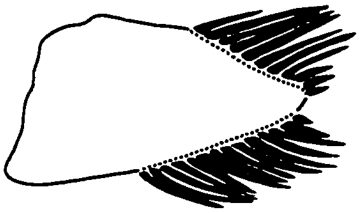


**A**



**B**

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**Figure 10.** Sensory papillae pattern of *Corcyrogobius lubbocki*.

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**_Corcyrogobius lubbocki_**

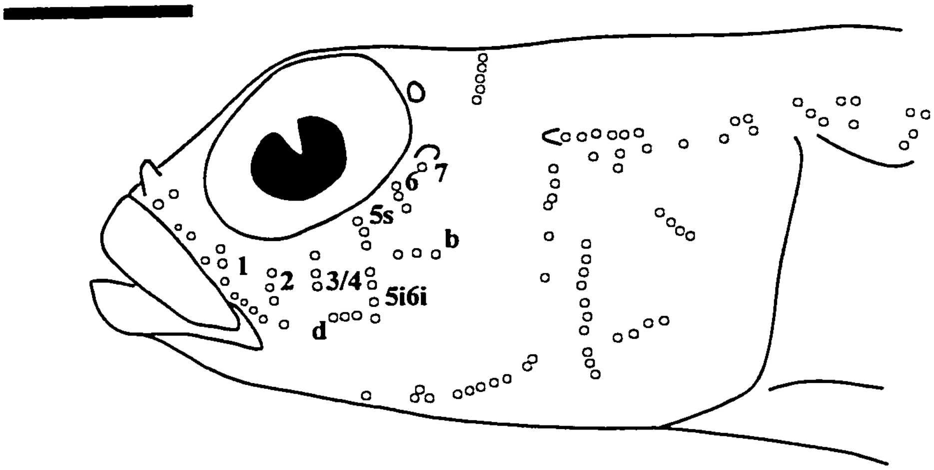

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**Figure 11.** Sensory papillae pattern of *Elacatinus oceanops*.

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*Elacatinus oceanops*

**ANSP 108746**

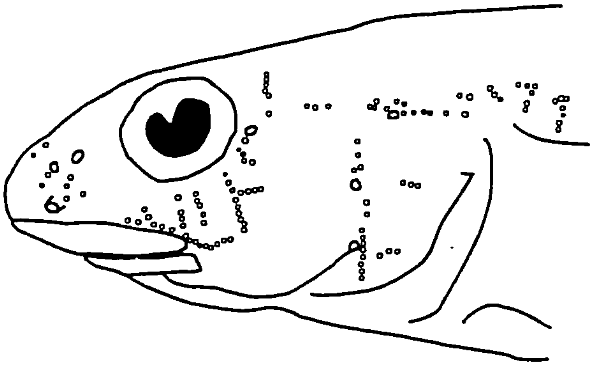

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**Figure 12.** Sensory papillae pattern of *Tigrigobius janssi*.

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# *Tigrigobius janssi*

LACM 32524-46 paratype

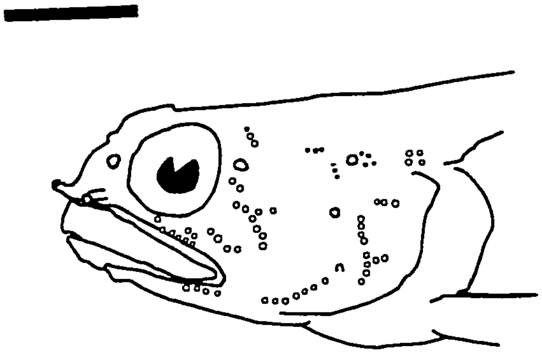

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**Figure 13.** Cladogram produced with all outgroups in the analysis. The consensus tree is shown, produced from 108 equally most parsimonious trees. Statistics for the 108 trees: ci-54; ri-87, tree length-309.

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```
    ╓═ Hypothetical Outgroup
╟═77╫═ Vanneaugobius
    ╟═ Gobius
    ║           ╓═ Microgobius
    ║       ╓═72╨═ Parrella
    ║   ╓═74╨═ Bollmannia
    ╙═76╢   ╓═ Aboma etheostoma
        ╙═75╢   ╓═ Enypnias seminudus
            ╙═73╢   ╓═ Gobiosoma (Gobiosoma) sp. nov. H
                ╟═71╢   ╓═ G. (Austrogobius) parri
                ║   ╙═69╢   ╓═ G. (Go.) ginsburgi
                ║       ╙═67╫═ G. (Go.) longipala
                ║           ║   ╓═ G. (Go.) bosc
                ║           ╙═65╢   ╓═ G. (Garmannia) paradoxum
                ║               ╙═63╨═ G. (Ga.) robustum
                ║   ╓═ G. (Au.) spilotum
                ╙═70╢   ╓═ G. (Au.) grosvenori
                    ╙═68╢   ╓═ G. (Ga.) chiquita
                        ╙═66╢       ╓═ G. (Ga.) spes
                            ║   ╓═62╨═ G. (Ga.) schultzi
                            ╙═64╢   ╓═ G. (Ga.) hildebrandi
                                ╙═61╢   ╓═ G. (Go.) sp. nov. B
                                    ╙═60╢   ╓═ G. (Ga.) homochroma
                                        ╙═59╢       ╓═ Barbulifer
                                            ║   ╓═56╨═ Aruma
                                            ╙═58╢       ╓═ Pycnomma
                                                ║       ╓═53╫═ Eleotrica
                                                ║       ║   ╙═ Chriolepis
                                                ║   ╓═55╨═ Gymneleotris
                                                ╙═57╢   ╓═ Gobulus
                                                    ╙═54╢   ╓═ Nes
                                                        ╙═52╨═51

    ╓═ Evermannichthys
╟═51╢   ╓═ Risor
    ╙═50╢   ╓═ Ginsburgellus
        ╙═49╢   ╓═ Elacatinus (Tigrigobius) janssi
            ╙═48╫═ G. (El.) puncticulatum
                ╟═ G. (Ti.) dilepis
                ╟═ G. (Ti.) macrodon
                ╟═ G. (Ti.) multifasciatum
                ╟═ G. (Ti.) saucrum
                ╟═ G. (Ti.) zebrella
                ║   ╓═ G. (Ti.) gemmatum
                ╟═47╨═ G. (Ti.) pallens
                ║   ╓═ G. (El.) oceanops
                ╙═46╫═ G. (El.) horsti
                    ╙═ G. (El.) xanthiprora
```

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**Figure 14.** Consensus tree with *Aboma* as the only outgroup in the analysis. The tree is produced from 212 most equally parsimonious trees with the following statistics: ci-59, ri-89, tree length 251.

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```
    ╓═ Aboma etheostoma
╟═67╬═ Enypnias seminudus
    ║                       ╓═ Gobiosoma (Garmannia) robustum
    ║                   ╓═57╨═ G. (Ga.) paradoxum
    ║               ╓═59╨═ G. (Gobiosoma) bosc
    ║           ╓═61╬═ G. (Go.) longipala
    ║           ║   ╙═ G. (Go.) ginsburgi
    ║       ╓═63╨═ G. (Austrogobius) parri
    ║   ╓═65╨═ G. (Go.) sp. nov H
    ╙═66╢   ╓═ G. (Au.) spilotum
        ╙═64╢   ╓═ G. (Au.) grosvenori
            ╙═62╢   ╓═ G. (Garmannia) chiquita
                ╙═60╢       ╓═ G. (Ga.) spes
                    ║   ╓═56╨═ G. (Ga.) schultzi
                    ╙═58╢   ╓═ G. (Ga.) hildebrandi
                        ╙═55╢   ╓═ G. (Go.) sp. nov. B
                            ╙═54╢   ╓═ G. (Ga.) homochroma
                                ╙═53╢       ╓═ Barbulifer
                                    ║   ╓═50╨═ Aruma
                                    ╙═52╢           ╓═ Pycnomma
                                        ║       ╓═47╬═ Eleotrica
                                        ║       ║   ╙═ Chriolepis
                                        ║   ╓═49╨═ Gymneleotris
                                        ╙═51╢   ╓═ Gobulus
                                            ╙═48╢   ╓═ Nes
                                                ╙═46╢   ╓═ Evermannichthys
                                                    ╙═45╢   ╓═ Risor
                                                        ╙═44╨═43
```

```
    ╓═ Ginsburgellus
╟═43╢   ╓═ Elacatinus (Tigrigobius) janssi
    ╙═42╬═ G. (El.) puncticulatum
        ╟═ G. (Ti.) dilepis
        ╟═ G. (Ti.) macrodon
        ╟═ G. (Ti.) multifasciatum
        ╟═ G. (Ti.) saucrum
        ╟═ G. (Ti.) zebrella
        ║   ╓═ G. (Ti.) gemmatum
        ╟═41╨═ G. (Ti.) pallens
        ║   ╓═ G. (El.) oceanops
        ╙═40╬═ G. (El.) horsti
            ╙═ G. (El.) xanthiprora
```

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**Figure 15.** Consensus tree with a hypothetical outgroup and all other outgroups eliminated. The consensus tree was produced from 36 equally parsimonious trees with the following statistics; ci-64, ri-89, tree length 289.

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```
    ╓═ Hypothetical Outgroup
╞═68╬═ Aboma etheostoma
    ║   ╓═ Enypnias seminudus
    ╙═67╣   ╓═ Gobiosoma (Gobiosoma) sp. nov. H
        ╞═66╣   ╓═ G. (Austrogobius) parri
        ║   ╙═64╣   ╓═ G. (Go.) ginsburgi
        ║       ╙═62╬═ G. (Go.) longipala
        ║           ║   ╓═ G. (Go.) bosc
        ║           ╙═60╣   ╓═ G. (Garmannia) paradoxum
        ║               ╙═58╩═ G. (Ga.) robustum
        ║   ╓═ G. (Au.) spilotum
        ╙═65╣   ╓═ G. (Au.) grosvenori
            ╙═63╣   ╓═ G. (Ga.) chiquita
                ╙═61╣       ╓═ G. (Ga.) spes
                    ║   ╓═57╩═ G. (Ga.) schultzi
                    ╙═59╣   ╓═ G. (Ga.) hildebrandi
                        ╙═56╣   ╓═ G. (Go.) sp. nov. B
                            ╙═55╣   ╓═ G. (Ga.) homochroma
                                ╙═54╣       ╓═ Barbulifer
                                    ║   ╓═51╩═ Aruma
                                    ╙═53╣           ╓═ Pycnomma
                                        ║       ╓═48╬═ Eleotrica
                                        ║       ║   ╙═ Chriolepis
                                        ║   ╓═50╩═ Gymneleotris
                                        ╙═52╣   ╓═ Gobulus
                                            ╙═49╣   ╓═ Nes
                                                ╙═47╣   ╓═ Evermannichthys
                                                    ╙═46╣   ╓═ Risor
                                                        ╙═45╩═44
```

```
    ╓═ Ginsburgellus
╞═44╣   ╓═ Elacatinus (Tigrigobius) janssi
    ╙═43╬═ Gobiosoma (El.) puncticulatum
        ╟═ G. (Ti.) dilepis
        ╟═ G. (Ti.) macrodon
        ╟═ G. (Ti.) multifasciatum
        ╟═ G. (Ti.) saucrum
        ╟═ G. (Ti.) zebrella
        ║   ╓═ G. (Ti.) gemmatum
        ╟═42╩═ G. (Ti.) pallens
        ║   ╓═ G. (El.) oceanops
        ╙═41╬═ G. (El.) horsti
            ╙═ G. (El.) xanthiprora
```

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**Figure 16.** Consensus tree with a *Vanneaugobius* as the only outgroup. The consensus tree was produced from 12 equally parsimonious trees with the following statistics; ci-60, ri-88, tree length 270.

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```
    ╓═ Vanneaugobius
╟═67╫═ Aboma etheostoma
    ║   ╓═ Gobiosoma (Austrogobius) parri
    ╙═66╢   ╓═ Enypnias seminudus
        ╙═65╢   ╓═ G. (Gobiosoma) ginsburgi
            ╟═64╫═ G. (Go.) longipala
            ║   ║   ╓═ G. (Go.) bosc
            ║   ╙═62╫═ G. (Go.) sp. nov. H
            ║       ║   ╓═ G. (Garmannia) paradoxum
            ║       ╙═60╨═ G. (Ga.) robustum
            ║   ╓═ G. (Au.) spilotum
            ╙═63╢   ╓═ G. (Au.) grosvenori
                ╙═61╢   ╓═ G. (Ga.) chiquita
                    ╙═59╢       ╓═ G. (Ga.) spes
                        ║   ╓═57╨═ G. (Ga.) schultzi
                        ╙═58╢   ╓═ G. (Ga.) hildebrandi
                            ╙═56╢   ╓═ G. (Go.) sp. nov. B
                                ╙═55╢   ╓═ G. (Ga.) homochroma
                                    ╙═54╢       ╓═ Barbulifer
                                        ║   ╓═51╨═ Aruma
                                        ╙═53╢               ╓═ Pycnomma
                                            ║       ╓═48╫═ Eleotrica
                                            ║       ║   ╙═ Chriolepis
                                            ║   ╓═50╨═ Gymneleotris
                                            ╙═52╢   ╓═ Gobulus
                                                ╙═49╢   ╓═ Nes
                                                    ╙═47╢   ╓═Evermannichthys
                                                        ╙═46╨═45
```

```
    ╓═ Risor
╟═45╢   ╓═ Ginsburgellus
    ╙═44╢   ╓═ Elacatinus (Tigrigobius) janssi
        ╙═43╫═ G. (El.) punctulatum
            ╟═ G. (Ti.) dilepis
            ╟═ G. (Ti.) macrodon
            ╟═ G. (Ti.) multifascatum
            ╟═ G. (Ti.) saucrum
            ╟═ G. (Ti.) zebrella
            ║   ╓═ G. (Ti.) gemmatum
            ╟═42╨═ G. (Ti.) pallens
            ║   ╓═ G. (El.) oceanops
            ╙═41╫═ G. (El.) horsti
                ╙═ G. (El.) xanthiprora
```

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**Figure 17.** Consensus tree with a hypothetical outgroup and *Vanneaugobius* as outgroups. The consensus tree was produced from 921 equally parsimonious trees with the following statistics; ci-58, ri-88, tree length 304.

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```
    ╔═ Hypothetical Outgroup
╠═70╬═ Vanneaugobius
    ║   ╔═ Aboma etheostoma
    ╚═69╣   ╔═ Enypnias seminudus
        ╚═68╣   ╔═ Gobiosoma (Gobiosoma) sp. nov. H
            ╠═67╣   ╔═ G. (Austrogobius) parri
            ║   ╚═65╣   ╔═ G. (Go.) ginsburgi
            ║       ╚═63╬═ G. (Go.) longipala
            ║           ║   ╔═ G. (Go.) bosc
            ║           ╚═61╣   ╔═ G. (Garmannia) paradoxum
            ║               ╚═59╩═ G. (Ga.) robustum
            ║   ╔═ G. (Au.) spilotum
            ╚═66╣   ╔═ G. (Au.) grosvenori
                ╚═64╣   ╔═ G. (Ga.) chiquita
                    ╚═62╣       ╔═ G. (Ga.) spes
                        ║   ╔═58╩═ G. (Ga.) schultzi
                        ╚═60╣   ╔═ G. (Ga.) hildebrandi
                            ╚═57╣   ╔═ G. (Go.) sp. nov. B
                                ╚═56╣   ╔═ G. (Ga.) homochroma
                                    ╚═55╣       ╔═ Barbulifer
                                        ║   ╔═52╩═ Aruma
                                        ╚═54╣           ╔═ Pycnomma
                                            ║       ╔═49╬═ Eleotrica
                                            ║       ║   ╚═ Chriolepis
                                            ║   ╔═51╩═ Gymneleotris
                                            ╚═53╣   ╔═ Gobulus
                                                ╚═50╣   ╔═ Nes
                                                    ╚═48╣   ╔═ Evermannichthys
                                                        ╚═47╩═46
```

```
    ╔═ Risor
╠═46╣   ╔═ Ginsburgellus
    ╚═45╣   ╔═ Elacatinus (Tigrigobius) janssi
        ╚═44╬═ G. (El.) puncticulatum
            ╠═ G. (Ti.) dilepis
            ╠═ G. (Ti.) macrodon
            ╠═ G. (Ti.) multifasciatum
            ╠═ G. (Ti.) saucrum
            ╠═ G. (Ti.) zebrella
            ║   ╔═ G. (Ti.) gemmatum
            ╠═43╩═ G. (Ti.) pallens
            ║   ╔═ G. (El.) oceanops
            ╚═42╬═ G. (El.) horsti
                ╚═ G. (El.) xanthiprora
```

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**Figure 18.** Consensus tree with *Microgobius* group as the outgroup. The consensus tree was produced from 625 equally parsimonious trees with the following statistics; ci-58, ri-88, tree length 299.

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```
    ╔═ Microgobius
╠═72╬═ Bollmannia
    ║   ╔═ Parrella
    ╚═71╣               ╔═ Eleotrica
        ║           ╔═62╩═ Chriolepis
        ║       ╔═66╩═ Pycnomma
        ║   ╔═69╩═ Gymneleotris
        ╚═70╣   ╔═ Gobulus
            ╠═68╣   ╔═ Nes
            ║   ╚═65╣   ╔═ Evermannichthys
            ║       ╚═61╣   ╔═ Risor
            ║           ╚═59╣   ╔═ Ginsburgellus
            ║               ╚═57╣   ╔═ Elacatinus (Tigrigobius) janssi
            ║                   ╚═55╬═ G. (El.) puncticulatum
            ║                       ╠═ G. (Ti.) dilepis
            ║                       ╠═ G. (Ti.) macrodon
            ║                       ╠═ G. (Ti.) multifasciatum
            ║                       ╠═ G. (Ti.) saucrum
            ║                       ╠═ G. (Ti.) zebrella
            ║                       ║   ╔═ G. (Ti.) gemmatum
            ║                       ╠═53╩═ G. (Ti.) pallens
            ║                       ║   ╔═ G. (El.) oceanops
            ║                       ╚═52╬═ G. (El.) horsti
            ║                           ╚═ G. (El.) xanthiprora
            ║   ╔═ G. (Garmannia) homochroma
            ╚═67╣   ╔═ Aruma
                ╠═63╩═ Barbulifer
                ║   ╔═ G. (Go.) sp. nov. B
                ╚═64╣   ╔═ G. (Ga.) hildebrandi
                    ╚═60╣   ╔═ G. (Ga.) chiquita
                        ╚═58╣   ╔═ G. (Austrogobius) grosvenori
                            ╚═56╣   ╔═ G. (Au.) spilotum
                                ╚═54╣       ╔═ Enypnias seminudus
                                    ║   ╔═49╩═ Aboma etheostoma
                                    ╚═51╣   ╔═ G. (Go.) sp. nov. H
                                        ╚═50╣   ╔═ G. (Au.) parri
                                            ╚═48╣   ╔═ G. (Go.) ginsburgi
                                                ╚═47╬═ G. (Go.) longipala
                                                    ║   ╔═ G. (Go.) bosc
                                                    ╚═46╣   ╔═ G. (Ga.) robustum
                                                        ╚═45╩═44

    ╔═ G. (Ga.) paradoxum
╠═44╣   ╔═ G. (Ga.) schultzi
    ╚═43╩═ G. (Ga.) spes
```

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**Figure 19.** Consensus tree with a hypothetical outgroup and the *Microgobius* group as outgroups. The consensus tree was produced from 318 equally parsimonious trees with the following statistics; ci-57, ri-87, tree length 308.

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```
    ┌─ Hypothetical Outgroup
├─75┼─ Bollmannia
    │   ┌─ Microgobius
    └─74┤   ┌─ Parrella
        └─73┤               ┌─ Eleotrica
            │           ┌─64┴─ Chriolepis
            │       ┌─68┴─ Pycnomma
            │   ┌─71┴─ Gymneleotris
            └─72┤   ┌─ Gobulus
                ├─70┤   ┌─ Nes
                │   └─67┤   ┌─ Evermannichthys
                │       └─63┤   ┌─ Risor
                │           └─61┤   ┌─ Ginsburgellus
                │               └─59┤   ┌─ Elacatinus (Tigrigobius) janssi
                │                   └─57┼─ Gobiosoma (El.) puncticulatum
                │                       ├─ G. (Ti.) dilepis
                │                       ├─ G. (Ti.) macrodon
                │                       ├─ G. (Ti.) multifasciatum
                │                       ├─ G. (Ti.) saucrum
                │                       ├─ G. (Ti.) zebrella
                │                       │   ┌─ G. (Ti.) gemmatum
                │                       ├─54┴─ G. (Ti.) pallens
                │                       │   ┌─ G. (El.) oceanops
                │                       └─53┼─ G. (El.) horsti
                │                           └─ G. (El.) xanthiprora
                │       ┌─ Barbulifer
                │   ┌─65┴─ Aruma
                └─69┤   ┌─ G. (Garmannia) homochroma
                    └─66┤   ┌─ G. (Gobiosoma) sp. nov. B
                        └─62┤   ┌─ G. (Ga.) hildebrandi
                            └─60┤       ┌─ G. (Ga.) spes
                                │   ┌─56┴─ G. (Ga.) schultzi
                                └─58┤   ┌─ G. (Ga.) chiquita
                                    └─55┤   ┌─ G. (Austrogobius) grosvenori
                                        └─52┤   ┌─ G. (Au.) spilotum
                                            └─51┤       ┌─ Enypnias seminudus
                                                │   ┌─48┴─ Aboma etheostoma
                                                └─50┤   ┌─ G. (Go.) sp. nov. H
                                                    └─49┤   ┌─ G. (Au.) parri
                                                        └─47┴─46


    ┌─ G. (Go.) ginsburgi
├─46┼─ G. (Go.) longipala
    │   ┌─ G. (Go.) bosc
    └─45┤   ┌─ G. (Ga.) paradoxum
        └─44┴─ G. (Ga.) robustum
```

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**Figure 20.** Consensus tree with *Gobius* as the outgroup. The consensus tree was produced from 36 equally parsimonious trees with the following statistics: ci-64, ri-89, tree length 274.

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```
    ╓── Gobius
╟─68╫── Aboma etheostoma
    ║   ╓── Enypnias seminudus
    ╙─67╢   ╓── Gobiosoma (Gobiosoma) sp. nov. H
        ╟─66╢   ╓── G. (Austrogobius) parri
        ║   ╙─64╢   ╓── G. (Go.) ginsburgi
        ║       ╙─62╫── G. (Go.) longipala
        ║           ║   ╓── G. (Go.) bosc
        ║           ╙─60╢   ╓── G. (Garmannia) paradoxum
        ║               ╙─58╨── G. (Ga.) robustum
        ║   ╓── G. (Au.) spilotum
        ╙─65╢   ╓── G. (Au.) grosvenori
            ╙─63╢   ╓── G. (Ga.) chiquita
                ╙─61╢       ╓── G. (Ga.) spes
                    ║   ╓─57╨── G. (Ga.) schultzi
                    ╙─59╢   ╓── G. (Ga.) hildebrandi
                        ╙─56╢   ╓── G. (Go.) sp. nov. B
                            ╙─55╢   ╓── G. (Ga.) homochroma
                                ╙─54╢       ╓── Barbulifer
                                    ║   ╓─51╨── Aruma
                                    ╙─53╢           ╓── Pycnomma
                                        ║       ╓─48╫── Eleotrica
                                        ║       ║   ╙── Chriolepis
                                        ║   ╓─50╨── Gymneleotris
                                        ╙─52╢   ╓── Gobulus
                                            ╙─49╢   ╓── Nes
                                                ╙─47╢   ╓── Evermannichthys
                                                    ╙─46╢   ╓── Risor
                                                        ╙─45╨─44


    ╓── Ginsburgellus
╟─44╢   ╓── Elacatinus (Tigrigobius) janssi
    ╙─43╫── G. (El.) puncticulatum
        ╟── G. (Ti.) dilepis
        ╟── G. (Ti.) macrodon
        ╟── G. (Ti.) multifasciatum
        ╟── G. (Ti.) saucrum
        ╟── G. (Ti.) zebrella
        ║   ╓── G. (Ti.) gemmatum
        ╟─42╨── G. (Ti.) pallens
        ║   ╓── G. (El.) oceanops
        ╙─41╫── G. (El.) horsti
            ╙── G. (El.) xanthiprora
```

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**Figure 21.** Consensus tree with a hypothetical outgroup and *Gobius* as the outgroups. The consensus tree was produced from 72 equally parsimonious trees with the following statistics; ci-60, ri-88, tree length 305.

