

Systematics of Gobiidae

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The family Gobiidae includes what are considered the typical gobies: small, usually marine fishes, with separate spinous and rayed dorsal fins and pelvic fins often joined into a disc, that live on or in the substrate and are generally inconspicuous. Color patterns may range from brightly patterned to drab and camouflaged. The composition of this family has changed since the description of the first *Gobius* by Linnaeus (1758), but it has always been the most speciose of gobioid taxa, and the one that contains the most well-known examples of goby biology and ecology. Various classifications based on morphology have delineated Gobiidae as the largest of six to nine gobioid families (Miller, 1973; Hoese, 1984; Harrison, 1989; Pezold, 1993; Nelson, 2006); reevaluations of gobioid systematics based on molecular data have shown that the smaller, distinctive families historically separated from the bulk of gobioid taxa are actually nested within the larger groups (Akihito *et al.*, 2000; Wang *et al.*, 2001; Thacker, 2003; Rüber and Agorreta, 2011, Chapter 1.2 of this volume). A revised six-family clade-based classification (Thacker, 2009) identifies a Gobiidae that includes all genera of the former taxa Gobiinae, Microdesmidae, Ptereleotridae, Schindleriidae,

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and Kraemeriidae (*Kraemia* recovered within Gobionellidae by Thacker [2003] but assigned to Gobiidae when analyzed in the context of more comprehensive sampling.) This monophyletic Gobiidae includes 1,107 species at this writing (calculated from an unpublished list of gobiid species compiled by Edward Murdy, augmented with data from the online version of the Catalog of Fishes [Eschmeyer, 2008]). The 165 genera included in Gobiidae are listed in Table 1.10.1.

Table 1.10.1 Valid genera of Gobiidae.

<i>Acentrogobius</i>	<i>Afurcagobius</i>	<i>Aioliops</i>
<i>Akko</i>	<i>Amblyeleotris</i>	<i>Amblygobius</i>
<i>Amoya</i>	<i>Anatirostrum</i>	<i>Aphia</i>
<i>Arcygobius</i>	<i>Arenigobius</i>	<i>Aruma</i>
<i>Asterropteryx</i>	<i>Aulopareia</i>	<i>Austrolethops</i>
<i>Barbulifer</i>	<i>Barbuligobius</i>	<i>Bathygobius</i>
<i>Benthophiloides</i>	<i>Benthophilus</i>	<i>Bollmannia</i>
<i>Bryaninops</i>	<i>Buenia</i>	
<i>Cabillus</i>	<i>Caffrogobius</i>	<i>Callogobius</i>
<i>Caspiosoma</i>	<i>Cerdale</i>	<i>Chriolepis</i>
<i>Chromogobius</i>	<i>Clarkichthys</i>	<i>Corcyrogobius</i>
<i>Coryogalops</i>	<i>Coryphopterus</i>	<i>Cristatogobius</i>
<i>Croilia</i>	<i>Cryptocentroides</i>	<i>Cryptocentrus</i>
<i>Crystallogobius</i>	<i>Ctenogobiops</i>	
<i>Deltentosteus</i>	<i>Didogobius</i>	<i>Discordipinna</i>
<i>Drombus</i>		
<i>Ebomegobius</i>	<i>Echinogobius</i>	<i>Economidichthys</i>
<i>Egglestonichthys</i>	<i>Ego</i>	<i>Elacatinus</i>
<i>Eleotrica</i>	<i>Enypnias</i>	<i>Evermannichthys</i>
<i>Eviota</i>	<i>Exyrias</i>	
<i>Favonigobius</i>	<i>Feia</i>	<i>Flabelligobius</i>
<i>Fusigobius</i>		
<i>Gammogobius</i>	<i>Ginsburgellus</i>	<i>Gladiogobius</i>
<i>Glossogobius</i>	<i>Gobiodon</i>	<i>Gobiopsis</i>
<i>Gobiosoma</i>	<i>Gobitrichonotus</i>	<i>Gobius</i>
<i>Gobiusculus</i>	<i>Gobulus</i>	<i>Gorogobius</i>
<i>Grallenia</i>	<i>Gunnellichthys</i>	<i>Gymneleotris</i>
<i>Hazeus</i>	<i>Hetereleotris</i>	<i>Heteroplopomus</i>
<i>Hyrcanogobius</i>		
<i>Istigobius</i>		
<i>Kelloggella</i>	<i>Knipowitschia</i>	<i>Kraemia</i>
<i>Larsonella</i>	<i>Lebetus</i>	<i>Lesueurigobius</i>

