

Systematics of the Family Gobionellidae

Frank Pezold¹

The classification adopted for this text (Thacker, 2009) is the culmination of recent molecular analyses comparing mitochondrial gene sequences of gobioid fishes. My observations and comments are largely focused on their relevance to the recognition of a family Gobionellidae including the previously recognized subfamily Gobionellinae (Pezold, 1993; Larson, 2001; Thacker, 2003) i.e. gobionellines *sensu stricto*, and the amblyopines, oxudercines and sicydiines (*sensu* Pezold, 1993). Additional observations are given on the Gobiidae clade (*sensu* Thacker 2009), and the sister group relationship proposed between the Butidae and the two goby clades recovered by Thacker (2009). The clade-based classification proposed by Thacker (2009) names putative monophyletic groups, but no synapomorphy is given for the family Gobionellidae, or for any of the families recognized therein.

Origins of the Gobionellinae

Bleeker (1874) was the first person to use a derivative of *Gobionellus* for a grouping of taxa above the genus-level. The subphalanx Gobionelli identified by Bleeker contained the genera *Gobionellus* and *Synechogobius*, a synonym of *Acanthogobius*. Other species recognized as gobionellines today were scattered across several other named suprageneric groups along with non-gobionelline species (see Larson, 2001 for a synopsis). Miller (1973) first proposed a subfamily Gobionellinae as one of seven subfamilies of the Gobiidae. In his classification, gobioid fishes were simply split between two families - a monotypic Rhyacichthyidae and the Gobiidae which contained the roughly 2000 other species. Gobionellinae *sensu* Miller (1973) included typical gobiids like *Gobionellus*, *Stenogobius*, and *Oxyurichthys* (all three genera later recognized as members of a monophyletic *Stenogobius* group by

Author's address: ¹Texas A&M University - Corpus Christi, Corpus Christi, TX 7841, USA. E-mail: frank.pezold@tamucc.edu

Larson , 2001), as well as species generally recognized now as amblyopines and periophthalmines. Miller (1973) recognized another large group of gobies as the Gobiinae which was largely consistent with the Gobiinae of today, but also included microdesmids, *Rhinogobius*, sicydiines and ptereleotines.

Kraemeriidae formed another subfamily, as did *Tridentiger* and *Triaenopogon*. Subsequently, Birdsong *et al.* (1988) recognized 32 groups of gobioid fishes (based upon postcranial axial osteology), half of which were hypothesized as monophyletic. A *Gobionellus* Group was characterized by a shared spinous dorsal-fin pterygiophore insertion pattern of 3-12210, 2 epurals and 26 vertebrae. None of the characters could be identified as a synapomorphy. Included in the group were *Calamiana*, *Ctenogobius*, *Gnatholepis*, *Gobionellus*, *Mugilogobius*, *Oligolepis*, *Oxyurichthys*, *Pseudogobiopsis*, *Stenogobius* and *Tamanka*.

Harrison (1989) recognized a monophyletic *Ctenogobius* lineage including *Ctenogobius*, *Gnatholepis*, *Gobionellus*, *Evorthodus*, *Gobioides*, *Oligolepis*, *Stenogobius*, Sicydiinae and *Awaous* based upon shared derived features of the palatopterygoquadrate complex. A monophyletic *Oxyurichthys* lineage was also proposed based upon shared possession of a shared stubby palatine. This latter group included its gobionelline namesake *Oxyurichthys* and representative amblyopines and oxudercines.