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```
    ╓─ Hypothetical Outgroup
╟─69╫─ Gobius
    ║   ╓─ Aboma etheostoma
    ╙─68╢   ╓─ Enypnias seminudus
        ╙─67╢   ╓─ Gobiosoma (Gobiosoma) sp. nov. H
            ╟─66╢   ╓─ G. (Austrogobius) parri
            ║   ╙─64╢   ╓─ G. (Go.) ginsburgi
            ║       ╙─62╫─ G. (Go.) longipala
            ║           ║   ╓─ G. (Go.) bosc
            ║           ╙─60╢   ╓─ G. (Garmannia) paradoxum
            ║               ╙─58╨─ G. (Ga.) robustum
            ║   ╓─ G. (Au.) spilotum
            ╙─65╢   ╓─ G. (Au.) grosvenori
                ╙─63╢   ╓─ G. (Ga.) chiquita
                    ╙─61╢       ╓─ G. (Ga.) spes
                        ║   ╓─57╨─ G. (Ga.) schultzi
                        ╙─59╢   ╓─ G. (Ga.) hildebrandi
                            ╙─56╢   ╓─ G. (Go.) sp. nov. B
                                ╙─55╢   ╓─ G. (Ga.) homochroma
                                    ╙─54╢   ╓─ Aruma
                                        ╙─53╫─ Barbulifer
                                            ║               ╓─ Pycnomma
                                            ║           ╓─47╨─ Eleotrica
                                            ║       ╓─49╨─ Chriolepis
                                            ║   ╓─51╨─ Gymneleotris
                                            ╙─52╢   ╓─ Gobulus
                                                ╙─50╢   ╓─ Nes
                                                    ╙─48╢   ╓─ Evermannichthys
                                                        ╙─46╫─ Risor
                                                            ╙─45
```

```
    ╓─ Ginsburgellus
╟─45╢   ╓─ Elacatinus (Tigrigobius) janssi
    ╙─44╫─ G. (El.) puncticulatum
        ╟─ G. (Ti.) dilepis
        ╟─ G. (Ti.) macrodon
        ╟─ G. (Ti.) multifasciatum
        ╟─ G. (Ti.) saucrum
        ╟─ G. (Ti.) zebrella
        ║   ╓─ G. (Ti.) gemmatum
        ╟─43╨─ G. (Ti.) pallens
        ║   ╓─ G. (El.) oceanops
        ╙─42╫─ G. (El.) horsti
            ╙─ G. (El.) xanthiprora
```

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**Figure 22.** Consensus tree with a hypothetical outgroup and *Vanneaugobius* and *Gobius* as outgroups. The consensus tree was produced from 72 equally parsimonious trees with the following statistics; ci-57, ri-88, tree length 307.

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```
    ╔═ Hypothetical Outgroup
╠═71╬═ Gobius
    ║   ╔═ Vanneaugobius
    ╚═70╣   ╔═ Aboma etheostoma
        ╚═69╣   ╔═ Enypnias seminudus
            ╚═68╣   ╔═ Gobiosoma Gobiosoma sp. nov. H
                ╠═67╣   ╔═ G. Austrogobius parri
                ║   ╚═65╣   ╔═ G. Go. ginsburgi
                ║       ╚═63╬═ G. Go. longipala
                ║           ║   ╔═ G. Go. bosc
                ║           ╚═61╣   ╔═ G. Garmannia paradoxum
                ║               ╚═59╩═ G. Ga. robustum
                ║   ╔═ G. Au. spilotum
                ╚═66╣   ╔═ G. Au. grosvenori
                    ╚═64╣   ╔═ G. Ga. chiquita
                        ╚═62╣       ╔═ G. Ga. spes
                            ║   ╔═58╩═ G. Ga. schultzi
                            ╚═60╣   ╔═ G. Ga. hildebrandi
                                ╚═57╣   ╔═ G. Go. sp. nov. B
                                    ╚═56╣   ╔═ G. Ga. homochroma
                                        ╚═55╣   ╔═ Aruma
                                            ╚═54╬═ Barbulifer
                                                ║           ╔═48
                                                ║       ╔═50╩═ Chriolepis
                                                ║   ╔═52╩═ Gymneleotris
                                                ╚═53╣   ╔═ Gobulus
                                                    ╚═51╣   ╔═ Nes
                                                        ╚═49╩═47
```

```
    ╔═ Eleotrica
╠═48╩═ Pycnomma
```

```
    ╔═ Evermannichthys
╠═47╬═ Risor
    ║   ╔═ Ginsburgellus
    ╚═46╣   ╔═ Elacatinus Tigrigobius janssi
        ╚═45╬═ G. El. puncticulatum
            ╠═ G. Ti. dilepis
            ╠═ G. Ti. macrodon
            ╠═ G. Ti. multifasciatum
            ╠═ G. Ti. saucrum
            ╠═ G. Ti. zebrella
            ║   ╔═ G. Ti. gemmatum
            ╠═44╩═ G. Ti. pallens
            ║   ╔═ G. El. oceanops
            ╚═43╬═ G. El. horsti
                ╚═ G. El. xanthiprora
```

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**Figure 23.** Diagrammatic representation of the cheek myology of *Gobionellus oceanicus*.

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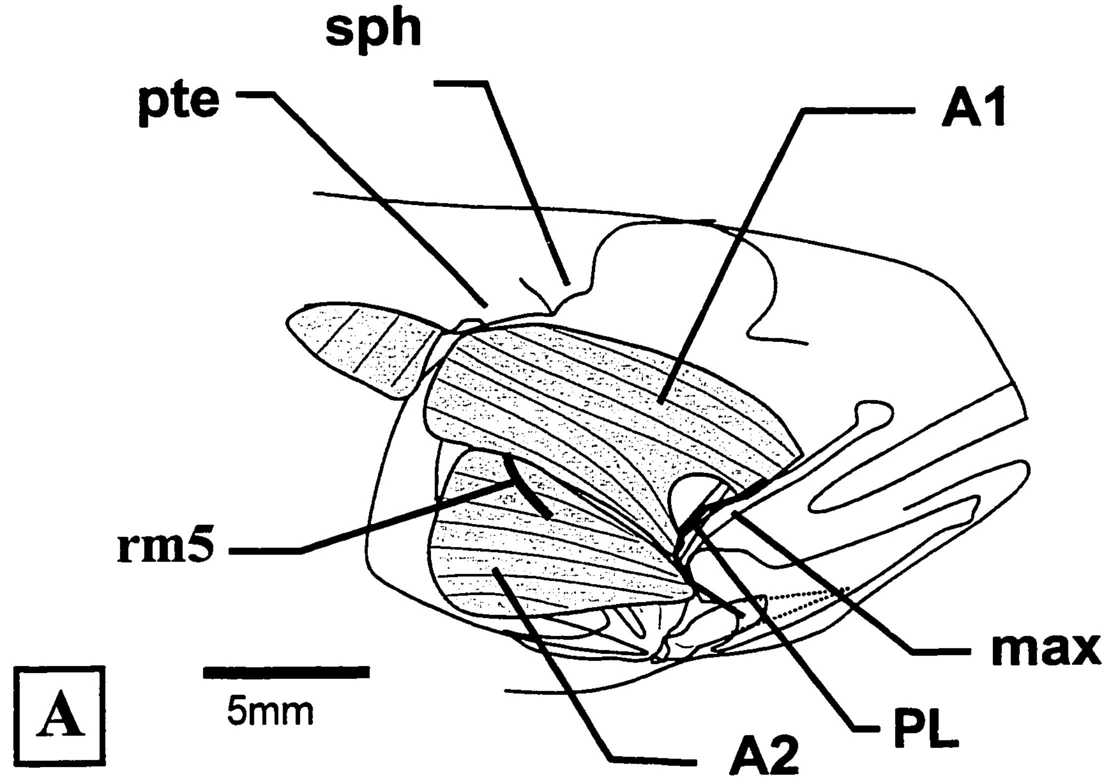
# *Gobionellus oceanicus*

FMRI Indian River collection



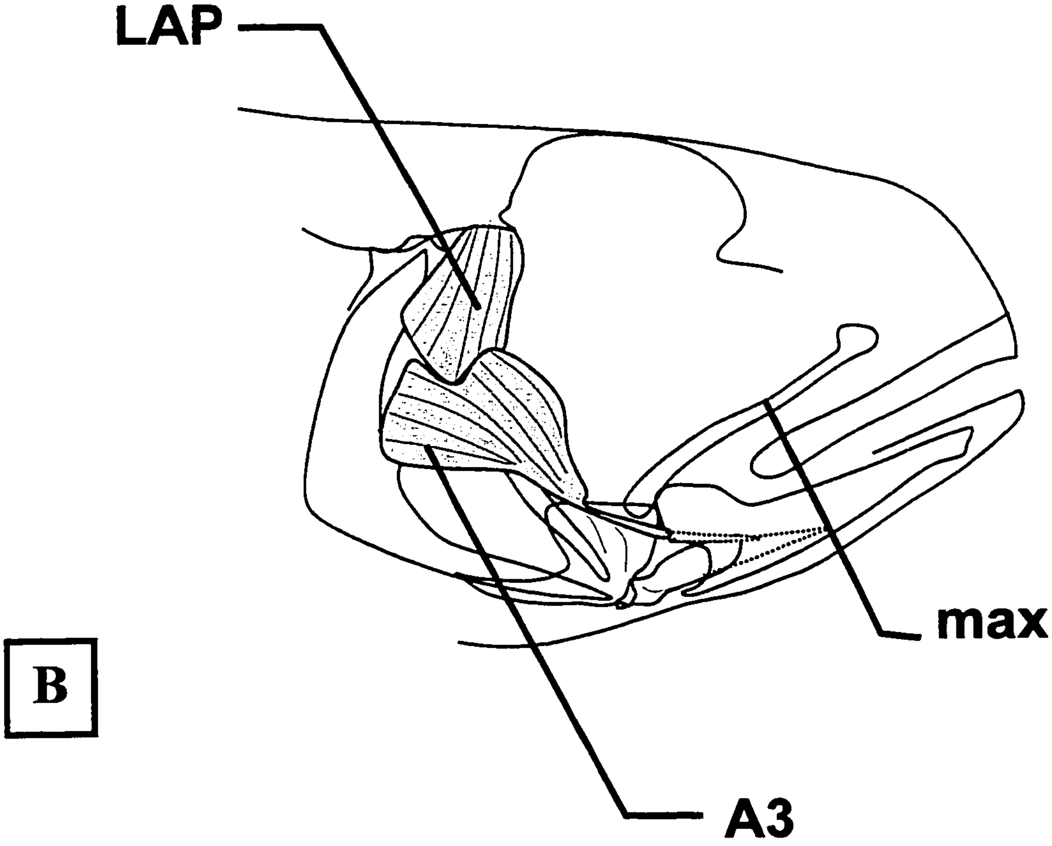


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**Figure 24.** Diagrammatic representation of the cheek myology of *Aruma histrio*.

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*Aruma histrio*

CAS 79602

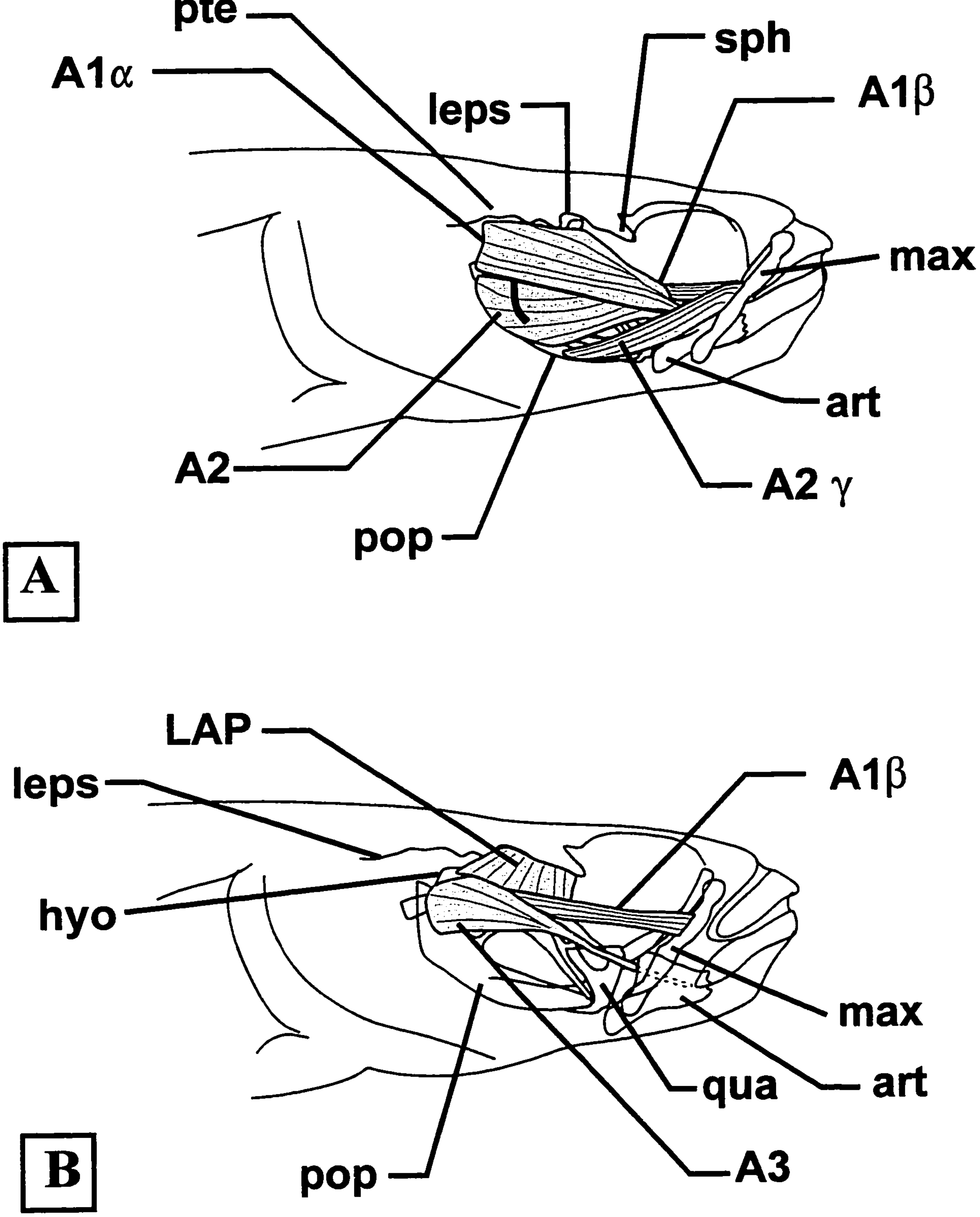

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**Figure 25.** Diagrammatic representation of the cheek myology of *Gobiosoma longipala.* External myology (A) and inner muscles of the suspensorium (B).

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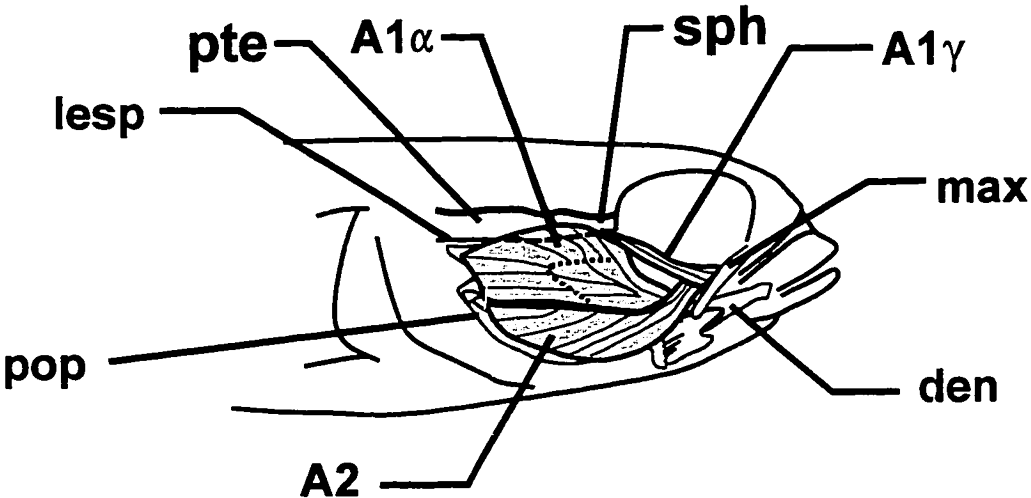
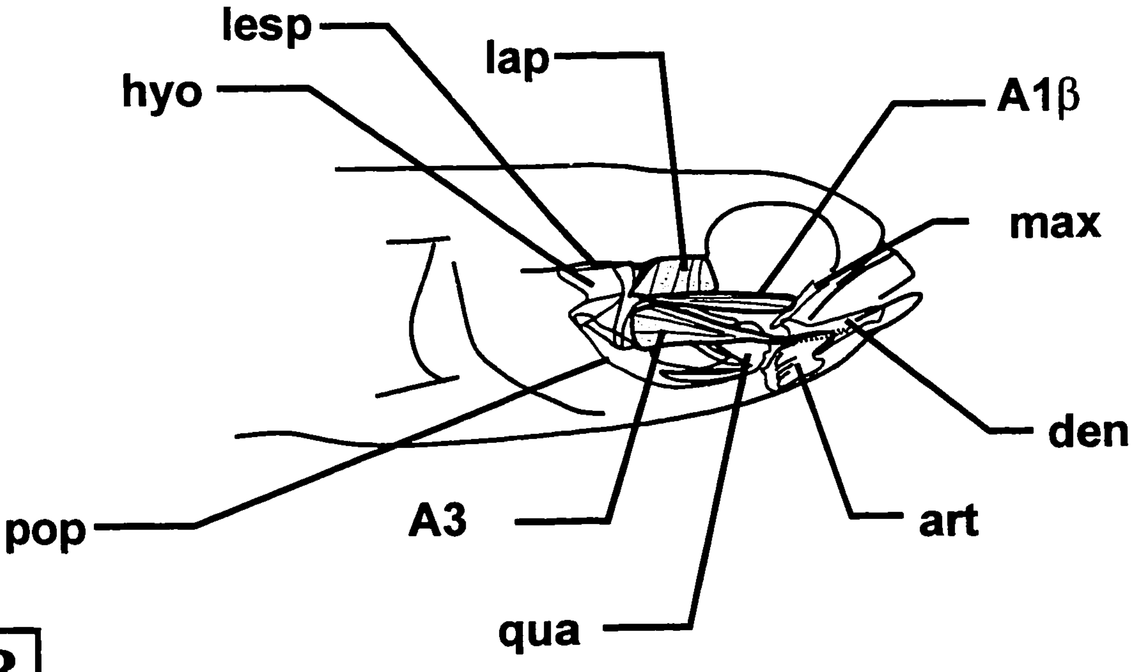
*Gobiosoma longipala*

**GCRL 815**



**A**



**B**

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**Figure 26.** Diagrammatic representation of the cheek myology of *Evermannichthys spongicola.* External myology (A) and inner muscles of the suspensorium (B).

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*Evermannichthys spongicola*

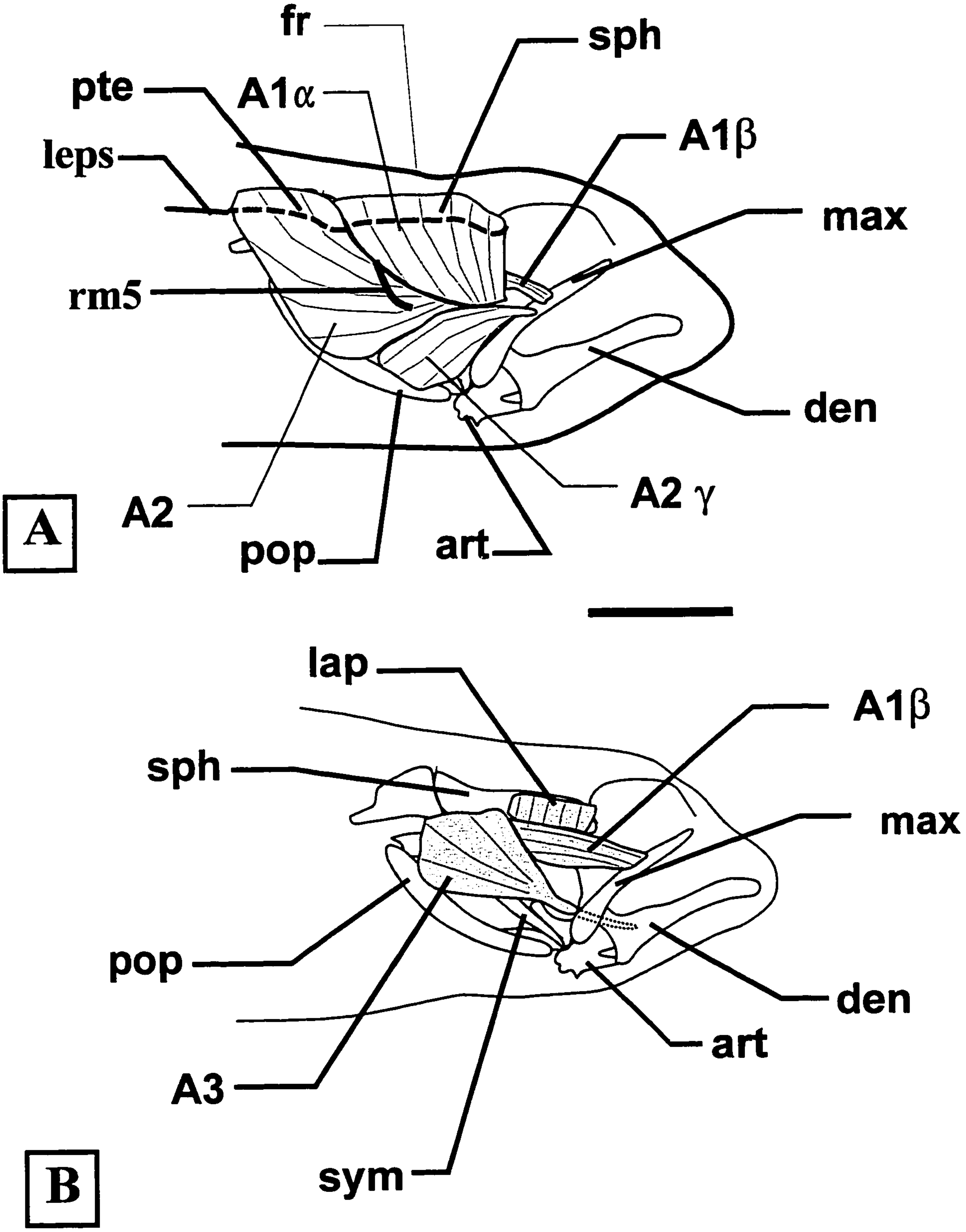

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**Figure 27.** Diagrammatic representation of the cheek myology of *Pycnomma semisquamatum.* External myology (A) and inner muscles of the suspensorium (B).