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<i>Lobulogobius</i>	<i>Lophiogobius</i>	<i>Lophogobius</i>
<i>Lotilia</i>	<i>Lubricogobius</i>	<i>Luposicya</i>
<i>Lythrypnus</i>		
<i>Macrodontogobius</i>	<i>Mahidolia</i>	<i>Mangarinus</i>
<i>Mauligobius</i>	<i>Mesogobius</i>	<i>Microdesmus</i>
<i>Microgobius</i>	<i>Millerigobius</i>	<i>Minysicya</i>
<i>Myersina</i>		
<i>Nemateleotris</i>	<i>Nematogobius</i>	<i>Neogobius</i>
<i>Nes</i>	<i>Nesogobius</i>	
<i>Obliquogobius</i>	<i>Odondebuenia</i>	<i>Ophiogobius</i>
<i>Oplopomops</i>	<i>Oplopomus</i>	<i>Opua</i>
<i>Oxymetopon</i>		
<i>Padogobius</i>	<i>Palatogobius</i>	<i>Palutrus</i>
<i>Papillogobius</i>	<i>Parachaeturichthys</i>	<i>Paragobiodon</i>
<i>Paragunnellichthys</i>	<i>Paratrimma</i>	<i>Pariah</i>
<i>Parioglossus</i>	<i>Parkraemeria</i>	<i>Parrella</i>
<i>Pascua</i>	<i>Phyllogobius</i>	<i>Platygobiopsis</i>
<i>Pleurosicya</i>	<i>Polyspondylogobius</i>	<i>Pomatoschistus</i>
<i>Porogobius</i>	<i>Priolepis</i>	<i>Proterorhinus</i>
<i>Psammogobius</i>	<i>Pseudaphya</i>	<i>Psilogobius</i>
<i>Psilotris</i>	<i>Ptereleotris</i>	<i>Pycnomma</i>
<i>Rhinogobiops</i>	<i>Risor</i>	<i>Robinsichthys</i>
<i>Schindleria</i>	<i>Signigobius</i>	<i>Siphonogobius</i>
<i>Silhouettea</i>	<i>Speleogobius</i>	<i>Stonogobius</i>
<i>Sueviota</i>	<i>Sufflogobius</i>	
<i>Tasmanogobius</i>	<i>Thorogobius</i>	<i>Tomiyamichthys</i>
<i>Trimma</i>	<i>Trimmatom</i>	<i>Tryssogobius</i>
<i>Valenciennea</i>	<i>Vanderhorstia</i>	<i>Vanneaugobius</i>
<i>Varicus</i>	<i>Vomerogobius</i>	
<i>Wheelerigobius</i>		
<i>Yongeichthys</i>		
<i>Zebrus</i>	<i>Zosterisessor</i>	

Tropical reef habitats are particularly rich in gobiids, but they are often inconspicuous due to their small size and ecology. Generally gobies will occupy crevices or interstices in the reef or rocky substrate, and many notable examples of mutualisms between gobies and invertebrates, particularly the burrow-digging snapping shrimps, have been documented (Karplus and Thompson, 2011, Chapter 4.4 of this volume). The reproductive strategy of gobiids is unusual compared to most fishes, and requires more investment and parental care. Typically, gobies will lay their eggs demersally, in a nest

area prepared and guarded by the male; eggs bear adherent filaments and are fixed in an adhesive sperm trail. The clutch of eggs is then monitored and cared for by the male, until larvae hatch out and begin an extended planktonic larval period (Breder and Rosen, 1966; Ruple, 1984). Some of the reef-dwelling species exhibit protogynous hermaphroditism, with females transforming into males as needed in response to social and environmental cues (Cole, 1990, 2008). Gobiids are also notable for their long larval lives, both in absolute length and considered as a percentage of total lifespan. As indicated by otoliths, the larval life of a small gobiid (*Trimma nasa*) totaled 33.9 days, or 38.7% of the total lifespan of 87 days (Winterbottom and Southcott, 2008). Species of *Eviota* experience lifespans as short as 59 days total, with 41.8% of that time spent as larvae (Depczynski and Bellwood, 2005, 2006).

Finally, one of the most well-known characteristics of gobiids is their small adult size, including species that become mature at 8-10mm standard length (*Eviota*, *Trimma*, *Trimmatom*), and those that exhibit not just size reduction, but morphological simplification likely the result of paedomorphosis (such as *Schindleria*; Johnson and Brothers, 1993; Watson and Walker, 2004; Thacker and Grier, 2005; Nelson, 2006). The miniaturization, reduction, and simplification common among gobiid, gobies has hindered efforts to determine phylogeny, and although a fair amount of data has been gathered, more comprehensive phylogenetic surveys are clearly necessary to definitively determine relationships among gobiids.