Pezold (1993) recognized the subfamily Gobionellinae as one of five subfamilies of the Gobiidae. Although not diagnosed, the Gobionellinae included all species characterized by two anterior interorbital pores, two epurals and a 3-12210 spinous dorsal pterygiophore pattern. It also included some taxa in which one or more of these characters were modified to represent autapomorphies (e.g. *Gobioides* with a 3-12201 pterygiophore pattern) or convergences with taxa in other subfamilies (e.g. a single epural in various species of *Gobionellus*, *Ctenogobius*, *Evorthodus*, *Gobioides* and *Awaous* [Pezold 2004]). Pezold (1993) also included three groups of gobies previously determined as monophyletic by Birdsong *et al.* (1988), (the *Acanthogobius*, *Astrabe* and *Chasmichthys* groups) and suggested they might themselves form a monophyletic temperate northern Pacific group. Monophyly was not proposed for the Gobionellinae; none of the three unifying characters was recognized as a synapomorphy because of limited understanding of character state distributions and polarities. Monophyly was hypothesized by Pezold (1993) for the revised subfamilies Gobiinae and Amblyopinae, in addition to the Sicydiinae and Oxudercinae proposed as monophyletic by earlier studies (Hoese, 1984; Harrison, 1989; Murdy, 1989).

The subfamily Gobionellinae was also recognized by Larson (2001). Adding to the characters observed by Pezold (1993), she indicated they also possess 25-28 vertebrae and 2 or 3 (occasionally 4) anal pterygiophores before the first hemal spine. The temperate northern Pacific gobionellines are characterized by a proliferation of vertebrae however, having counts as high as 42 in some species. In addition to the northern Pacific group, she recognized two other groups proposed as monophyletic: a *Mugilogobius* group and a *Stenogobius* group. The *Mugilogobius* group is characterized by a number of characters. These include the absence of an anterior nasal pore (reduction of the canals on the snout with a

single pore on each canal anterior to the orbits), the presence of villi on the head, infraorbital pores present in those species with oculoscapular canals, and sensory papillae on the cheek primarily organized as longitudinal rows. Larson (2001) regarded all but the infraorbital pores as derived features. The *Stenogobius* species group was found to be characterized by canals on the snout including a pair of pores anterior to the orbits, no villi on the head, no infraorbital pores on the oculoscapular canal, and sensory papillae on the cheeks forming transverse rows. Only the loss of the infraorbital pore was regarded as evolutionarily derived. However, Larson (2001) refrained from naming the *Mugilogobius* and *Stenogobius* groups because no single derived feature was possessed by all members of either clade. Larson (2001) diagnosed 12 genera in the *Mugilogobius* group and provided a synoptic evaluation of relationships among the genera. The *Stenogobius* group identified by Larson (2001) is largely consistent with the *Ctenogobius* lineage of Harrison (1989).

In a phylogenetic analysis of *Gobionellus* species, Pezold (2004) examined relationships among genera of the *Stenogobius* group and delimited six monophyletic genera - *Ctenogobius*, *Evorthodus*, *Gobioides*, *Oligolepis*, *Oxyurichthys* and *Stenogobius*. The genus *Gobionellus* was differentially diagnosed, but evidence for monophyly not including *Gobioides* species was equivocal. Species historically assigned to *Gobionellus* (e.g. Gilbert and Randall, 1979) fell into two groups - a *Gobionellus-Gobioides* clade sister to an *Awaous-Stenogobius* clade, and a *Ctenogobius-Oxyurichthys* clade which was in turn sister group to an *Evorthodus-Oligolepis* clade.

Molecular analyses and the emergence of Gobionellidae

The first attempt to examine gobioid relationships using gene sequences was by Akihito *et al.* (2000). They compared partial sequences (380 bp) of the mtDNA gene cytochrome *b* for 28 gobioid fishes. Six species clusters, loosely joined by branches with low bootstrap values, were recovered. Of note was the high support for the grouping of the representative amblyopine species (*Taenioides limicola*) and the representative oxudercine species (*Periophthalmus argentilineatus*). In Akihito *et al.*'s study (2000) these two species were then clustered with three gobionelline species (*Acanthogobius flavigaster*, *Tridentiger bifasciatus* and *Tridentiger obscurus*), but with low support. These findings promised that more insight might be obtained from mtDNA sequences because they corroborated Harrison's (1989) placement of *Periophthalmus* and *Taenioides* in the Gobionellinae based on shared derived features of the suspensorium. Akihito *et al.*'s (2000) analysis also associated *Micropercops swinhonis*, an odontobutid sleeper, with this group, but again with low support. These results suggested that, while promising, the information obtained from mtDNA analyses would have to be interpreted cautiously and corroborated

with other datasets, and that taxon sampling would need to be broadened and increased to more adequately represent the diversity comprised by gobioid fishes.

