

Phylogenetic Analysis of the Genus *Gobionellus* (Teleostei: Gobiidae)

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A cladistic analysis of the gobiid fish genus *Gobionellus* primarily using characters of the postcranial axial skeleton and the cephalic lateralis system gave evidence that the genus as historically conceived is polyphyletic. Its present recognition relies upon characters common to many species of gobiionelline gobies. One group of six species is most closely related to the genus *Gobioides*. This group includes *Gobionellus oceanicus* and retains the name *Gobionellus*. *Gobionellus* is diagnosed by an extensive oculoscapular canal running from the snout to above the rear margin of the operculum with a unique A'BCDFHKL' pore pattern, a distally flared fourth neural spine that is spatulate in five of the six species, a vertical row of neuromasts on the rear field of the operculum, and elongate gill rakers on the anterior surface and lobes on the posterior surface of the epibranchial of the first gill arch. No unequivocal synapomorphies are offered for the genus excluding *Gobioides*. Fifteen species previously assigned to *Gobionellus* are more closely related to species in the genera *Oxyurichthys*, *Oligolepis*, and *Evorthodus*. These species are removed to the resurrected genus *Ctenogobius* of which *Ctenogobius fasciatus* is the type species. *Ctenogobius* is diagnosed by an abbreviated oculoscapular canal that terminates above the preoperculum with an A'BCDFH' pattern, a simple or triangulate fourth neural spine, a diagonal posterior opercular neuromast row, and a lack of lobes or gill rakers on the anterior surface of the first epibranchial. The lack of lobes or gill rakers on the anterior surface of the first epibranchial is synapomorphic for the genus. One species originally placed in *Gobionellus*, *Oxyurichthys stigmalophius*, exhibits two synapomorphies diagnostic of *Oxyurichthys*—a transversely bifid third neural spine and no preopercular canal. It also shares other derived features found in most species of *Oxyurichthys*—a rounded margin on the tongue, a membranous crest on the nape, a shortened palatine bone, and a single row of teeth in the upper jaw. Putative synapomorphies of the gobiionelline genera *Evorthodus*, *Gobioides*, *Oligolepis*, and *Stenogobius* are discussed.

FISHES referred to the genus *Gobionellus* are widespread in subtropical and tropical coastal waters of the Americas and West Africa. They are common from northern Peru to Baja California in the Pacific, from southern Brazil to North Carolina and Bermuda in the Atlantic and throughout the Gulf of Guinea region in the eastern Atlantic. Little is known about the biology of most species and some are uncommon across much of their ranges. Most appear to prefer protected waters with soft sediments and may be very abundant where discovered.

Ginsburg (1932) recognized 14 species of *Gobionellus* in six subgenera. He distinguished this group from the genera *Rhinogobius*, *Ctenogobius*, and *Gobius* by the relative number of second dorsal- and anal-fin rays, and the form of caudal fin. Species of *Gobionellus* were characterized as having one fewer ray in the second dorsal fin than in the anal fin and an elongate caudal fin. Ginsburg noted that species in the other three genera had an equal number of elements for both fins, or one fewer in the anal fin than in the second dorsal fin, and a blunt or rounded

caudal fin. As the three other genera were at that time “catchalls,” receiving species that could not be distinguished from a general gobiid condition (small, fusiform, bottom-dwelling fishes with united ventral fins), Ginsburg was in fact comparing *Gobionellus* to a large cross-section of gobies (for examples of the taxa represented in these genera, see Robins and Lachner, 1966; Hoese and Winterbottom, 1979). Ginsburg also separated *Gobionellus* from the morphologically similar *Oxyurichthys* by the number of tooth rows in the upper jaw. *Oxyurichthys* was noted to have a single row, whereas the 14 species of *Gobionellus* that Ginsburg (1932) recognized had two or more.

Two of the 14 nominal species Ginsburg (1932) initially placed in *Gobionellus*, *Biat luzonica* and *Biat fontanesii* were not seen by him. These two species differ from the other members of the genus by a number of features but most prominently in having an oculoscapular canal with a single median anterior interorbital pore (C, see Materials and Methods), a single pair of pores on the snout (B), a posterior otic

pore (E) and a supraotic pore (G); a 3–22110 first dorsal fin pterygiophore pattern; and a broad gill opening (restricted in all the other species). In actuality, these taxa are not closely related to any species of *Gobionellus* but instead belong to the subfamily Gobiinae (Pezold, 1993). Both nominal species of *Biat* are apparently synonyms of *Amblyeleotris fontanesii* (Hoese and Steene, 1978; Gilbert and Randall, 1979).

Since Ginsburg's revision, 11 new species have been described or moved to *Gobionellus* from other genera. The addition of three of these species nullified Ginsburg's (1932) diagnosis. These were *Gobionellus daguae* (including *Gobionellus panamensis*, see Gilbert and Randall, 1979) and *Gobionellus liolepis*, described by Ginsburg (1953), and *Gobionellus stigmalophius*, which was described by Mead and Böhlke (1958). Both *G. daguae* and *G. liolepis* have the same number of rays in the second dorsal and anal fins. *Gobionellus stigmalophius* has a single row of teeth in the upper jaw. Although large individuals of *G. liolepis* develop two complete rows and large males of *G. daguae* may also develop a second row, smaller individuals of these species have a single row of teeth in the upper jaw. When Mead and Böhlke (1958) described *G. stigmalophius*, they considered it a "highly modified *Gobionellus*" and felt that with its inclusion "the generic limits of *Gobionellus* and *Oxyurichthys* closely approach one another." Gilbert and Randall (1979) believed *G. stigmalophius* and *Oxyurichthys microlepis* to be congeneric but did not place the two genera in synonymy pending further studies of these and several similar genera, including *Evorthodus*, *Paroxyurichthys*, *Oligolepis*, and *Waitea*. In fact, *Paroxyurichthys* was later discovered to be a junior synonym of *Gobionellus* (Pezold, 1991) based upon a specimen of *Gobionellus oceanicus*. The reference to *Waitea* (based upon a communication to the authors by D. Hoese) was most likely to *Waitea stomias*, which is demonstrated later in this work to be a species of *Oligolepis*.

As suggested by Gilbert and Randall (1979), the limits of *Oxyurichthys* and *Gobionellus* did not merely approach one another; they could not be distinguished. The only character state for *Gobionellus* not violated by the additions noted above was the elongate caudal fin—a state found in a number of disparate gobioid genera. In essence, the problem of an ever more inclusive *Gobionellus* was that none of the diagnostic character states was uniquely derived at the level used. Diagnostic characters have previously been offered for *Oxyurichthys*, *Stenogobius* and *Gobionellus* as recognized here (Pezold, 1991)

but the species included in the latter genus were not given.

In this paper, I offer a hypothesis on the relationships of all species presently included in *Gobionellus* and present diagnoses with postulated synapomorphies for *Gobionellus* and related genera resulting from this analysis. *Gobionellus* is restricted to six species. Fifteen species formerly included in *Gobionellus* are assigned to the genus *Ctenogobius* (sensu Robins and Lachner, 1966). All references to *Ctenogobius* and *Gobionellus* hereafter are used in this restricted sense. One species, *G. stigmalophius*, is removed to the genus *Oxyurichthys* and *Oxyurichthys occidentalis* Boulenger, a West African species, is formally reassigned to *Gobionellus* (Miller [1981] assigned the species to *Gobionellus*, but neither he, nor subsequent authors, gave an explanation for the reassignment). The six species of *Gobionellus* recognized herein are redescribed in Pezold (2004).

MATERIALS AND METHODS

The study focused on features of the postcranial axial osteology and the cephalic lateralis for three reasons. First, these characters have been shown useful in diagnosing supraspecific taxa: postcranial axial osteology by Birdsong (1975) and Birdsong et al. (1988); cephalic free neuromast patterns by Iljin (1930), Miller (1973), and Hoese (1983) and cephalic lateralis canal structure by Lachner and McKinney (1979), Takagi (1989), and Pezold (1993). As these character suites exhibit sufficient stability in a group notorious for labile characters, they are often effective in diagnosing genera and occasionally higher taxa as well. Second, when this study was initiated in the early 1980s our understanding of gobioid relationships was much more vague than it is today. Although questions of character state polarity within the Gobioidi still remain, the polarization of states was much more tentative than simply because we knew much less about the distribution of character states across the numerous gobioid taxa. A survey of numerous taxa for character suites could be undertaken relatively easily. Finally, focusing on the sensory system and postcranial osteological characters was appealing in that they offered the opportunity for potentially independent assessments of relationships. The different embryological origins (ectoderm vs mesoderm) of these characters enhance the possibility of independent evolutionary changes where not constrained by selection or linkage. Because Miller et al. (1980) illustrated the conflicting information offered by skeletal and lateralis char-

acters, other characters were included in the analysis that follows if they appeared informative in diagnosing generic limits for the ingroup species.

Comparative collections used for the examination of the cephalic lateralis, and free sensory papillae are listed in Pezold (1993). Specimens of *Gobionellus* examined are listed in Pezold (2004), whereas specimens of *Ctenogobius* are listed in Materials Examined. Characters examined included extent of oculoscapular canal development, oculoscapular canal pore patterns, presence/absence of preopercular canal, preopercular canal pore number, and free neuromast configurations on the cheek and opercle. Canal and canal pore terminology follows Takagi (1957) and Akihito et al. (1984). Pore names (*sensu* Takagi, 1957) are used in discussions and notated using the lettering system of Akihito et al. (1984) when reporting configurations for a taxon and labeling illustrations. The system of Akihito et al. (1984) has been modified such that, when interorbital pores are single and median in position, they are underlined (as C and/or D). Pore names given in discussions are followed by the designator letter of the "Akihito system" in parentheses. Free neuromast patterns are described in reference to topographic location unless otherwise indicated. All lateralis drawings were made with a dissecting microscope and camera lucida.

Features of the postcranial osteology were examined from radiographs and cleared-and-stained specimens. Specimens examined are included in Birdsong et al. (1988). Characters examined were shape of the basihyal; placement of the first pterygiophore of the spinous dorsal fin; placement of the first pterygiophore of the second dorsal fin; number of precaudal anal fin pterygiophores; number of precaudal vertebrae; number of caudal vertebrae; relative number of segmented rays to vertebrae; form of the third neural spine; form of the fourth neural spine; extent of neural arch completion over the caudal vertebrae; number of epurals; and first dorsal fin pterygiophore insertion pattern. The first dorsal fin pterygiophore insertion pattern is given as a formula following Birdsong (1975) and Birdsong et al. (1988). Shape of the basihyal and third neural spine was determined from cleared-and-stained material and by dissection.

Twenty characters were coded for the analysis. Characters found to be phylogenetically uninformative were not included in the matrix. Much additional information on character state distributions for the postcranial axial skeleton has been previously given in Birdsong et al.

(1988) and for the oculoscapular canal system in Pezold (1993).

Monophyly of *Gobionellus* (as historically conceived) was tested and phylogenetic relationships among its species were described by comparing them to other gobionelline species (Pezold, 1993) with which they have previously been confused or for which close relationships have been suggested (e.g., Mead and Böhlke, 1958; Gilbert and Randall, 1979; Birdsong et al., 1988). The outgroup species are all members of the *Stenogobius* group of the Gobionellinae recognized by Larson (2001). Gobionellines in the northern Pacific *Acanthogobius*, *Astrabe*, and *Chasmichthys* groups were not included in the analysis, nor were a number of Indo-Pacific genera related to *Mugilogobius*. Larson (2001) proposed two species groups within the Gobionellinae on the basis of four characters. Species of the *Stenogobius* group, which would include all species historically placed in *Gobionellus* (with the exception of *A. fontanesii*), differ from the *Mugilogobius* group in having anterior nasal pores (A) present, no villi on the head, no infraorbital pores (E) and (usually) transverse rows of free neuromasts on the cheek. The latter two features she proposed as derived states within the gobionellines. Larson's *Mugilogobius* and *Stenogobius* groups are at this time united to one another and to the northern Pacific group of gobionellines solely by plesiomorphic traits.