Gobiidae are so diverse and such an important part of reef faunas that they have been studied as exemplars of a variety of evolutionary and ecological patterns. The coral-perching species of *Gobiodon* have provided one of the few clear examples of sympatric speciation by host shift, and the only such example from a marine system (Munday *et al.*, 2004). *Gobiodon* have also been studied to compare the impact of habitat degradation on ecological generalists as compared to specialists (Munday, 2004). Phylogenetic studies of the seven-spined cleaner gobies of the Caribbean have provided insights into larval transport and retention, as well as the tempo and ecological correlates of speciation (Rüber *et al.*, 2003; Rüber and Zardoya, 2005; Taylor and Hellberg, 2003, 2005). In each of these cases, understanding of phylogeny has been a crucial first step in exploring various hypotheses of evolutionary and ecological change.

Phylogeny of taxa and groups within Gobiidae has not been determined with morphological characters. Several surveys of morphological character patterns across Gobiidae have been performed, including osteology of the fins and axial skeleton (Birdsong *et al.*, 1988), suspensorium, branchial

apparatus and pectoral girdle (Akihito, 1986; Harrison, 1989), and configuration of cephalic sensory pores (Pezold, 1993; Takagi, 1989). In particular, the study of Birdsong *et al.* (1988), although not phylogenetic, provided a breakdown of Gobiidae into groups of genera with common patterns of skeletal characters. These included temperate Pacific-rim *Acanthogobius*, *Astrabe*, and *Chasmichthys* groups; the New World tropical *Gobiosoma* and *Microgobius* groups; the Old World temperate *Gobius* and *Pomatoschistus* groups; and the highly diverse tropical marine *Priolepis* and *Bathygobius* groups. Pezold's (1993) study not only surveyed the cephalic pore configurations of a comprehensive sample of Gobiidae, but also proposed a diagnostic character for the group (former Gobiinae only): a single cephalic interorbital pore, rather than a pair of pores. He also noted that most of those taxa possess a common dorsal fin pterygiophore pattern and vertebral number, the same as that of the *Bathygobius* and *Priolepis* groups. Clearly, there are characters valuable for identifying gobiid groups; however, there are relatively few and they do not seem to show entirely consistent patterns, particularly when former families Microdesmidae, Ptereleotridae, Kraemeriidae, and Schindleriidae are included as part of gobiid diversity.

Given that Gobiidae is such a speciose group, it is not surprising that it is difficult to generalize about their morphology or biology. The most outstanding question still to be addressed in consideration of gobioid relationships is inference of the phylogeny of groups within Gobiidae. A robust phylogeny will enable evolutionary consideration of the wealth of interesting biological and ecological patterns documented among gobiids. Phylogenetic analysis of morphological characters has been performed for some subgroups (Gill, 1994; Thacker, 2000), others have been investigated with molecular data (Rüber *et al.*, 2003; Taylor and Hellberg, 2003, 2005), or a combination (Thacker and Cole, 2002; Harold *et al.*, 2008), and gobiids have been included in larger molecular phylogenetic hypotheses (Thacker, 2003, 2009; Thacker and Hardman, 2005). Patterns of morphological character distribution may be reconsidered in conjunction with molecular phylogenetic results, and generally it is the case that morphological character distribution correlates fairly well, but not completely, with clades proposed based on DNA sequence (Thacker, 2009). Within Gobiidae, the most notable results based on analysis of molecular data are that the large *Priolepis* group (Birdsong *et al.*, 1988) is not monophyletic, and that New World taxa are placed in several different clades (three in that hypothesis, comprising *Cerdale* plus *Microdesmus*; *Gobiosoma*, *Risor*, and *Barbulifer*; and *Coryphopterus* plus *Lophogobius*), nested within the more diverse Indo-

Pacific fauna (Thacker, 2003, 2009). Overall, the development of gobiid systematics seems to be progressing in much the same pattern as seen for the entire Gobioidae: distinctive groups are delineated and singled out from the majority of taxa, and as data accumulate, it is revealed that this perceived distinctiveness is simply a part of the range of diversity in the larger group. Comprehensive surveys of both morphology and molecular data will be required to further evaluate gobiid relationships, and to reveal the systematics of this diverse group.

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