Following the Akihito *et al.* (2000) study, Wang *et al.* (2001) analyzed complete sequences of the 12s rRNA gene for 43 gobioid species spanning 32 genera in eight families or subfamilies. Their findings first identified some of the major groupings recognized in the classification followed here (Thacker, 2009). Significantly, a monophyletic Butinae was determined to be the sister group to a clade containing two monophyletic groups. One of these groups included the Gobionellinae, Sicydiinae and Oxudercinae (all *sensu* Pezold, 1993); the other monophyletic group consisted of the Gobiinae (*sensu* Pezold, 1993) plus the Microdesmidae (Ptereleotridae of Thacker, 2000). It was first noted by Wang *et al.* (2001) that the molecular phylogeny based on mtDNA was supported by the reduction of 6 branchiostegals to 5 for the clade containing these two monophyletic groups. They also observed that the lineage including the gobiines and microdesmids (ptereleotrids of Thacker 2000) shared a derived trait, the possession of a single epural, while most species in the gobionelline clade have two epurals. A single epural also appears in some gobionellines and most sicydiines, but that was interpreted as homoplasious, representing a parallel evolutionary trend within the gobionelline clade. Subsequently, Kim *et al.* (2004) sequenced the complete mitochondrial genome of *Acanthogobius hasta*. Their phylogenetic analysis used the 12S rRNA gene sequences available from GenBank (from Wang *et al.*, 2001) and the sequence for *Acanthogobius hasta* derived from their research. The four clades recognized by Wang *et al.* (2001) were supported and *A. hasta* was placed among the gobionellines.

Sixty-seven gobioid species from 51 genera in 12 families or subfamilies were examined by Thacker (2003) in an analysis using complete sequences of three other mitochondrial genes - ND1, ND2 and COI. As observed by Wang *et al.* (2001), two monophyletic clades of gobies were obtained - one including the gobionellines and another with gobiines (both *sensu* Pezold 1993). As observed by Wang *et al.* (2001), the clade including the Gobionellinae also contained the Amblyopinae, Sicydiinae and Oxudercinae. However, Thacker (2003) found the oxudercines were paraphyletic if the representative amblyopine in the analysis, *Odontamblyopus rubicundus*, was excluded. The sicydiines were grouped with a paraphyletic set of gobionellines previously recognized by Larson (2001) as monophyletic (the *Stenogobius* group) due to the loss of an oculoscapular canal pore. *Kraemeria cunicularia*, the sole representative of the Kraemeriidae in the analysis, was grouped in another gobionelline clade with a mix of species from the putative monophyletic *Mugilogobius* group (Larson, 2001) and a northern Pacific gobionelline species.

Consistent with the findings of Wang *et al.* (2001), Thacker (2003) recovered the Ptereleotridae (and Microdesmidae *sensu* Thacker 2000) with the Gobiinae (*sensu* Pezold 1993). The Gobiinae were also

recovered as paraphyletic (Thacker, 2003). Interestingly, the microdesmids were polyphyletic in the clade, with New World species grouped with New World gobiines and an Old World species, *Gunnellichthys monostigma*, with Old World gobiines. Ptereleotrids were sister to a clade containing *Gunnellichthys* and two species of Schindleriidae. The Microdesmidae and Ptereleotridae were not recovered as sister groups and neither was found to be monophyletic, contrary to the revision of the Microdesmidae by Thacker (2000) using morphological characters and other morphological studies (Randall and Hoese, 1985; Rennis and Hoese, 1987).

A study by Thacker and Hardman (2005) using complete sequences of ND1, ND2, COI and cytochrome *b* genes focused on basal gobioid relationships, but also included two gobiid species in the analysis. The phylogeny produced found the Butinae to be paraphyletic. This was due to *Butis butis* sharing a clade with the two gobiids instead of with other members of its subfamily.