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*Pycnomma semisquamatum*

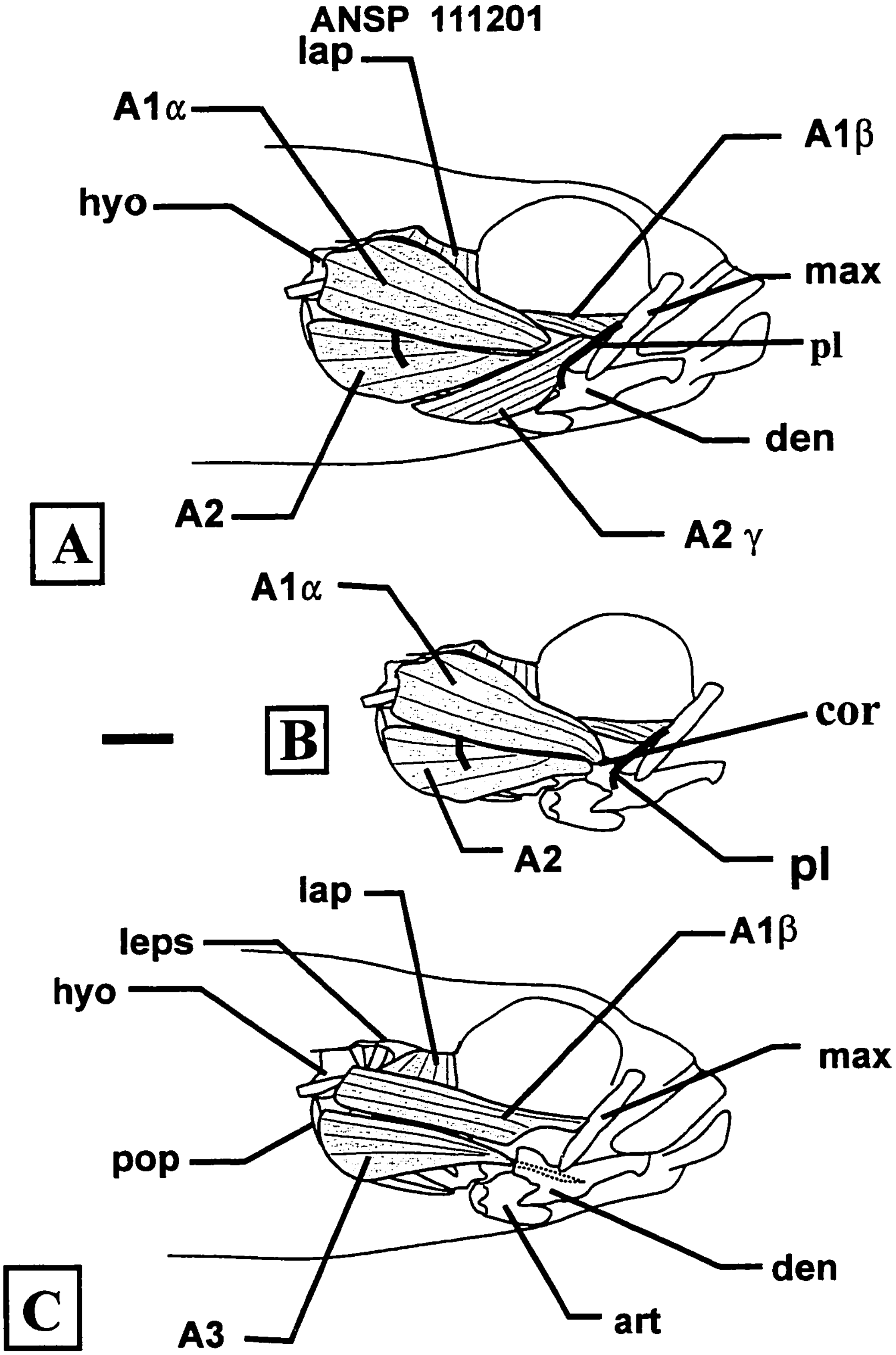

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**Figure 28.** Diagrammatic representation of the cheek myology of *Chromogobius sp. nov.* External myology (A) and inner muscles of the suspensorium (B).

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*Chromogobius sp. nov.*

**JVT-90-512**

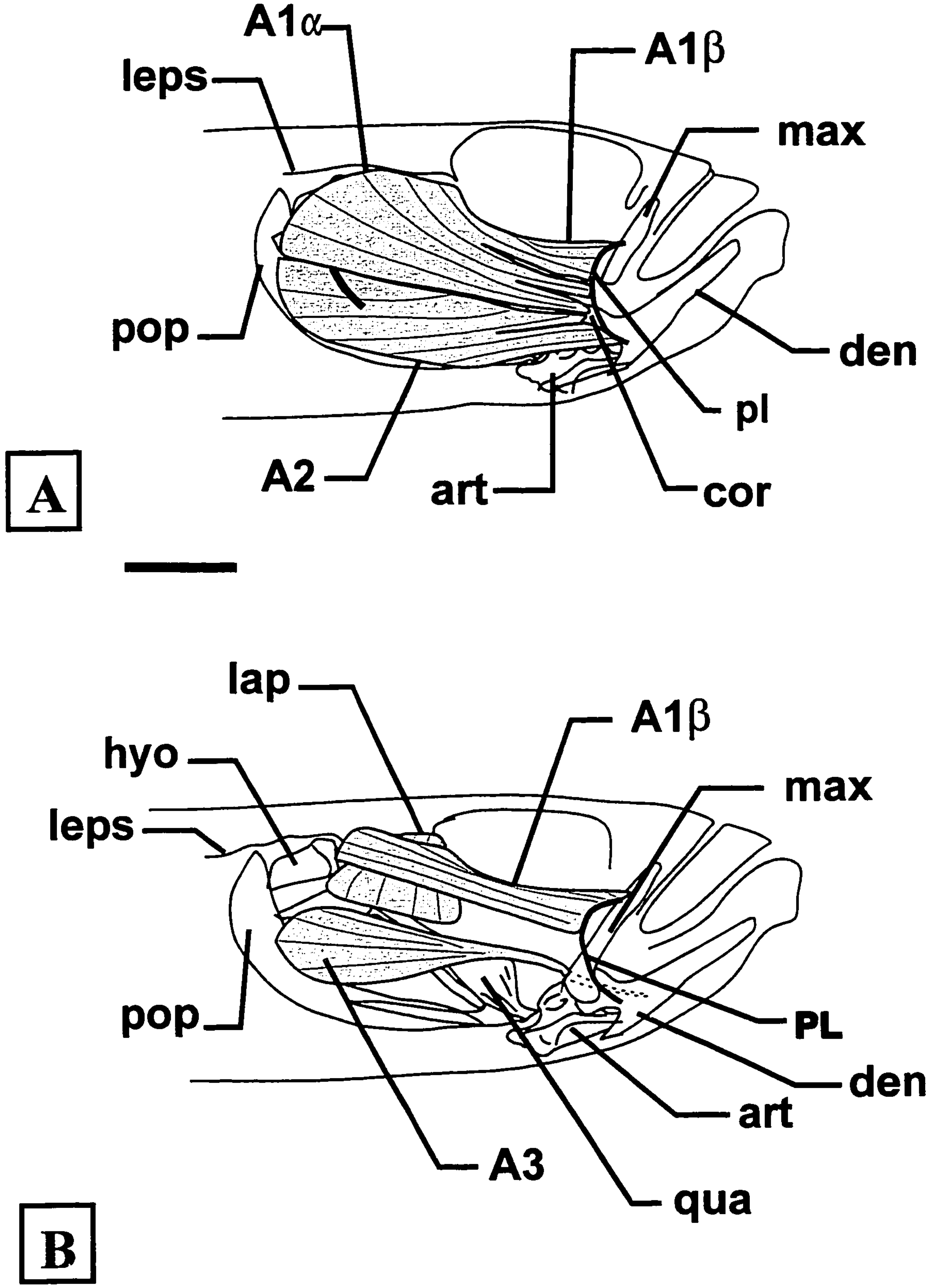

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**Figure 29.** Diagrammatic representation of the cheek myology of *Gobiosoma ginsburgi*. External myology (A) and inner muscles of the suspensorium (B).

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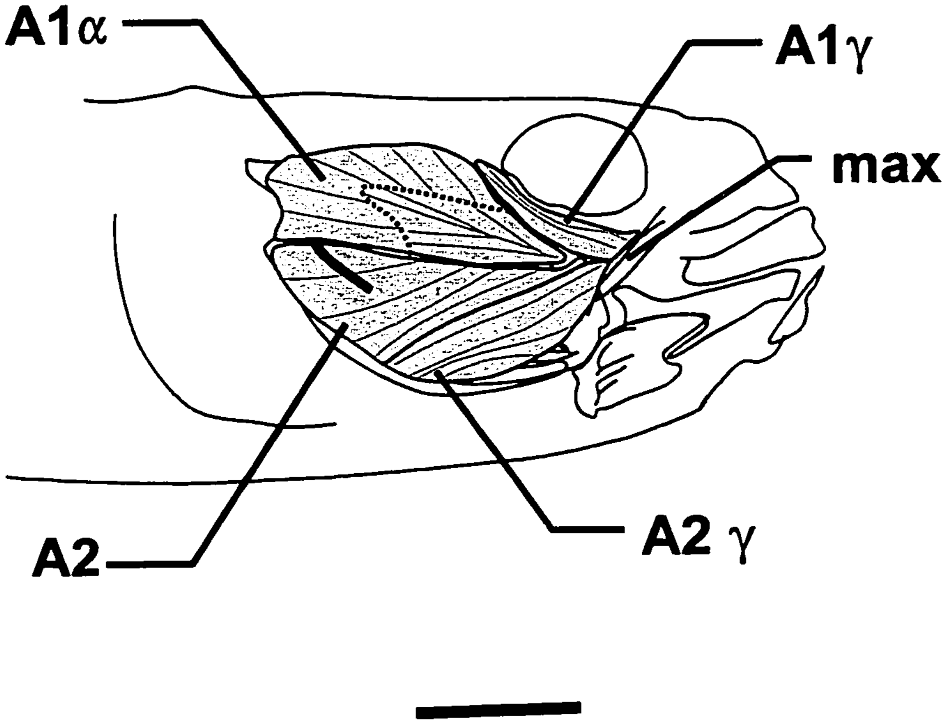
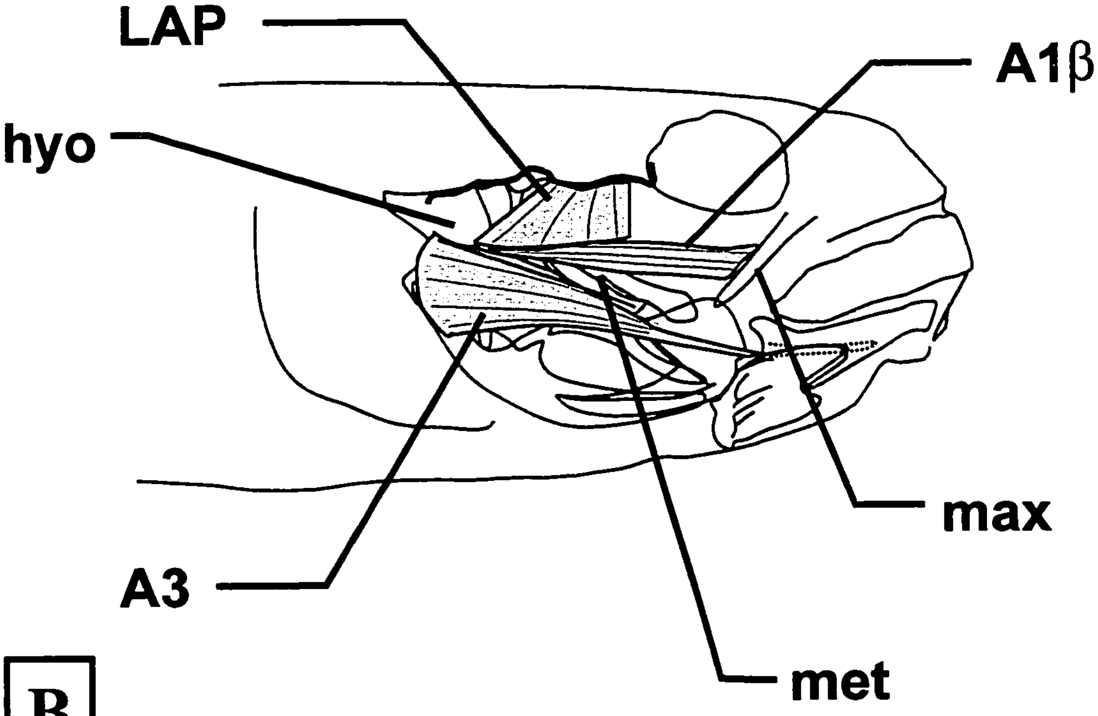
## *Gobiosoma ginsburgi*

### ANSP 101975



A



B

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**Figure 30.** Diagrammatic representation of the cheek myology of *Zebrus zebrus*. External myology (A) and inner muscles of the suspensorium (B).

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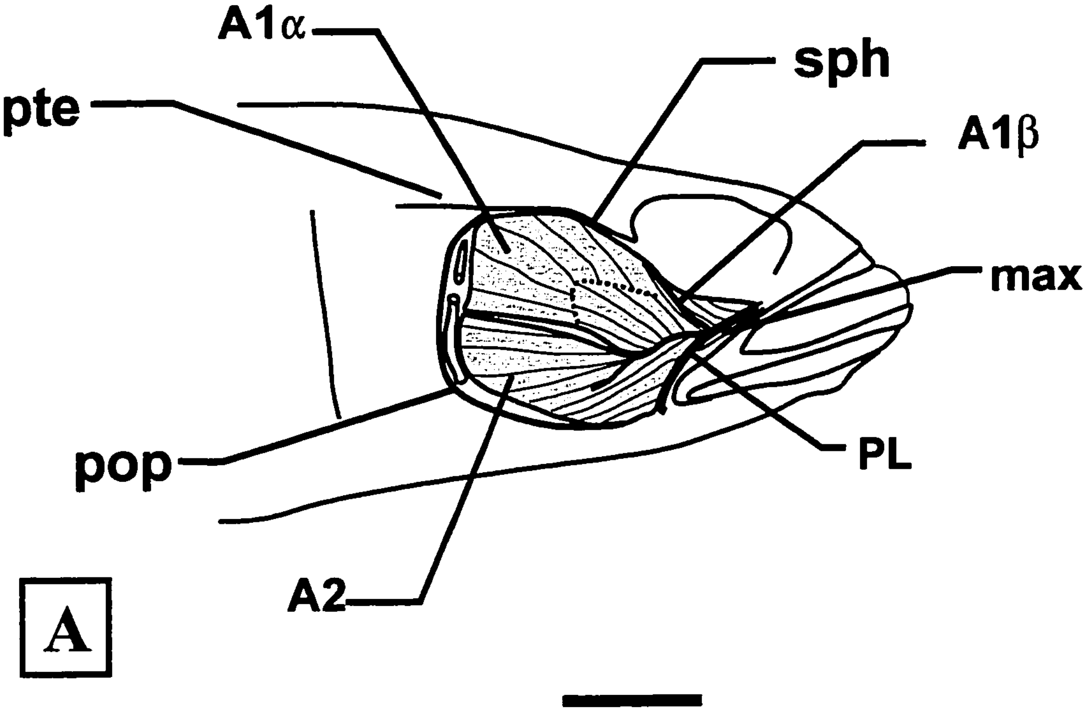
## *Zebrus zebrus*

### BMNH 1980.3.5:21



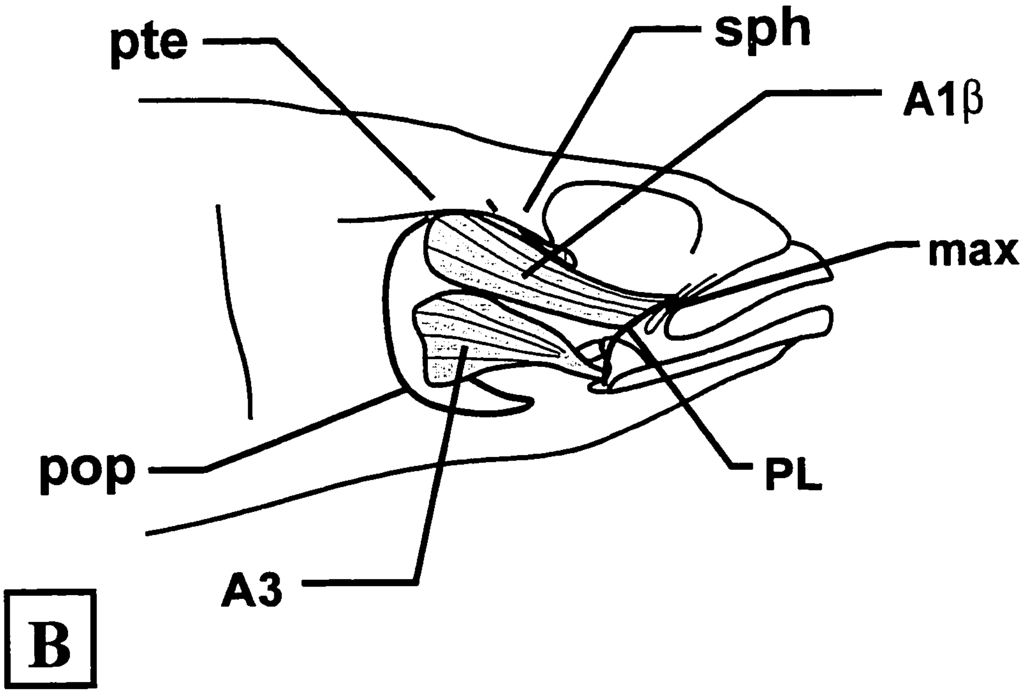


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**Figure 31.** Diagrammatic representation of the cheek myology of *Dormitator latifrons*. External myology (A) and inner muscles of the suspensorium (B).

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*Dormitator latifrons*

AMNH 32955

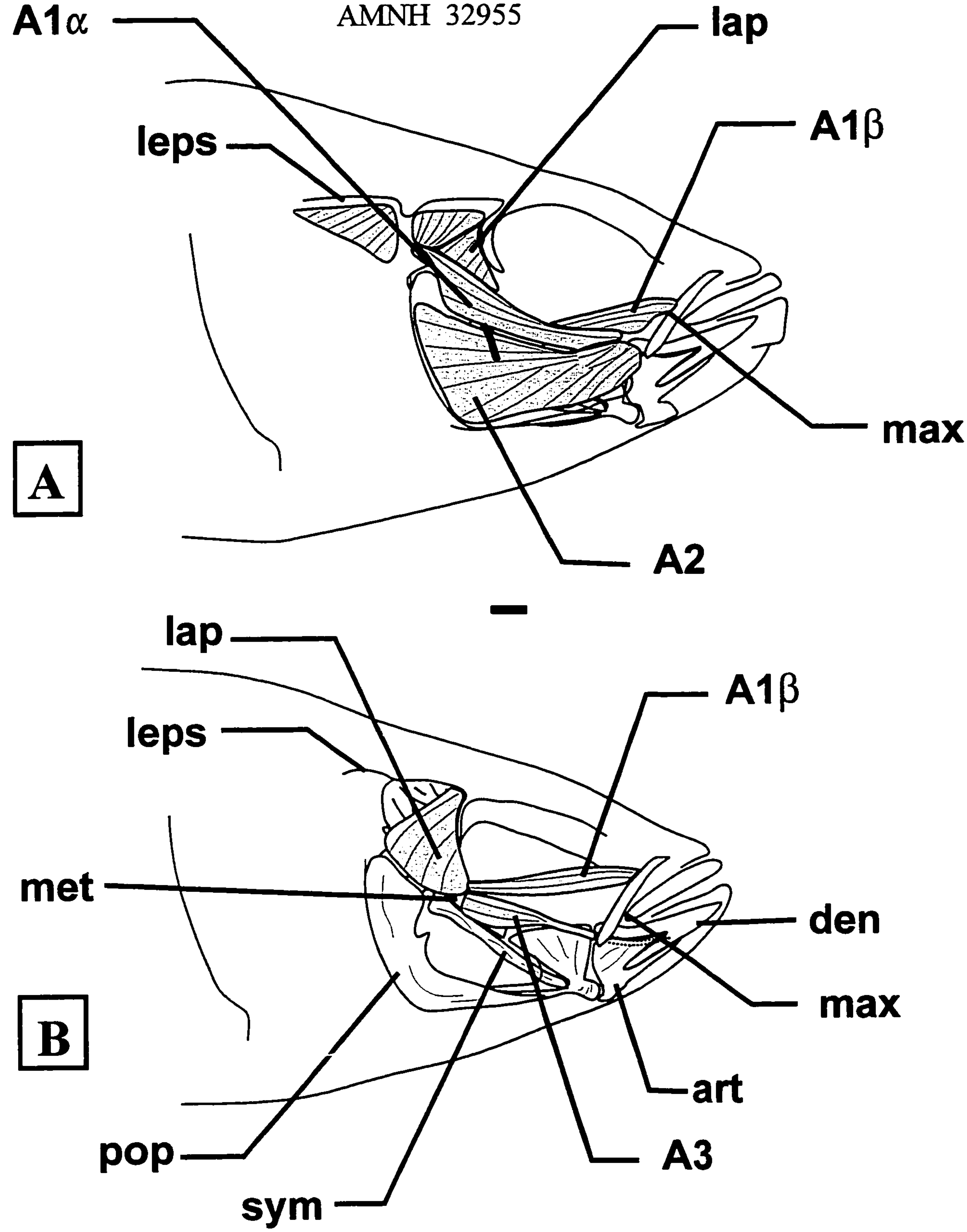

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**Figure 32.** Diagrammatic representation of the cheek myology of *Aboma etheostoma*. External myology (A) and inner muscles of the suspensorium (B).

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*Aboma etheostoma*

**GCRL 13035**

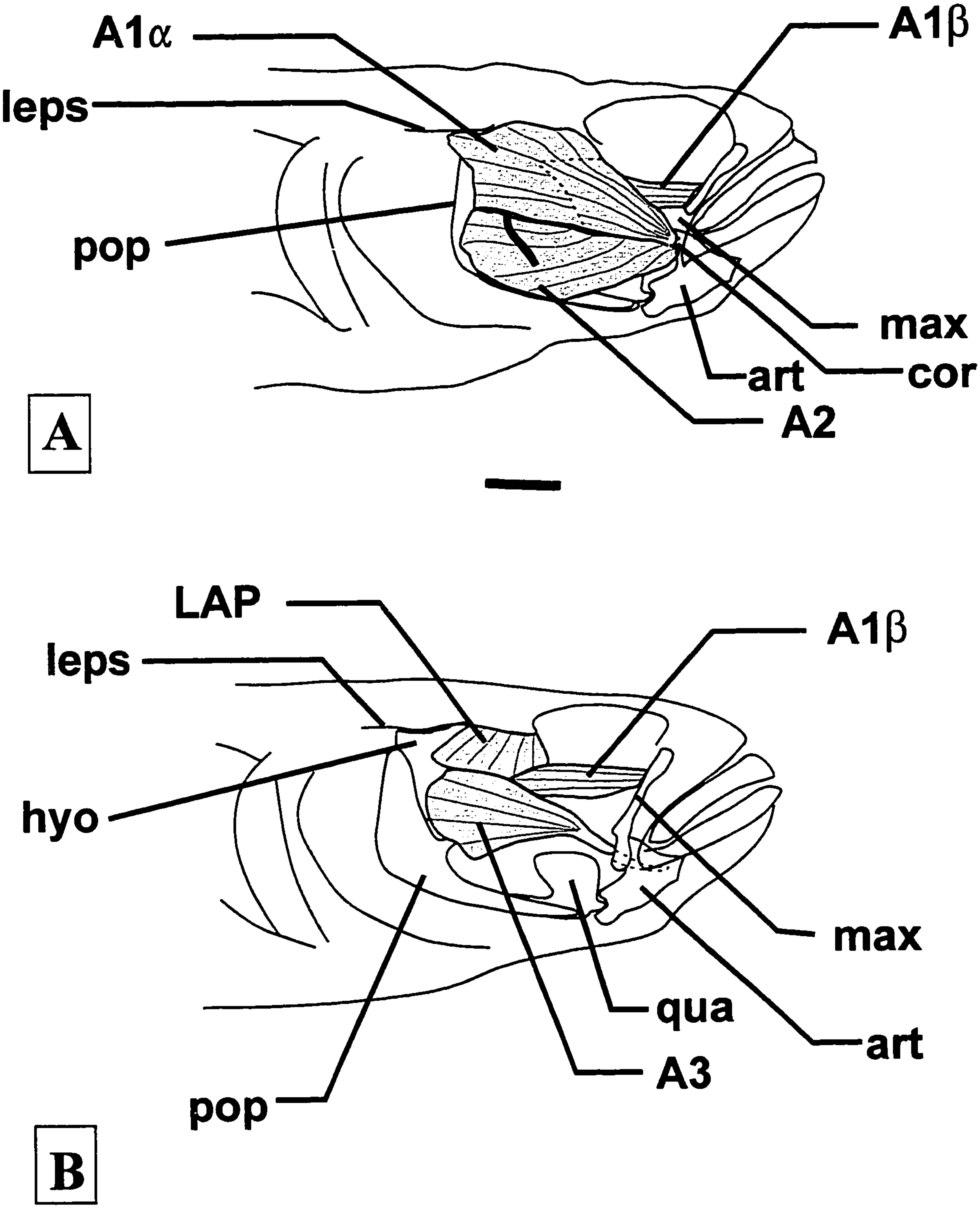

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**Figure 33.** Diagrammatic representation of the cheek myology of *Sufflogobius bibarbatus*. External myology (A) and inner muscles of the suspensorium (B).