Phylogenetic analysis was accomplished using PAUP* (D. Swofford, Phylogenetic Analysis Using Parsimony, 4.0 beta 10 vers., Sinauer Press, unpubl.) and NONA (P. Goloboff, NONA vers. 2.0., unpubl.). Heuristic searches were performed using TBR branch-swapping algorithms. Trees were collapsed if minimum branch length equaled zero. All characters were unweighted and character states were unordered (nonadditive). Bremer support values (Bremer, 1994) were calculated using SEPAL (B. Salisbury, SEPAL: strongest evidence and parsimony analyzer, vers. 1.4. Yale University, New Haven, CT, unpubl.). The data matrix constructed is given in the appendix. Character state polarity among study taxa (ingroup and gobionelline outgroups) was determined by rooting the cladogram using the outgroup method (Farris, 1982; Nixon and Carpenter, 1993). Cladograms were rooted using a hypothetical taxonomic unit representing putative ancestral character states (Lundberg, 1972) derived from a survey of states observed in *Rhyacichthys aspro* (Rhyacichthyidae), the sister group to all other gobioid fishes (Miller, 1973; Springer, 1983), odontobutids (*sensu* Hoese and Gill, 1993) and butine eleotrids (the Eleotridae are recognized here as

including the Butinae and Eleotrinae of Hoese and Gill, 1993, but not the Gobiidae). Character conditions for the hypothetical outgroup are denoted by "0" in the matrix and character state descriptions that follow, with four exceptions. Cheek papillae orientation (character 9), first dorsal fin pterygiophore insertion pattern (15), the relative number of second dorsal fin and anal fin rays (17) and epural number (20) show ambiguous distributions among basal gobioid taxa. The hypothetical outgroup state was denoted as unknown (?) for those characters. Trees were constructed and edited using WinClada (K. Nixon, BETA vers. 0.9.9, unpubl.) and CorelDRAW (2002 Corel Corporation, unpubl.).

RESULTS

Both character suites were phylogenetically informative and results applying to higher levels of gobioid relationships have been previously published (Birdsong et al., 1988; Pezold, 1993). Characters useful in assessing generic affinities of species of *Gobionellus* and *Ctenogobius* and included in the analysis are listed below. The cladistic analyses using PAUP and NONA produced two most parsimonious trees, each with a branch length of 43. A strict consensus tree with a branch length of 45, consistency index of 0.69 and retention index of 0.90 is shown in Figure 1. In the consensus tree, *Gobionellus* is part of a clade including *Gobioides*. The *Gobioides*/*Gobionellus* clade has an *Awaous*/*Stenogobius* clade as its sister group. *Ctenogobius* is part of a polytomy (12 branches) including one clade of six species of *Ctenogobius*, an *Oxyurichthys* clade and an *Evorthodus*/*Oligolepis* clade. The two most parsimonious cladograms from which the consensus tree was formed differ in the position of *Ctenogobius stigmaturus* as a sister group to a *Ctenogobius*/*Oxyurichthys*/*Evorthodus*/*Oligolepis* clade or as part of a *Ctenogobius* clade; and in *Ctenogobius* being placed as either the sister group to *Oxyurichthys* (Fig. 2) or as the sister group (excluding *C. stigmaturus*) to an *Oxyurichthys*/*Evorthodus*/*Oligolepis* clade.

The consensus tree indicates that *Gobionellus* and *Ctenogobius* are more closely related to other taxa than to one another. Character states are listed and described for each character used in the analysis and followed by a discussion of distributions among ingroup taxa and other gobioid fishes. Character numbers correspond to those given in the data matrix (Appendix 1). The consistency index for each character follows the character state descriptions.

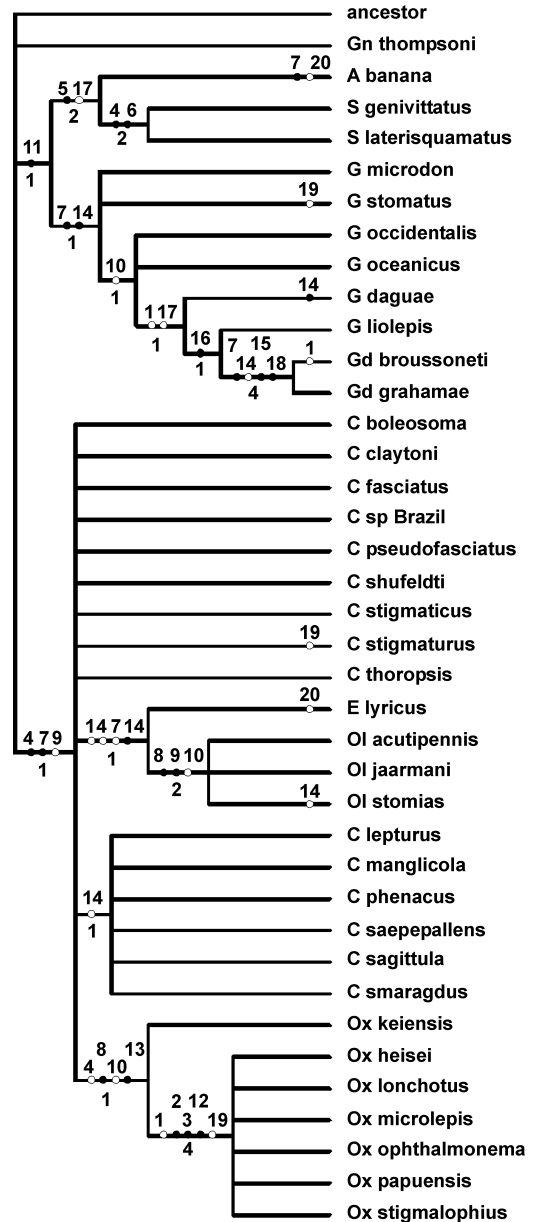


Fig. 1. Strict consensus tree of four cladograms generated by parsimony analysis of 20 characters for a hypothetical outgroup and 38 species of the gobioline "*Stenogobius* group" sensu Larson (2001). The cladogram has a branch length of 45, a consistency index of 0.69 and a retention index of 0.90. Bremer support indices are indicated beneath branches. Character state changes are indicated on the branches with number given above. Homoplastic changes are shown by white circles.

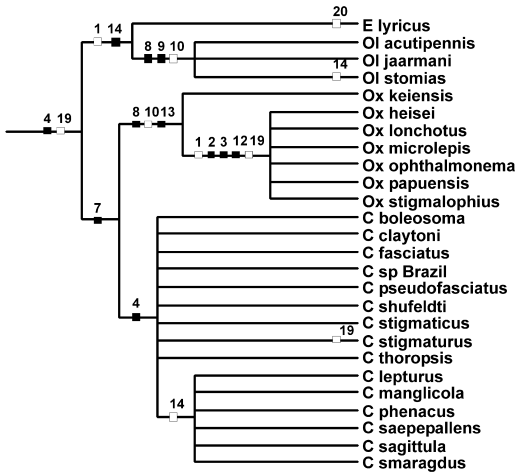


Fig. 2. Cladogram illustrating alternative most parsimonious reconstruction of relationships of species of *Ctenogobius* with other gobionellines. In this resolution, *Oxyurichthys* is the sister group to a monophyletic *Ctenogobius*. Character numbers are noted above the state changes indicated on branches. Homoplastic changes are shown by white circles.

Number of upper jaw tooth rows (1).—(0) multiple rows; (1) single row. (0.25). Basal gobioids have multiple rows of teeth in the upper jaw. Single rows of teeth appear in the scydiines, oxuderines (Murdy, 1989), and the *Mugilogobius* group gobionellines *Gobiopterus* and *Calamiana variegata* (Larson, 2001).

Within the *Stenogobius* group gobionellines, a single row of teeth in the upper jaw has been observed in *Evorthodus* (Ginsburg, 1931; Dawson, 1967, 1969), *Oxyurichthys* (except for *Oxyurichthys keiensis*) and several species of *Gobioides* (Murdy, 1998). A single row also occurs in *Gobionellus daguae* and *G. liolepis* (Ginsburg, 1953) and *Oligolepis*. Large males of *G. daguae* may develop a second row of teeth. Additional specimens of *G. liolepis* have just recently been collected on a STRI-NMNH cruise off the coast of El Salvador. The several specimens collected are all larger than the types examined in this study. All of these specimens have developed a second complete row of fine teeth in the upper jaw (J. Van Tassell, pers. comm.). I reran the analysis changing the state for *G. liolepis* to reflect two rows of teeth in the upper jaw and the results, including consistency and tree length, were unchanged, except for the distribution of states for this character. A single row of teeth appeared as parallel developments in *G. daguae* and *Gobioides africanus* instead of a reversal as in the cladogram presented (Fig. 1). One can legitimately code this character either way, depending upon whether one emphasizes the ap-

pearance of a single row through individuals as large as those observed in the type series or the ultimate achievement of two rows. I chose to emphasize the significance of the presence of the single row as did Meek and Hildebrand (1928) and Ginsburg (1953).

Tongue form (2).—(0) truncate or emarginate; (1) rounded. (1.00). Emarginate or truncate tongues were observed in the butines *Parviparma straminea*, *Oxyeleotris* sp. (blackbanded gudgeon), *Ophiocara porocephala*, *Butis melanostigma*, and *Bostrychus africanus* and the eleotrinus *Gobiomorus*, *Dormitator*, *Eleotris*, *Erotelis smaragdus*, *Hypseleotris compressa*, *Leptophylipnus*, *Mogurnda mogurnda*, and *Guavina guavina*. Among the *Stenogobius* group gobionellines (sensu Larson, 2001), the derived condition was only found in *Oxyurichthys*, with the exception of *Ox. keiensis* in which the plesiomorphic condition was observed.

Palatopterygoid strut (3).—(0) palatine extending midway along ectopterygoid; (1) palatine elongate, reaching or nearly reaching quadrate and reinforced with subequal or very reduced ectopterygoid; (2) palatine short, not reaching along more than the dorsal third of ectopterygoid. (1.00). Harrison (1989) described the plesiomorphic condition for the palatopterygoid strut in gobioids (as part of a palatopterygoquadrate complex) as consisting of a palatine extending half the length of the ectopterygoid. In the most basal species, an ossified endopterygoid also forms a prominent part of the strut.

All but one species of *Oxyurichthys* has a shortened palatine in which the posteroventral process of the palatine is reduced and the ectopterygoid forms the lower part of the palatopterygoid strut (state 2; Harrison, 1989). All other species of the *Stenogobius* group (sensu Larson, 2001) included in this study have an elongate palatine extending nearly to or meeting the quadrate (state 1).

The elongate palatine is typical of gobionellines and has been proposed by Harrison (1989) as a derived condition for gobioid fishes. Larson (2001) found the elongate condition present in most *Mugilogobius*-group gobionellines. The elongate palatine described for these taxa forms the major portion of the palatopterygoid strut, with the ectopterygoid reduced to a small splint behind the lower tip of the palatine in the most extreme cases. Although a similar palatine structure has been observed in the gobiines *Luciogobius grandis* and *Gobiodon* (Harrison, 1989), the ectopterygoid forms a major part of the palatopterygoid strut and could not

be considered subequal to the palatine. An elongate palatine also appears in a number of eleotrids (Akihito, 1969; Harrison, 1989), and the odontobutid *Odontobutis obscura* (Akihito, 1969). The ectopterygoids in these species are long but are subequal to the palatine, splintlike and bordered by the palatine along most of the anteroventral side. All of these species have endopterygoids forming a major portion of the strut. Regarding the constitution of the strut as a whole, not just the relative reach of the palatine along the ectopterygoid, the strut seen in the gobionellines examined here is distinct.

