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Evidence for a Monophyletic Gobiinae

Frank Pezold

Sixty-nine different oculoscapular canal pore configurations are described for 129 gobioid genera. A modified oculoscapular canal structure consisting of a single median anterior interorbital pore and a single terminal pair of nasal pores located near the posterior nares is recognized as synapomorphic for the gobiid subfamily Gobiinae. Some member genera and species have lost the anterior interorbital pore or the oculoscapular canal itself but are included based on relationships determined by other characters. The apomorphic feature is concordant with other diagnostic nonpolarized characters. Gobiines have one epural and most species have a 3-22110 first dorsal-fin pterygiophore insertion pattern, two prehemal pterygiophores, and 26 or 27 vertebrae. A new classification of gobioid fishes is proposed to accommodate results presented here and to integrate information obtained from the competing two-family and six-family classifications now in use.

The limits of family-level taxa within the Gobioidei are poorly defined and a matter of much debate. Harrison (1989) recently summarized the major arguments, including the problem of using different, and often conflicting, character suites on which to base gobioid classifications. I will not review specific arguments of the conflict here, readers are referred

TABLE 1. CONTEMPORARY GOBIOID CLASSIFICATIONS AND PROPOSED MODIFICATIONS. (*) signifies a monophyletic taxon.

Miller (1973)	Hoese (1984)	Proposed
Family*	Family*	Superfamily*
Rhyacichthyidae	Rhyacichthyidae	Rhyacichthyoidea
Family*	Family	Family*
Gobiidae	Eleotrididae	Rhyacichthyidae
Subfamily	Family*	Superfamily*
Eleotrinae	Kraemeriidae	Gobioidea
Subfamily	Family*	Family
Pirskeninae	Microdesmidae	Eleotrididae
Subfamily*	Family*	Family*
Xenisthminae	Xenisthmidae	Kraemeriidae
Subfamily	Family*	Family*
Gobionellinae	Gobiidae	Microdesmidae
Subfamily	Subfamily	Family*
Tridentigerinae	Amblyopinae	Xenisthmidae
Subfamily	Subfamily	Family*
Gobiinae	Gobiinae	Gobiidae
Subfamily*	Subfamily*	Subfamily*
Kraemeriinae	Oxudercinae	Amblyopinae
	Subfamily*	Subfamily*
	Sicydiinae	Gobiinae
		Subfamily
		Gobionellinae
		Subfamily*
		Oxudercinae
		Subfamily*
		Sicydiinae

to Harrison's work for further information. Two classifications of gobioid fishes are currently in use: a classification that recognizes two families, with the Gobiidae comprising seven subfamilies; and one that recognizes six families, with the Gobiidae comprising four subfamilies. Both classifications accept poly- or paraphyletic family-level taxa; nonmonophyletic subfamilies are allowed explicitly (Miller, 1973) or implicitly (Springer, 1983) in the two-family classification, and nonmonophyletic families are proposed in the six-family concept (Hoese, 1984).

Miller (1973) recognized a Gobiidae encompassing all gobioid species but one (about 2000 species) and a Rhyacichthyidae containing that one species, *Rhyacichthys aspro* (Table 1). The Gobiidae as proposed by Miller share two derived features: one or two epurals and a reduced cephalic lateralis system. *Rhyacichthys aspro* forms the primitive sister group to all other gobioids. It has three epurals and a well-developed lateralis on the head. Springer (1983) strengthened Miller's classification with additional gobiid synapomorphies, supported recognition of the xenisthmines as a distinct subfamily within the Gobiidae, and provided four synapomorphies for all gobioid fishes. By Millers's classification, seven subfamilies encompass the diversity obtained within the Gobiidae. Other than the Xenisthminae, however, only the Kraemeriinae could be delimited by apomorphic features (Table 1).

Hoese (1984) divided gobioid fishes into six families: Rhyacichthyidae, Eleotrididae, Gobiidae (including four subfamilies), Xenisthmidae, Microdesmidae, and Kraemeriidae (Table 1). Of these, all but the Eleotrididae were characterized by at least one derived character state. Subsequently, Springer (1988) followed Hoese and accepted the Xenisthmidae as a valid family. Within the Gobiidae, monophyly has been proposed for the sicydiines (Hoese, 1984; Harrison, 1989) and the oxudercines (Murdy, 1989). Species of the subfamily Amblyopinae as presented by Hoese (1984) and Birdsong et al. (1988) do not share any derived character states. I have noted in an unpublished manuscript (cited in Birdsong et al., 1988) that *Gobioides*, previously placed in the Amblyopinae, shares several derived features of the cephalic lateralis with *Gobionellus*, a member of Hoese's Gobiinae. Harrison (1989) also noted that *Gobioides* shares a derived palatine condition with *Gobionellus* and

TABLE 2. OCULOSCAPULAR CANAL STRUCTURES AND PORE PATTERNS OBSERVED OR REPORTED IN LITERATURE CITED. Pore terminology follows Akihito et al. (1984). Dots signify canal absent in that region. "0" indicates canal present, but pore is absent from that position. "f" refers to a single pore resulting from the fusion of two separate portions of the canal and their terminal pores. "x" indicates a pore is present. For pores C and D, a "2" indicates paired, separate interorbital canals are present with a pair of pores, whereas "1" indicates a connection between the canals with a single median pore exhibited.