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***Sufflogobius bibarbatus***

**PJM Collection**

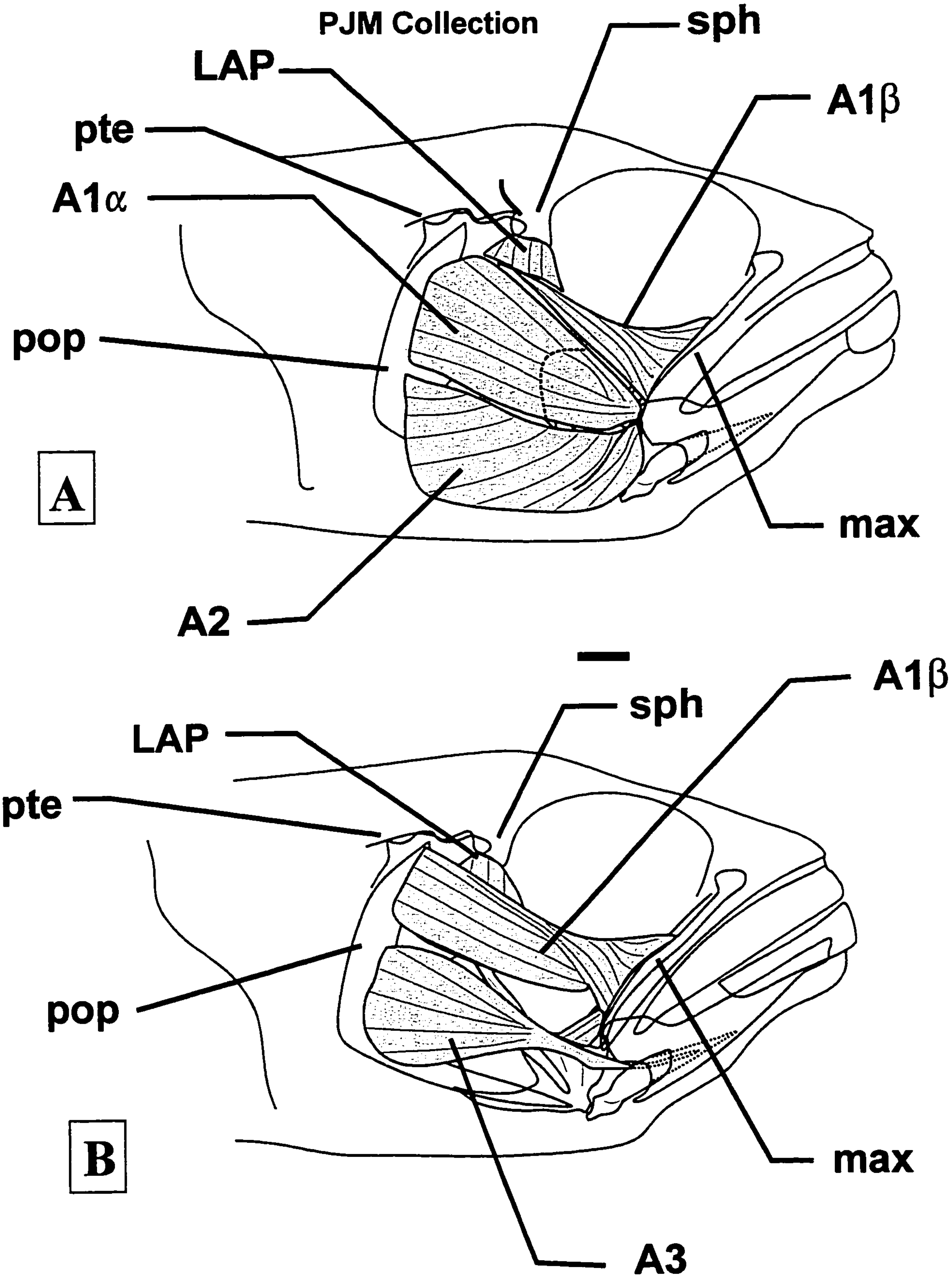

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**Figure 34.** Diagrammatic representation of the cheek myology of *Chriolepis minutilis*. External myology (A) and inner muscles of the suspensorium (B).

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## *Chriolepis minutilis*

**LACM 20148**

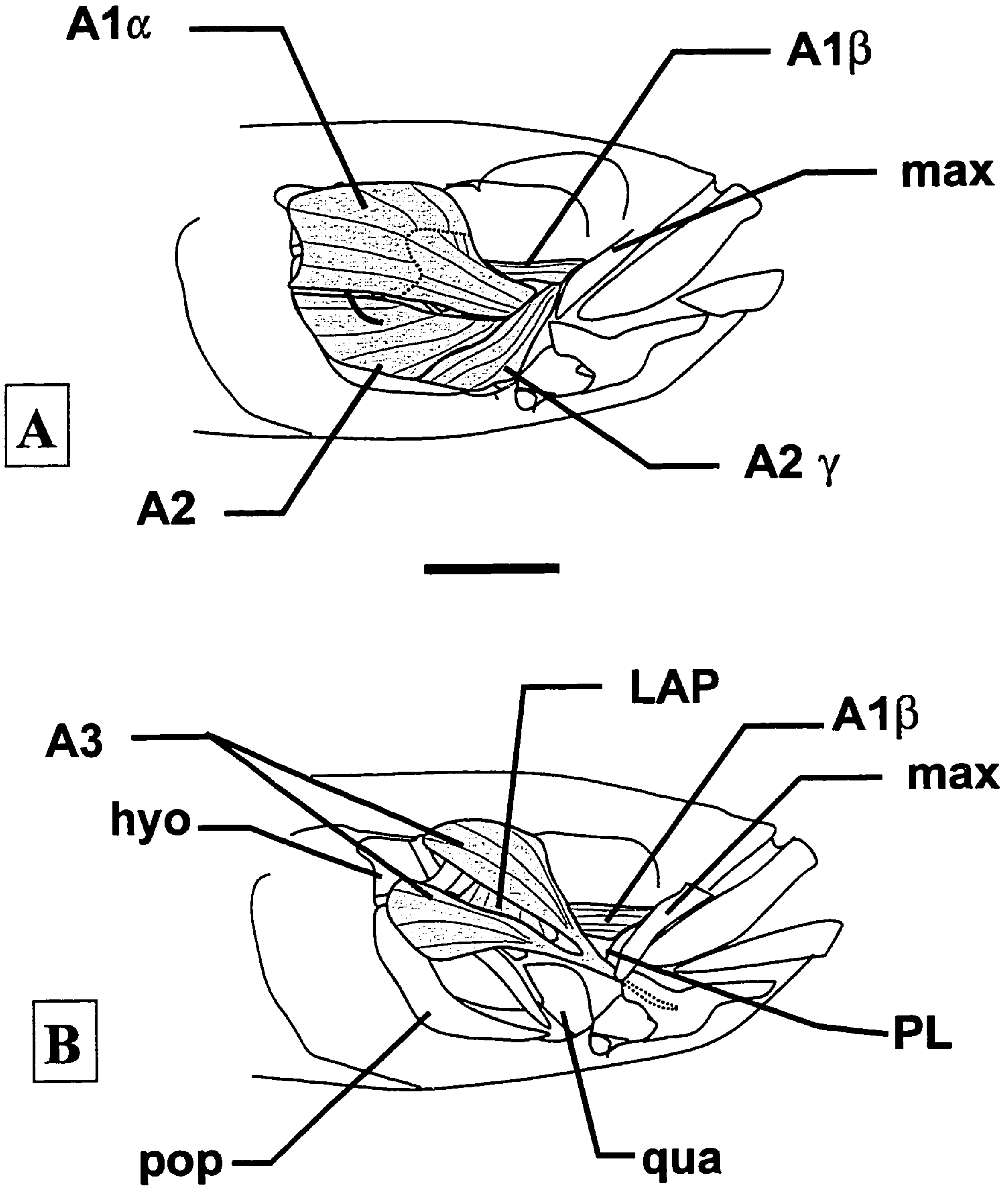

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**Figure 35.** Diagrammatic representation of the cheek myology of *Coryphopterus eidolon*. External myology (A) and inner muscles of the suspensorium (B).

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# *Coryphopterus eidolon*

**AMNH 38288**

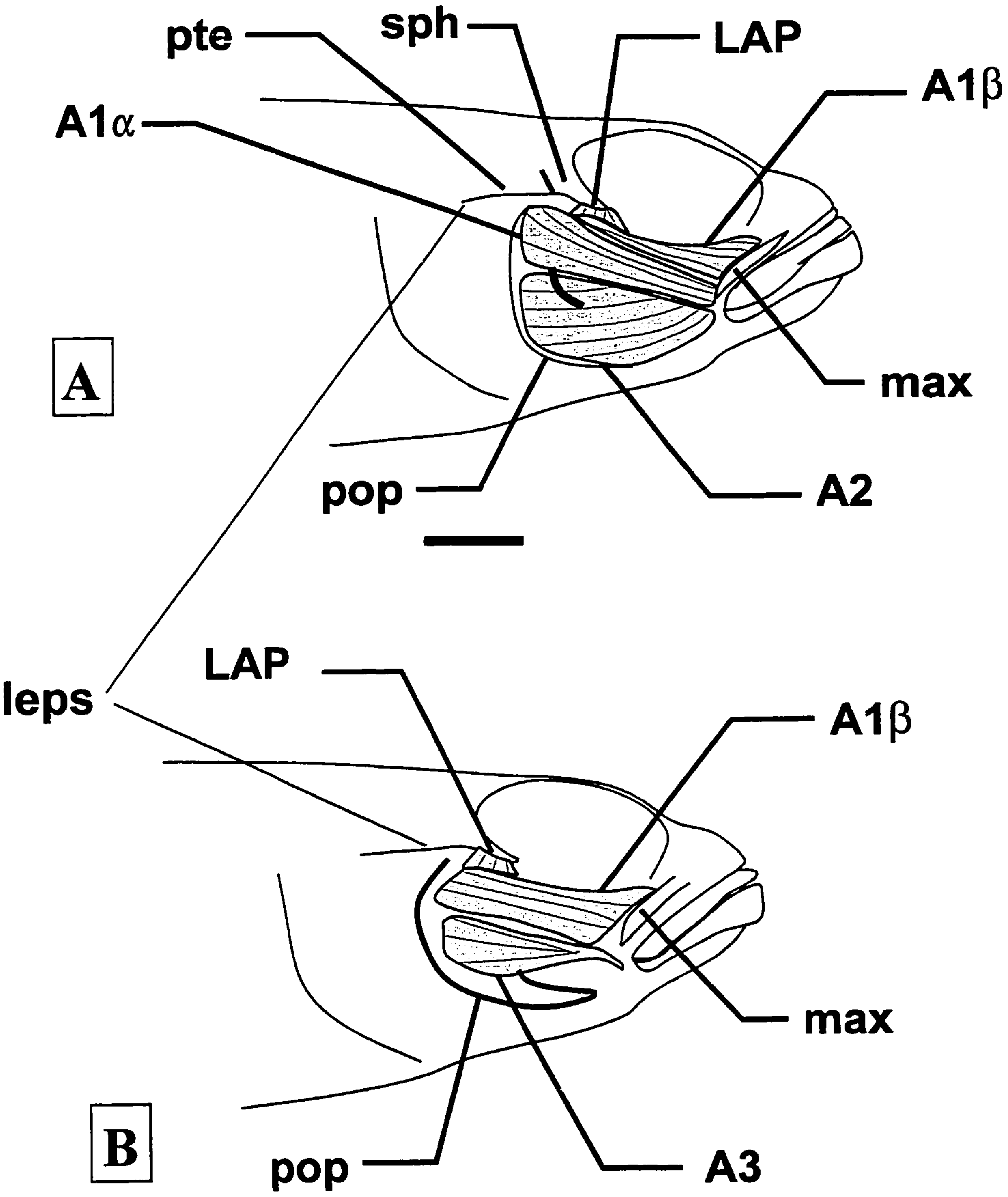

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**Figure 36.** Diagrammatic representation of the cheek myology of *Gobiosoma nudum*. External myology (A) and inner muscles of the suspensorium (B).

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## *Gobiosoma nudum*

**GCRL V73:11523**

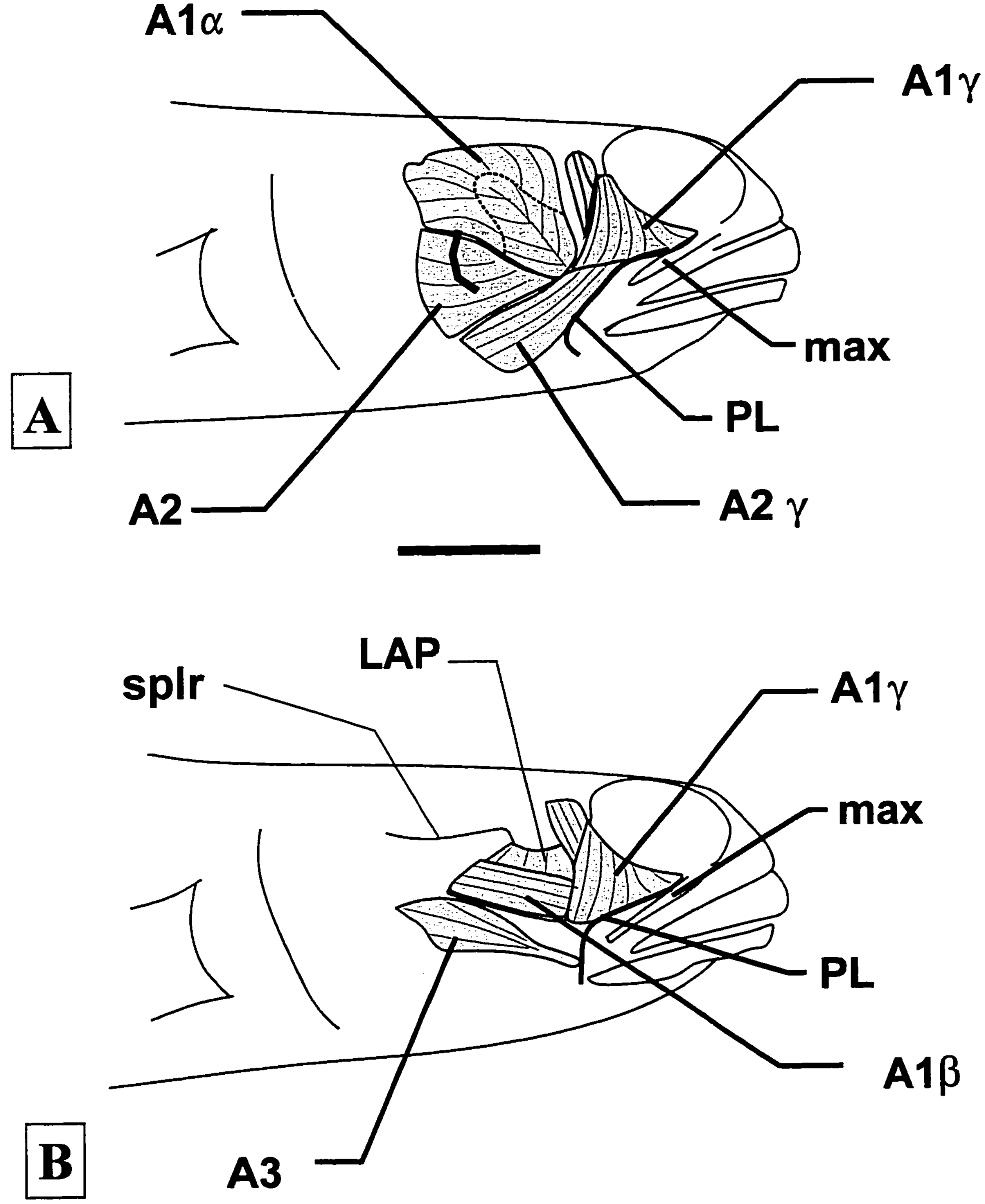

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**Figure 37.** Diagrammatic representation of the cheek myology of *Bollmannia chlamydes*.

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## *Bollmania chlamydes*

**SU 42777**

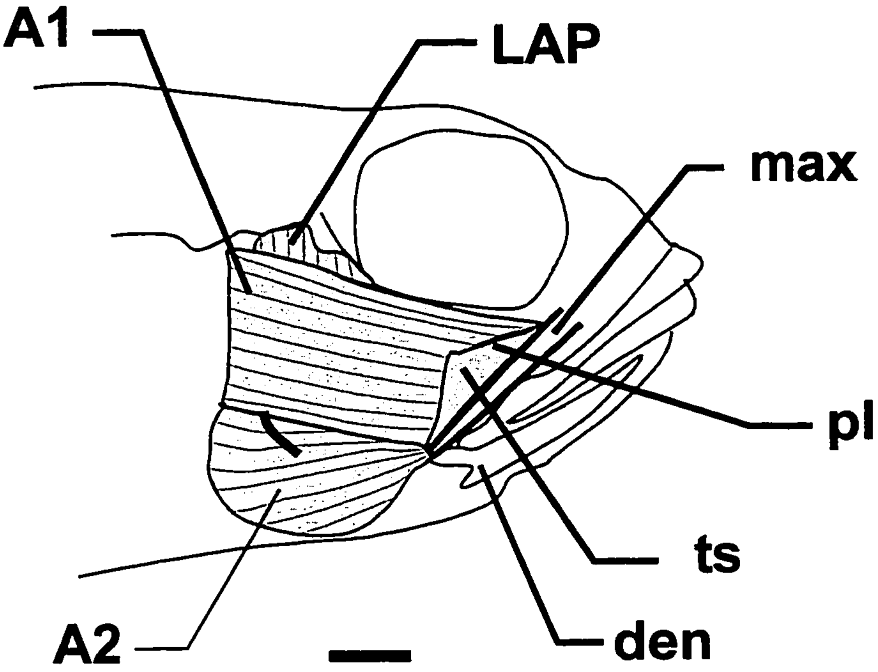

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**Figure 38.** Diagrammatic representation of the cheek myology of *Gobulus cresentalis*. External myology (A) and inner muscles of the suspensorium (B).

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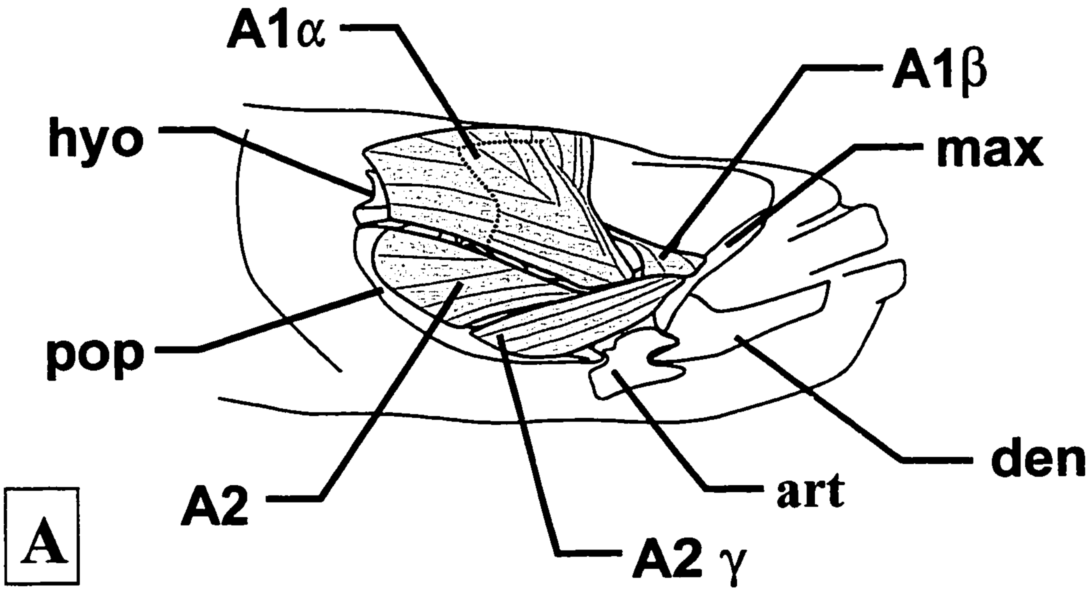
# *Gobulus crescentalis*

## LACM 32562-49



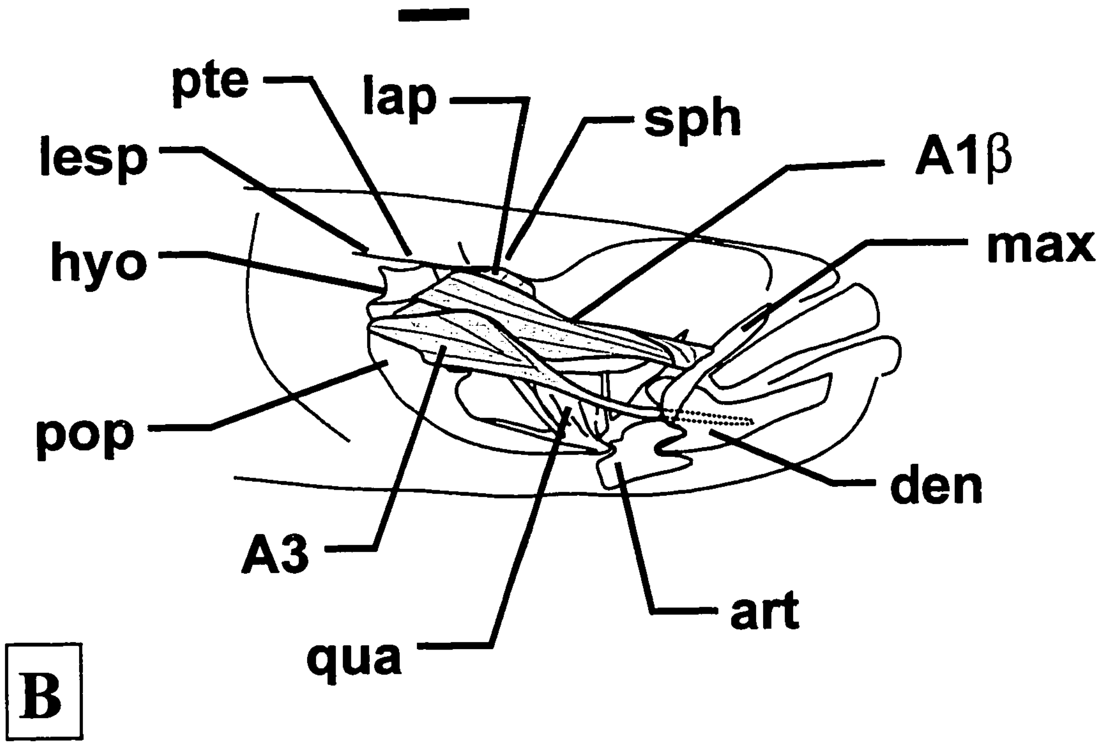


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**Figure 39.** Barbels and sensory papillae arrangement in *Barbulifer* and *Gobiosoma spilotum*.

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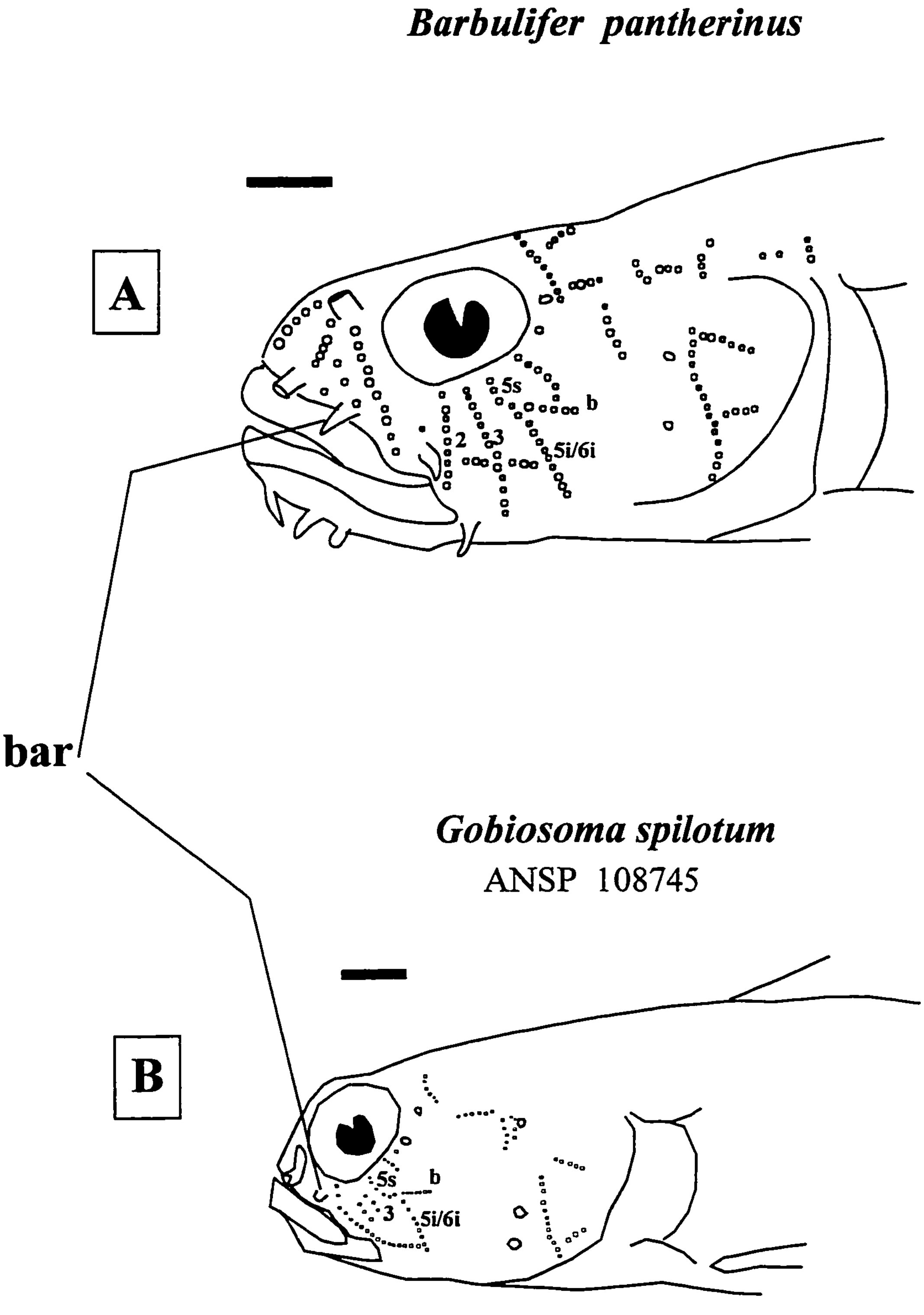

***Barbulifer pantherinus***

***Gobiosoma spilotum***
ANSP 108745

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**Figure 40.** Pelvic disc showing a complete disc with the anterior membrane extending to the end of the pelvic spine (A) and a partly separate disc with a highly reduced anterior membrane and nearly separate fins (B).