According to Harrison (1989), a shortened palatine as seen in *Oxyurichthys* also appears in the oxudercines and the amblyopines *Taenioides cirratus* and *Trypauchen vagina*. Murdy (1989) and Murdy and Shibukawa (2001) reported this state for the amblyopine genera *Trypauchen*, *Brachyamblyopus*, and *Odontamblyopus*. Although Harrison used the character to associate the oxudercines, *Taenioides* and *Trypauchen* in an *Oxyurichthys* lineage, Murdy (1989) discounted the similarity between the oxudercine and amblyopine forms because of a greater reduction of the palatines in the oxudercines specimens he examined. This is not apparent in Harrison's illustrations nor the illustration in Murdy and Shibukawa (2001). Harrison's illustrations do show a difference in the form of the ectopterygoid between the amblyopines *T. cirratus* and *T. vagina* and the oxudercines and *Oxyurichthys*. The latter group has elongate ectopterygoids forming the lower portion of the strut. *Oxyurichthys* has a splintlike, teardrop-shaped ectopterygoid with an attenuated anterior process. The amblyopines have more bluntly formed, rectangular ectopterygoids (Harrison, 1989; Murdy and Shibukawa, 2001). In a molecular phylogeny for gobioid fishes derived from sequence data for three protein-coding mitochondrial genes, Thacker (2003) presented representative amblyopines and oxudercines as a sister clade to selected scydiines and *Stenogobius* gobionellines. Her analysis did not include *Oxyurichthys* but did include *Evorthodus* and *Ctenogobius*. If *Oxyurichthys* is a sister group to *Ctenogobius* as proposed here, then the similarities between the palatopterygoquadrate struts of *Oxyurichthys* and those of the amblyopines and oxudercines are likely caused by convergence. This conclusion may be supported by differences in the form of the ectopterygoid among these taxa.

Gill rakers on the anterior side of first epibranchial (4).—(0) unmodified gill rakers present; (1) fleshy lobe-like gill rakers present; (2) no rakers, tufts of small papillae present; (3) no rak-

ers, clumps of large papillae present (Fig. 3). (0.75). The presence of gill rakers on the first gill arch is ancestral for gobioid fishes. Gill rakers are present on the anterior surface of the epibranchial of the first gill arch, in varying numbers, in *R. aspro* (Miller, 1973:407), the butines *P. straminea*, *Oxyeleotris* sp. (blackbanded gudgeon), *O. porocephala*, *B. melanostigma*, and *Bostrychus africanus* and the eleotrids *Gobiomorus*, *Dormitator*, *Eleotris*, *E. smaragdus*, *H. compressa*, *Leptophilypnus*, *M. mogurnda*, and *G. guavina*. Rakers in the eleotrids and *R. aspro* vary from many thin and elongate rakers as seen in *Dormitator* to small prickly knobs as observed in *M. mogurnda* and *B. melanostigma*, but they are not fleshy lobes.

Species of *Ctenogobius* have a first gill arch with tufts of tiny papillae on the first epibranchial but no gill rakers or lobes and four or five broad, triangulate, unconnected rakers on the ceratobranchial. There are no rakers or lobes on the first epibranchial in species of *Stenogobius*, but there are tufts of large papillae present; the rakers on the first ceratobranchial are reduced and joined by a low membrane. Species of *Gobionellus* have slender gill rakers on the upper arch and, with the exception of *G. daguae*, on the lower portion as well. *Gobionellus daguae* has a few broad rakers on the first ceratobranchial similar to those found in *Ctenogobius*, *Oxyurichthys*, *Oligolepis*, and *Evorthodus*. *Oxyurichthys*, *Oligolepis*, and *Evorthodus* have lobelike structures on the anterior side of the first epibranchial. Lobes are also found on the epibranchial of species of *Gobionellus*, but they are not on the anterior side and, therefore, do not appear to be homologous. *Evorthodus* may have a single long raker in addition to lobes on the upper arch. Lobes on the anterior side of the first epibranchial are also found in some species assigned to the Gobiinae (e.g., Hoese and Allen, 1977).

Fleshy lobes on pectoral fin girdle (5).—(0) none; (1) present. (1.00). The pectoral girdle is smooth in *R. aspro*, odontobutids and most eleotrids. A large platelike flap is found on the pectoral girdle of *P. straminea*. Fleshy protuberances (lobes) and folds are found in some species of Gobionellinae (Larson, 2001:fig. 9). Larson (2001) discussed the presence of these structures in a number of *Mugilogobius* group genera. Fleshy structures on the pelvic girdle are also seen in several northern Pacific endemics. Lobes are present in *Chaeturichthys stigmatias* and a long fold is found in *Acanthogobius flavimanus*, both members of the *Acanthogobius* group sensu Birdsong et al. (1988). *Quietula*

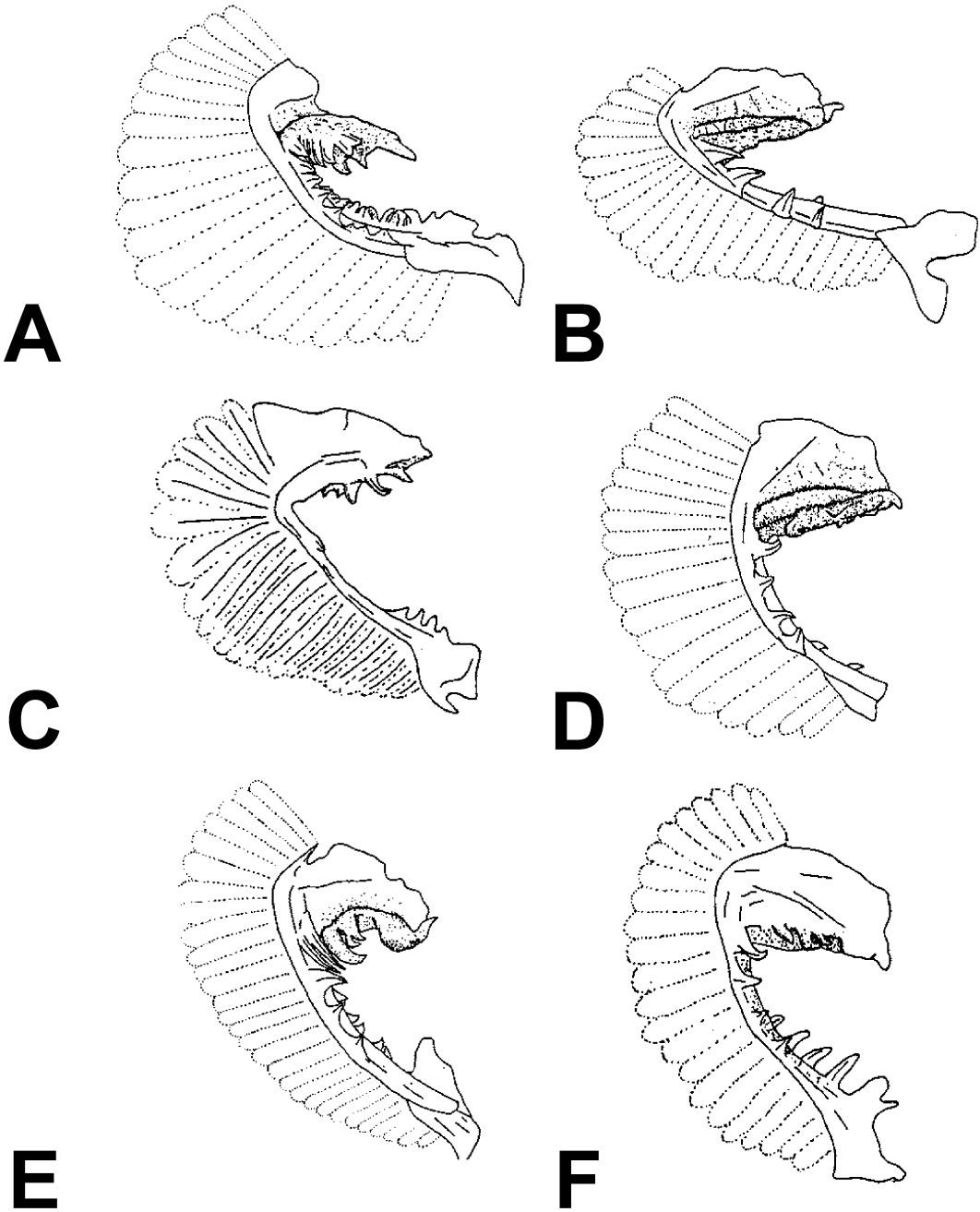


Fig. 3. An illustration of the first gill arch (right lateral view) as found in (A) *Gobionellus oceanicus*, (B) *Ctenogobius fasciatus*, (C) *Evorthodus lyricus*, (D) *Oligolepis acutipennis*, (E) *Oxyurichthys stigmalophius*, and (F) *Oxyurichthys keiensis*. Examples of observed states for character 4, gill rakers associated with the anterior epibranchial, are unmodified gill rakers present on anterior epibranchial surface (3A), fleshy lobelike rakers present (C–F) and no rakers present, only small tufts of papillae (B).

y-cauda, a member of the *Chasmichthys* group (Birdsong et al., 1988) has lobes as well. Among the *Stenogobius* group gobionellines, only *Awaous* and *Stenogobius* have lobes.

Anterior nares position relative to cephalic lateralis (6).—(0) nares lateral to canals on snout; (1) nares medial to snout canals. (1.00). The basal gobioid condition is for each naris to be lateral

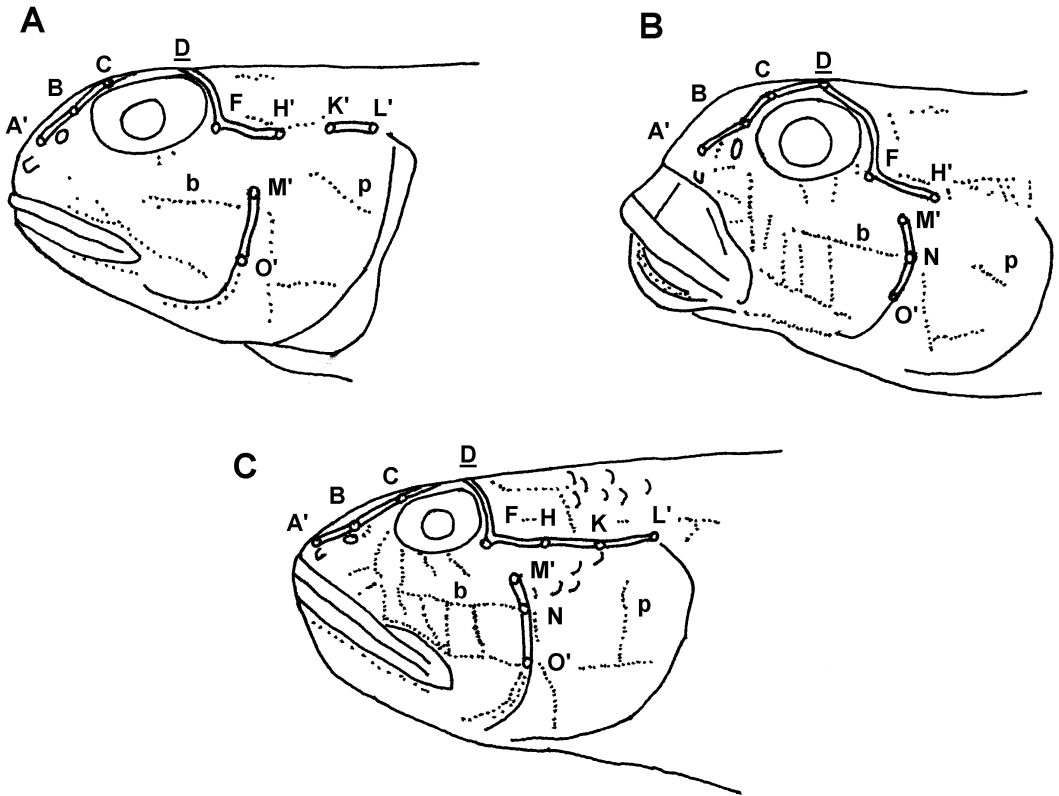


Fig. 4. Lateral view of the oculoscapular canals, preopercular canals and sensory papillae rows of the cheek and opercle in (A) *Oligolepis acutipennis*, (B) *Ctenogobius lepturus*, and (C) *Gobionellus occidentalis*. Canal pores are labeled according to Akihito et al. (1984) with unpaired pores underlined. Labeled neuromast rows are posterior opercular row (p) and horizontal midcheek row (b).

to the cephalic lateralis canals on the snout. In fact, state one was only observed in *Stenogobius* (Pezold, 1991).