In the most comprehensive molecular analysis of gobioid fishes to date, Thacker (2009) pulled together data from her earlier studies, work by Miya *et al.* (2003) and added information for a number of taxa to offer a phylogeny based on four mtDNA genes for 107 gobioid species and 41 outgroup species. Salient features of the resultant phylogeny are: a monophyletic Butidae as sister-group to two goby clades; a shift of the Kraemeriidae from the Gobionellidae/Gobionellinae clade (Thacker, 2003) to the Gobiidae/Gobiinae clade where it is now aligned with *Fusigobius* and *Coryphopterus* (instead of with *Pandaka*, *Gobiopterus* and *Acanthogobius*); sicydiines, amblyopines and oxudercines are part of the Gobionellidae clade; gobionellines outside of the *Stenogobius* Group are recovered as paraphyletic instead of monophyletic per Thacker (2003); the Microdesmidae and Ptereleotridae are each indicated as monophyletic instead of polyphyletic per Thacker (2003); and there is no division of gobiids into New World and Old World clades as recovered by Thacker (2003).

Some of the larger patterns of relationship (e.g. butine sleepers as sister group to gobies, and gobies comprising two major divisions - one including gobiines and the other gobionellines) are generally concordant with information from morphological studies (Hoese and Gill, 1993; Pezold, 1993). The devil is in the details however, even when comparing molecular studies, as noted in the previous paragraph. Yet as more studies are attempted, the information accrued offers a hefty heuristic tool for testing hypotheses of monophyly and unraveling gobioid evolution. Another outcome presents more of a challenge than an aid – undiagnosed lineages determined by similarities of gene sequences. Classifications based upon morphology have been moving progressively towards the elucidation of monophyletic groups distinguished by features hypothesized to represent evolutionary novelties for the said groups, coupled with continuing analyses of different suites of features. This is embodied in all classifications since Miller

(1973). The most recent classification presented by Thacker (2009) is particularly significant as it represents a departure from this philosophy, and it is not unique (Frost, 2006). The classification is clade-based as determined from analyses of mtDNA genes, instead of taxa being proposed based upon synapomorphies. There are some cautions advisable in this approach. There has been some notable instability in the progression of phylogenies that have been constructed (examples given in the previous paragraph). Broadening taxon sampling can reduce the impact of long branch attraction and is also needed to incorporate taxa critical to understanding the evolution of character states among gobioids, a group noted for its plasticity. Some attention is also necessary to which portions of the mtDNA genome are sequenced and the length of sequence read. In addition, although multiple genes are frequently used, presumably to avoid confusion of gobioid phylogeny with the reconstruction of a gene tree, the genes in all of the preceding molecular analyses are part of the mtDNA genome and thus are inherited together. In reality the addition of linked genes may be simply the addition of sequence. With those caveats in mind, the phylogenies constructed offer much insight, but demand greater corroboration through the addition of more taxa, additional independent genes and complementary morphological analyses.

Ecology and distribution of the Gobionellinae

The Gobionellinae *sensu stricto* are found in tropical and temperate seas except for the northeastern Atlantic Ocean, the Mediterranean Sea and Ponto-Caspian. Most inhabit estuaries while some are freshwater species. The few species associated with coral reef habitats are typical of sand or fine sedimentary substrates. The *Mugilogobius* group predominates in the Indo-West Pacific and temperate Australia. Species in the *Stenogobius* group are also present in the Indo-West Pacific, and are the only gobionellines in the Western and East-Central Atlantic Ocean. The *Chasmichthys*, *Astrabe* and *Acanthogobius* groups identified by Birdsong *et al.* (1988) are endemic to the temperate northern Pacific and features of the post-cranial axial skeleton suggest that they may be part of a larger monophyletic clade that includes other genera endemic to the area. There are an estimated 370 species in 55 genera.