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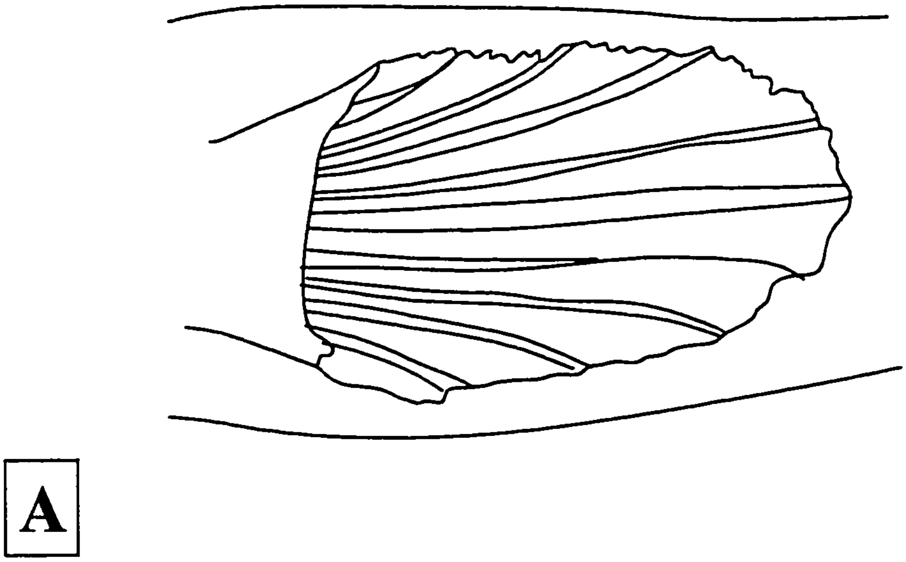

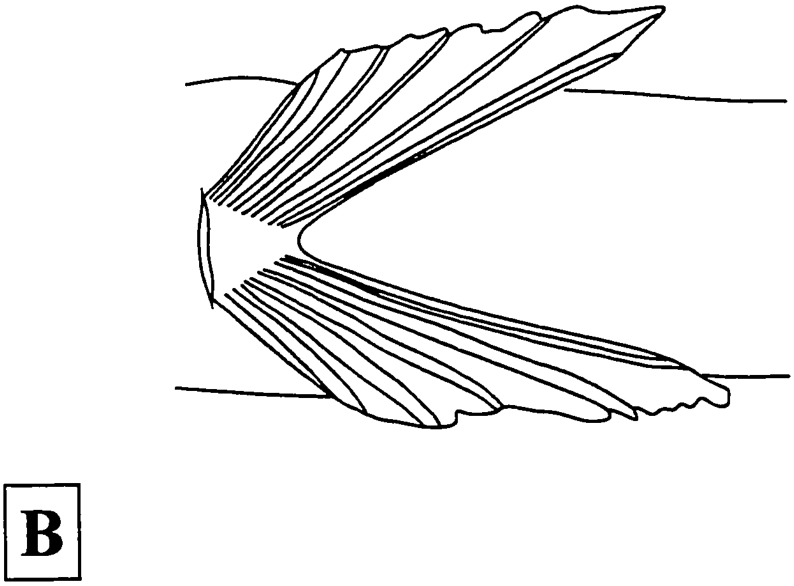

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**Figure 41.** Pelvic fin ray with elongate dorsal process (A) and with a typical non-elongate process (B).

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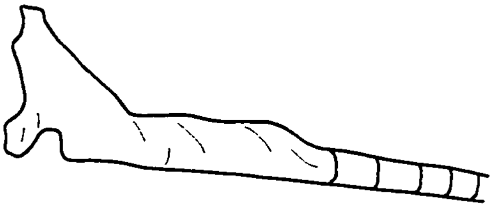

**A**

**B**

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**Figure 42.** Supraoccipital with lateral wings. Dorsal view with anterior at top of page.

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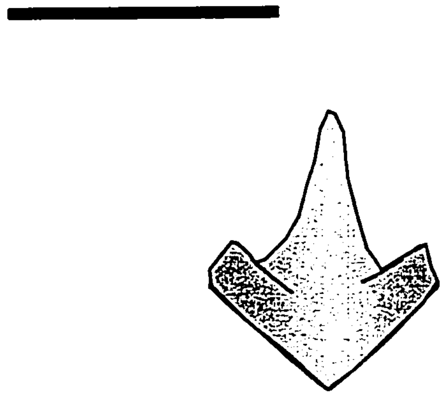

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**Figure 43.** Supraoccipital with reduced lateral wings. Dorsal view with anterior at top of page.

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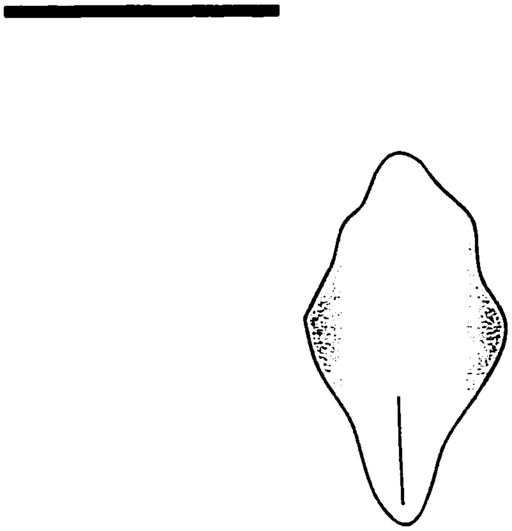

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**Figure 44.** Suspensorial bones showing the metapterygoid's not overlapping the quadrate and a complete preopercle bridge (A) and the metapterygoid's overlapping the quadrate and an incomplete preopercle bridge (B).

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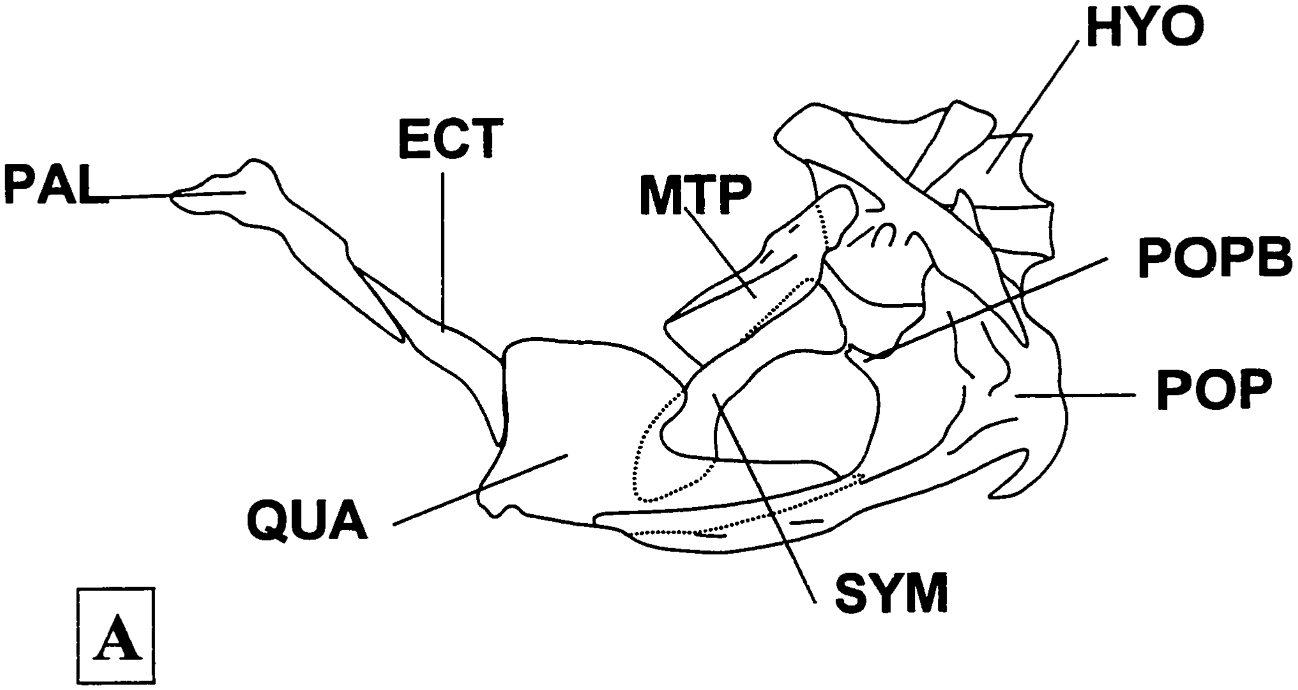

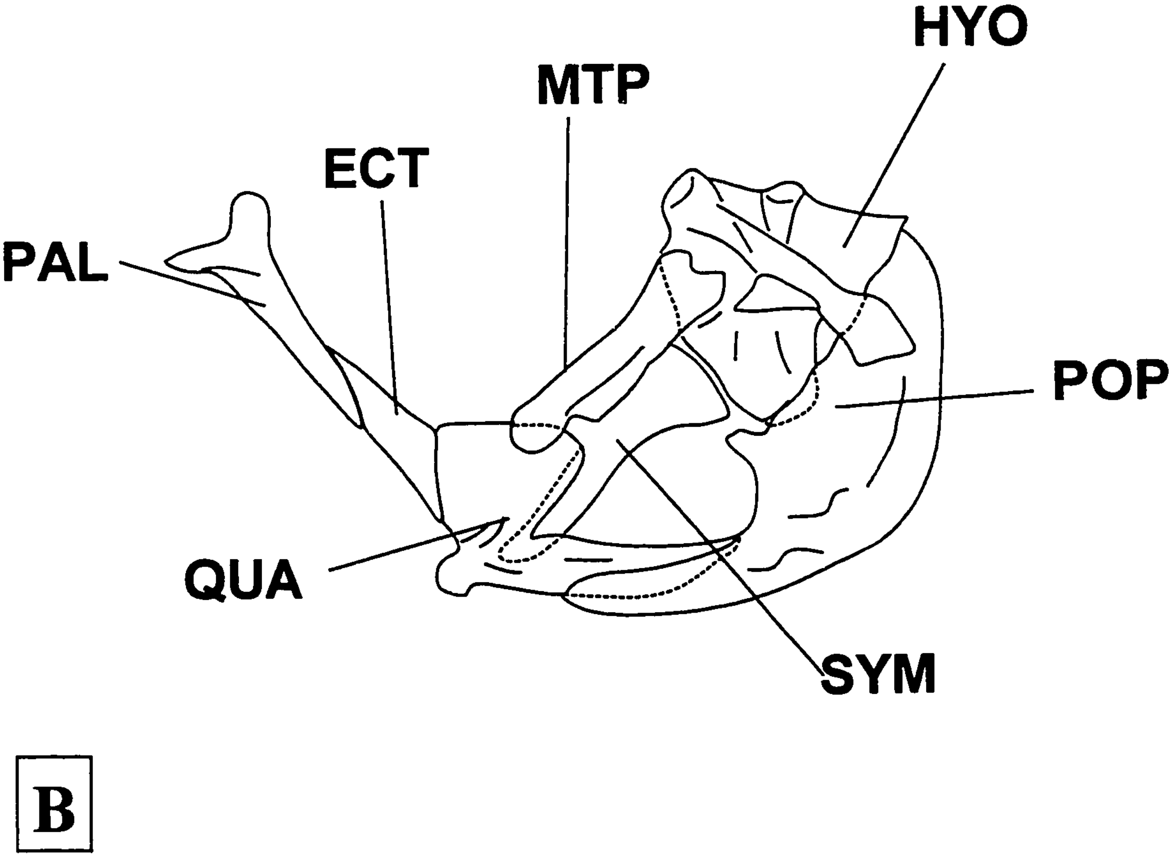

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**Figure 45.** Sensory papillae pattern of *Gobiolepis sp. nov.* B.

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*Gobiolepis sp. nov. b*

**ANSP 127758**

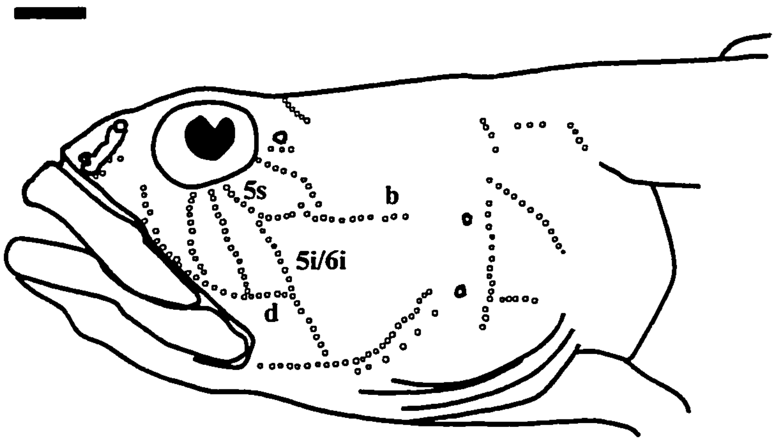

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**Figure 46.** Sensory papillae pattern of *Gobiolepis grosvenori*.

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## *Garmannia grosvenori*

**ANSP 101167 paratype**

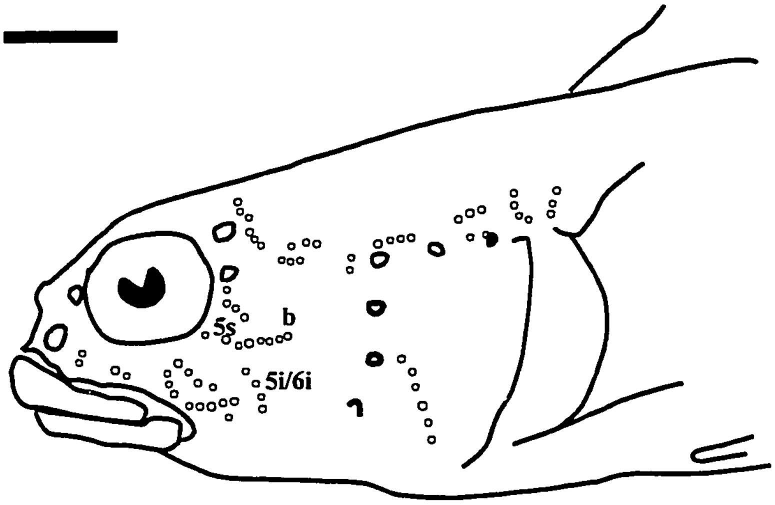

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**Figure 47.** Sensory papillae pattern of *Gobiolepis spilotum*.

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## *Gobiosoma spilotum*

ANSP 108745

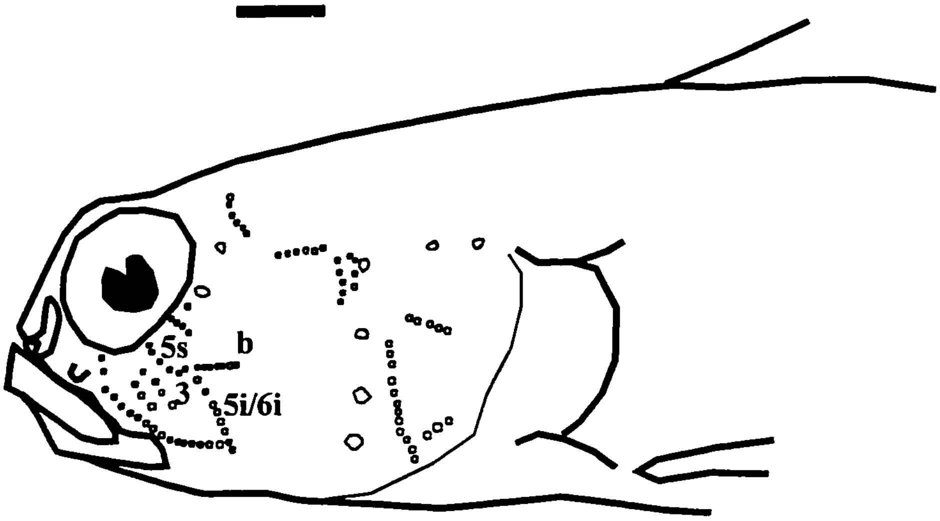

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**Figure 48.** Sensory papilla pattern of *Gobiosoma bosc*.

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*Gobiosoma bosc*

**ANSP 76139**

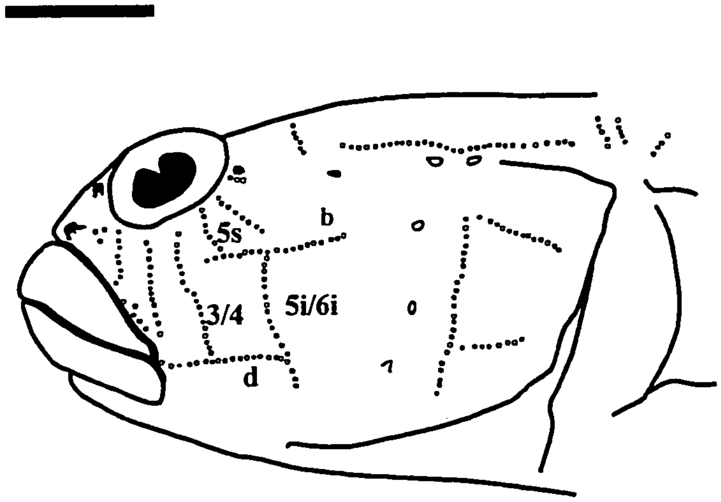

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**Figure 49.** Sensory papillae pattern of *Gobiosoma robustum*.

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*Gobiosoma robustum*

**ANSP 161571**

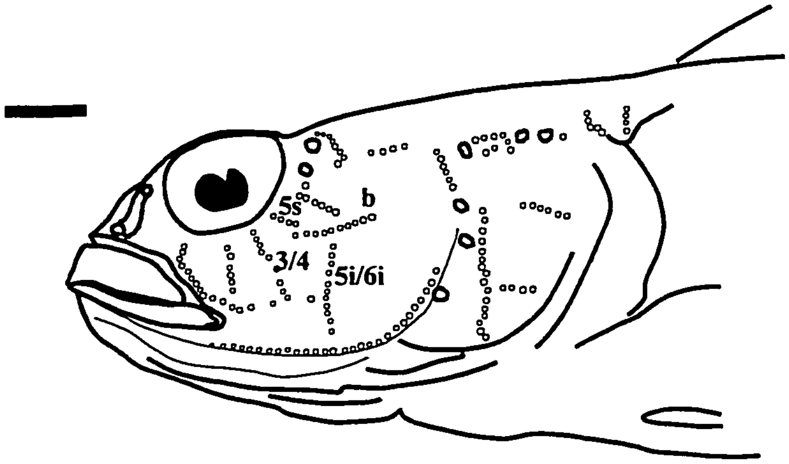

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**Figure 50.** Sphenotic with one lateral process.

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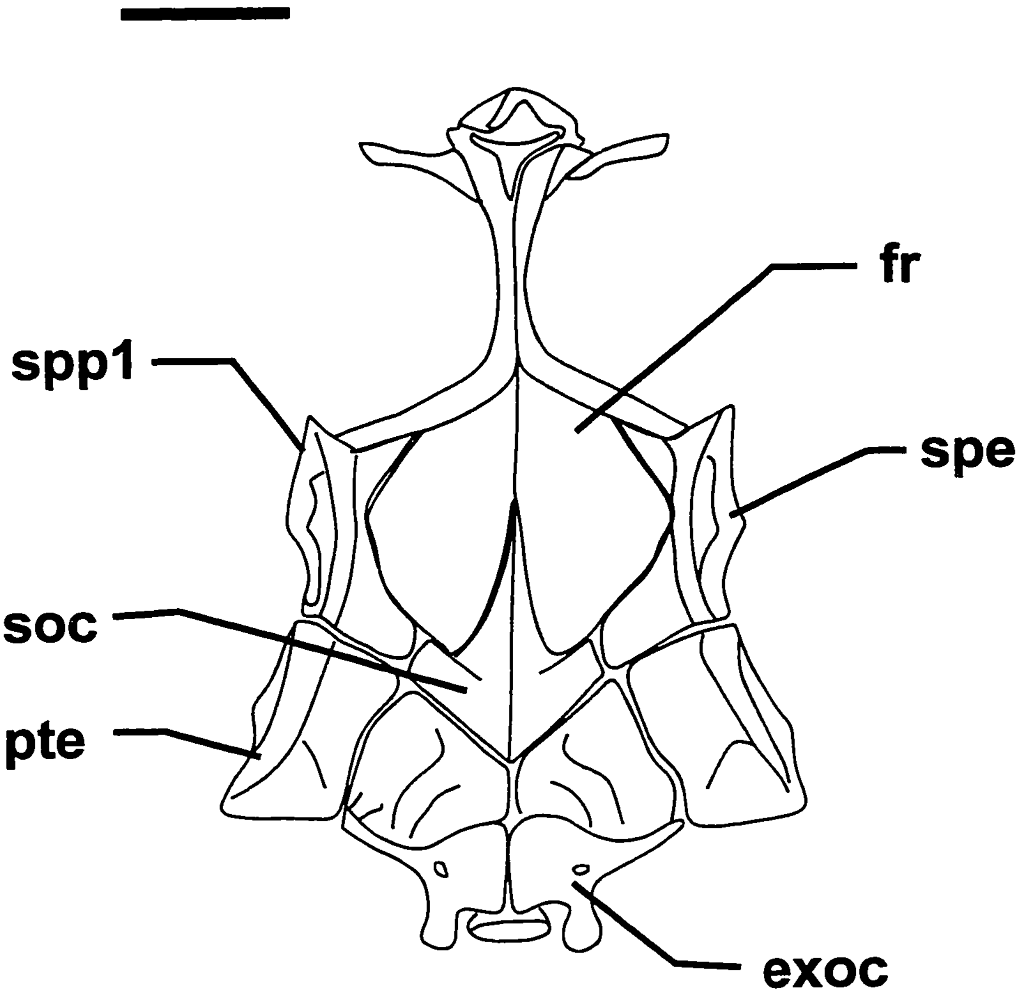

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**Figure 51.** Sphenotic with two lateral processes.