Oculoscapular canal (7).—(0) complete laterally (continuous from orbit to rear margin of opercle) with A'BCDEFGHIJKL' pattern; (1) complete laterally with A'BCDFHJKL' pattern; (2) complete laterally with A'BCDFHKL' pattern (Fig. 4C); (3) complete laterally with A'BD \underline{F} HKL' pattern; (4) abbreviate laterally, terminating above preopercle with A'BCDFH' pattern (Fig. 4B); (5) disjunct laterally with a separate portion above rear opercle and A'BCDFH' K'L' pattern (Fig. 4A). (0.83). Akihito (1986) reasoned that the primitive gobioid oculoscapular canal is probably an interrupted canal with a disjunct temporal portion as it is common across many gobioid taxa (for examples, see Pezold, 1993). However, Takagi (1989) suggested a general evolutionary trend in gobioid fishes from well developed to reduced cephalic sensory canal formation. This is consistent with the occurrence of complete oculoscapular canals in the Rhyacichthyidae

(Miller, 1973), and a long canal running from near the tip of the snout to the opercular margin is also seen in butine genera *Butis*, *Bostrychus*, *Oxyeleotris*, and *Ophiocara* (Pezold, 1993). An extensive lateral oculoscapular canal is considered plesiomorphic in this study. Pores A'BCDEFGHIJKL' are observed in several basal eleotrid genera with extensive canals—the butines *Bostrychus*, *Butis*, and *Oxyeleotris* (Pezold, 1993). There is a tendency toward loss of pores among the gobioids, even within the butines. Pore G is lost in *Ophiocara*, G, C, and E in some *Bostrychus*, and G, C, E, and I in *Parviparma*. A complete oculoscapular canal with pores A'BCDEFGHIJKL' is regarded as the ancestral gobioid state herein.

There are at least five different oculoscapular canal structures (Pezold, 1993) occurring among the study taxa (*Awaous* exhibits more than one; see Watson, 1992, 1996; Pezold, 1993). Of the five, only the disjunct pattern (state 5) spans the two clades containing *Ctenogobius* and *Gobionellus*, occurring in *Evorthodus*, *Gnatholepis*, *Oligolepis*, and *Stenogobius*. This pat-

tern is also seen in the sicydiine genera *Sicyopus*, *Lentipes*, and *Stiphodon*. In the cladogram, this pattern is the basal state from which the other four states, all unique among gobioid fishes, are derived.

The A'BCDFHKL' oculoscapular pore pattern is unique to *Gobionellus*. In the cladogram, this extensive canal structure is derived from the disjunct state and is the precursor to the state described for *Gobioides* below. An extensive canal (with a different pore pattern) appears independently in *Awaous*. Similar reversals to an extensive and continuous oculoscapular canal (with different pore patterns) are seen in the gobiines *Bathygobius* and *Gobius* (Akihito and Meguro, 1980; Ahnelt, 2001) and the sicydiines *Sicydium* and *Sicyopterus* (Parenti and Maciolek, 1993; Pezold, 1993).

In *Gobioides*, the anterior interorbital pores (C) are lost, resulting in an A'BDFHKL' oculoscapular pore pattern. The oculoscapular canals are separate between the orbits. Anterior interorbital pores (C) are absent in oxudercine specimens identified as *Apocryptes bato* and *Parapocryptes cantonensis*, but they also lack much of the oculoscapular canal system (Pezold, 1993). These oxudercine species have lost the anterior portion of the nasal or snout canals leaving them with only a single pair of snout canal pores (B). Some gobionellines of the northern Pacific, such as *A. flavimanus*, *C. stigmatias* and *Q. y-cauda*, have also lost the anterior interorbital pores. These species have very different canal systems from the form seen in *Gobioides* (Pezold, 1993), showing a reduction in the extent of the snout canals in particular. *Mahidolia* and some of the gobiiosominines lack anterior interorbital pores as well; all of these species are believed to have attained this condition from a single-pored state, and thus the condition would not be homologous. In short, the canal structure and the pore patterns in all of the taxa noted above differ from the condition observed in *Gobioides*.

Ctenogobius and *Oxyurichthys* have an A'BCDFH' pore pattern. Abbreviated temporal portions of the oculoscapular canal as found in these two genera are also seen in *Redigobius*, *Fusiogobius*, *Gobiodon*, *Tukugobius bucculentus* and the gobiiosominines examined but differ in the pores present—their canal structures are not regarded as homologous.

Preopercular canal pores (8).—(0) canal present with three pores, M'NO' (Fig. 4B–C); (1) canal present with two pores, M'O' (Fig. 4A); (2) canal absent. (1.00). Preopercular canals have no more than three pores in gobioids (M'NO') and

this condition is regarded as plesiomorphic for the family. The canal is completely lost in *Oxyurichthys* and has been reduced independently to a two-pore state in *Oligolepis*. Outside of the *Stenogobius* group gobionellines, the canal and its associated pores have been lost or reduced to the two-pore state independently many times (e.g., Takagi, 1989, Larson, 2001). This character is variable in *G. oceanicus*—approximately 5% of the specimens examined here had two pores (state 1) in both preopercular canals, nearly 10% had two pores in one canal and three in the other.

Cheek papillae orientation (9).—(0) longitudinal (Fig. 4A); (1) transverse (Fig. 4B–C). (1.00). Larson (2001) characterized the scattered, unorganized state found in *R. aspro* as the plesiomorphic condition for gobioid fishes. This same approach was taken in initial analyses, but I. J. Harrison (unpubl.) notes that *Rhyacichthys* “shows several unusual and specialized characters” and suggests that the organization of the cephalic sensory papillae might be another example of specialization. A longitudinal pattern is observed in the putative rhyacichthyid *Protogobius attiti* (Watson and Pollabauer, 1998; for discussion, see Shibukawa et al., 2001) and odontobutids (Hoese and Gill, 1993), but both states 0 and 1 are found across other eleotrids. The outgroup state was designated as unknown. Within the Gobionellinae, state 0 predominates among species of the *Mugilogobius* group (Larson, 2001) and the northern Pacific species (the *Chasmichthys*, *Acanthogobius*, and *Astrabe* groups of Birdsong et al., 1988; Akihito et al., 1984). Within the *Stenogobius* group, only *Oligolepis* exhibits state 0.

Anteriad extension of horizontal cheek papillae row “b” (10).—(0) not reaching second transverse suborbital row (Fig. 4B); (1) reaching second transverse row (Fig. 4C). (0.33). The plesiomorphic condition is a midcheek horizontal row (“b” row) (Miller and Wongrat, 1979) that does not reach anteriad as far as the second transverse suborbital row.

The midcheek horizontal suborbital papillae row extends forward to reach the second transverse suborbital row of a series that starts at the anterior eye margin in *Gobioides* and *Gobionellus* with the exception of *Gobionellus microdon* and *Gobionellus stomatus*. It reaches only the third row in *G. microdon* and only the third or fourth row in *G. stomatus*. The derived condition appears independently in both *Oligolepis* and in most *Oxyurichthys* (specimens examined for the

latter genus varied with the row reaching the third or second transverse suborbital rows).

There are three transverse suborbital rows anterior to the end of row “b” in all specimens of *Ctenogobius* examined. The same is true for *Stenogobius genivittatus* (Akihito et al., 1984:fig. 156), *Awaous banana*, *Awaous ocellaris* (Akihito et al., 1984:fig. 131), and *Evorthodus lyricus*. *Oligolepis acutipennis* lacks well-developed transverse rows, whereas *Oligolepis stomias* has a condition similar to *Evorthodus* and *Ctenogobius* (although the transverse rows are still reduced). Position homology for this row with midcheek horizontal rows seen in the sicydiines and *Gnatholepis* is not clear. Papillae row patterns of the cheek in the latter taxa have poorly developed midcheek horizontal rows at best, and where formed they are on the posterior field.

Posterior opercular papillae row (p) (11).—(0) diagonal (Fig. 4A–B); (1) vertical (Fig. 4C). (1.00). The general gobioid condition is a diagonal *p* row crossing the subopercle-opercle symphysis, disjunct from both the anterior opercular and subopercular rows (Sanzo, 1911; Akihito et al., 1984; this study).

Gobionellus, Gobioides, Awaous, and Stenogobius have a vertical (perpendicular to the long axis of the fish) *p* row. The *p* row is not confluent with the anterior opercular row but does reach the subopercular row in most specimens.

Several species of *Eleotris*, both species of *Eretelis*, and *Leptophilypnus fluviatilis* (Akihito et al., 1984; Miller, 1998; Pezold and Cage, 2002) have a *p* row that usually connects with the anterior opercular and subopercular rows. It is archlike in orientation and is diagonally inclined as it crosses the opercular/subopercular juncture. The upper portion of the row is directed toward the anterior opercular row when not actually connected. In some species of *Eleotris* the *p*-row may appear as two intersecting rows, with a diagonal upper row intersected by a vertical lower row. Shared possession of these row types may be indicative of relationship among *Eleotris*, *Eretelis*, and *Leptophilypnus*, but the conformations appear to be homoplastic to the rows seen in *Gobionellus* and the other gobiids noted.

Nape crest (12).—(0) without a membranous crest; (1) membranous crest present. (1.00). Most gobioid fishes, including *Rhyacichthys*, odontobutids and eleotrids, do not have a crest on the nape. A membrane is observed in some gobiines (e.g., *Lophogobius*, *Cristatogobius*, *Cryptocentroides*). Among the *Stenogobius* group gobiionellines, the derived state is found in *Oxyurichthys*.

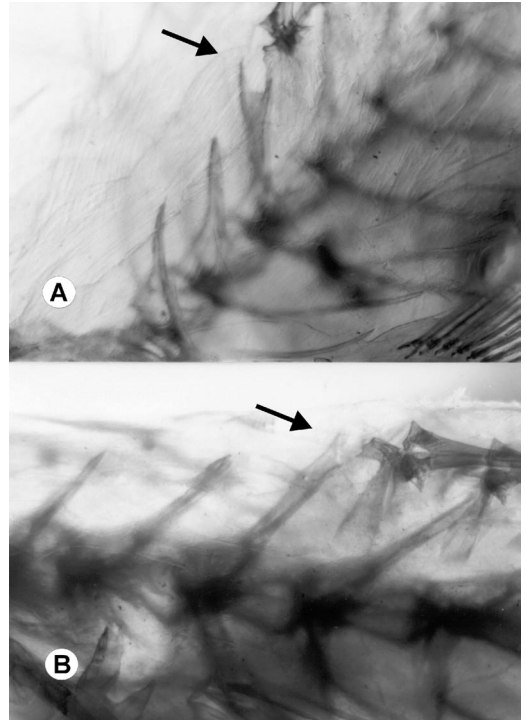


Fig. 5. Transversely bifid third neural spine of (A) *Oxyurichthys keiensis* and (B) *Oxyurichthys stigmalophius*. Arrows indicate the third neural spines which precede the first dorsal fin pterygophore.

Third neural spine (13).—(0) spikelike with one point; (1) transversely broad and bifid (1.00; Fig. 5). The typical gobioid condition, and that observed in *Rhyacichthys*, odontobutids, and eleotrids, consists of a single spine tip. The bifid condition, not observable in radiographs, has been observed only in species of *Oxyurichthys*.