Valid Genera of the Subfamily Gobionellinae

Northern Pacific Group:

Acanthogobius Gill, 1859

Amblychaeturichthys Bleeker, 1874
Astrabe Jordan and Snyder, 1901
Chaenogobius Gill, 1859
Chaeturichthys Richardson, 1844
Clariger Jordan and Snyder, 1901
Clevelandia Eigenmann and Eigenmann, 1888
Eucyclogobius Gill, 1862
Eutaeniichthys Jordan and Snyder, 1901
Gillichthys Cooper, 1864
Gymnogobius Gill, 1863
Ilypnus Jordan and Evermann, 1896
Lepidogobius Gill, 1859
Lethops Hubbs, 1926
Leucopsarion Hilgendorf, 1880
Lophiogobius Günther, 1873
Luciogobius Gill, 1859
Polyspondylogobius Kimura and Wu, 1994
Pterogobius Gill, 1863
Quietula Jenkins and Evermann, 1895
Sagamia Jordan and Snyder, 1901
Suruga Jordan and Snyder, 1901
Tridentiger Gill, 1859
Typhlogobius Steindachner, 1880
***Mugilogobius* Group**
Brachygobius Bleeker, 1874
Caecogobius Berti and Ercolini, 1991
Chlamydogobius Whitley, 1930
Eugnathogobius Smith, 1931
Gobiopterus Bleeker, 1874
Hemigobius Bleeker, 1874
Mistichthys Smith, 1902

Mugilogobius Smitt, 1899
Nesogobius Whitley, 1929
Paedogobius Iwata, Hosoya and Larson, 2001
Pandaka Herre, 1927
Papuligobius Chen and Kottelat, 2003
Pseudogobiopsis Koumans, 1934
Pseudogobius Popta, 1922
Redigobius Herre, 1927
Rhinogobius Gill, 1859
Schismatogobius Beaufort, 1912
Stigmatogobius Bleeker, 1874
Tamanka Herre, 1927
Tasmanogobius Scott, 1935
Tukugobius Herre, 1927
***Stenogobius* Group**
Awaous Valenciennes, 1837
Ctenogobius Gill, 1858
Evorthodus Gill, 1859
Gnatholepis Bleeker, 1874
Gobioides Lacepède, 1800
Gobionellus Girard, 1858
Oligolepis Bleeker, 1874
Oxyurichthys Bleeker, 1857
Parawaous Watson, 1993
Stenogobius Bleeker, 1874

Acknowledgments

Doug Hoese provided information on genera and species of gobioid fishes. Kathleen Cole, Ryan Chabarria, Marcelo Kovacic and Luke Tornabene reviewed the manuscript and contributed helpful commentary and suggestions.

References

- Akihito, Prince, A. Iwata, T. Kobayashi, K. Ikeo, T. Imanishi, H. Ono, Y. Umehara, C. Hamamatsu, K. Sugiyama, Y. Ikeda, K. Sakamoto, A. Fumihito, S. Ohno, and T. Gojobori. 2000. Evolutionary aspects of gobioid fishes based upon a phylogenetic analysis of mitochondrial cytochrome *b* genes. *Gene* 259: 5-15.
- Birdsong, R.S., E.O. Murdy and F.L. Pezold. 1988. A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships. *Bulletin of Marine Science* 42: 174-214.
- Bleeker, P. 1874. Esquisse d'un systeme naturel des Gobioides. *Archives Nerlandaises des Sciences Exactes et Naturelles* 9: 289-331.
- Frost, D.R., T. Grant, J.N. Faivovich, R.H. Bain, A. Haas, C.F.B. Haddad, R.O. De Sa', A. Channing, M. Wilkinson, S.C. Donnellan, C.J. Raxworthy, J.A. Campbell, B.L. Blotto, P. Moler, R.C. Drewes, R.A. Nussbaum, J.D. Lynch, D.M. Green and W.C. Wheeler. 2006. The Amphibian Tree of Life. *Bulletin of the American Museum of Natural History* 297,: 370 pp.
- Gilbert, C.R. and J.E. Randall. 1979. Two new western Atlantic species of the gobiid fish genus *Gobionellus*, with remarks on characteristics of the genus. *Northeast Gulf Science* 3: 27-47.
- Harrison, I.J. 1989. Specialization of the gobioid palatoquadrate complex and its relevance to gobioid systematics. *Journal of Natural History* 23:235-353.
- Hoese, D.F. 1984. Gobioidi: relationships In: *Ontogeny and systematics of fishes*, H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall Jr. and S.L. Richardson (Eds.). *American Society of Ichthyologists and Herpetologists Special Publication* 1: pp. 588-591,
- Hoese, D.F. and A.C. Gill. 1993. Phylogenetic relationships of eleotridid fishes (Perciformes: Gobioidi). *Bulletin of Marine Science* 52(1): 415-440.
- Kim, I-C., H.-S. Kweon, Y.J. Kim, C.-B. Kim, M.C. Gye, W.-O. Lee, Y.-S. Lee and J.-S. Lee. 2004. The complete mitochondrial genome of the jaeveline goby, *Acanthogobius hasta* (Perciformes: Gobiidae) and phylogenetic considerations. *Gene* 336: 147-153.