Taxa	Oculoscapular pores											
	A	B	C	D	E	F	G	H	I	J	K	L
1	x	x	2	2	x	x	x	x	x	x	x	x
2	x	x	2	1	x	x	x	x	x	x	x	x
3	x	x	2	1	x	x	0	x	x	x	x	x
4	x	x	0	1	0	x	0	x	x	x	x	x
5	x	x	0	1	0	x	0	x	0	x	x	x
6	x	x	2	1	0	x	0	x	0	x	x	x
7	x	x	2	1	0	x	0	x	0	0	x	x
8	x	x	0	1	0	x	0	x	0	0	x	x
9	x	x	2	1	0	x	0	f	0	0	f	x
10	x	x	2	1	x	x	0	x	x	x	x	·
11	x	x	2	1	0	x	x	x	·	·	x	x
12	x	x	2	1	x	x	0	x	·	·	x	x
13	x	x	2	1	0	x	0	x	·	·	x	x
14	x	x	2	1	0	x	0	x	·	·	·	·
15	x	0	2	1	0	x	0	x	·	·	·	·
16	·	x	2	1	x	x	x	x	·	·	x	x
17	·	x	2	1	x	x	0	x	·	·	x	x
18	·	x	2	1	0	x	0	x	·	·	x	x
19	·	x	2	1	x	x	0	x	·	·	·	·
20	·	x	2	1	x	x	x	·	·	·	·	·
21	·	·	2	0	0	x	0	x	·	·	x	x
22	·	·	2	2	0	x	0	x	·	·	·	·
23	·	·	2	1	0	x	0	x	·	·	·	·
24	·	·	2	1	0	x	x	·	·	·	·	·
25	·	·	2	2	x	·	·	·	·	·	x	x
26	·	·	·	2	0	x	0	x	·	·	·	·
27	·	·	2	1	x	x	·	·	·	·	·	·
28	·	·	2	1	0	x	·	·	·	·	·	·
29	·	·	2	0	0	x	·	·	·	·	·	·
30	·	x	1	1	x	x	x	f	0	0	f	x
31	·	x	0	1	x	x	x	f	0	0	f	x
32	·	x	1	1	x	x	x	x	0	x	x	x
33	·	x	1	1	x	x	x	x	·	·	x	x
34	·	x	1	1	0	x	x	x	·	·	x	x
35	·	x	1	1	x	x	0	x	·	·	x	x
36	·	x	1	1	0	x	0	x	·	·	x	x
37	·	x	1	1	x	x	x	x	·	·	·	·
38	·	x	1	1	0	x	x	x	·	·	·	·
39	·	x	1	1	x	x	0	x	·	·	·	·
40	·	x	1	0	x	x	0	x	·	·	·	·
41	·	x	1	1	0	x	0	x	·	·	·	·
42	·	x	1	1	x	x	x	·	·	·	·	·
43	·	x	1	1	x	x	·	·	·	·	·	·
44	·	x	1	0	x	x	·	·	·	·	·	·
45	·	x	1	1	0	x	·	·	·	·	·	·
46	·	x	1	1	·	·	·	·	·	·	·	·
47	·	·	1	1	x	x	·	·	·	·	·	·
48	·	·	1	0	x	x	·	·	·	·	·	·
49	·	·	1	1	·	·	·	·	·	·	·	·
50	·	x	0	1	x	x	x	x	·	·	x	x
51	·	x	0	1	0	x	x	x	·	·	x	x

TABLE 2. CONTINUED.

Taxa	Oculoscapular pores											
	A	B	C	D	E	F	G	H	I	J	K	L
52	·	x	0	1	x	x	0	x	·	·	·	·
53	·	x	0	1	0	x	0	x	·	·	x	x
54	·	x	0	0	0	x	0	x	·	·	x	x
55	·	x	0	1	0	x	·	·	·	·	x	x
56	·	x	0	0	x	·	·	·	·	·	x	x
57	·	x	0	1	0	x	x	x	·	·	·	·
58	·	x	0	1	x	x	0	x	·	·	·	·
59	·	x	0	1	0	x	0	x	·	·	·	·
60	·	x	0	0	0	x	0	x	·	·	·	·
61	·	x	0	1	x	x	·	·	·	·	·	·
62	·	x	0	1	0	x	·	·	·	·	·	·
63	·	x	0	0	x	·	·	·	·	·	·	·
64	·	x	0	1	·	·	·	·	·	·	·	·
65	·	x	·	·	·	·	·	·	·	·	·	·
66	·	·	·	2	x	·	·	·	·	·	·	·
67	·	·	·	·	x	x	0	x	·	·	·	·
68	·	·	·	·	x	x	·	·	·	·	·	·
69	·	·	·	·	·	·	·	·	·	·	x	x

associated genera. The remaining members of the Amblyopinae, the *Trypauchen* and *Taenioides* groups of Birdsong et al. (1988), have a derived fin element to vertebra ratio of 2:1. Transferring *Gobioides* to the Gobiinae results in three gobiid subfamilies out of four hypothesized as monophyletic. The Gobiinae still contains the bulk of gobioid fishes, however; and its monophyly is unconfirmed.

Analysis of the oculoscapular canal system in gobioid fishes revealed a number of distinctive structures. In this paper, I propose that a unique modification of the anterior oculoscapular canal is synapomorphic for most of the species included in Hoese's Gobiinae. This delimitation of the Gobiinae results in the remnant group of genera being placed in an additional subfamily, the Gobionellinae, for which monophyly is not established. Incorporation of this assemblage into a version of Hoese's classification modified to reflect phylogenetic information presented by Springer (1983) obtains a further refinement of gobioid relationships. Acceptance of the Gobionellinae as a subfamily has a heuristic value similar to that provided by recognition of the Eleotrididae.