Fourth neural spine (14).—(0) thin spine; (1) triangulate; (2) slightly flared along its length; (3) pikelike, flared along its length with rearward extension just above the base; (4) spatulate with thin base. (0.67; Figs. 6–7). Most gobioids have simple, thin neural spines (Larson, 2001; this study). The fourth neural spine is broadly flared distally, spatulate but constricted at the base in most *Gobionellus*. The fourth neural spine in *G. daguae* (Fig. 6D) is not spatulate like that seen in the other species of *Gobionellus* but is broadened distally with a caudad extension above the base.

A similar structure to the distally flared fourth neural spine described above has been observed in *Oxudercus dentatus* (Murphy, 1989). Larson (2001) described the second through fifth neural spines as variably expanded and bifid or

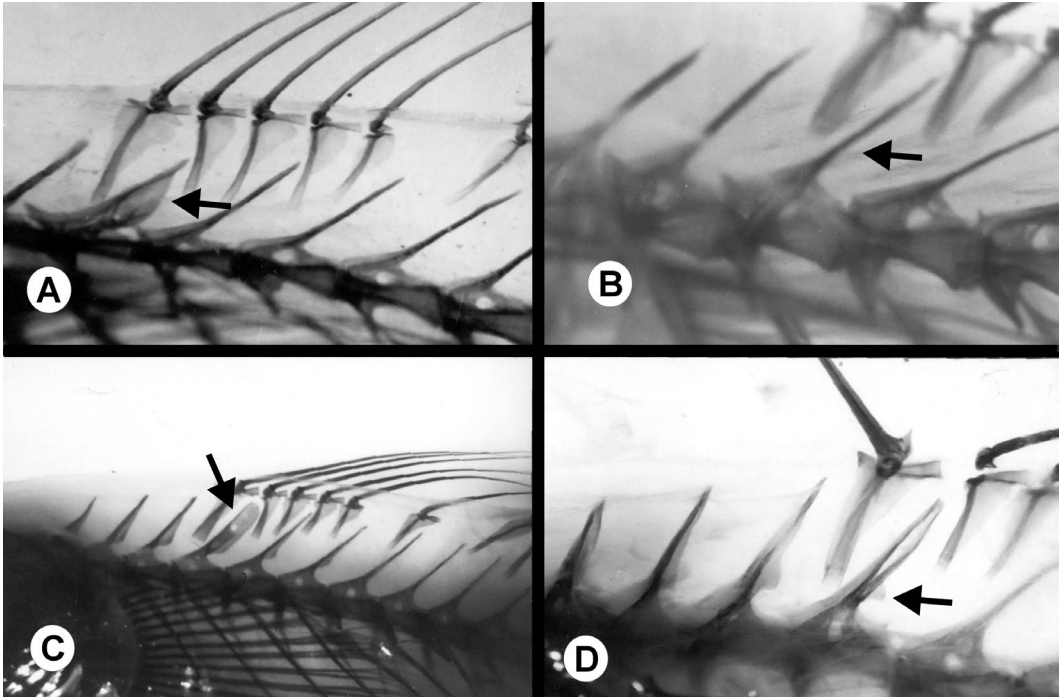


Fig. 6. The fourth neural spine in (A) *Ctenogobius smaragdus*, (B) *Ctenogobius shufeldti*, (C) *Gobionellus microdon*, and (D) *Gobionellus daguae*. Arrows indicate the fourth neural spines which follow the insertion of the first dorsal fin pterygiophore. The arrow in (D) points to the horizontal posterior flange on the fourth neural spine of *Gobionellus daguae*.

split for *Mugilogobius* and some related gobiionelline genera, noting the character does not appear in all specimens within a species nor all species within a genus. *Evorthodus* and most species of *Oligolepis* have a fourth neural spine very slightly expanded throughout its length ending in a pointed tip (state 2; Fig. 7). *Oligolepis stomias* and some species of *Ctenogobius* have a broad-based triangulate fourth neural spine (state 1).

First dorsal fin pterygiophore pattern (15).—(0) 3–12210; (1) 3–12201. (1.00). Although the ancestral condition for first dorsal fin pterygiophore pattern is a matter of debate (see Larson, 2001:32 for a synopsis), the gobiionellines generally exhibit a 3–12210 pattern. *Gobioides* is an exception showing the derived state (Birdsong et al., 1988; Murdy, 1998). The outgroup was coded as unknown.

Dorsal fin confluence (16).—(0) separate or barely connected at base; (1) broadly confluent. (1.00). Basal gobioid fishes have separate dorsal fins. Confluent dorsal fins are found in amblyopine species. Confluent dorsal fins are also found in *Ptereleotris monoptera* (Randall and Hoese, 1986). Although rarely observed, conflu-

ent dorsal fins have appeared independently in gobioids at least twice. Although they were not connected in the specimen of *Gobiodon quinquestrigatus* examined in this study, the trait is variably expressed in some species of *Gobiodon* (R. Winterbottom, pers. comm.). Dawson (1967) reported that the dorsal fins were frequently connected basally in *E. lyricus* but not *Evorthodus minutus*. *Gobionellus liolepis* and all species of *Gobioides* have confluent dorsal fins (Murdy, 1998).

The presence of the dorsal fin connection in both the amblyopines and the other diverse taxa is regarded as convergent with the condition seen in *Gobioides* and *Gobionellus*. *Gobioides* differs from the amblyopines in jaw structure, including the palatopterygoid strut (Harrison, 1989), in the form of the cephalic lateralis canals and papillae, and does not have the 2:1 ratio of soft rays to underlying vertebrae, a feature synapomorphic for the amblyopines (Pezold, 1993; Murdy, 1998).

Number of second dorsal and anal fin rays (17).—(0) one more ray in second dorsal fin than anal fin; (1) equal number of rays in second dorsal and anal fins; (2) one more ray in anal fin than

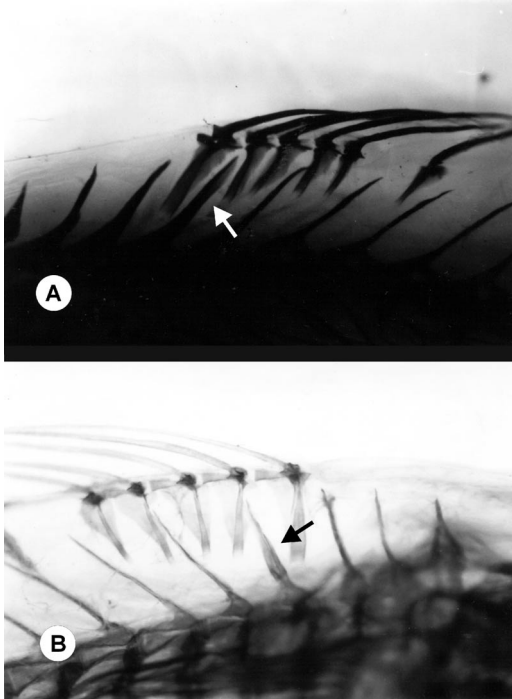


Fig. 7. The fourth neural spine in (A) *Evorthodus lyricus* and (B) *Oligolepis acutipennis*. Arrows indicate the fourth neural spine which follow the insertion of the first dorsal fin pterygiophore.

second dorsal fin. (0.67). Two conditions have usually been observed in *R. aspro*, one more second dorsal-fin ray than anal-fin ray or an equal number of rays in the two fins (Miller, 1973; Larson, 2001), although Akihito et al. (1984) reported two more in the anal fin than the second dorsal fin for this species. The odontobutids generally have at least one more ray in the second dorsal fin than the anal fin (Akihito et al., 1984; Iwata et al., 1985; Larson, 2001). Among eleotrids states 0 and 1 are generally observed (Akihito et al., 1984; Larson, 2001; this study), but Akihito et al. (1984) reported state 2 in *Butis amboinensis*, *Ophieleotris* sp. and *Hypseleotris cyprinoides*. In this study, state 2 was also found characteristic of *Dormitator latifrons*, *Dormitator lebretonis*, and *Dormitator maculatus*, and *Hypseleotris compressa*. The ancestral state was coded as unknown.

Among gobionellines, one more dorsal-fin ray or equal numbers of rays were the predominant states observed in the *Mugilogobius* group by Larson (2001). Of the gobionelline species examined in this study, *G. liolepis*, *G. daguae*, *Gobioides*, *Stenogobius*, and *Awaous* had equal numbers of second dorsal- and anal-fin elements. All others had one more ray in the anal fin than

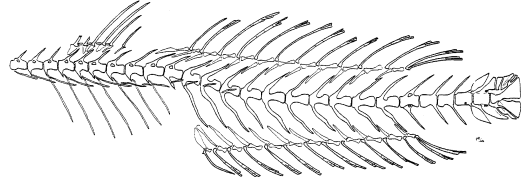


Fig. 8. Drawing of the postcranial axial skeleton *Ctenogobius shufeldti* (UMMZ 155326) illustrating incompletely formed neural arches over the caudal vertebrae. Incomplete arches lack neural foramina.

the second dorsal fin. The cladogram hypothesizes two separate origins of state one from ancestors having one more ray in the anal fin than the second dorsal fin.

Median/caudal fin confluence (18).—(0) anal fin and second dorsal fin separate from caudal fin; (1) both fins connected to caudal fin. (1.00). Among basal gobioids all median fins are separate. Within the Gobionellinae, state 1 is observed only in *Gobioides* (with the exception of *Gobioides africanus* [Murphy, 1998]). Although connected median and caudal fins are obtained in the amblyopines, the condition is not homologous to that observed in *Gobioides* for reasons given under character 16. Thacker (2000) demonstrated that a continuous median fin-fold was synapomorphic for the genus *Microdesmus* within the monophyletic Microdesmidae.

Neural arches of caudal vertebrae (19).—(0) complete; (1) incompletely formed (0.25; Fig. 8). Among gobioid fishes, including *Rhyacichthys*, odontobutids and eleotrids, the neural arches of the last few caudal vertebrae are incompletely formed. The possession of incompletely formed arches in additional vertebrae is regarded as a derived condition. *Evorthodus*, *Oligolepis*, *Ox. keiensis*, most species of *Ctenogobius* and *G. stomatus* have incompletely developed neural arches over all or most of the caudal vertebrae. The condition of the neural arch reverses to complete over the caudal vertebrae in *C. stigmaturus* and all species of *Oxyurichthys* except *Ox. keiensis*. Among other gobioids, the scyidiines and the oxudercine *Boleophthalmus boddarti* are also characterized by incomplete neural arches over the caudal vertebrae, and Birdsong (1988) reported reduced neural arches over the caudal vertebrae in the gobiine *Robinsichthys arrowsmithensis*.

Epural number (20).—(0) three; (1) two; (2) one. (0.50). Three epurals are found in *Rhyacichthys* (Miller, 1973) and sporadically in some odontobutids (Akihito, 1986). Most eleotrids have two epurals. The hypothetical ancestor was cod-

ed as “?” for this feature because of the lability in basal gobioids. This character is also labile within the gobiionellines studied here. A single epural was variably observed in specimens of *G. liolepis*, *Ctenogobius lepturus*, *Ctenogobius manglicola*, *Ctenogobius saepepallens*, *C. stigmaturus*, an undescribed species of *Ctenogobius* from Brazil, *Gobioides sagitta*, *Ol. stomias* and *Oxyurichthys lonchotus*. One specimen of *Ox. keiensis* had three. Larson (2001) reported two epurals in all members of the *Mugilogobius* group except for *Brachygobius* and *Chlamydogobius* and *Calamiana paludosus*. In her analysis, she used the modal number if there was variation within a species. Using that approach, *Awaous* and *Evorthodus* have a single epural; all others studied here have a mode of two.

DISCUSSION

The data demonstrate that *Gobionellus* as historically conceived is polyphyletic. The evidence indicates that two lineages exist within the genus that are more closely related to other gobiionellines than to one another. One group of six species, paraphyletic in the analysis, includes *G. oceanicus* and retains the name *Gobionellus*. The six species recognized are *G. daguae*, *G. liolepis*, *G. microdon*, *G. occidentalis*, *G. oceanicus*, and *G. stomatus*. The species are redescribed in another work.