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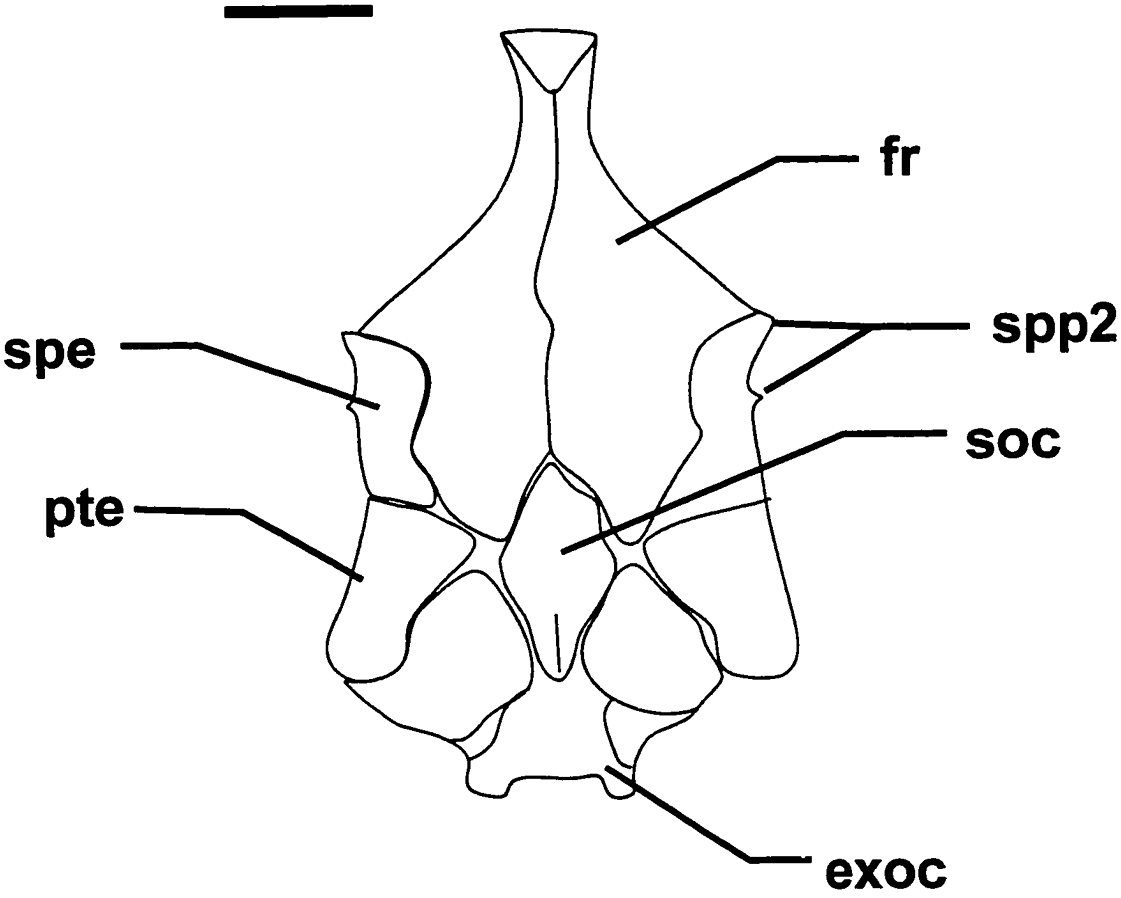

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**Figure 52.** Cladogram with new classification terminology.

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```
    ╓═ Outgroup
╟═68╬═ Aboma etheostoma
    ║   ╓═ Enypnias seminudus
    ╙═67╣   ╓═ Gobiosoma sp. nov. H
        ╟═66╣   ╓═ Gobiosoma parri
        ║   ╙═64╣   ╓═ Gobiosoma ginsburgi                      Gobiosoma
        ║       ╙═62╬═ Gobiosoma longipala
        ║           ║   ╓═ Gobiosoma bosc
        ║           ╙═60╣   ╓═ Gobiosoma paradoxum
        ║               ╙═58╩═ Gobiosoma robustum
        ║   ╓═ Gobiolepis spilotum
        ╙═65╣   ╓═ Gobiolepis grosvenori
            ╙═63╣   ╓═ Gobiolepis chiquita
                ╙═61╣       ╓═ Gobiolepis spes                            Gobiolepis
                    ║   ╓═57╩═ Gobiolepis schultzi
                    ╙═59╣   ╓═ Gobiolepis hildebrandi
                        ╙═56╣   ╓═ Gobiolepis sp. nov. B
                            ╙═55╣   ╓═ Gobiolepis homochroma
                                ╙═54╣       ╓═ Barbulifer
                                    ║   ╓═51╩═ Aruma
                                    ╙═53╣           ╓═ Pycnomma
                                        ║       ╓═48╬═ Eleotrica
                                        ║       ║   ╙═ Chriolepis
                                        ║   ╓═50╩═ Gymneleotris
                                        ╙═52╣   ╓═ Gobulus
                                            ╙═49╣   ╓═ Nes
                                                ╙═47╣   ╓═ Evermannichthys
                                                    ╙═46╣   ╓═ Risor
                                                        ╙═45╩═44
```