MATERIALS AND METHODS

Collections examined are listed below. *Ctenogobius* and *Gobionellus* specimens are listed in Pezold (1984). Information was drawn from the literature for: *Chromogobius* (Miller, 1971); *Corcyrogobius* (Miller, 1972a); *Didogobius* (Miller, 1965); *Egglestonichthys* (Miller and Wongrat, 1979); *Eviota* (Lachner and Karnella, 1978, 1980); *Gobiopsis* (Lachner and McKinney, 1978, 1979); *Gobius* (Miller, 1974; Miller and El-Tawil, 1974); *Gorogobius* (Miller, 1978b); *Knipowitschia* (Miller, 1972b); *Monishia* (Miller, 1978a); *Odondebuenia* (Miller and Tortonese, 1968); *Thorogobius* (Miller, 1969); *Zebrus* (Miller, 1977); and gobiosominines (Böhlke and Robins, 1968). Descriptions of gobies from works on the following regions were also used: Chagos Archipelago (Winterbottom and Emery, 1986); east central Atlantic Ocean (Miller, 1981); Japan (Akihito et al., 1984); Macaronesia (Miller, 1984). Early papers by Sanzo (1911) and Iljin (1930) on gobioid relationships also provided descriptions of the lateralis canals of European gobies.

Canal and canal pore terminology follows Takagi (1957) and Akihito et al. (1984). Pore names (Takagi, 1957) are used in discussions, whereas the lettering system of Akihito et al. (1984) is used to report pore configurations for a taxon. All drawings were made using a Wild M-5 dissecting microscope and camera lucida.

Where preopercular canals are present in gobiids, the canals have no more than three pores. Reduction to a two-pored canal or the total loss of the canal has occurred independently many times (e.g., Takagi, 1989). The preopercular canal system was, therefore, considered separately from the more complex oculoscapular system because (1) preopercular canal modifications often appear independently of oculo-

TABLE 3. GENERA EXHIBITING OCULOSCAPULAR CANALS AND PORE PATTERNS DESCRIBED IN TABLE 2.

1. *Butis, Bostrychus*[a]
2. *Oxyeleotris*
3. *Ophiocara*
4. *Bostrychus*[a]
5. *Parviparma*
6. *Awaous*[a]
7. *Gobionellus*
8. *Gobioides*
9. *Sicydium, Sicyopterus*
10. *Xenisthmus*
11. *Awaous*[a]
12. *Tridentiger*
13. *Evorthodus, Gnatholepis, Lentipes, Oligolepis, Sicyopus, Stenogobius, Stiphodon*
14. *Ctenogobius, Oxyurichthys*
15. *Tukugobius*[a]
16. *Coryphopterus*[a]
17. *Pterogobius,*[a] *Rhinogobius*
18. *Pterogobius,*[a] *Sagamia, Tukugobius*[a]
19. *Redigobius, Nemateleotris*
20. *Bryaninops*
21. *Amblychaeturichthys*
22. *Chaenogobius*[a,b]
23. *Knipowitschia*
24. *Chaenogobius*[a,b]
25. *Hypseleotris*[a]
26. *Hyrcanogobius*
27. *Pseudogobius*
28. *Chaenogobius*[a,b]
29. *Stigmatogobius*
30. *Bathygobius,*[a] *Gobius,*[a] *Mauligobius*
31. *Bathygobius*[a]
32. *Fusigobius,*[a] no connection between J and K.
33. *Acentrogobius,*[a] *Amblyeleotris,*[a] *Amblygobius, Asterropteryx, Barbuligobius,*[a] *Bathygobius,*[a] *Bollmannia,*[a] *Cabillus, Caffrogobius, Callogobius,*[a,b] *Coryphopterus,*[a] *Cristatogobius, Cryptocentroides, Cryptocentrus,*[a] *Ctenogobiops, Drombus, Exyrias, Favonigobius, Fusiogobius,*[a] *Gladiogobius, Glossogobius,*[a] *Gobius,*[a] *Hazeus, Heteroplopomus, Istigobius,*[a] *Macrodontogobius, Mangarinus, Monishia, Myersina,*[a] *Oplopomus, Signigobius, Silhouettea, Thorogobius, Valenciennea, Vanderhorstia,*[a] *Yongeichthyes, Zebrus*
34. *Bollmannia,*[a] *Gobius*[a]
35. *Amblyeleotris,*[a] *Buenia, Cryptocentrus,*[a] *Enypnias,*[a] *Gobiosoma,*[a] *Gobiusculus, Istigobius,*[a] *Pomatoschistus*[a]
36. *Pomatoschistus*[a]
37. *Acentrogobius,*[a] *Callogobius,*[a,b] *Chromogobius, Discordipinna, Flabelligobius, Glossogobius,*[a] *Millerigobius, Myersina,*[a] *Odondebuenia, Vanderhorstia*[a]
38. *Fusigobius*[a] (specimens of *F. neophytus* examined here)
39. *Elacatinus, Enypnias,*[a] *Eviota,*[a,b] *Garmannia, Ginsburgellus, Gobiodon, Gobiosoma,*[a] *Gorogobius, Heteroeleotris,*[a,b] *Tomiyamichthys*
40. *Paragobiodon*
41. *Gobiosoma,*[a] *Pomatoschistus*[a]

TABLE 3. CONTINUED.