Although the extensive oculoscapular canal with an ‘BCDFHKL’ pore pattern is unique to *Gobionellus*, it is most likely the precursor for the condition found in *Gobioides* as depicted in the cladogram. The expanded fourth neural spine as seen in *Gobionellus*, however, is also presented as a synapomorphy for the *Gobioides*/*Gobionellus* clade, being subsequently lost in *Gobioides*. The characters in conflict with the fourth neural spine as a synapomorphy for *Gobionellus* are the relative number of second dorsal and anal fin rays (17), the confluence of the dorsal fins (16), forward extent of the midcheek suborbital (“b”) papillae row (10), and the number of teeth in the upper jaw (1). Four species, *G. oceanicus*, *G. occidentalis*, *G. daguae*, and *G. liolepis* share the forward extent of the “b” row with *Gobioides*. *Gobionellus daguae* and *G. liolepis* have an equal number of anal- and second dorsal-fin rays as seen in *Gobioides*. *Gobionellus liolepis* forms the sister group to *Gobioides* with which it shares confluent dorsal fins. *Gobionellus occidentalis*, *G. oceanicus*, and *G. liolepis* share pigmentary features not used in the analysis and approach *Gobioides* in elongate body form, but *G. daguae* seems misplaced as it is reminiscent of *Stenogobius* with a stockier morphology and distinctive

pigmentation. The fourth neural spine in *G. daguae*, although expanded, is not rounded distally, and lacks the spatulate form seen in these other species of *Gobionellus*.

All six species of *Gobionellus* also have a vertical posterior opercular papillae row, and elongate gill rakers on the anterior surface and lobes on the posterior surface of the epibranchial of the first gill arch. All species but *G. stomatus* have complete neural arches. It has been suggested by I. J. Harrison (unpubl.) that the presence of lobes on the posterior surface of the first epibranchial could be a synapomorphy for *Gobionellus*. Whether or not the morphology of the posterior surface of the first epibranchial is a synapomorphy for the genus remains to be tested. It does appear to differ from that observed for other *Stenogobius* group gobiionellines, but more information is required on the details of gill arch morphology (beyond the anterior surface of the ceratobranchial and epibranchial of the first arch) to better define characters and assess the homologies and polarities of their associated states.

Gobionellus is not combined with *Gobioides* here because of the clear synapomorphies delimiting *Gobioides*, the relatively few phylogenetically informative characters available to this study and the likelihood that possibly two characters (shape of the fourth neural spine and posterior epibranchial lobes) may be synapomorphic for *Gobionellus*. For the sake of nomenclatural stability, it is best to continue to recognize *Gobioides* and *Gobionellus* until more substantial support is offered for one alternative or the other.

The other group, comprising 15 species, is *Ctenogobius*; *C. fasciatus* is the type species. Although shown in the consensus tree as part of a polytomy including *Oxyurichthys* and an *Evorthodus*/*Oligolepis* clade, one of the two most parsimonious trees supports monophyly based upon a derived condition for the first gill arch (Fig. 2). The epibranchial of the first gill arch lacks lobes and rakers but has small tufts of papillae (Fig. 3). The ceratobranchial has four or five broad, triangulate rakers. The relationship between *Ctenogobius* and *Evorthodus* is consistent with the molecular phylogeny of gobioid fishes presented by Thacker (2003). In her phylogeny, which did not include *Gobionellus*, *Gobioides*, *Oxyurichthys* or *Oligolepis*, *Evorthodus*, and *Ctenogobius* formed a clade sister to a clade of three *Gnatholepis* species. The *Evorthodus*-*Ctenogobius*-*Gnatholepis* clade of the molecular phylogeny is in turn sister to *Awaous*-*Stenogobius* and sicydiines. It is also of note that Thacker’s molecular phylogeny supports the recognition of a *Steno-*

gobius group of Gobionellinae as proposed by Larson (2001), distinct from *Mugilogobius* and the northern Pacific species. In fact, by her analysis, the amblyopines and oxudercines form a sister group to the *Stenogobius* group gobionellines and sicydiines.

In addition to the synapomorphy of the epibranchial structure of the first gill arch, *Ctenogobius* is characterized by a combination of other features shared with other members of the polytomy: an abbreviated cephalic lateralis canal with an A'BCDFH' pattern, a diagonal posterior opercular papillae row and reduced neural arches over the caudal vertebrae (reversed in one species). Most species have a simple fourth neural spine, but it is broad-based and triangulate in six species (Fig. 6). The polarity of this character is ambiguous. Contrary to the cladograms, geographic character-state distributions suggest a recent derivation of the simple spine, as a reversal from a basally broad, triangulate spine. As noted by Pezold and Gilbert (1987), both eastern Pacific species of *Ctenogobius*, the sole west African species, *C. lepturus*, and three of the western Atlantic species (*C. phenacus*, *C. saepepallens*, and *C. smaragdus*) have a broad-based triangulate fourth neural spine. The triangulate spine found in *Oligolepis stomias* parallels the condition found in *Ctenogobius*.

Species assigned to *Ctenogobius* are *Ctenogobius boleosoma*, *Ctenogobius claytoni*, *Ctenogobius fasciatus*, *C. lepturus*, *C. manglicola*, *Ctenogobius phenacus*, *Ctenogobius pseudofasciatus*, *C. saepepallens*, *Ctenogobius sagittula*, *Ctenogobius shufeldti*, *Ctenogobius smaragdus*, *Ctenogobius stigmaticus*, *C. stigmaturus*, and *Ctenogobius thoropsis*. An undescribed species from Brazil is also included in this genus. *Gobionellus atripinnis* and *Gobionellus comma* are regarded as synonyms of *C. claytoni* and *C. saepepallens*, respectively. A full description of the genus *Ctenogobius* and a review of and key to its species will be given elsewhere.

Gobioides is distinguished by two synapomorphies: a 3–12201 first dorsal pterygiophore pattern (Birdsong et al., 1988; Murdy, 1998) and an oculoscapular canal extending from near the anterior nares to the rear margin of the opercle with an A'BDFHKL' pore pattern. As indicated by the pattern, paired nasal canals are present and separate between the orbits and the anterior interorbital pores (C) are absent. Most species also have confluent median and caudal fins. As noted above, the genus shares several derived conditions with *Gobionellus*. Murdy (1998) has reviewed the species of this genus.

Species of *Stenogobius* are united by two synapomorphies in the cladogram—the anterior nares are medial to the oculoscapular canals (Pe-

zold, 1991) and the raker morphology of the epibranchial of the first gill arch. The lateralis canals also terminate high on the snout near the posterior nares and the first gill arch has very small gill rakers which are united by a low membrane on the ceratobranchial (Watson, 1991; this study). Both of the latter features are also considered possible synapomorphies.

The genus *Oligolepis* is delimited by two synapomorphies: transverse suborbital papillae rows of the cheek are reduced to form a longitudinal pattern and the preopercular canal has only two terminal pores (M'O'). The epibranchial of the first gill arch has a single, simple fleshy lobe on the anterior surface (Fig. 3), which may also be synapomorphic in that the conditions observed in *Evorthodus* and *Oxyurichthys* include either multiple structures on the epibranchial or if a single lobe is present, the lobe has a fingerlike, bifid or trifurcate structure. Species included in this genus are *Oligolepis jaarmani* (= *Oxyurichthys jaarmani*), *Oligolepis nijsseni* (= *Oxyurichthys nijsseni*), *Oligolepis acutipennis* and *Oligolepis stomias* (= *W. stomias*). The genus *Waitea* has been distinguished by an extremely elongate jaw and a lanceolate caudal fin (Smith, 1941). These states occur only in males. Similar sexual dimorphism, although not as extreme, occurs in some species of *Ctenogobius* and in *Oxyurichthys keiensis*. *Waitea* is placed in synonymy here with *Oligolepis*. The *Oligolepis* sp. illustrated by Akihito et al. (1984) appears to be *Ol. stomias*. *Oligolepis jaarmani* and *Ol. nijsseni* do not possess any of the apomorphies described below for *Oxyurichthys*.

The genus *Evorthodus* was diagnosed by Ginsburg (1931) and Dawson (1967). Teeth primarily form a single row in both jaws, particularly in females and juveniles. Teeth are incisiform and truncate in juveniles, bifid or entire, but incisiform in females and conical or caniniform in adult males (Dawson, 1967, 1969). Although this character was coded as an identical state to the single row of teeth observed in *Oxyurichthys*, *Oligolepis*, *G. africanus* and two species of *Gobionellus*, the presence of incisiform teeth in juveniles and females is synapomorphic for the genus *Evorthodus*, and a single epural appears as a synapomorphy for *Evorthodus* in this analysis. Epural number is a labile character in gobioid fishes showing intraspecific variation in the related gobionelline genera *Ctenogobius* and *Oligolepis* (Birdsong et al., 1988) and was coded in its modal form in this study and by Larson (2001). Murdy (1989) described *retractor dorsalis* muscle and fifth ceratobranchial structures that may also prove synapomorphic for *Evorthodus*.

The genus *Oxyurichthys* contains about 16 spe-

cies, all of which share two synapomorphies: a transversely broad and bifid third neural spine (Fig. 5) and no preopercular canal (F. Pezold and H. K. Larson, unpubl. data). All species of *Oxyurichthys*, except for *Ox. keiensis*, also share three other synapomorphies: a sharply rounded fleshy tongue, a single row of teeth in the upper jaw (with partial second rows appearing in a few species) and a shortened palatine which does not form part of the lower palatopterygoquadrate strut. All but *Ox. keiensis* also show a reversal to complete neural arches over the caudal vertebrae. Although all of the representative species in the cladogram other than *Ox. keiensis* have a membranous crest on the nape, it is also lacking in other members of the genus (Pezold, 1998). Other diagnostic characters for the genus, excluding *Ox. keiensis*, are given by Pezold (1991). *Gobionellus stigmalophius* exhibits all five of the synapomorphies listed above and is also reassigned to *Oxyurichthys*. *Oxyurichthys* also has an elongate longitudinal suborbital neuromast row (row b). A review of the species of this genus is being completed with Helen Larson.

MATERIAL EXAMINED

Comparative materials examined for postcranial osteology are listed in Birdsong et al. (1988) and those studied for cephalic lateralis structure and free sensory papillae distribution patterns are listed by Pezold (1993). Species of Rhyacichthyidae, Odontobutidae, Butinae (Eleotridae) and *Stenogobius* group gobionellines (Gobiidae) examined are given below with the collection number followed by the number of individuals in parentheses. Additional information was obtained from Hoese and Gill (1993), Miller (1973) and Springer (1983). Specimens of *Gobionellus* examined are given in Pezold (2004), whereas specimens of *Ctenogobius* are listed below by species, region, and museum catalog number with the number of individuals given in parentheses. Type material is indicated with the original binomen. Institutional abbreviations are as in Leviton et al. (1985).

Rhyacichthyidae. *Rhyacichthys aspro*: CAS 32758(1), USNM 247300(5).

Odontobutidae. *Micropercops dabryi*: USNM 83982(1). *Micropercops* sp.: USNM 112474(6), USNM 112475(2), USNM 112508(1). *Odontobutis obscurus*: USNM 86108(1), USNM 71419(5), USNM 84004(1), USNM 86412(5). *Percottus glehni*: USNM 86108(1), USNM 105188(1). *Percottus pleskei*: USNM 77008(1).

Butinae. *Bostrychus africanus*: CAS-SU 40431(1). *Bostrychus sinesis*: USNM 46802(1), USNM 576093(1), USNM 85907(6). *Butis ambroinensis*:

USNM 51953(1); USNM 272625(3). *Butis butis*: USNM 135895(1); USNM 161618(4), USNM 261350(13), USNM 268461(7), ANSP 63023-9(17). *Butis gymnopomus*: USNM 161176(4), USNM 161177(1). *Butis koilatodoni*: USNM 161233(3). *Bostrychus melanopterus*: USNM 87928(2). *Kribia kribensis*: CAS-SU 63034(1), CAS-SU 63035(1), USNM 118789(3), USNM 118790(1). *Odonteleotris* sp.: MCZ 49560(2). *Ophiocara porocephala*: CAS-SU 38579(4). *Oxyeleotris lineolata*: CAS SU 25582(4). *Oxyeleotris marmorata*: USNM 230238(2), ANSP 87352(3), CAS 49455(2). *Oxyeleotris* sp.: USNM 103362(1), USNM 119618(1). *Parviparma straminea*: CAS-SU 29701(1).