- Larson, H.K. 2001. A revision of the gobiid fish genus *Mugilogobius* (Teleostei: Gobioidei), and its systematic placement. *Records of the Western Australian Museum* Suppl. 62: 1-233.
- Miller, P.J. 1973. The osteology and adaptive features of *Rhyacichthys aspro* (Teleostei: Gobioidei) and the higher classification of gobioid fishes. *Journal of Zoology, London* 171: 397-434.
- Miya, M., H. Takeshima, H. Endo, N.B. Ishiguro, J.G. Inoue, T. Mukai, T.P. Satoh, M. Yamaguchi, A. Kawaguchi, K. Mabuchi, S.M. Shirai and M. Nishida. 2003. Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 26: 121-138.
- Murdy, E.O. 1989. A taxonomic revision and cladistic analysis of the oxudercine gobies (Gobiidae: Oxudercidae). *Records of the Australian Museum* Suppl. 11: 1-93.
- Pezold, F. 1993. Evidence for a monophyletic Gobiinae. *Copeia* 1993: 634-643.
- Pezold, F. 2004. A phylogenetic analysis of the genus *Gobionellus* (Teleostei, Gobiidae). *Copeia* 2004: 260-280.
- Randall, J.E. and D.F. Hoese. 1985. Revision of the Indo-Pacific dartfishes, genus *Ptereleotris* (Perciformes: Gobioidei). *Indo-Pacific Fishes* 7: 1-36.
- Rennis D.S. and Hoese, D.F. 1987. Aioliops, a new genus of ptereleotrine fish (Pisces: Gobioides) from the tropical Indo-Pacific with descriptions of four new species. *Records of the Australian Museum* 39: 67-84.
- Thacker, C. 2000. Phylogeny of the wormfishes (Teleostei: Gobioidei: Microdesmidae). *Copeia* 2000: 940-957.
- Thacker, C.E. 2003. Molecular phylogeny of the gobioid fishes. *Molecular Phylogenetics and Evolution* 26(3): 354-368.
- Thacker, C.E. 2009. Phylogeny of Gobioides and placement within Acanthomorpha, with a new classification and investigation of diversification and character evolution. *Copeia*

2009: 93-104.

Thacker, C.E. and M.A. Hardman. 2005. Molecular phylogenetics of basal gobioid fishes:

Rhyacichthyidae, Odontobutidae, Xenisthmidae, Eleotridae (Teleostei: Perciformes: Gobioidi). *Molecular Phylogenetics and Evolution* 37(3): 858-871.

Wang, H-Y., M.-P. Tsai, J. Dean, and S.-C. Lee. 2001. Molecular phylogeny of gobioid fishes

(Perciformes: Gobioidi) based on mitochondrial 12S rRNA sequences. *Molecular Phylogenetics and Evolution* 20(3): 390-408.