42. *Pleurosicya*
43. *Eviota,*[a,b] *Gobiopsis*[a,b]
44. *Eviota*[a,b]
45. *Risor*
46. *Stonogobiops*[a,b]
47. *Eviota*[a,b]
48. *Eviota*[a,b]
49. *Stonogobiops*[a,b]
50. *Barbuligobius,*[a] *Bathygobius*[a]
51. *Mahidolia*
52. *Gobiopsis*[a,b]
53. *Acanthogobius, Gobiomorus, Parachaeturichthys*
54. *Chaeturichthys, Deltentosteus, Gobiopsis,*[a,b] *Hetereleotris*[a]
55. *Hemieleotris, Leptophilypnus, Schismatogobius*
56. *Gobitrichinotus, Kraemeria*[b]
57. *Callogobius,*[a,b] *Parrella, Vanderhorstia*[a]
58. *Gobiopsis,*[a,b] *Ptereleotris*[a]
59. *Aruma, Chasmichthys, Didogobius, Eleotrica, Pycnomma, Suruga*
60. *Barbulifer, Callogobius*[a,b]
61. *Gobiopsis,*[a,b] *Ptereleotris*[a]
62. *Callogobius,*[a,b] *Parkraemeria, Quietula*
63. *Apocryptes*[a]
64. *Apocryptes,*[a] *Boleophthalmus, Parapocryptes*
65. *Scartelaos*
66. *Gobiomorphus,*[a,b] *Hypseleotris*[a]
67. *Gobiopsis*[a,b]
68. *Percottus*
69. *Gobiomorphus*[a,b]

[a] Genera with more than one pore pattern for the oculoscapular canal.
[b] Genera in which the oculoscapular canal is completely lost in some species.

scapular canal changes; (2) there are relatively few, simple states possible for the preopercular canal; and (3) similar, but nonhomologous, conditions have apparently arisen a number of times within the family.

RESULTS

Sixty-nine different oculoscapular canal pore patterns were observed and/or derived from published accounts (Tables 2–3). Although this information does not include all gobioid taxa, 129 genera are represented in the tables. Genera with species lacking oculoscapular canals were noted only if canals were present in some species.

Pore configurations outlined in Tables 2 and 3 range from patterns unique to specific genera to patterns shared by many diverse taxa. A large group of "typical" gobiids usually assigned to the subfamily Gobiinae (e.g., Hoese, 1984) is characterized by an oculoscapular canal with a single median anterior interorbital pore (pore

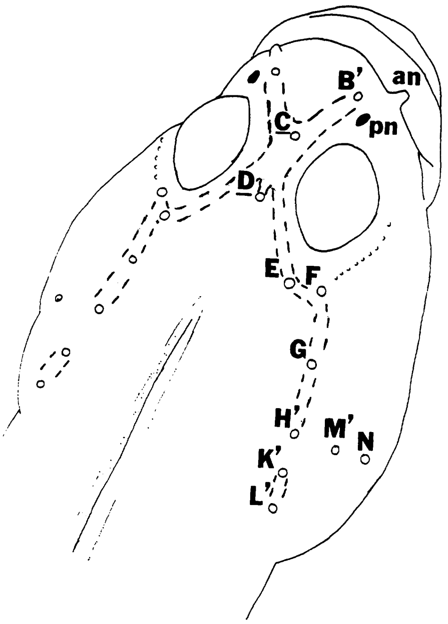

Fig. 1. The oculoscapular canal and pores of *Cryptocentroides insignis.* Canal pores labeled as in Akihito et al. (1984). Dotted lines indicate canal. Terminal pores indicated by '. an = anterior nares, pn = posterior nares.

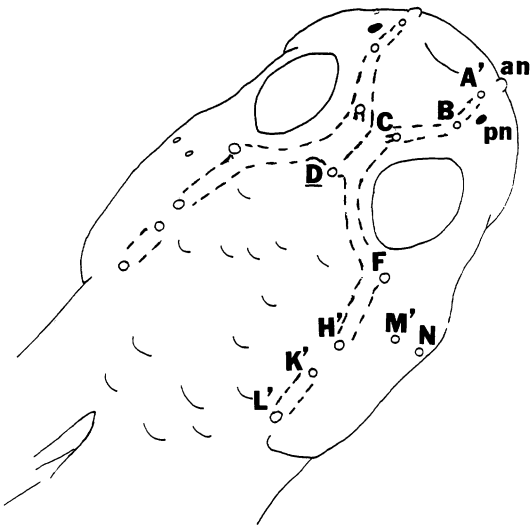

Fig. 2. The oculoscapular canal and pores of *Evorthodus lyricus.* Labeling as in Figure 1.

C). The canal terminates in a single pair of pores (B') near the posterior nares (Fig. 1). This modification of the lateralis is unique among gobioid fishes. The more general condition is illustrated in Fig. 2.

Takagi (1989) noted that species with the modified oculoscapular pore arrangement usually have a single, unified interorbital canal (his type III condition). One exception he found was *Callogobius okinawae,* in which the canals are separate although a single anterior interorbital pore is present. Other species of *Callogobius* have canals united and a single pore, or no pore. Takagi presented evidence that a unified interorbital canal is a specialization found only within gobies and some blennioid fishes.