Gobionellinae (*Stenogobius* group). *Awaous guineensis*: CAS-SU 55635(2). *Awaous stamineus*: ANSP 29510-13(4), CAS 52267(2). *Awaous banana*: ANSP 144525(3), CAS-SU 18573(3), FMNH 93277(3), UF 30510(1), USNM 272622(1), UTMSI 334(3). *Awaous transandeanus*: CAS 42775(2), TNHC 11519(1), TNHC 11506(1), TNHC 11509(1), TNHC 11511(1). *Awaous* sp.: ANSP 149484(1). *Euorthodus lyricus*: CAS 57067(1), CAS 52392(3), CAS 52394(3), TCWC 3283.1(3), TNHC 10623(29), UF 100059(12), USNM 144040(1), UNOVC 4306(15). *Gnatholepis anjerensis*: USNM 126530(2). *Gnatholepis cauerensis*: CAS 51548(1). *Gnatholepis thompsoni*: CAS-SU 8364(1), UMMZ 174286(5). *Gobioides africanus*: BMNH 1939.7.12.33(1). *Gobioides ansorgii*: BMNH 1909.10.29.110-112(3), BMNH 1968.11.15.77(1). *Gobioides broussoneti*: ANSP 121256(2), CAS-SU 21381(1), USNM 233612(11). *Gobioides grahamae*: BMNH 1925.10.28.464(1), BMNH 1925.10.28.465(1), BMNH 1950.5.15.41(1), BMNH 1959.3.17.161(1). *Gobioides peruanus*: USNM 123616(1). *Gobioides sagitta*: BMNH 1862.1.24.27.29(3). *Oligolepis acutipennis*: UMMZ 100537(25), USNM 139345(1), RMNH 14325(3). *Oligolepis jaarmani*: USNM 217267(8), USNM 217266(2). *Oligolepis nijsseni*: ZMA 115270(2). *Oligolepis stomias*: USNM 51816(1), USNM 257137(13), USNM 258782(9), USNM 99296(1). *Oxyurichthys auchenolepis*: RMNH 4506(2). *Oxyurichthys cornutus*: CAS-SU 33137(10). *Oxyurichthys heisei*: NLU 64915(2). *Oxyurichthys keiensis*: RUSI 17043(8), RUSI 16786(1). *Oxyurichthys lonchotus*: ANSP 23350(1), ANSP 90998(3), ANSP 28055-56(2), CAS 23328(14), CAS 51062(17), UMMZ 196868(1), USNM 126533(1), USNM 50698(1). *Oxyurichthys microlepis*: ANSP 88946(1), UMML 14353(4), UMMZ 100268(4), UMMZ 100539(5). *Oxyurichthys ophthalmomema*: FMNH 91547(10). *Oxyurichthys papuensis*: BPBM 7354(2), LACM 37382-2(1). *Oxyurichthys paulae*: USNM 346922(2). *Oxyurichthys stigmalophius*: ANSP 81233(1), ANSP 81855(1), ANSP 144295(1), UMML 3992(1). *Oxyurichthys tentacularis*: ANSP 100179(1), NLU 71393(9). *Oxyuri-*

chthys takagi: CAS 51047(13), CAS 51059(4). *Stenogobius genivittatus*: ANSP 86151(9); ANSP 28016-19(4), BPBM 26373(4), BPBM 26380(2), CAS 51056(7), CAS 52011(3), USNM 99878(1). *Stenogobius gymnopomus*: RMNH 4552(4). *Stenogobius laterisquamatus*: ZMA 116477(2); WAM P27847-007(3), WAM P28206-002(1), NLU 62766(4).

Ctenogobius boleosoma. New Jersey: ANSP 130090(1). Delaware: ANSP 73745(1). Bermuda: MCZ 32987(1). North Carolina: USNM 123295(1); USNM 123301(2); USNM 123298(6); USNM 123299(1). South Carolina: ANSP 142663(24); ANSP 142664(1); USNM 265067(3); USNM 133064(3); USNM 29673(3), syntypes, *Gobius encaeomus*. Georgia: ANSP 71066(1). Florida: UF/FSU 13575(115); ANSP 96801(1); ANSP 113042(1); USNM 123305(4); USNM 265068(1); USNM 123303(3); USNM 30860(40), syntypes, *Gobius boleosoma*. Alabama: USNM 127465(1). Mississippi: USNM 265008(1). Louisiana: USNM 123319(1). Texas: ANSP 115760(1); ANSP 73643(2); ANSP 115719(1); ANSP 99216(2); ANSP 73849(3). Mexico: GCRL 2879(18); USNM 192269(1). Belize: USNM 265001 (1). Bahamas: ANSP 98654(1). Cuba: USNM 265011(1); USNM 178955(1). Jamaica: USNM 265071(1). Dominican Republic: USNM 265069(1). Puerto Rico: UMMZ 172793(16); ANSP 144506(1); ANSP 144488(3); USNM 86910(1); USNM 55695(1); USNM 114657(1). Guadeloupe: ANSP 144487(2). Martinique: ANSP 113089(5). Panama: GCRL 4669(66); GCRL 12227(1); ANSP 146903(1); USNM 148716(1); USNM 123344(2); USNM 265000(1); USNM 205204(1); USNM 226379(1); USNM 81825(1). Colombia: GCRL 4787(24); USNM 38655(3). Curaçao: ANSP 144507(4). Venezuela: GCRL 15513(9); USNM 123273(1). BRAZIL: MAPA 1502(6 [of 35]); AMNH 3836(13); MO-FURG 80-111(3); ANSP 121172(3); ANSP 121173(1); ANSP 121182(2); AMNH 20746(1); AMNH 20705(1).

Ctenogobius claytoni. Texas: UMMZ 167639(1), holotype, *Gobionellus atripinnis*. Tamaulipas: SU 68864(2). Vera Cruz: FMNH 3740(1), holotype, *C. claytonii*; FMNH 3741, 16900-16902(4), paratypes, *Gobius claytonii*; FMNH 16903-16906(4), paratypes, *G. claytonii*; FMNH 4572, 16907-16910(5); UMMZ 184472(2); UMMZ 184456(1); UMMZ 184609(1); TNHC 11277(1); TNHC 11287(6); UMMZ 181796(7; one cleared and stained), paratypes, *G. atripinnis*; UMMZ 187725(4), paratypes, *G. atripinnis*; UMMZ 187703(7); UMMZ 97727(3); UMMZ 187763(1), paratype, *G. atripinnis*.

Ctenogobius fasciatus. Florida: IRCZM 7544 (2). Honduras: UMMZ 199685(1). Costa Rica: TU 24861(2); TU 24877(28); UMMZ 180655(3); UF 11139(10); UF 11176(5); UF 10268(6); UF/FSU 17695(3); UF/FSU 17624(4); UF/FSU 17727(1);

UF/FSU 17670(1); UF/FSU 17645(4). Panama: USNM 81874(1); USNM 81875(4); USNM 81876(2); USNM 81819(3); USNM 148715(1); SU 18574(10); FMNH 32186-32188(3); FMNH 32184(1); GCRL 7846(15); GCRL 12773(5); GCRL 10282(2); GCRL 10266(2); GCRL 12777(9); GCRL 3280(1); UF 35956(1); ANSP 122357(1); ANSP 122358(1). Venezuela: UMMZ 147507(31); UMMZ 147536(1); USNM 194104(1). Trinidad: USNM 7549(1), lectotype, *C. fasciatus*; USNM 198110(1), paralectotype, *C. fasciatus*; AMNH 26394(2). Barbados: ROM 36366(91); ROM 36216(88); ROM 24325(2); ROM 36363(1). Dominica: USNM 199703(1); USNM 199704(2); USNM 199705(1). Dominican Republic: UF 30402(1). Haiti: UMMZ 167222(7).

Ctenogobius lepturus. Ghana: USNM 264991(2). Congo: MNHN 1967-416(28).

Ctenogobius manglicola. Mexico: SU 3095(1), holotype, *Gobius manglicola*; GCRL 4421(23); GCRL 2771(9); GCRL 2658(35). Guatemala: GCRL 5849(57). El Salvador: GCRL 5030(17). Costa Rica: GCRL 3529(180). Panama: AMNH 73935 (60); USNM 123251(2); USNM 81826(2); USNM 101374(1); USNM 119328(2); USNM 123250(6); USNM 123248(15); USNM 123347(17). Colombia: GCRL 5142(15); USNM 123252 (3). Peru: GCRL 22308(20).

Ctenogobius sp. Piaui: MCZ 46857(2). Espirito Santo: FMNH 93278(2); FMNH 93258(13); FMNH 92356(1); FMNH 93268(4). Rio De Janeiro: FMNH 86668(5); UF 19210(2); UF 19209(2); ANSP 121210(2); ANSP 121211(1). Rio Grande Do Sul: UF34127(2); UF 34129(4); MO-FURG 80-150(2); DZUFRGS 0952(1); UF 34128(1); MAPA 1718(3); MAPA 1498(1); DZUFRGS 1023(3); DZUFRGS 0701(1); DZUFRGS 0946(1); MO-FURG 80-34(6 of 35); MAPA 1501(2).

Ctenogobius phenacus. French Guiana: UF 34132(1), holotype, *Gobionellus phenacus*; USNM 244153(3), paratypes; USNM 264990(7), paratypes. Surinam: USNM 226247(2), paratypes; USNM 226248(1), paratype. Venezuela: MBUCV-V 14128(2), paratypes.

Ctenogobius pseudofasciatus. Trinidad: UF 31201(1), paratype. Venezuela: UMMZ 147535(1). Panama: FMNH 32178(1); USNM 81824(1), paratype; USNM 105109(1), paratype; USNM 123264(1), paratype; USNM 205202(1), paratype. Costa Rica: USNM 201589 (1), paratype; ANSP 109179(1), paratype; UF/FSU 17696(1), paratype; UF 13517(1); paratype; UF 13518(1), paratype; UF 13519(1), paratype; UF 13520(1), paratype. Honduras: UMMZ 199544(1). Belize: FMNH 82076(1); FMNH 86680(1). Florida: TNHC 10859(1);

UF100057(13); IRCZM 5086(4); IRCZM 5102(7); IRCZM 7358(11); IRCZM 7363(5); IRCZM 7543(3).

Ctenogobius saepepallens. Brazil (Bahia): GCRL 10917(1). Trinidad: MCZ 58720(1). Venezuela (Isla Cubagua): ANSP 109181(7), holotype, *Gobionellus comma*; LACM 20634(1), paratype, *G. comma*; LACM 20635(1), paratype, *G. comma*; UF 12793(1), paratype, *G. comma*. Panama: MCZ 47646(1); GCRL 4668(1); MCZ 58718(14). Colombia (Isla Providencia): UF 24450(1); UF 19103(6); UF 25851(1). Belize: FMNH 86618(1); FMNH 77684(5); FMNH 77681(5); FMNH 77685(1); FMNH 77687(3); FMNH 77682(5); FMNH 77686(3); FMNH 77683(5). Mexico (Cozumel): UMMZ 9458(2). Grand Cayman: UF 13521(25), paratypes, *Gobionellus saepepallens*; UF 13523(2), paratypes, *G. saepepallens*; UF 13522(5), paratypes, *G. saepepallens*; ANSP 109177(3), paratypes, *G. saepepallens*; ANSP 109178(20), paratypes, *G. saepepallens*. Puerto Rico: UPR 2412(4), paratypes, *G. saepepallens*; UF 23017(12); USNM 114656(1). Virgin Islands: UPR 1766(1), paratype, *G. saepepallens*; GCRL 1999(2); UF 13524(1), paratype, *G. saepepallens*. Antigua: CAS 37270(1); UF 12759(1), paratype, *G. saepepallens*; UF 11304(7), paratypes, *G. saepepallens*. Dominica: USNM 199706(1), paratype, *G. saepepallens*. Bahamas: ANSP 147349(5); UMMZ 186507(2), paratypes, *G. saepepallens*; ANSP 100519(38), paratypes, *G. saepepallens*; ANSP 109180(1), holotype, *G. saepepallens*; ANSP 86135(1), paratype, *G. saepepallens*; AMNH 25792(2) paratypes, *G. saepepallens*; AMNH 24936(59); FMNH 73908(2), paratypes, *G. saepepallens*; USNM 201590(2), paratypes, *G. saepepallens*. Florida: ANSP 84784(1); ANSP 96802(1); UF 7050(1); USNM 167676(2). North Carolina: MPM 33435(1); MPM uncat. stn. 52 (1); MPM uncat. stn. 87 (1); MPM uncat. stn. 76 (2).