```
    ╓═ Ginsburgellus
╟═44╣   ╓═ Tigrigobius janssi
    ╙═43╬═ Tigrigobius puncticulatum
        ╟═ Tigrigobius dilepis
        ╟═ Tigrigobius macrodon
        ╟═ Tigrigobius multifasciatum          Tigrigobius
        ╟═ Tigrigobius saucrum
        ╟═ Tigrigobius zebrella
        ║   ╓═ Tigrigobius gemmatum
        ╟═42╩═ Tigrigobius pallens
        ║   ╓═ Elacatinus oceanops
        ╙═41╬═ Elacatinus horsti               Elacatinus
            ╙═ Elacatinus xanthiprora
```

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**Figure 53.** Expanded cladogram (part I) showing nodes and characters.

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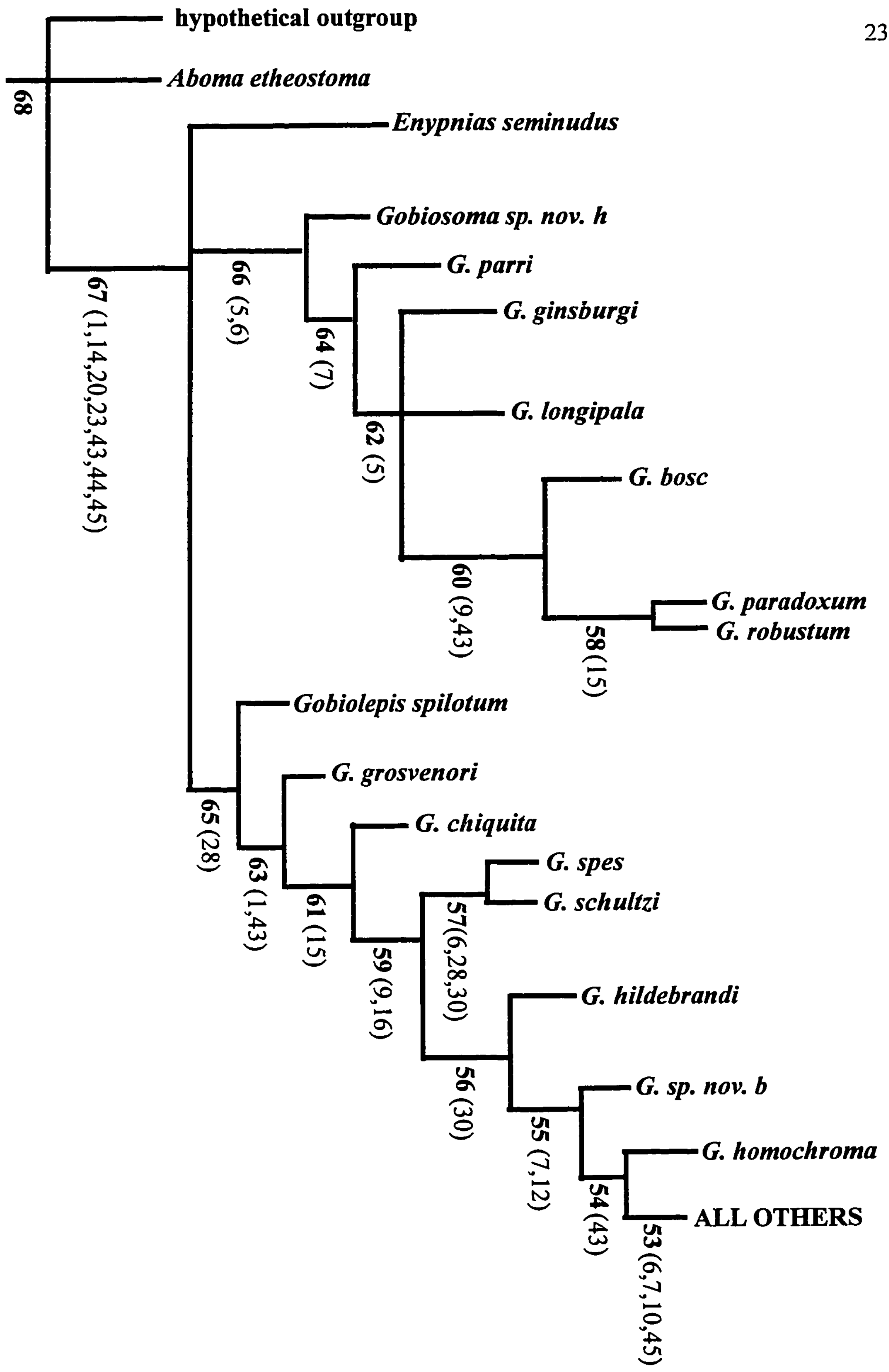

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**Figure 54.** Expanded cladogram (part II) showing nodes and characters.

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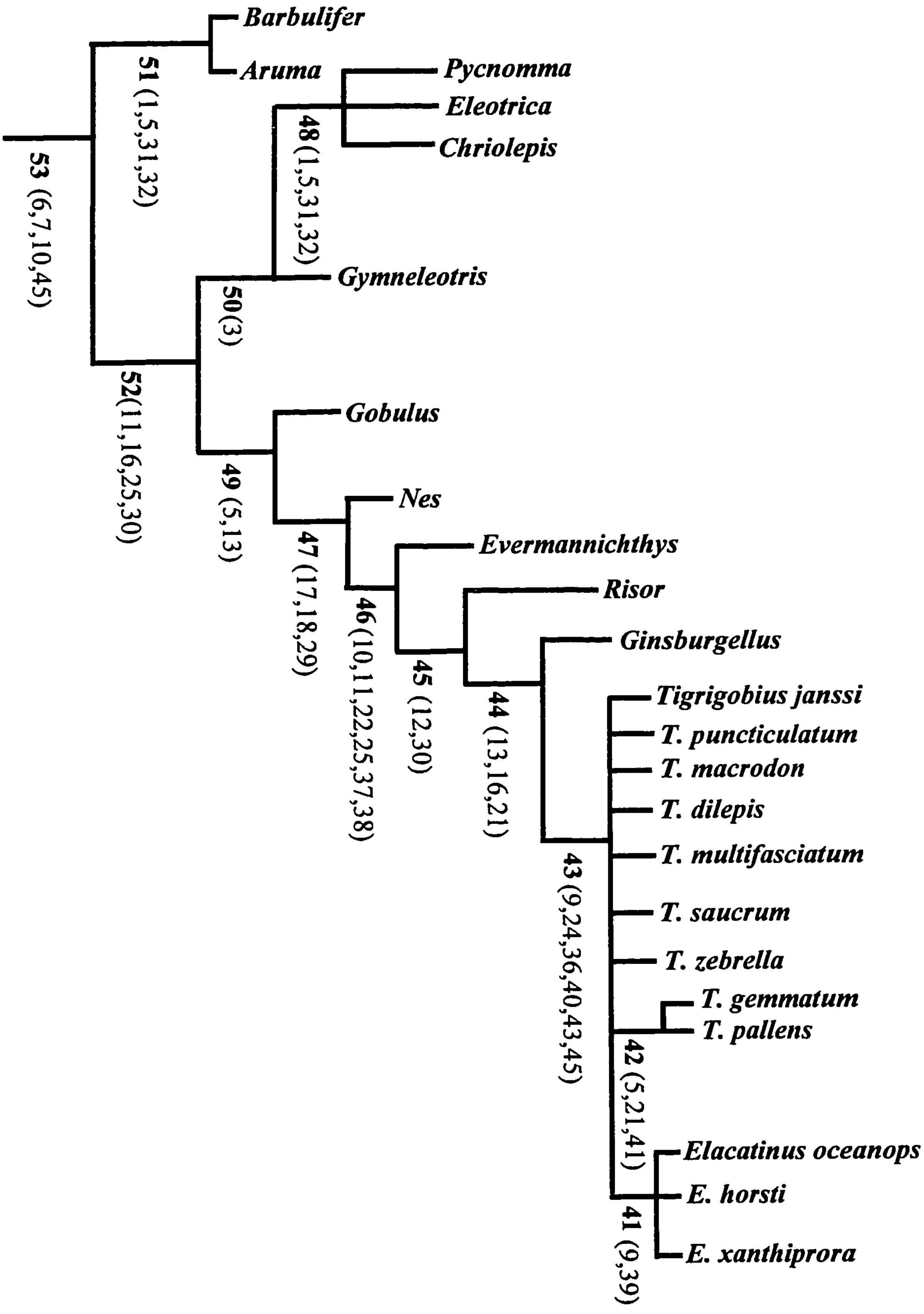

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**Figure 55.** Distribution of species in the genus *Gobiosoma*.

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*Gobiosoma bosc*

*Gobiosoma ginsburgi*

*Gobiosoma sp. H*

*Gobiosoma longipala*

*Gobiosoma nudum*

*Gobiosoma paradoxum*

*Gobiosoma parri*

*Gobiosoma robustum*

# Distribution of species of *Gobiosoma*

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**Figure 56.** Distribution of species in the genus *Gobiolepis*.

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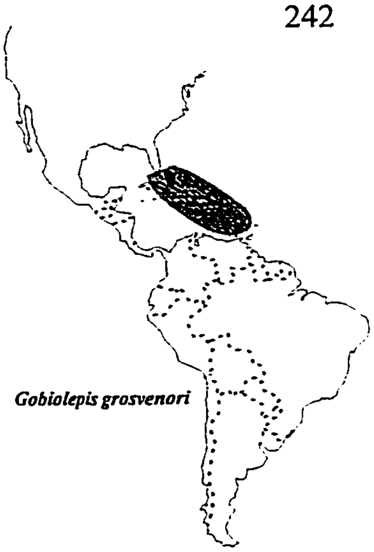
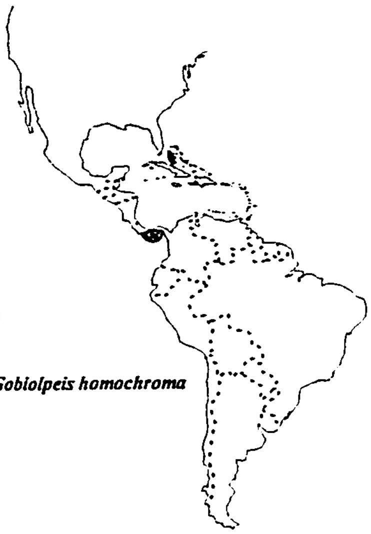
*Gobiolepis chiquita*

*Gobiolepis sp B*



*Gobiolepis grosvenori*

*Gobiolepis hildebrandi*



*Gobiolpeis homochroma*

*Gobiolepis schultzi*

*Gobiolepis spilotum*

*Gobiolepis spes*

# Distribution of species of *Gobiolepis*

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**Figure 57.** Distribution of species in the genus *Tigrigobius*.

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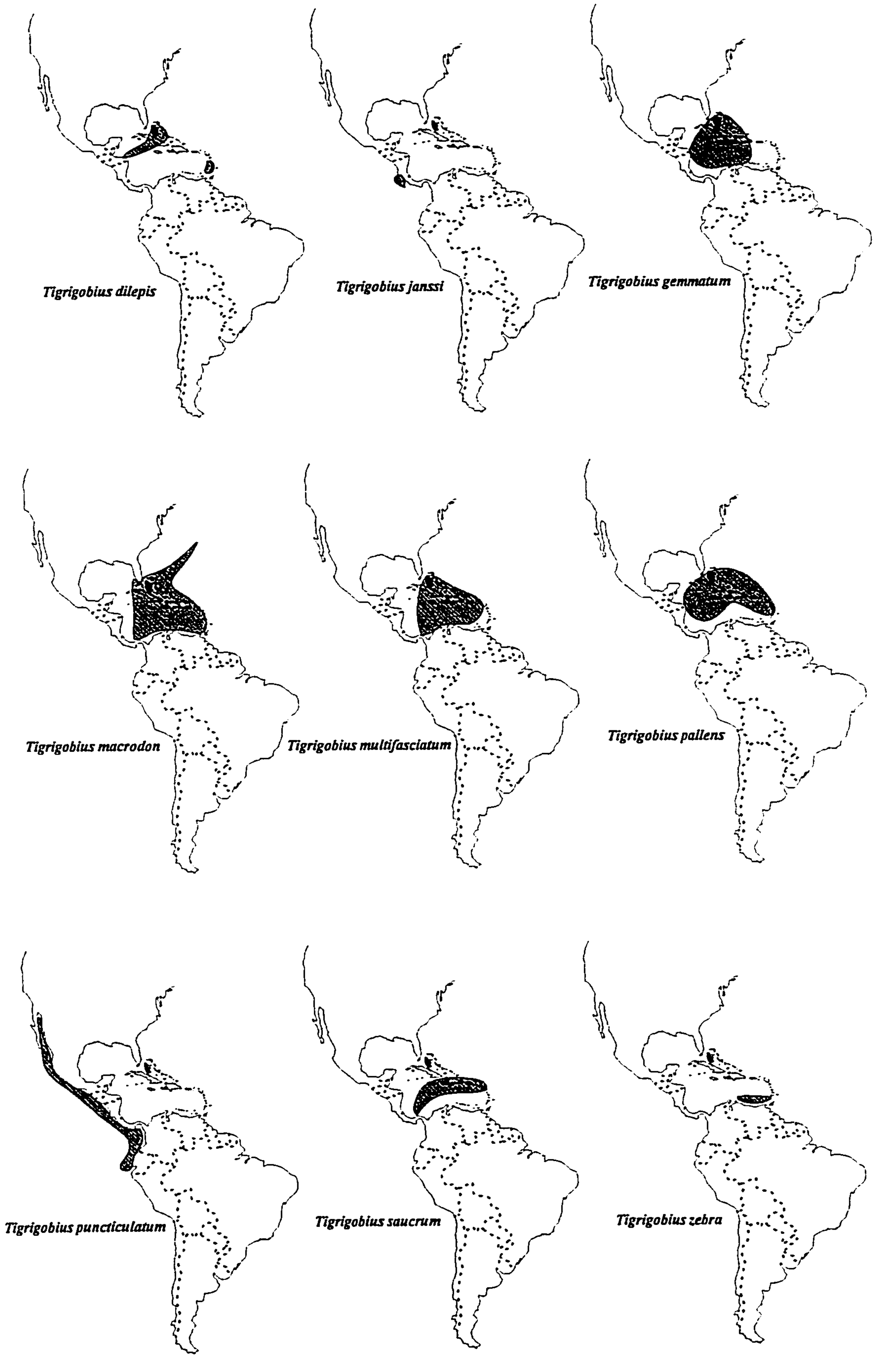
# Distribution of species of *Tigrigobius*



*Tigrigobius dilepis*

*Tigrigobius janssi*

*Tigrigobius gemmatum*

*Tigrigobius macrodon*

*Tigrigobius multifasciatum*

*Tigrigobius pallens*

*Tigrigobius puncticulatum*

*Tigrigobius saucrum*

*Tigrigobius zebra*

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**Figure 58.** Distribution of species in the genus *Elacatinus*.

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# Distribution of *Elacatinus*

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# Appendix

## Materials Examined

Species are listed according to the classification presented here and are divided into the following categories: (1) the arrangement of the species proposed herein (*Gobiosoma, Gobiolepis, Tigrigobius,* and *Elacatinus*); (2) genera closely related to those in category 1; (3) outgroups included in the study and (4) comparative material. Numbers of specimens are given in parentheses, first the number of cleared and stained individuals followed by the number of specimens in the lot. When only one number appears, the lot consists only of alcoholic specimens.

***Gobiosoma***

*Gobiosoma bosc*

UF 70961 (24). Bay-mouth Bar at mouth of Alligator Harbor, Florida, USA. Western Atlantic.

AMNH 42914 (4/16). Norrasetuck Creek, Amityville, New York, USA. Western Atlantic.

AMNH 67726 (3). Patuxent River, Maryland. Western Atlantic.

AMNH 67220 (4). Barnegate Bay, New Jersey. Western Atlantic.

AMNH 30143 (100). Currituck Sound, North Carolina. Western Atlantic.

AMNH 64119 (1). Virgina Institute of Marine Science beach, Virginia. Western Atlantic.

AMNH 083189 (3). Dauphin Island, Alabama. Gulf of Mexico.

AMNH 083125 (1). Dauphin Island, Alabama. Gulf of Mexico.

*Gobiosoma ginsburgi*

USNM 87655 Holotype (1). Cape Charles, Virginia. Western Atlantic.

CAS 32506 (1). Cape Kennedy, Ponce de Leon Inlet, Florida. Western Atlantic.

ANSP 91251 (1). York River, Virginia. Western Atlantic.

ANSP 101911 (2). Cold Spring Harbor, New Jersey. Western Atlantic.

ANSP 101917 (1). Old Bare Shoal, Delaware. Western Atlantic.

ANSP 101949 (2). Mispillion Cove, Delaware. Western Atlantic.

ANSP 101975 (1/30). Delaware Bay, New Jersey. Western Atlantic.

ANSP 120943 (24). Brandywine Shoal, Delaware Bay. Western Atlantic.

ANSP 138785 (1). Oldman Creek, Cape May Co., New Jersey. Western Atlantic.

ANSP 145929 (1). North Inlet, Bly Creek, South Carolina. Western Atlantic.

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AMNH 36083 (3). Long Island Sound, Oyster Bay, New York. Western Atlantic.

*Gobiosoma sp. nov.* H

CAS 30998 (7). Sebastian Vizcaino Bay, Mexico. Eastern Pacific.

CAS CAS 167494. Rocky Bluff Bay, Gulf of California, Mexico. Eastern Pacific.

GCRL 15468 (10). Playas Arenosas, Puerto Penasco, Sonora, Mexico. Eastern Pacific.

GCRL 21732 (1/17). Roca del Toro, Puerto Penasco, Sonora, Mexico. Eastern Pacific.

*Gobiosoma longipala*

USNM 86158 Holotype (1). Boca Grande, Florida. Gulf of Mexico.

ANSP 106132 (1). Pine Island Sound, Florida. Gulf of Mexico.

ANSP 106137 (2). Sanibel Island, Florida. Gulf of Mexico.

GCRL 815 (2/26). Belle Fontaine beach, Mississippi. Gulf of Mexico.

GCRL 989 (4). Biloxi Bay, Mississippi. Gulf of Mexico.

GCRL 2523 (13). Dogs Keys Pass, Mississippi. Gulf of Mexico.

*Gobiosoma nudum*

FMNH 8467 Paratype (1). Panama.

FMNH 8461 (1). Paratype. Panama.

FMNH 8468 (1). Panama.

FMNH 98464 (1). Panama.

USNM 185087 (2). Miraflores Locks, Panama Canal, Panama. Eastern Pacific.

USNM 322690 (2). Panama City, Panama. Eastern Pacific.

USNM 338279 (1). Miraflores Locks, Panama Canal, Panama. Eastern Pacific.

USNM 338280 (12). Reef off French Fort, Panama. Eastern Pacific.

GCRL 3502 (10). Punta Paitillo, Panama. Eastern Pacific.

GCRL 12360 (9). Venado Beach, Isla Venado, Panama. Eastern Pacific.

GCRL 11523 (11). Venado Beach, Isla Venado, Panama. Eastern Pacific.

GCRL 15608 (6). Naos Island, Panama. Eastern Pacific.

*Gobiosoma paradoxum*:

CAS 6198 (1). Baja California sur, Mexico. Eastern Pacific.

CAS 103765 (1). Mazatlan, Sinaloa State, Mexico. Eastern Pacific.

CAS 153130 (1/10). Costa Rica. Eastern Pacific.

ANSP 110685 (2/10). Kobbe Army Base, Venado Beach, Panama. Eastern Pacific.

GCRL 3351 (21). Venado Beach, Panama. Eastern Pacific.

GCRL 5623 (15). Fort Kobbe, Panama. Eastern Pacific.

GCRL 8497 (316). Miraflores Locks, Panama. Eastern Pacific.

AMNH 73441 (8/152). Pearl Islands, Gulf of Panama. Eastern Pacific.

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*Gobiosoma parri*

USNM 93177 Holotype (1). Uruguay. Western Atlantic.

ANSP 80831 (4). Puerto de Montevideo, Uruguay. Western Atlantic.

ANSP 121399 (1/1). Puerto de Montevideo, Uruguay. Western Atlantic.

UF 19907 (3). Maceio, Ponta Verde, Alagoas, Brazil. Western Atlantic.

*Gobiosoma robustum*

USNM 92802 Holotype (1). Corpus Christi, Texas. Gulf of Mexico.

ANSP 161571 (6). Rockefeller Wildlife Refuge, Louisiana. Gulf of Mexico.

ANSP 79129 (3). Beaumont, Neches River, Texas. Gulf of Mexico.

ANSP 84583 (8). Sanibel, Florida. Gulf of Mexico.

ANSP 84591 (24). Boca Grande, Florida. Gulf of Mexico.

ANSP 84592 (29). Lemon Bay, Englewood, Florida. Gulf of Mexico.

ANSP 110707 (1). Largo Maracaibo, Venezuela. Western Atlantic.

GCRL 536 (28). Ship Island, Mississippi, Gulf of Mexico.

GCRL 1238 (30). Horn Island, Mississippi. Gulf of Mexico.

GCRL 1240 (38). Horn Island, Mississippi, Gulf of Mexico.

AMNH 52376 (2/19). Pirates Cove, Ozello, Florida. Gulf of Mexico.

***Gobiolepis***

*Gobiosoma sp. nov.* B

ANSP 127758 (25). Paratype MS. Miraflores Locks, Panama. Western Atlantic.

ANSP 127759 (2/2). Paratype MS. Miraflores Locks, Panama. Western Atlantic.

*Gobiosoma chiquita*

CAS 166911 (2/84). San Carlos Bay, Gulf of California, Mexico. Eastern Pacific.

ANSP 91261 (1). Punta Penasco, Gulf of Baja California, Mexico. Eastern Pacific.

UF 21759 (11). Rocky Point, Puerto Penasco, Gulf of California, Mexico. Eastern Pacific.

GCRL 21744 (15). Choya Bay, Roca del Toro, Sonora, Mexico. Eastern Pacific.

GCRL 15469 (60). Playas Arenosas near Cholla Bay, Sonora, Mexico. Eastern Pacific.

GCRL 21638 (33). Playas Arenosas near Cholla Bay, Sonora, Mexico. Eastern Pacific.

GCRL 21842 (6). La Paz Harbor, Baja California, Mexico. Eastern Pacific.

*Gobiosoma grosvenori*

ANSP 101167 Paratype (1). Boca Chita Pass between Sand Key and Ragged Key, Florida. Western Atlantic.

ANSP 114114 (1). Great Exuma Island, Culmer's Cay, Bahamas. Western Atlantic.

ANSP 117425 (2). Basin Harbor Cay, Bahamas. Western Atlantic.

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ANSP 152669 (1). Dowlings Shoal, Sand Island, Anguilla. Western Atlantic.

UF 214380 (2/3). Boca Chita Pass, N of Sands Key, Florida, USA. Western Atlantic.

UF 214381 (1). Cubaguas Island, Venezuela. Caribbean Sea.

AMNH 28287 (3). Little Abaco, S. side Black Point, Bahama Islands. Western Atlantic.

*Gobiosoma hildebrandi*

USNM 107297 Holotype (1). Gatun Locks, Panama.

ANSP 110684 Paratype (1/1). Gatun Locks, Panama.

GCRL 11609 (56). Miraflores spillway, Panama Canal, Panama.

GCRL 12730 (3/52). Gatun Locks, Panama Canal, Panama.

GCRL 14504 (112). Pedro Miguel Locks, Panama Canal Zone, Panama.

*Gobiosoma homochroma*

USNM 293555 (1/9). Darien Provence, Rio Pirre, Panama. Eastern Pacific.

*Gobiosoma schultzi*

ANSP 110706 (1/1). Lago Maracaibo, Venezuela. Western Atlantic.

ANSP 161571 (6). Rockefeller Wildlife Refuge, Cameron Co., Louisiana. Western Atlantic.

UF 25410 (1). E shore of Lago Maracaibo, Estado de Zulia, Venezuela. Western Atlantic.

UF 25412 (1). La Rosa, Distrito Bolivar, Estado de Zulia, Venezuela. Western Atlantic.

*Gobiosoma spes*

ANSP 144483 (10). Isla Grande, San Juan, Puerto Rico, West Indies. Western Atlantic.

ANSP 144504 (10). Tortugera Lagoon, Costa Rica. Western Atlantic.

*Gobiosoma spilotum*

ANSP 108745 (2/9). Pulpit Point, Panama. Caribbean Sea.

ANSP 110681 (1/1). Limon Bay, Panama. Caribbean Sea.

ANSP 126532 (3). Rio de Janerio, Brazil. Western Atlantic.

GCRL 12704 (83). Gatun Locks, Colon, Panama.

GCRL 8698 (31). Gatun Locks, Colon, Panama.

*Gobiosoma yucatana*

USNM 205368 Holotype (1). Quintana Roo, Mexico. Caribbean Sea.

ANSP 114538 Paratype (1). Ciudad Chetumal Harbor, Quintana Roo, Mexico. Caribbean Sea.

UF 228326 (6). Ciudad Chetumal, Quintana Roo, Mexico. Caribbean Sea.

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**Tigrigobius**

*Gobiosoma dilepis*

ANSP 100815 Holotype (1). Conception Island, Bahama Islands. Western Atlantic.

ANSP 100816 Paratype (1). Conception Island, Bahama Islands. Western Atlantic.

ANSP 102208 (2/10). Georgetown, Grand Cayman Island, Cayman Islands. Caribbean Sea.

ANSP 102950 (6). Georgetown, Grand Cayman Island, Cayman Islands. Caribbean Sea.

ANSP 108753 (1). Little St. Vincent Island, Grenadine Islands. Caribbean Sea.

ANSP 112712 (1). Gulf of Gonave, St. Marc Channel, Haiti. Caribbean Sea.

ANSP 153709 (1). Union Island, Grenadine Islands. Caribbean Sea.

UF 12381 (7). SW corner of Grand Cayman Island, Cayman Islands. Caribbean Sea.

UF 12382 (9). Paradise Rocks, Grand Cayman, Cayman Islands. Caribbean Sea.

UF 12384 (4). Paradise Rocks, Grand Cayman, Cayman Islands. Caribbean Sea.

UF 12401 (4). Paradise Rocks, Georgetown, Grand Cayman, Cayman Islands. Caribbean Sea.

UF 12452 (8). Paradise Rocks, Georgetown, Grand Cayman, Cayman Islands. Caribbean Sea.

UF 14032 (2). Great Exuma Island, Bahama Islands. Western Atlantic.

UF 18839 (3). NW end of Providence Island, [Isla de Providencia], Colombia. Caribbean Sea.

UF 18880 (5). NE of Crab Cay, Isla de Providencia, Colombia. Caribbean Sea.

UF 20826 (5). N of Catalina Island, Lawrence Reef, Isla de Providencia, Colombia. Caribbean Sea.

UF 24880 (3). NW side of Isla de Providencia, Colombia. Caribbean Sea.

UF 25385 (1). SE of Three Brothers Islettes, Isla de Providencia, Colombia. Caribbean Sea.

UF 25810 (2). Western end of Three Brothers Keys, Isla de Providencia, Colombia. Caribbean Sea.

UF 25852 (1). NE end of Isla de Providencia, Colombia. Caribbean Sea.

*Gobiosoma gemmatum*

ANSP 98888 (1). Tobago Island, Charlotteville, Trinidad/Tobago. Caribbean Sea.

ANSP 102206 (3). Georgetown, Grand Cayman Island, Cayman Islands. Caribbean Sea.

ANSP 108755 (16). Little St. Vincent Island, Grenadine Islands. Caribbean Sea.

ANSP 111194 (1). Exumas, Bahama Islands. Western Atlantic.

ANSP 112713 (1). Gulf of Gonave, St. Marc Channel, Haiti. Western Atlantic.

ANSP 119240 (1). San Bias, Holandes Cays, Panama. Caribbean Sea.

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AMNH 26076 (6/63). Hog Cay, Ragged Islands, Bahama Islands. Western Atlantic.

*Elacatinus janssi*

LACM 32524-46 Paratypes (3/40). Costa Rica. Eastern Pacific.

LACM 32524-47 Paratype (1/1). Costa Rica. Eastern Pacific.

*Elacatinus sp. nov.*

USNM 322686 (9). Isla San Ignacio de Farallon, Gulf of California, Mexico. Eastern Pacific.

USNM 322688 (1). Isla San Pedro Martir, Gulf of California, Mexico. Eastern Pacific.

USNM 322689 (5). Isla San Ignacio de Farallon, Gulf of California, Mexico. Eastern Pacific.

*Gobiosoma macrodon*

USNM 170896 Holotype (1). Port-au-Prince Bay, Haiti. Caribbean Sea.

ANSP 102172 (1/1). Crawl Key, Monroe Co., Florida. Western Atlantic.

ANSP 70992 (2). Sanibel, Florida. Western Atlantic.

ANSP 79168 (10). Crawl Key, Florida. Western Atlantic.

ANSP 106140 (5). Madeira Beach, Florida. Gulf of Mexico.

ANSP 108754 (1). St. George Harbor, Grenada. Caribbean Sea.

ANSP 119179 (2). Isla Zapatilla, Bocas del Toro, Panama. Caribbean Sea.

ANSP 147844 (3). Off Paget Island, Bermuda. Western Atlantic.

ANSP 147847 (36). Baileys Bay, Bermuda. Western Atlantic.

ANSP 168620 (2/18). Patch reef off Coney Island, Bermuda. Western Atlantic.

AMNH 16924 (2). South Channel, Tarpon Springs, Florida. Gulf of Mexico.

*Gobiosoma multifasciatum*

ANSP 72206 (4). New Providence Island, Bahama Islands. Western Atlantic.

ANSP 96790 (1). Little Camanoe Island, British Virgin Islands. Caribbean Sea.

ANSP 98608 (1). Treasure Island, Salt Cay, Great Bahamas Bank, Bahama Islands. Western Atlantic.

ANSP 100514 (1/1). New Providence Island, Great Bahama Bank, Bahama Islands. Western Atlantic.

ANSP 102221 (7). Georgetown, Grand Cayman Island, Cayman Islands. Caribbean Sea.

ANSP 130006 (1). Isla Syndare, Port de Gustavia, St. Barthelemy. Caribbean Sea.

ANSP 137513 (1). Fourche Island, St. Barthelemy. Caribbean Sea.

ANSP 143032 (3). Reefs of San Blas Point, Panama. Caribbean Sea.

ANSP 144945 (28). Silver Cay, Great Bahama Bank, Bahama Islands. Western Atlantic.

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AMNH 23621 (15/94). Eleuthra Island, Current Rock, Bahama Islands. Western Atlantic.

*Gobiosoma pallens*

ANSP 92732 (12). Sandy Cay, Great Bahamas Bank, Bahama Islands. Western Atlantic.

ANSP 102216 (5). SW corner of Grand Cayman Island, Cayman Islands. Caribbean Sea.

ANSP 102237 (13). Georgetown, Grand Cayman Island, Cayman Islands. Caribbean Sea.

ANSP 120661 (1). San Bias Archipelago, Molandes Cays, Panama. Caribbean Sea.

ANSP 149296 (1). Shelf edge of Margarita Reef, Puerto Rico. Caribbean Sea.

ANSP 152667 (1). Dowlings Shoal, Sand Island, Anguilla. Caribbean Sea.

ANSP 152683 (5). Gulf of Gonave, St. Marc Island, Haiti. Caribbean Sea.

ANSP 152697 (10). Little St. Vincent Island, Grenadine Islands. Caribbean Sea.

ANSP 108749 (1). Admiralty Bay, Bequia Island, Grenadine Islands. Caribbean Sea.

AMNH 23971 (2). Nurse Cay, Ragged Island, Bahama Islands. Western Atlantic.

AMNH 26071 (1/5). Hog Cay, Ragged Islands, Bahama Islands. Western Atlantic.

AMNH 23237 (1). Cat Island, Bahama Islands. Western Atlantic.

AMNH 26014 (5). Nurse Cay, Ragged Islands, Bahama Islands. Western Atlantic.

AMNH 28421 (1). W. side Western Plana Cay, Reef B2, Bahama Islands. Western Atlantic.

AMNH 31061 (1). Flamingo Cay, Ragged Islands, Bahama Islands, Western Atlantic.

AMNH 30965 (2). Nurse Cay, Ragged Islands, Bahama Islands, Western Atlantic.

*Elacatinus puncticulatus*

ANSP 70075 Holotype (1) of *Gobiosoma rubrifrons* Fowler 1944.

CAS 31374 (1/12). Punta San Guellermo, Sonora, Mexico. Eastern Pacific.

CAS 147835 (1/14). Bahia San Lucas, Baja California, Mexico. Eastern Pacific.

CAS 161742 (11). Port Parker, Costa Rica. Eastern Pacific.

CAS 161744 (1). Port Parker, Costa Rica. Eastern Pacific.

AMNH 73449 (2/12). Bartolome Island, Pearl Islands, Gulf of Panama. Eastern Pacific.

*Gobiosoma saucrum*

ANSP 92985 Holotype (1). South Cay, Jamaica. Caribbean Sea.

ANSP 113024 (1). Harbor west of Point Caracoli, Martinique. Caribbean Sea.

ANSP 119235 (4). San Bias, Holandes Cay, Panama. Caribbean Sea.

ANSP 119245 (4). San Lias Archipelago, Salada Cay, Panama. Caribbean Sea.

ANSP 121917 (1). Port-au-Prince Bay, Pelican Cays, Haiti. Caribbean Sea.

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ANSP 134982 (1). Harbor west of Point Caracoli, Martinique. Caribbean Sea.

UF 11521 (2). Bird Island, Antigua, Leeward Islands. Caribbean Sea.

UF 11939 (1). Green Island, Antigua, Leeward Islands. Caribbean Sea.

UF 18842 (3). NW side of Providencia Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 19106 (2). W side of Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 20829 Lawrence Reef N of Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 28853 (1). E of Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

AMNH 33578 (2/9). Lameshur Bay, St. John, US Virgin Islands, Caribbean Sea.

*Gobiosoma zebrella*

ANSP 53387 Holotype (1). Monos Island, Trinidad. Caribbean Sea.

ANSP 101771 (2/13). Estado Sucre, Venezuela. Caribbean Sea.

ANSP 101785 (10). Golfo de Cariaco, Estado Sucre, Venezuela. Caribbean Sea.

ANSP 119234 (2). Boca del Toro, Callego Cay, Panama. Caribbean Sea.

***Elacatinus***

*Elacatinus atronasum*

ANSP 110690 Paratype (1). Long Island, Bahama Islands. Western Atlantic.

ANSP 110901 Paratype (1). Eleuthera Island, Bahama Islands. Western Atlantic.

ANSP 110900 Paratype (1). Long Island, Bahama Islands. Western Atlantic.

UF 223435 Paratype (2). NW tip of Long Island, Bahama Islands. Western Atlantic.

AMNH 26241 Paratype (1). Little San Salvador, Bahama Islands. Western Atlantic.

*Elacatinus chancei*

CAS 137276 Paratype (2). Barbados. Western Atlantic.

ANSP 110687 (1/1). Portsmouth, Prince Rupert Bay, Dominica. Caribbean Sea.

*Elacatinus digueti*

SIO70-167 (8). Bahia Chamela, Islas Cocinas, Mexico. Eastern Pacific.

SIO67-40 (7). Pearl Islands, Isla Saboga, Panama. Eastern Pacific.

SIO67-37 (5). Pearl Islands, Isla San Jose, Panama. Eastern Pacific.

SIO65-345 (2/28). Cabeza de Mechudo, Baja California, Mexico. Eastern Pacific.

*Elacatinus evelynae*

ANSP 110559 Holotype (1). Nassau, Bahama Islands. Western Atlantic.

USNM 198661 Paratypes (5). Soufriere Bay at Scotts Head, Dominica. Caribbean Sea.

ANSP 110566 Paratypes (4). Green Cay, Bahama Islands. Western Atlantic.

ANSP 110563 Paratype (1). Green Cay, Bahama Islands. Western Atlantic.

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UF 223473 Paratypes (5). Albuquerque Cay, N end of North Cay, Nicaragua. Caribbean Sea.

AMNH 30411 (1/1). Leeward Islands, Antigua. Western Atlantic.

AMNH 28445 (1). W side West Plana Cay, Bahamas. Western Atlantic.

AMNH 34645 (1). Frazer's Hog Cay, Bahama Islands. Western Atlantic.

AMNH 30224 (1). Leeward Islands, Antigua. Western Atlantic.

AMNH 29353 (1). Berry Islands, Bahama Islands. Western Atlantic.

AMNH 30958 (1). N side of Antigua. Western Atlantic.

AMNH 31275 (1). Acklin's Island, Bahama Islands. Western Atlantic.

AMNH 33130 (1). Little Inagua, Bahama Islands. Western Atlantic.

AMNH 37816 (1). No data.

*Elacatinus genie*

ANSP 110574 Holotype (1). Nassau, Bahama Islands. Western Atlantic.

ANSP 110575 Paratype (1). North Cay, Bahama Islands. Western Atlantic.

UF 206614 (5). SW end of Water Cay, Jumentos group, Bahama Islands. Western Atlantic.

AMNH 33126 (4). Little Inagua, Bahama Islands. Western Atlantic.

AMNH 34146 (1). Eastern Plana Cay, Bahama Islands. Western Atlantic.

AMNH 34222 (1). Samana Cay, Bahama Islands. Western Atlantic.

AMNH 34744 (2). Mamma Rhoda Rock, Berry Islands, Bahama Islands. Western Atlantic.

AMNH 34316 (1). Port Nelson Harbour, Rum Cay, Bahama Islands. Western Atlantic.

AMNH 34379 (1). Conception Island, Bahama Islands. Western Atlantic.

AMNH 35509 (3). Little San Salvador, West Bay, Bahama Islands. Western Atlantic.

AMNH 35329 (2). Great Stirrup Cay, Bahama Islands. Western Atlantic.

*Elacatinus horsti*

UF 13664 (1). Little San Salvador, Bahama Islands. Western Atlantic.

UF 14471 (7). Georgetown, Grand Cayman, Cayman Islands. Caribbean Sea.

UF 14521 (4). Georgetown, Grand Cayman, Cayman Islands. Caribbean Sea.

UF 17270 (1). NW end of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 17272 (1). NW end of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 17273 (1). NW end of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

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UF 17274 (2). NW end of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 17275 (2). NW end of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 17278 (1). NW end of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 19880 (1). E side of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 23385 (3). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 23422 (1). NW end of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 23435 (4). Off Santa Catalina Harbor, Isla de Providencia, Colombia. Caribbean Sea.

UF 23468 (1). WNW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 23540 (2). NW part of Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 23543 (1). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 23545 (7). Channel mouth area, Isla de Providencia, Colombia. Caribbean Sea.