The single AIP is a stable character for gobiines, with only two of the 129 genera containing a species showing a reversal from the single-pored to the two-pored state. One species of *Coryphopterus, C. hyalinus,* has two anterior interorbital pores [see Smith and Tyler (1977) for cladistic evidence supporting a reversal]. The interorbital or anterior portion of the right and left oculoscapular canals initially develop separately in gobioid fishes and may fuse later in development. Consequently, developmental truncation could lead to reversals to the two-pored (unconnected canal) state (D. Hoese, pers. comm.). The Indo-Pacific genus *Bryaninops* is tentatively included in the Gobiinae because of its relationship to *Pleurosicya* (Larson, 1985). These are small obligate symbionts associated with corals and sea grasses. All the species of *Bryaninops* and *Coryphopterus hyalinus* have shortened snout canals with a single pair of nasal pores. Because some species of *Bryaninops* show variability in the connection of the posterior interorbital section of the oculoscapular canal ontogenetically (Larson, 1985), the condition of the anterior section is probably secondarily derived. Several other gobiid genera (Tables 2–3: 17–20) have reduced canals on the snout and a single pair of nasal pores, but do not have united anterior interorbital canals.

D. Hoese (pers. comm.) has observed a species of *Nesogobius* with two pairs of pores on the snout (A and B in Table 3) and a single median anterior interorbital pore. Because I have not seen this genus, and have no information on other species of the genus, I cannot comment on the derivation of the canal structure.

Species with the derived anterior interorbital condition (single AIP and one pair of nasal pores; Tables 2–3: 30 and 32–46) usually have a supraotic pore (E in Table 2; not in 34, 36, 38, 41, 45, and 46) and/or a posterior otic pore (G in Table 2; lacking in 35, 36, 39–41, and 43–46). Takagi (1989) also noted the general association of the supraotic and posterior otic pores with the interorbital canal modification. The association of one or both of these pores may be diagnostic for some gobiine genera (e.g., *Amblygobius, Asterropteryx, Cabillus, Caffrogobius,*

Table 2: 33), but their presence in a number of gobioid fishes lacking the modified interorbital, including some eleotridids (Table 2: 1–3), indicates they are plesiomorphic for the Gobiinae.

Subfamily Gobiinae

Diagnosis.—A single anterior interorbital pore present, one pair of nasal pores (posterior), interorbital portion of oculoscapular canal fused; anterior interorbital pore, posterior nasal pores, interorbital section of oculoscapular canal or entire oculoscapular canal lost in some species. One epural; most species with 3-22110 first dorsal-fin pterygiophore insertion pattern or derivative; most species with 26 or 27 vertebrae and two prehemal pterygiophores.

The Gobiinae as recognized here include the *Priolepis, Microgobius, Gobius, Bathygobius, Gobiosoma, Pomatoschistus,* and *Kelloggella* groups of Birdsong et al. (1988). Included genera are listed in Appendix 1. Although some members of these groups have lost the anterior interorbital pore, their generic or generic group relationships may be recognized by other characters. The bulk of the gobiine species I recognize have either a 3-22110 or 3-221110 first dorsal pterygiophore insertion pattern and a single epural, although these osteological characters are not polarized herein. Most other insertion patterns found in the gobiines are more easily derived from the 3-22110 or 3-221110 patterns than the 3-1220 pattern. An exception is *Pomatoschistus* which has 3-122100 and 3-1221000 patterns (Birdsong et al., 1988). Until conflicting information is obtained from characters that can be polarized, *Pomatoschistus* is retained in the Gobiinae.

The single anterior interorbital pore delimits a smaller group than the Gobiinae of Hoese (1984); however, it still includes most gobiids (Birdsong et al., 1988). Recognition of the Gobiinae as defined here also leaves a number of gobiids (though smaller) outside of a monophyletic subfamily (Appendix 2). Addressing this problem (and ignoring the problem of the relationships of the included species for the moment), I follow Hoese (1984) and recognize six families of gobioids as well as five subfamilies of gobiids (Table 1). Distinguishing major gobioid lineages as families is more informative to individuals not familiar with the intricacies of gobioid systematics than designating the lineages subfamilies. A species' family membership is more often referenced by nonsystematists than is its membership in other categories above the genus level. Using families to delimit lower levels of relationship than those of Miller (1973) also permits greater information retrieval within the Gobiidae; natural subfamilies and possibly tribes may be discerned. To incorporate phylogenetic information presently obtained only in the two-family classification proposed by Miller (1973), as developed by Springer (1983), I propose the use of two superfamilies, the Gobioidea (=Gobiidae of Miller, 1973; Springer, 1983) and Rhyacichthyoidea (includes the Rhyacichthyidae of Miller, 1973; Springer, 1983; Hoese, 1984).

For those gobies outside of the Gobiinae, Sicydiinae, Oxudercinae, and Amblyopinae, the name Gobionellinae proposed by Miller (1973) may be used. However, the names Brachygobiinae, Chaeturichthyinae, Platygobiinae, and Luciogobiinae may also be available (Bleeker, 1874). Birdsong et al. (1988) proposed three monophyletic groups placed here with the gobionellines, the *Acanthogobius, Astrabe,* and *Chasmichthys* groups (Appendix 2). Species contained in all three of these groups show elevated vertebral numbers (30–42), and members of the *Astrabe* and *Chasmichthys* groups have posteriorly displaced insertions of the first dorsal fin.