Ctenogobius sagittula. California: SU 9893(4); SU 12944(1). Mexico: AMNH 5558(6); CAS 51045(4); LACM 1025(35); LACM 34081-2(5); FMNH 57530(3); MCZ 27881(1); SU 169(8); UMMZ 178590(2); UMMZ 184865(27); UMMZ 172256(15); USNM-BOC 2755(2); USNM 39636(3), syntypes, *Gobius longicaudus*; USNM 59456(7); USNM 46655(1); USNM 123265(6); USNM 214515(1); USNM 30936(7); USNM 43740(3); USNM 265002(1). El Salvador: FMNH 12018(2); FMNH 93706(2); GCRL 16554(4); GCRL 16562(1); USNM 87200(3); USNM 220642(2). Costa Rica: FMNH 86669(3); FMNH 91226(1); LACM 2700(1); LACM 2889(2). Panama: ANSP 151059(1); FMNH 8469(3); MCZ 46472(2); MCZ 46482(1); UF 16208(10); UMMZ 180724(2); USNM 81961(2);

USNM 79013(3); USNM 123260(1); USNM 123258(2); USNM 265005(1); USNM 123259(1); USNM 81821(1); USNM 81818(1); USNM 81820(3). Central America: BMNH 1861-8-13-26(1), holotype, *Euctenogobius sagittula*. Colombia: CAS 51041(2); CAS 64211(2); FMNH 58481(2); FMNH 86693(10); USNM 257662(7); USNM 257678(235+); USNM 265085(1); USNM 257667(3); USNM 257679(243+). Ecuador: SU 9291(4); USNM 88785(2).

Ctenogobius shufeldti. North Carolina: UMMZ 126274(6); USNM 123238(2); USNM 123240(2). South Carolina: USNM 59074(8); USNM 123237(1); USNM 123244(1); ANSP 149878(3); UMMZ 155196(3). Georgia: GCRL 16980(2); UF 25089(1); UMMZ 155219(7); USNM 298633(30); USNM 346221(16); USNM 131223(1). Florida (Atlantic Coast): IRCZM 5100(5); IRCZM 5101(2); TNHC 10834(1); UF 7585(4); UF 7741(8); UF 7742(1); UF 7743(1); UF 7744(3); UF 7745(4); UF 7746(1); UF 7747(14); UF 7748(11); UF 7749(3); UF 7750(2); Florida (Gulf Coast): UF 4381(7); UF/FSU 5334(7); TU 103016(2); TU 120046(1); TU120073(1); UMMZ 163443(3); ANSP 72835(2); ANSP 72981(1); ANSP 73030(13); ANSP 73069(1). Alabama: UMMZ 163590(28). Mississippi: ANSP 55812-15(4). GCRL 2066(1); GCRL 2067(1); GCRL 2777(1); GCRL 2778(1); GCRL 2779(3); TU 122420(2); TU 122465(5); TU 122501(8); UMMZ 155431(2); UMMZ 163654(4). Louisiana: USNM 35202(12), syntypes, *Gobius shufeldti*; USNM 123239(1); USNM 123241(1); USNM 123249(1); ANSP 70796(1); FMNH 51061(2); FSC 10872(47); TU 266(18); UF 33927(3); UMMZ 155326(9); UNOVC 656(708); UNOVC 763(15); UNOVC 769(33); UNOVC 787(223); UNOVC 1232(3); UNOVC 1770(22). Louisiana-Texas (Sabine Lake): ANSP 99078(7); ANSP 115695(2). Texas: TCWC 1619.1(1); USNM 123245(1).

Ctenogobius smaragdus. Florida (Atlantic Coast): IRCZM 309(4); IRCZM 2560(4); IRCZM 2606(5); IRCZM 4842(5); TNHC 10860(16); TNHC 10884(1); UF 4807(1); UF 7756(3); UF 11602(14); UF 19336(1); UF 28776(1); UF 28778(1); UMMZ 189754(10). Florida (Gulf Coast): ANSP 71056-65(10); ANSP 71067(1); CAS 51043(7); LACM 1448(6); UF/FSU 24720(7); UF 3433(5); UF 9231(1). Cuba: MNHN 1257(1), holotype, *Gobius smaragdus*; USNM 4769(2); USNM 37461(1); USNM 264987(1). Virgin Islands: USNM 78150(1). Belize: FMNH 86666(1); FMNH 86677(1). Venezuela: GCRL 15514(2). Brazil: CAS-SU 52379(1); GCRL 9621(46); MCZ 4624(1); MCZ 13077(1); SU 52386(1); UF 19211(20).

Ctenogobius stigmaticus. Florida: TNHC

10703(1); UF 30509(1); UMMZ 13450(1). Mississippi: GCRL 13824(3). Texas: NLU 69898(4). Cuba: MCZ 13104(1), holotype, *Smaragdus stigmaticus*; MCZ 13122(3); MCZ 13923(2); SU 1936(6). Antigua: USNM 170308(1). Guadeloupe: ANSP 144494(1). Honduras: FMNH 86678(1). Brazil (Rio De Janeiro): UF 19212(1); UF 19903(1); MCZ 4622(22); UMMZ 201445(2).

Ctenogobius stigmaturus. Bermuda: ANSP 148421(1); ANSP 148422(4); ANSP 148423(1); ANSP 148424(14); GCRL 19604(6); GCRL 19605(2); USNM 178903(2); USNM 178904(2). Florida: ANSP 96784(1); CAS 52007(1); IRCZM 1750(4); IRCZM 2564(60); IRCZM 4005(6); UF/FSU 13247(1); UF/FSU 9152(5); UF/FSU 13245(2); UF/FSU 13255(3); UE/FSU 11467(1); UF 7081(43); UF 37133(59); UMMZ 1446(6); UMMZ 189866(10); USNM 35004(1); USNM 57330(31); USNM 57365(4); USNM 57431(2); USNM 57450(8); USNM 65327(1); USNM 73097(3); USNM 89868(1); USNM 89869(2); USNM 89870(1); USNM 89871(1); USNM 89872(2); USNM 89873(1); USNM 89883(1); USNM 89884(1); USNM 264985(1). Cuba: USNM 82512(2). Belize: AMNH 24615(5). Panama: AMNH 73937(16).

Ctenogobius thoropsis. Surinam: FMNH 90554(1), holotype, *Gobionellus thoropsis*; FMNH 94890(2), paratypes. Brazil: USNM 214066(1), paratype; USNM 264992(1), paratype.

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APPENDIX 1. CHARACTER STATE MATRIX FOR *Gobionellus*, *Ctenogobius*, RELATED GOBIONELLINES, AND COMPOSITE OUTGROUP.

Taxon	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Outgroup	0	0	0	0	0	0	0	0	?	0	0	0	0	0	?	0	?	0	0	?
<i>Gobionellus daguae</i>	1	0	1	0	0	0	2	0	0	1	1	0	0	3	0	0	1	0	0	1
<i>G. liolepis</i>	1	0	1	0	0	0	2	0	0	1	1	0	0	4	0	1	1	0	0	1
<i>G. microdon</i>	0	0	1	0	0	0	2	0	0	0	1	0	0	4	0	0	2	0	0	1
<i>G. occidentalis</i>	0	0	1	0	0	0	2	0	0	1	1	0	0	4	0	0	2	0	0	1
<i>G. oceanicus</i>	0	0	1	0	0	0	2	0	0	1	1	0	0	4	0	0	2	0	0	1
<i>G. stomatus</i>	0	0	1	0	0	0	2	0	0	1	1	0	0	4	0	0	2	0	0	1
<i>Ctenogobius boleosoma</i>	0	0	1	1	0	0	0	0	0	1	1	0	0	4	0	0	2	0	1	1
<i>C. claytoni</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	0	0	0	2	0	1	1
<i>C. fasciatus</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	0	0	0	2	0	1	1
<i>C. lepturus</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	0	0	0	2	0	1	1
<i>C. manglicola</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	1	0	0	2	0	1	1
<i>C. sp. (Brazil)</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	1	0	0	2	0	1	1
<i>C. phenacus</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	0	0	0	2	0	1	1
<i>C. pseudofasciatus</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	1	0	0	2	0	1	1
<i>C. saepepallens</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	0	0	0	2	0	1	1
<i>C. sagittula</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	1	0	0	2	0	1	1
<i>C. shufeldti</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	1	0	0	2	0	1	1
<i>C. smaragdus</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	0	0	0	2	0	1	1
<i>C. stigmaticus</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	1	0	0	2	0	1	1
<i>C. stigmaturus</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	0	0	0	2	0	1	1
<i>C. thoropsis</i>	0	0	1	2	0	0	4	0	0	0	0	0	0	0	0	0	2	0	0	1
<i>Oxyurichthys keiensis</i>	0	0	1	1	0	0	4	2	0	1	0	0	1	0	0	0	2	0	1	1
<i>Ox. heisei</i>	1	1	2	1	0	0	4	2	0	1	0	1	1	0	0	0	2	0	0	1
<i>Ox. lonchotus</i>	1	1	2	1	0	0	4	2	0	1	0	1	1	0	0	0	2	0	0	1
<i>Ox. microlepis</i>	1	1	2	1	0	0	4	2	0	1	0	1	1	0	0	0	2	0	0	1
<i>Ox. ophthalmonema</i>	1	1	2	1	0	0	4	2	0	1	0	1	1	0	0	0	2	0	0	1
<i>Ox. papuensis</i>	1	1	2	1	0	0	4	2	0	1	0	1	1	0	0	0	2	0	0	1
<i>Ox. stigmaphius</i>	1	1	2	1	0	0	4	2	0	1	0	1	1	0	0	0	2	0	0	1
<i>Oligolepis acutipennis</i>	1	0	1	1	0	0	5	1	1	1	0	0	0	2	0	0	2	0	1	1
<i>Ol. jaarmani</i>	1	0	1	1	0	0	5	1	1	1	0	0	0	2	0	0	2	0	1	1
<i>Ol. stomias</i>	1	0	1	1	0	0	5	1	1	1	0	0	0	1	0	0	2	0	1	1
<i>Gobioides broussoneti</i>	0	0	1	0	0	0	3	0	0	1	1	0	0	0	1	1	1	1	0	1
<i>Gobioides grahamae</i>	1	0	1	0	0	0	3	0	0	1	1	0	0	0	1	1	1	1	0	1
<i>Evorthodus lyricus</i>	1	0	1	1	0	0	5	0	0	0	0	0	0	2	0	0	2	0	1	2
<i>Stenogobius genivittatus</i>	0	0	1	3	1	1	5	0	0	0	1	0	0	0	0	0	1	0	0	1
<i>S. laterisquamatus</i>	0	0	1	3	1	1	5	0	0	0	1	0	0	0	0	0	1	0	0	1
<i>Awaous banana</i>	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	2
<i>Gnatholepis thompsoni</i>	0	0	1	0	0	0	5	0	0	0	0	0	0	0	0	0	2	0	0	1