UF 24402 (1). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 24530 (1). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 24744 (2). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 24766 (1). S of Channel Mouth area, NW of Santa Catalina Island, Isla de Providencia, Colombia. Carribean Sea.

UF 24951 (1). NW part of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 25748 (2). N end of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 26237 (4). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

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UF 28905 (1/5). W of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

AMNH 38296 (2). Grand Bahama, Bahama Islands, Western Atlantic.

*Elacatinus illecebrosum*

ANSP 110693 Holotype (1). Banco Chinchorro, Yucatan. Caribbean Sea.

CAS 31732 (5). Cocos-Banderas cays, Panama. Caribbean Sea.

UF 209621 (1). Banco Chinchorro near Cayo Norte. Caribbean Sea.

Smithsonian Res. Lab collection (4/4). Belize. Caribbean Sea.

*Elacatinus louisae*

ANSP 110691 Holotype (1). North side of Georgetown, Cayman Islands. Caribbean Sea.

ANSP 111073 Paratype (1). Crokked Island, Bahama Islands. Western Atlantic.

ANSP 111072 Paratype (1). Crokked Island, Bahama Islands. Western Atlantic.

UF 23386 (2). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 23467 (2). WNW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 23481 (4). S of Channel Mouth, Isla de Providencia, Colombia. Caribbean Sea.

UF 23542 (3). NW of Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 23547 (3). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 24745 (1). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 24767 (1). S of Channel Mouth area, NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 24777 (4). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 24809 (2). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 24842 (2). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 24952 NW part of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 25749 (4). N end of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 28887 (1). W side of Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

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AMNH 34500 (4). Hawksnest Creek, Cat Island, Bahama Islands. Western Atlantic.

*Elacatinus oceanops*

CAS 108365 Holotype (1). Garden Key, Dry Tortugas, Florida. Western Atlantic.

UF 11818 (2). Garden Key, Dry Tortugas, Florida. Western Atlantic.

UF 11837 (11). Loggerhead Key, Dry Tortugas, Florida. Western Atlantic.

UF 11868 (14). Loggerhead Key, Dry Tortugas, Florida. Western Atlantic.

UF 16014 (1). Delray Beach, Palm Beach County, Florida. Western Atlantic.

UF 16169 (23). Big Pine Key, Looe Key, Florida. Western Atlantic.

UF 17299 (3). Boca Raton, Palm Beach County, Florida. Western Atlantic.

UF 31247 (1). Sand Key, Florida Keys, Florida. Western Atlantic.

UF 46890 (5). Sand Key, Florida Keys, Florida. Western Atlantic.

AMNH 84022 (2). Florida middle ground. Gulf of Mexico.

N.J. State Aquarium Coll. (3/3). No locality data.

*Elacatinus prochilos*

ANSP 110628 Holotype (1). Port of Gustavia, St. Barthelemy. Caribbean Sea.

ANSP 110632 Paratype (1). Little St. Vincient Island, Grenadine Islands. Caribbean Sea.

ANSP 110629 Paratype (1). Port of Gustavia, St. Barthelemy. Caribbean Sea.

USNM 317003 (18). Charlotteville, Tobago. Caribbean Sea.

USNM 318695 (6). Charlotteville, Tobago. Caribbean Sea.

USNM 318823 (6). Little Tobago Island, Tobago. Caribbean Sea.

UF 15430 (1). English Harbor, Antigua, Leeward Islands. Caribbean Sea.

UF 24883 (1). NW side of Isla de Providencia, Colombia. Caribbean Sea.

UF 223438 (1). Devil's Table, Admiralty Bay, Bequia Island, Grenadine Islands. Caribbean Sea.

*Elacatinus randalli*

ANSP 110672 Holotype (1). Grenadine Islands, Lesser Antilles. Caribbean Sea.

ANSP 110674 Paratype (1/1). Cumberland Bay, St. Vincent Island. Caribbean Sea.

ANSP 110680 Paratype (1). Margarita Islands, Venezuela. Western Atlantic.

UF 15431 (2). Cumberland Bay, St. Vincent, Windward Islands. Caribbean Sea.

AMNH 26243 Paratype (1). Anse Mahaut, St. Vincent Island, Grenadines. Caribbean Sea.

*Elacatinus figaro*

N.J. State Aquarium coll. (3/3). Brazil. Western Atlantic.

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*Elacatinus tenox*

ANSP 110699 Holotype (1). Sta. TE-42, Prince Rupert Bay, Portsmouth, Dominica. Caribbean Sea.

*Elacatinus xanthiprora*

ANSP 110898 Holotype (1). Alligator Reef Light, Monroe Co., Florida. Western Atlantic.

USNM 118105 Paratype (1). Tortugas. Caribbean Sea.

UF 17271 (1). NW end of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 17276 (1). NW end of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 23427 (1). E side of Providence Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 24521 (1). Isla Santa Catalina, Colombia. Caribbean Sea.

UF 24797 (1/3). N of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

UF 28382 (2). Onslow Bay, North Carolina. Western Atlantic.

UF 30660 (4). Southern Onslow Bay, North Carolina. Western Atlantic.

UF 73226 (2). Florida Middle Ground, Florida. Gulf of Mexico.

UF 208312 (1). Lime Cay, Jamaica. Caribbean Sea.

## RELATED GENERA

### *Aboma*

*Aboma etheostoma*

CAS 103459 Holotype (1). Sinaloa State, Mexico. Eastern Pacific.

UF 224451 Paratype for *Gobiosoma polyporosum* (1). Farfan Point, Panama. Eastern Pacific.

GCRL 15934 (8). Farfan Point, Panama. Eastern Pacific.

GCRL 11153 (10). Boca Pedregal, Chiriqui, Panama. Eastern Pacific.

GCRL 13035 (1/9). Farfan Point, Panama. Eastern Pacific.

*Aboma lactipes*

SU 6569 (16). Tsuruga, Japan. Western Pacific.

*Aboma tsushimae*

SU 23526 (1). Kichi r Nagoya, Japan. Western Pacific.

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**Aruma**

*Aruma histrio*

USNM 35147 Holotype (1) Labeled as *Gobiosoma histrio*. Emeric, Guaymas, Mexico. Eastern Pacific.

CAS 79599 (1). Freshwater Bay, Gulf of California, Mexico. Eastern Pacific.

CAS 79600 (4). San Luis Island, Baja California, Mexico. Eastern Pacific.

CAS 79601 (1). La Partita, Gulf of California, Mexico. Eastern Pacific.

CAS 79602 (2/29). Guaymas, Gulf of California, Mexico. Eastern Pacific.

CAS 79603 (1). Las Tetas de Cobra, Gulf of California, Mexico. Eastern Pacific.

CAS 79604 (3). Punta Diggs, Baja California, Mexico. Eastern Pacific.

CAS 79605 (1). Punta de las Cuevas, Gulf of California, Mexico. Eastern Pacific.

ANSP 90821 (3). San Francisquito Bay, Baja California, Mexico. Eastern Pacific.

AMNH 12910 (1). San Francisquito Bay, Gulf of California. Eastern Pacific.

**Barbulifer**

*Barbulifer antennatus*

ANSP 110642 Holotype (1). Exuma Cays, Great Bahama Bank, Bahama Islands. Western Atlantic.

ANSP 110643 Paratype (1). Great Bahama Bank, Bahama Islands. Western Atlantic.

UF 9047 Paratype (1). New Providence, Bahama Islands. Western Atlantic.

UF 9216 Paratype (1). New Providence, Bahama Islands. Western Atlantic.

UF 10320 (1). New Providence, Bahama Islands. Western Atlantic.

AMNH 24035 (2). Cay south of Buena, Ragged Islands, Bahama Islands. Western Atlantic.

*Barbulifer ceuthoecus*

USNM 093749 (1). Key West, Florida. Western Atlantic.

USNM 265083 (1). Bahia Mochima, Venezuela. Western Atlantic.

USNM 317110 (1). Bloody Bay, Tobago. Caribbean Sea.

AMNH 28299 (2/21). Mangrove Cay, Abaco, Bahama, Bahama Islands. Western Atlantic.

*Barbulifer pantherinus*

CAS 117705 (10). Ensenada San Franciso, Sonora State, Mexico. Eastern Pacific.

CAS 149929 (3/52). Punta de las Cuevas, Ensenada San Francisco, Sonora State, Mexico. Eastern Pacific.

CAS 153631 (34). Baja California, Mexico. Eastern Pacific.

AMNH 12232 Syntypes (2). Label reads *Gobiosoma pantherinum*. Sargassum weed, Gulf of California [Baja California]. Eastern Pacific.

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***Chriolepis***

*Chriolepis minutillus*

USNM 322595 (3). Isla San Pedro Martir, Gulf of California. Eastern Pacific.

LACM 20058 (2). Bahia Ballenas, Isla Espiritu Santo, Gulf of California, Mexico. Eastern Pacific.

LACM 20060 (1). Isla Angel de la Guarda, Puerto Refugio, Gulf of California, Mexico. Eastern Pacific.

LACM 20148 (1/4). Isla Angel de la Guarda, Puerto Refugio, Gulf of California, Mexico. Eastern Pacific.

*Chriolepis cuneata*

LACM 32548-56 Paratype (1). Isla del Cano, E. side, Puntarenas, Costa Rica. Eastern Pacific.

LACM 32546-50 Paratype (2). Isla del Cano, N. side, Puntarenas, Costa Rica. Eastern Pacific.

LACM 32539-35 Paratype (2). Punta Catedral, Quepos, Isla Salera, Costa Rica. Eastern Pacific.

LACM 32499-47 Paratype (2). Punta Santa Elena, Costa Rica. Eastern Pacific.

*Chriolepis dialepta*

LACM 44820-2 (21). Isla del Coco, Roca Pan de Azucar, Costa Rica. Eastern Pacific.

*Chriolepis fisheri*

CAS 137262 Holotype (1). Barbados. Caribbean Sea.

***Eleotrica***

*Eleotrica cableae*:

CAS 23723 (1/26). I. Fernadina, Galapagos Islands. Eastern Pacific.

CAS 31203 (3). Santa Cruz, Academy Bay, Galapagos Islands. Eastern Pacific.

CAS 137537 (11). Academy Bay, Santa Cruz, Galapagos Islands. Eastern Pacific.

***Enypnias***

*Enypnias aceras*

USNM 107298 Holotype (1). Miraflores Locks, lower chamber, Panama Canal. Eastern Pacific.

FMNH 8459 (1). Panama.

*Enypnias seminudus*

FMNH 8457 (1). Panama.

CAS 106945 (1/10). Central America. Panama.

ANSP 110699 (6). Bahia Pinas, Panama. Eastern Pacific.

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**Evermannichthys**

*Evermannichthys convictor*

ANSP 111863 Paratype (1). Green Cay, Great Bahama Bank, Bahama Islands. Western Atlantic.

*Evermannichthys metzelaari*

ANSP 111872 (7/7). Conception Island, Great Bahama Bank, Bahama Islands. Western Atlantic.

ANSP 112410 (19). Conception Island, Bahama Islands. Western Atlantic.

AMNH 28752 (5/26). Grand Bahama, Bahama Islands. Western Atlantic.

*Evermannichthys silus*

ANSP 111865 Holotype (1). Samana Cay, Great Bahama Bank, Bahama Islands. Western Atlantic.

ANSP111866 Paratype (10). Samana Cay, Great Bahama Bank, Bahama Islands. Western Atlantic.

ANSP 111867 Paratype (1/1). Samana Cay, Bahama Islands. Western Atlantic.

UF 224151 Paratypes (2). Samana (Atwood) Cay, Bahama Islands. Western Atlantic.

*Evermannichthys spongicola*

USNM 160662 Paratype (1). Curacao. Caribbean Sea.

AMNH 82393 (3/10). Florida. Gulf of Mexico.

**Ginsburgellus**

*Ginsburgellus novemlineatus*

ANSP 71778 Holotype (1). San Andres Island. Caribbean Sea.

ANSP (13). Treasure Island, Salt Cay, Bahama Islands. Western Atlantic.

ANSP 115663 (5). Puerto Yabucoa, Puerto Rico. Caribbean Sea.

ANSP 121698 (4). Isla Syndare, Port de Gustavia, St. Barthelemy. Caribbean Sea.

ANSP 124695 (34). Port Castries, Vigie Point, St. Lucia. Caribbean Sea.

ANSP 144946 (93). Silver Cay, Great Bahama Bank, Bahama Islands. Western Atlantic.

ANSP 85835 (13). Salt Cay, Bahama Islands. Western Atlantic.

AMNH 34259 (4/7). W. end Atwood (Samara) Cay, Bahama Islands. Western Atlantic.

FMNH 101221 (1). Palo Reef, Eastern cut outside, Puerto Rico. Caribbean Sea.

**Gobulus**

*Gobulus hancocki*

CAS 118449 (1). San Carlos Bay, Sonora, Mexico. Eastern Pacific.

CAS 118450 (1). Moreno Rocks, Bahia San Carlos, Baja California, Mexico. Eastern Pacific.

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*Gobulus crescentalis*

USNM 214508 (1). Scammons Lagoon, Stony Island, Baja California, Mexico. Eastern Pacific.

LACM 32547-54 (4). Isla del Canao, Puntarenas, Costa Rica. Eastern Pacific.

LACM 32549-61 (4). Isla del Cano, Puntarenas, Costa Rica. Eastern Pacific.

LACM 32562-49 (1/9). Isla del Cano, N. side, Puntarenas, Costa Rica. Eastern Pacific.

GCRL 3624 (2). Playa el Coco, Guanacaste, Costa Rica. Eastern Pacific.

GCRL 9076 (1). Isla Venado, Panama. Eastern Pacific.

GCRL 11890 (1). Chatham Bay, Cocos Island, Costa Rica. Eastern Pacific.

GCRL 15072 (8). Playa del Coco, Guanacaste, Costa Rica. Eastern Pacific.

AMNH 05621 (2). Aqua Verde Bay, Townsed Albatross expedition. Eastern Pacific.

***Gymneleotris***

*Gymneleotris seminudus*:

CAS 30930 (1). Venados Island, Mexico. Eastern Pacific.

CAS 31000 (1). Pajaro Island, Mexico. Eastern Pacific.

CAS 118461 (1). Partida Island, Gulf of California, Mexico. Eastern Pacific.

CAS 118462 (1). Bahia San Lucas, Baja California, Mexico. Eastern Pacific.

CAS 149932 (1). Punta de las Cuevas, Sonora State, Mexico. Eastern Pacific.

CAS 157881 (1). Port Parker, Costa Rica. Eastern Pacific.

CAS 157882 (1). Gulf of Nicoya, Costa Rica. Eastern Pacific.

CAS 167498 (1). Port Utria, Colombia. Eastern Pacific.

MCZ 44759 (1/3). Rey Island, Perlas Islands, Panama. Eastern Pacific.

ANSP 111897 (1). La Plata Island, Ecuador. Eastern Pacific.

ANSP 134939 (1/1). Port Parker, Costa Rica. Eastern Pacific.

SIO 61-262-58A (1). Baja California, Mexico. Eastern Pacific.

***Nes***

*Nes longus*

USNM 118106 (1). Dry Tortugas, Florida. Western Atlantic.

ANSP 111198 (2). Lower Matecumbe Key, Florida. Western Atlantic.

ANSP 133224 (2/18). Castle Harbor, Bermuda. Western Atlantic.

ANSP 147247 (2). Athol Island, Great Bahama Bank, Bahamas. Western Atlantic.

UF 11305 (2). Green Island, Antigua, Leeward Islands. Caribbean Sea.

UF 13802 (4). Green Cay, Bahama Islands. Western Atlantic.

UF 24888 (1). NW side of Isla de Providencia, Colombia. Caribbean Sea.

UF 25073 (1). E coast of Isla de Providencia, Colombia. Caribbean Sea.

UF 25859 (1). NE end of Isla de Providencia, Colombia. Caribbean Sea.

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AMNH 24944 (1). Hawksnest Creek, Cat Island, Bahama Islands. Western Atlantic.

***Pariah***

*Pariah scotius*

UF 224150 Paratype (1). Conception Island, Bahama Islands. Western Atlantic.

AMNH 26096 (3). W. side of Conception Island, Bahama Islands. Western Atlantic.

***Psilotris***

*Psilotris alepis*

USNM 197515 (1). Havana, Cuba. Caribbean Sea.

UF 12343 (1). Prospect Point, Grand Cayman, Cayman Islands. Caribbean Sea.

GCRL 11122 (2). Isla Mira, San Blas, Panama. Caribbean Sea.

AMNH 21298 (1). Little Inagua, Bahama Islands. Western Atlantic.

*Psilotris batrachodes*

UF 10728 (1). West shore of Grand Cayman Island, Cayman Islands. Caribbean Sea.

UF 11338 (2). Carlisle Bay, Antigua. Caribbean Sea.

UF 11397 (1). Falmouth Harbour in Windward Bay, Antigua. Caribbean Sea.

UF 12389 (1). SW corner of Grand Cayman, Cayman Islands. Caribbean Sea.

UF 12390 (1). Georgetown, Grand Cayman, Cayman Islands. Caribbean Sea.

UF 12391 (2). SE corner of Grand Cayman, Cayman Islands. Caribbean Sea.

UF 25662 (1). NW edge of Three Brothers (Bailey Cays), Isla de Providencia, Colombia. Caribbean Sea.

AMNH 29032 (1). W. side West Plana Cay, Bahama Islands. Western Atlantic.

AMNH 28802 (1/1). Grand Bahama Island, Bahama Islands. Western Atlantic.

AMNH 29067 (1). W. side West Plana Cay, Bahama Islands. Western Atlantic.

AMNH 29052 (1). W. side West Plana Cay, Bahama Islands. Western Atlantic.

AMNH 28422 (1). W. side West Plana Cay, Bahama Islands. Western Atlantic.

AMNH 28899 (1). Deep Water Cay, Grand Bahama, Bahama Islands. Western Atlantic.

AMNH 34535 (1). West Bay, Little Salvador, Bahama Islands. Western Atlantic.

*Psilotris celsus*

UF 24889 (1). NW side of Isla de Providencia, Colombia. Caribbean Sea.

UF 25815 (1). West end of Three Brothers Keys, Isla de Providencia, Colombia. Caribbean Sea.

UF 234400 (1). Gray's Reef National Santuary, Georgia, USA. Western Atlantic.

AMNH 31210 (1). Salinas Point, Acklin's Islands, Bahama Islands. Western Atlantic.

*Psilotris kaufmani*

UF 21336 Paratype (1). NW of Santa Catalina Island, Isla de Providencia, Colombia. Caribbean Sea.

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***Pycnomma***

*Pycnomma roosevelti*

FMNH 96484 (1). Little Hog Island, Honduras. Caribbean.

FMNH 101362 (1). Lajas, Margarita Reef, outside reef, Puerto Rico. Caribbean Sea.

FMNM 83964 (1). Sergeants Cay, Belize. Caribbean.

ANSP 149437 (1). La Parguera reef, Puerto Rico. Caribbean Sea.

*Pycnomma semisquamatum*

USNM 322622 (10). Isla Nalasco, Gulf of California, Mexico. Eastern Pacific.

USNM 322623 (2). Isla San Pedro Martir, Gulf of California, Mexico. Eastern Pacific.

ANSP 111201 (1/7). Baja California, Gulf of California, Mexico.. Eastern Pacific.

***Risor***

*Risor ruber*

ANSP 110614 (1/1). No locality data.

ANSP 110618 (1/1). No locality data.

AMNH 18566 (2). Bimini, Bahamas. Western Atlantic.

AMNH 18567 (6). Bimini, Bahamas. Western Atlantic.

AMNH 82835 (1). Florida. Gulf of Mexico.

AMNH 85155 (1). R/V Oregon II, Lat 26-11.00 N Long 83-39.30 W. Gulf of Mexico.

AMNH 085159 (1/1). Gulf of Mexico.

***Varicus***

*Varicus bucca*

FMNH 65608 Paratype (1). Oregon Sta. 2627. West Indies.

*Varicus imswe*

FMNH 83894 Holotype (1). Carrie Bow Cay, Belize. Caribbean Sea.

FMNH 83898 Paratype (1). Carrie Bow, Barrier reef, Belize. Caribbean Sea.

*Varicus vespa*

UF 72110 (1/3). Cape San Bias, Florida. Gulf of Mexico.

UF 72156 (1). Venice, Florida. Gulf of Mexico.

UF 72163 (1). Cape San Bias, Florida. Gulf of Mexico.

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## Outgroups Examined

***Bollmannia***

*Bollmannia chlamydes*

CAS 42777 (1/11). Gulf of Nicoya, Costa Rica. Eastern Pacific.

AMNH 16063 (5). N. of Aquacate Bay, Colombia.

AMNH 16066 (1). Solano Bay, Colombia.

*Bollmannia communis*

AMNH 83864 (2/3). Northern Gulf of Mexico.

*Bollmannia eigenmanni*

AMNH 83455 (1). Gulf of Mexico.

AMNH 83756 (1). Gulf of Mexico.

AMNH 85997 (1). Gulf of Mexico.

***Gobius***

*Gobius niger*

JVT Coll. (2/2). Canary Islands. Eastern Atlantic.

JVT 79-050 (4/4). Canary Islands. Eastern Atlantic.

*Gobius paganellus*

JVT-89-049 (1/1) Maderia. Eastern Atlantic.

JVT-85-044 (1/1) Canary Islands. Eastern Atlantic.

A. Brito Coll. (2/2). Cape Verde Islands. Eastern Atlantic

***Microgobius***

*Microgobius brevispinis*

CAS 133209 Paratype (1). Panama.

*Microgobius carri*

ANSP 144660 (1). La Parguera, Puerto Rico. Caribbean Sea.

AMNH 81570 (1). Pensacolo Beach, Florida. Gulf of Mexico.

*Microgobius cinctus*

AMNH 20935 Paratype (1). Carmen Island, Baja California, Mexico. Eastern Pacific.

*Microgobius gulosus*

ANSP 145439 (1). Pensacola Bay, Florida. Gulf of Mexico.

CAS 150875 (1/10). Cedar Keys, Florida. Gulf of Mexico.

AMNH 87239 (3/3). Little Dauphin Island, Alabama. Gulf of Mexico.

AMNH 22198 (5/5). Cedar Key, Florida. Western Atlantic.

*Microgobius miraflorensis*

CAS 106511 Holotype (1). Panama.

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*Microgobius meeki*

FMNH 72362 (1). Punterenos Estero, Costa Rica. Caribbean.

*Microgobius omostigma*

CAS 122214 Holotype (1). Rio Grande de Norte, Brazil. Western Atlantic.

AMNH 03857 (1). Natal, Brazil. Western Atlantic.

*Microgobius signatus*

ANSP 105209 (1). Estado Sucre, Venezuela. Western Atlantic.

MCZ 30602 (3/8). Havana, Cuba. Western Atlantic.

USNM 035164 (12). Cuba. Caribbean Sea.

*Microgobius thalassinus*

AMNH 65657 (1). Carteret Co., West Atlantic Beach, North Carolina. Western Atlantic.

**New Genus A**

ANSP 147645 (1/3). Puerto Rico. Caribbean Sea.

***Odondebuenia***

*Odondebuenia balearica*

USNM 048411 (2). Bay of Naples, Italy. Mediterranean.

***Parrella***

*Parrella ginsburgi*

CAS 146827 (1/19). Gulf of Nicoya, Costa Rica. Eastern Pacific.

*Parrella maxillaris*

USNM 322735 (1/82). Punta San Ignacio, Sonora, Mexico. Eastern Pacific.

LACM 22741 Paratype (1). Puerto Escondido, Gulf of California, Mexico. Eastern Pacific.

***Vanneaugobius***

*Vanneaugobius canariensis*

JVT-88-075 (2/2). Canary Islands. Eastern Atlantic.

JVT-88-069 (1/1). Canary Islands. Eastern Atlantic.

## Comparative Material

***Brachygobius***

*Brachygobius sp*: Aquarium coll. (7/7).

***Buenia***

*Buenia jeffreysii*: PJM Coll. (2/2).

***Bunaka***

*Bunaka herwerdeni*: AMNH 48525 (1).

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***Caffrogobius***

*Caffrogobius caffra*: PJM Coll. (2/2).

***Chaetuichthys***

*Chaetuichthys sciistius*: PJM Coll. (2/2).

***Chromogobius***

*Chromogobius quadrivittatus*: PJM Coll. (1/1). Mediterranean.

*Chromogobius sp.*: JVT-85-43 (1/1); JVT-88-065 (1/1); JVT-90-512 (1). Canary Islands. Eastern Atlantic.

***Coryphopterus***

*Coryphopterus eidolon*: AMNH 38288 (10).

***Deltentosteus***

*Deltentosteus quadramaculatus*: PJM Coll. (2/2). Mediterranean.

***Dormitator***

*Dormitator latifrons*: AMNH 32955 (1).

***Gobius***

*Gobius cobitus*: PJM Coll. (2/2). Mediterranean.

***Mauligobius***

*Mauligobius maderensis*: JVT-88-062 (6/6). Canary Islands. Eastern Atlantic.

***Padogobius***

*Padogobius markensii* (1). PJM collection. Italy. Mediterranean Sea.

***Pomatoschistus***

*Pomatoschistus pictus*: PJM Coll. (3/3). Mediterranean.

***Robinsichthys***

*Robinsichthys arrowsmithensis*: UF 234392 Paratype (1); UF 234393 Paratype (1).

***Stigmatogobius***

*Stigmatogobius sudanandio*: PJM Coll (1/1).

***Sufflogobius***

*Sufflogobius bibarbatus*: PJM Coll. (2/2).

***Thorogobius***

*Thorogobius epiphiatus*: JVT Coll. (2/2); PJM Coll. (1/1).

***Zebrus***

*Zebrus zebrus*: BMNH 1980.3.5:22 (1/1); BMNH 1980.3.5:21 (1).

***Zosterisessor***

*Zosterisessor ophiocephalus* : PJM Coll. (2/2).

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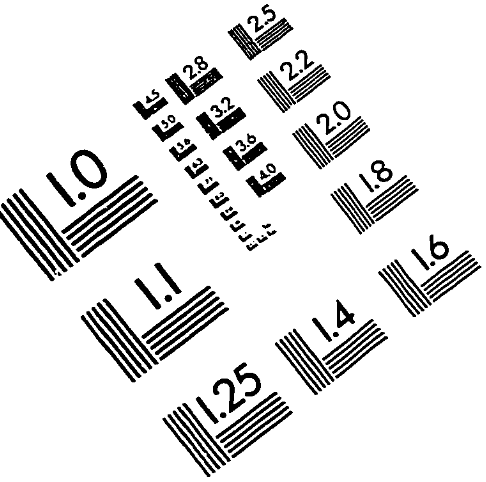

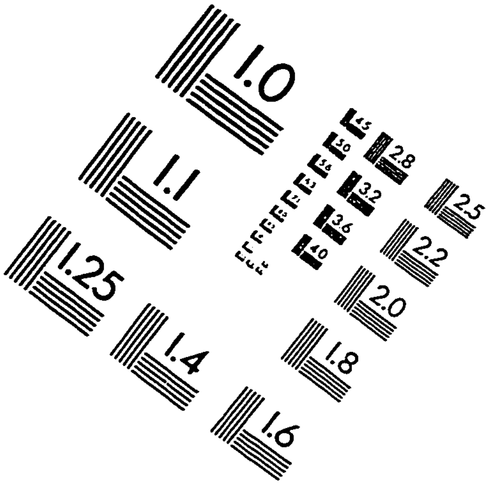

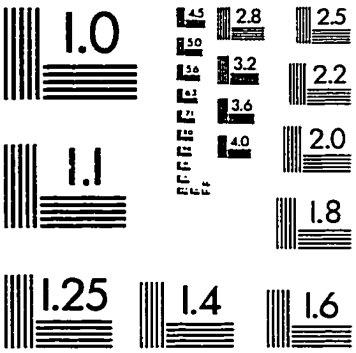

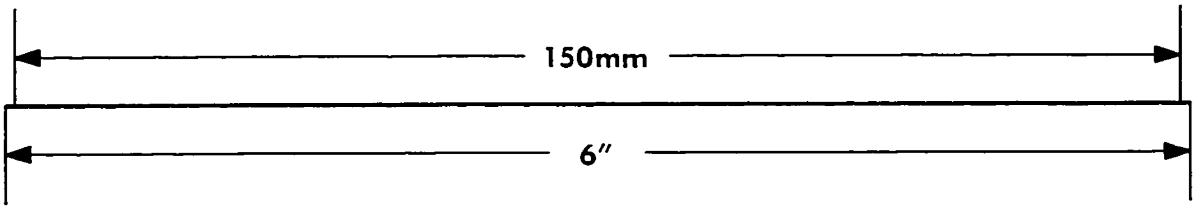

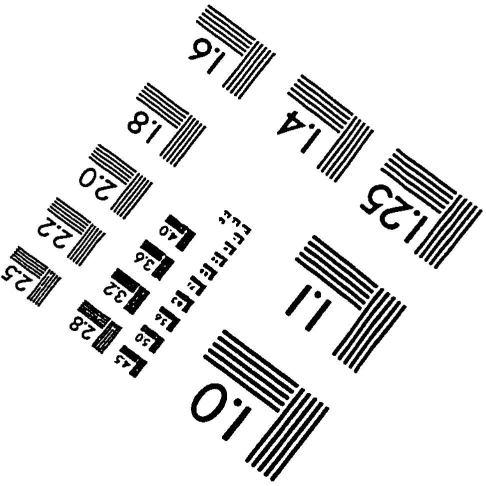

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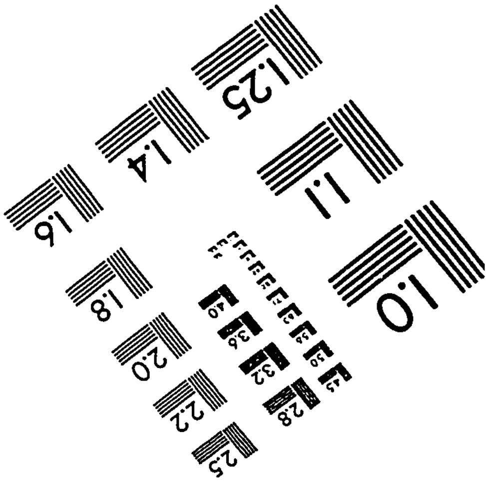

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