A posteriorly displaced first dorsal fin is often obtained in some eleotridids (*Guavina, Odontobutis, Ophieleotris, Gobiomorphus, Mogurnda*) and a few other gobiids (*Evermannichthys, Lethrops,* and *Synechogobius*). *Lethrops* and *Synechogobius,* both northern Pacific gobiid genera, are probably related to members of the *Astrabe* and *Chasmichthys* groups. The condition reported for *Evermannichthys* (Birdsong et al., 1988) is undoubtedly homoplastic. Posteriorly displaced first dorsal fins in eleotridids insert in the fourth interneural space. All members of the *Astrabe* group and two genera of the *Chasmichthys* group (*Clevelandia* and *Eucyclogobius*) have first pterygiophores inserting in the fifth through tenth interneural spaces. Insertions beyond the fourth interneural space are derived conditions, but polarity of the fourth interneural insertion is ambiguous.

The number of vertebrae offers less insight as a character than the first dorsal-fin insertion. Relatively high numbers of vertebrae (30 or more) are also found in eleotridids (*Gobiomorphus, Micropercops, Mogurnda, Odontobutis, Percottus, Philypnodon, Tateurndina*), kraemeriids (*Gobitrichonotus*), microdesmids (*Cerdale, Clarkichthys, Gunnellichthys, Microdesmus, Paragunnelichthys*) and other gobiids (*Deltentosteus, Evermannichthys, Gobioides, Lethrops, Neogobius, Nesogobius, Odontamblyopus, Ophiogobius, Pomatoschistus, Synechogobius, Taenioides, Trypauchen, Trypauchenichthys*). Considering the plasticity for vertebral number exhibited both in and between gobioid species (Birdsong et al., 1988), even transformation series of this character may offer little information at higher levels of universality. Although the concordance of first dorsal fin and vertebral number character states suggests the existence of a northern Pacific gobiid clade, its limits are poorly defined. The synapomorphies proposed by Birdsong et al. (1988) for the *Astrabe, Acanthogobius,* and *Chasmichthys* groups require further refinement and resolution against other character state distributions.

Although not delimited as a group in Appendix 2, Harrison (1989) hypothesized a relationship between the genera *Ctenogobius, Evorthodus, Gnatholepis, Gobioides, Gobionellus, Oligolepis,* and *Stenogobius* based upon an apomorphic palatine structure. The same structure was observed in *Awaous,* but that genus was suggested as the sister group to the sicydiines because of a synapomorphic suborbital free neuromast pattern. Although there is difference in detail, Harrison's general hypothesis of a close relationship of these genera, including *Awaous,* is supported by other derived features of the cephalic lateralis (Pezold, unpubl. cited in Birdsong et al., 1988). No formal group recognition is given here, however, because the relationship of these genera to other gobionellines, oxudercines, and sicydiines is unclear (Harrison, 1988; unpubl.).

Acceptance of the Gobiinae as defined by the derived oculoscapular canal confers new information on relationship for a large number of gobiids. The Gobionellinae simply becomes a smaller assemblage of convenience.

Material Examined

Institutional abbreviations follow Leviton et al. (1985) unless otherwise noted.

Acanthogobius flavimanus: CAS 52003 (4). *Acentrogobius caninus*: CAS 51065 (2). *Amblyeleotris fontanesii*: CAS-SU 26209 (1); CAS-SU 33073 (5); USNM 160741 (2). *A. randalli*: USNM 220085 (1). *A. steinitzi*: USNM 282957 (2). *Aphia minuta*: USNM 265060 (1). *Apocryptes bato*: UMMZ 187890 (9). *Awaous guineensis*: CAS-SU 55635 (2). *A. stamineus*: ANSP 29510–13 (4); *A. tajasica*: ANSP 144525 (3); FMNH 93277 (3); UF 30510 (1); University of Texas Marine Sciences Institute (UTMSI) 334 (3). *A. transandeanus*: TNHC 11519 (1); TNHC 11506 (1); TNHC 11509 (1); TNHC 11511 (1). *Awaous* sp.: ANSP 149484 (1). *Bathygobius soporator*: TNHC 10469 (5); TNHC 10809 (6). *Boleophthalmus boddarti*: CAS-SU 33141 (1). *Bollmannia chlamydes*: CAS 42777 (1). *B. communis*: USNM 195539 (1). *Bostrychus sinensis*: USNM 85907 (6). *Brachyamblyopus* sp.: USNM 243403 (45). *Butis butis*: USNM 261350 (13); ANSP 63023–39 (17). *Callogobius* sp.: CAS 5105 (16). *Chaenogobius urotaenia*: CAS 52005 (2). *Chaeturichthys stigmatias*: CAS-SU 61210 (5). *Coryphopterus glaucofrenum*: FMNH 48426 (2). *C. nicholsii*: CAS-SU 48966 (15). *Cryptocentroides insignis*: CAS 51064 (1). *Cryptocentrus cryptocentrus*: MNHN A.1166 (1); BMNH 1975.5.5.3–4 (2). *C. filifer*: FMNH 3814 (3); UMMZ 142629 (1); MNHN 7196 (1). *C. strigilliceps*: CAS 52009 (1). *Cryptocentrus* sp.: CAS 52010 (1); CAS 52006 (3). *Dormitator latifrons*: CAS-SU 55012 (1). *D. lebretoni*: ANSP 38675–78 (4). *D. maculatus*: MSU 1273 (2); MSU 7692 (4). *Dormitator* sp.: ANSP 99855 (2). *Drombus palackyi*: USNM 57971 (1). *Eleotris pisonis*: ANSP 99833 (3); ANSP 104302 (3); TNHC 8115 (2); TNHC 10473 (1). *E. picta*: ANSP 104165 (2). *Eleotris* sp.: CAS-SU 52359 (1); CAS-SU 52360 (2). *Erotelis smaragdus*: UMMZ 199452 (7); CAS-SU 19339 (2); CAS 51044 (1); ANSP 143106 (1). *Evorthodus lyricus*: UF 100059 (12); TNHC 10623 (29). *Favonigobius aliciae*: CAS 56374 (3). *F. reichei*: CAS-SU 38598 (1); USNM 258131 (4). *Fusigobius neophytus*: CAS-SU 9010 (2). *Ginsburgellus* sp.: USNM 170262 (1). *Glossogobius bicirrhosus*: CAS 51058 (12). *G. callidus*: ANSP 55287–9 (3). *G. giuris*: CAS 56375 (16). *Gnatholepis cauerensis*: CAS 51548. *G. thompsoni*: UMMZ 174286 (5). *Gobiodon quinquestrigatus*: CAS-SU 26717 (1). *Gobioides broussoneti*: USNM 233612 (11); ANSP 121256 (1). *G. africanus*: BMNH 1939.7.12.33 (1). *G. ansorgii*: BMNH 1968.11.15.77 (1). *G. grahamae*: BMNH 1959.3.17.161 (1). *Gobiomorphus australis*: USNM 265059 (1). *G. gobioides*: ANSP 122811 (45). *Gobiomorphus* sp.: USNM 210751 (5). *Gobiomorus dormitor*: CAS-SU 61392 (4). *Gobiosoma longipala*: UF 21835 (1). *Gobius niger*: CAS-SU 61441 (2). *G. paganellus*: CAS-SU 1688 (2). *Gobiopterus* sp.: USNM 217264 (3). *Guavina guavina*: CAS-SU 52357 (3). *Hemieleotris latifasciatus*: USNM 265050 (3); ANSP 71084–96 (13). *Hetereleotris zonatus*: USNM 210413 (1). *Hypseleotris cyprinoides*: USNM 262027 (39). *H. guntheri*: ANSP 31675–91 (16). *H. tohizonae*: USNM 143781 (1). *Istigobius ornatus*: CAS 46503 (5). *Leptophilypnus fluviatilis*: USNM 249722 (16); ANSP 122361 (7). *Lophogobius cyprinoides*: CAS 52008 (1); TNHC 10925 (2); TNHC 10862 (2). *Mahidolia mystacina*: CAS 51063 (1); MNHN 1965-217 (2); RMNH 15260 (1); MNHN 2967 (1). *Microgobius thalassinus*: UF 30508 (4). *Mogurnda mogurnda*: ANSP 89831 (3). *Mugilogobius abei*: CAS-SU 30266 (2); *Mugilogobius* sp.: USNM uncat. IIOE, Seychelles, stn. F-70 (2). *Odontamblyopus* sp.: USNM 86955 (9). *Oligolepis acutipennis*: UMMZ 100537 (25); RMNH 14325 (3). *O. jaarmani*: USNM 217267 (8); USNM 217266 (2). *O. stomias*: USNM 257137 (13); USNM 258782 (9); USNM 99296 (1). *Ophiocara porocephala*: CAS-SU 38579 (4). *Oplopomus oplopomus*: CAS 51589. *Oxyeleotris marmorata*: USNM 230328 (2); ANSP 87352 (3). *Oxyurichthys auchenolepis*: RMNH 4506 (2). *O. keiensis*: RUSI 17043 (8); RUSI 16786 (1). *O. lonchotus*: ANSP 23350 (1); ANSP 90998 (3); ANSP 28055–56 (2); CAS 23328 (14). *O. microlepis*: ANSP 88946 (1). *O. ophalmonema*: CAS 61040 (1). *O. papuensis*: LACM 37382-2 (1). *O. stigmalophius*: ANSP 81233 (1); ANSP 81855 (1). *O. tentacularis*: ANSP 100179 (1). *Oxyurichthys* sp.: CAS 51047 (75). *Parapocryptes cantonensis*: UMMZ 100616 (4). *Parrella ginsburgi*: CAS-SU 46827 (19). *Parviparma straminea*: CAS-SU 29701 (1). *Percottus glehni*: USNM 86108 (1). *Periophthalmus cantonensis*: CAS-SU 61102 (5). *Philypnodon grandiceps*: USNM 59976 (9). *Pomatoschistus microps*: ANSP 147148 (20); CAS-SU 32183 (3). *Porogobius schlegeli*: CAS-SU 63028 (2). *Ptereleotris calliurus*: USNM 118102 (4). *P. helenae*: CAS-SU 63565 (1). *Quietula ycauda*: CAS 41895 (5). *Redigobius balteata*: CAS 51061 (9). *R. bikolanus*: NLU uncat., John Lake Coll.: Australia. *R. dispar*: CAS-SU 69019 (4). *R. macrognathos*: CAS-SU 38647 (3). *Rhinogobius candidus*: CAS-SU 23185 (2). *R. kurodai*: CAS-SU 23529 (5). *R. hadropterus*: CAS-SU 23536 (5). *R. leavelli*: CAS-SU 32832 (3). *R. similis*: CAS-SU 58338 (3); RMNH 12509 (1). *R. taiwanus*: CAS-SU 23182 (1); CAS-SU 23104 (2); CAS-SU 23167 (1). *Rhyacichthys aspro*: USNM 247300 (5). *Sicydium pittieri*: CAS 52012 (3); TNHC 11524 (1); TNHC 11507 (1); TNHC 11499 (1); TNHC 11510 (1); TNHC 11521 (1). *S. plumieri*: USNM uncat. acc. no. 249592, Dominica (3). *Sicydium* sp.: MCZ 33968 (1). *Sicyopterus ouwensi*: CAS-SU 61629 (2). *Stenogobius genivittatus*: ANSP 86151 (9); ANSP 28016–19 (4); BPBM 26373 (4); BPBM 26380 (2); CAS 51056 (7); CAS 52011 (3). *S. gymnopomus*: RMNH 4552 (4). *S. laterisquamatus*: ZMA 116.477 (2); WAM P27847-007 (3); WAM P28206-002 (1); NLU 62766, Laloki River (4). *Stigmatogobius sadanundio*: USNM 263326 (4); ANSP 77797 (1). *Stiphodon elegans*: USNM 260937 (29). *Taenioides cirratus*: USNM 243405 (1). *Taenioides* sp.: USNM uncat. SOSC ref. no. 134, Madagascar (4); ANSP 63086–87 (2). *Tridentiger obscurus*: CAS-SU 6590 (3); CAS 52013 (3). *Trypauchen vagina*: USNM 119644 (1). *Tukugobius bucculentus*: CAS-SU 39400 (5); CAS-SU 26366 (5); CAS-SU 26363 (1). *T. carpenteri*: CAS-SU 26367 (5). *T. philippinus*: CAS-SU 38601 (5). *Tyntlastes brevis*: USNM 77581 (1). *Valenciennea longipinnis*: CAS 13762 (2); USNM 259429 (6). *V. muralis*: CAS 51060 (1). *V. sexguttatus*: CAS 59878 (2). *Vanderhorstia ornatissima*: CAS 59865. *Yongeichthyes criniger*: CAS-SU 9425 (1). *Y. nebulosus*: CAS-SU 20331 (3).

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APPENDIX 1. GENERA INCLUDED IN THE GOBIINAE

Members of the Tribe Gobiosomini are listed separately.

Acentrogobius, Amblyeleotris, Amblygobius, Amoya, Asterropteryx, Aulopareia, Austrolethops, Barbuligobius, Bathygobius, Bryaninops, Buenia, Cabillus, Caffrogobius, Callogobius, Chromogobius, Coryphopterus, Cristatogobius, Cryptocentroides, Cryptocentrus, Ctenogobiops, Didogobius, Discordipinna, Drombus, Egglestonichthys, Eviota, Exyrias, Favonigobius, Feia, Flabelligobius, Fusigobius, Garmannia, Gladiogobius, Glossogobius, Gobiodon, Gobiopsis, Gobius, Gobiusculus, Gorogobius, Hazeus, Hetereleotris, Heteroplopomus, Istigobius, Kelloggella, Lesueurigobius, Lophogobius, Lotilia, Luposicya, Lythrypnus, Macrodontigobius, Mahidolia, Mangarinus, Mauligobius, Millerigobius, Monishia, Myersina, Nematogobius, Odondebuenia, Oplopomops, Oplopomus, Opua, Parachaeturichthys, Paragobiodon, Paratrimma, Parkraemeria, Platygobiopsis, Pleurosicya, Pomatoschistus, Porogobius, Priolepis, Psammogobius, Psilogobius, Signigobius, Silhouettea, Stonogobiops, Sueviota, Tenacigobius, Thorogobius, Tomiyamichthys, Trimma, Trimmatom, Valenciennea, Vanderhorstia, Vanneaugobius, Yongeichthys, Zebrus, Zonogobius

Tribe Gobiosomini

Aruma, Barbulifer, Bollmannia, Chriolepis, Elacatinus, Eleotrica, Enypnias, Evermannichthys, Ginsburgellus, Gobiosoma, Gobulus, Gymneleotris, Microgobius, Nes, Ophiogobius, Palatogobius, Pariah, Parrella, Psilotris, Pycnomma, Risor, Robinsichthys, Varicus

APPENDIX 2. GENERA ASSIGNED TO THE GOBIONELLINAE

Members of the *Acanthogobius*, *Astrabe* and *Chasmichthys* groups, proposed monophyletic by Birdsong et al. (1988), are listed separately.

Aphia, Awaous, Brachygobius, Calamiana, Ctenogobius, Deltentosteus, Evorthodus, Gnatholepis, Gobioides, Gobionellus, Gobiopterus, Hyrcanogobius, Knipowitschia, Lethrops, Mesogobius, Mistichthys, Mugilogobius, Neogobius, Nesogobius, Oligolepis, Oxyurichthys, Pandaka, Pseudogobiopsis, Pseudogobius, Redigobius, Rhinogobius, Schismatogobius, Stenogobius, Stigmatogobius, Synechogobius, Tamanka, Tridentiger, Tukugobius, Vitraria, Vomerogobius

Acanthogobius Group

Acanthogobius, Amblychaeturichthys, Chaeturichthys, Lophiogobius, Pterogobius, Sagamia, Suruga

Astrabe Group

Astrabe, Clariger, Eutaeniichthys, Leucopsarion, Luciogobius, Typhlogobius

Chasmichthys Group

Chaenogobius, Chasmichthys, Clevelandia, Eucyclogobius, Gillichthys, Ilypnus, Lepidogobius, Quietula