Zootaxa 3266: 41–52 (2012)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Thalasseleotrididae, new family of marine gobioid fishes from New Zealand and temperate Australia, with a revised definition of its sister taxon, the Gobiidae (Teleostei: Acanthomorpha)

ANTHONY C. GILL[1,2] & RANDALL D. MOOI[3,4]

[1] *Macleay Museum and School of Biological Sciences, A12 – Macleay Building, The University of Sydney, New South Wales 2006, Australia. E-mail: anthony.c.gill@sydney.edu.au*

[2] *Ichthyology, Australian Museum, 6 College Street, Sydney, New South Wales 2010, Australia*

[3] *The Manitoba Museum, 190 Rupert Ave., Winnipeg MB, R3B 0N2 Canada. E-mail: rmooi@manitobamuseum.ca*

[4] *Department of Biological Sciences, 212B Biological Sciences Bldg., University of Manitoba, Winnipeg MB, R3T 2N2 Canada*

Abstract

Thalasseleotrididae **n. fam.** is erected to include two marine genera, *Thalasseleotris* Hoese & Larson from temperate Australia and New Zealand, and *Grahamichthys* Whitley from New Zealand. Both had been previously classified in the family Eleotrididae. The Thalasseleotrididae is demonstrably monophyletic on the basis of a single synapomorphy: membrane connecting the hyoid arch to ceratobranchial 1 broad, extending most of the length of ceratobranchial 1 (= first gill slit restricted or closed). The family represents the sister group of a newly diagnosed Gobiidae on the basis of five synapomorphies: interhyal with cup-shaped lateral structure for articulation with preopercle; laterally directed posterior process on the posterior ceratohyal supporting the interhyal; pharyngobranchial 4 absent; dorsal postcleithrum absent; urohyal without ventral shelf. The Gobiidae is defined by three synapomorphies: five branchiostegal rays; expanded and medially-placed ventral process on ceratobranchial 5; dorsal hemitrich of pelvic-fin rays with complex proximal head. This study represents a contribution to our ongoing clarification of the family Eleotrididae, which has served historically as a repository for genera not classified among the more derived gobioids (= Gobiidae as defined here).

Key words: Gobioidei, Gobiidae,Thalasseleotrididae new family, Eleotrididae, osteology, systematics

Introduction

The internal relationships and classification of the perciform suborder Gobioidei represent a major challenge in systematic ichthyology. There is no consensus on the number of families recognized (Akihito *et al*. 2000a: tab. 1; Thacker 2000) and the bulk of genera are undiagnosed by synapomorphies. The lack of resolution of relationships in part reflects the large size of the clade (which numbers more than 2,000 species), but also the paucity of comprehensive character surveys. In recent years we have been conducting a broad survey of osteological and myological characters of gobioids, particularly concentrating on “basal gobioids” (those with six branchiostegal rays), with the aim of contributing to an understanding of the internal relationships and classification of the Gobioidei. These ongoing anatomical studies and phylogenetic analyses have retrieved a sister-group relationship between a clade consisting of the five-branchiostegal-rayed taxa (which we herein define as the Gobiidae), and a clade consisting of two Australian and New Zealand marine eleotridid genera, *Thalasseleotris* Hoese & Larson and *Grahamichthys* Whitley. Although these genera have been noted as atypical among eleotridids (Hoese & Larson 1987; Hoese & Gill 1993), they have not been included in recent examinations of gobioid relationships.The purposes of this paper are to describe a new family for *Thalasseleotris* and *Grahamicthys* in order to reflect their sister-group status with the Gobiidae, and to document supporting evidence for the relationship, as well as for the monophyly of the new family and for the newly defined Gobiidae.

Accepted by R. Pethiyagoda: 2 Mar. 2012; published: 11 Apr. 2012

Materials and Methods

Our assessment of the distribution of characters documented herein is based on the examination of over 400 skeletal preparations representing around 170 gobioid genera (42 of the almost 50 genera of non-gobiid ("basal") gobioids; over 125 of the approximately 220 gobiid genera), including representatives of all major groups recognised by Birdsong *et al*. (1988). Collection details for these specimens will be listed in forthcoming papers by us on the relationships of basal gobioids, and on gobioid dorsal gill arch morphology. Our observations on the osteology of the new family are based on the following specimens (institutional abbreviations follow Eschmeyer, 1998a; C&S = cleared and stained for cartilage and bone following the methods of Taylor & Van Dyke, 1985; EtOH = alcohol preserved): *Grahamichthys radiata*, AMS I.27125-001 (1 C&S, 42.5 mm SL), AMS I.27272-001 (C&S, 43 mm SL), AMS I.41350-001 (1 C&S, 51.8 mm SL), MPM 43072 (3 EtOH, 31.6–36.6 mm SL), MPM 43073 (1 EtOH, 52.2 mm SL; 2 C&S, 46.5–51.3 mm SL), MPM 43270 (2 C&S, 29.5–31.7 mm SL); *Thalasseleotris adela*, AMS I.18241-035 (6 C&S paratypes, 20–27 mm SL), NMV A17805 (1 EtOH, 26.1 mm SL; 1 C&S, 25.5 mm SL); *T. iota*, AMS I.41347-001 (1 C&S, 28.0 mm SL); NMNZ 28333 (2 C&S, 13–15.5 mm SL; NMNZ 35077 (1 C&S, 29.2 mm SL).

Revised Definition of the Gobiidae Cuvier 1816

To justify the erection of the new family, and to discuss its relationships, it is first necessary to define and diagnose a demonstrably monophyletic Gobiidae. Over the past 25 or so years, various authors have recognised a number of families for the five-branchiostegal-rayed gobioid taxa on the basis of their distinctive morphologies, including Kraemeriidae, Ptereleotridae, Microdesmidae, Schindleriidae, Trypauchenidae, Gunnellichthyidae and Gobioididae (e.g., Akihito *et al*. 1984; Hoese 1984; Nelson 1984, 1994, 2006; Birdsong *et al*. 1988; Eschmeyer 1998b,c; Akihito *et al*. 2000b; Senou *et al*. 2004). In contrast, our unpublished studies of morphological characters, as well as recent molecular studies (e.g., Wang *et al*. 2001; Thacker 2003, 2009), indicate that these families are nested within the more traditional Gobiidae (i.e., the subfamilies Gobiinae, Gobionellinae, Sicydiinae, Oxudercinae and Amblyopinae), and are thus not cladistically defensible. We therefore diagnose a monophyletic Gobiidae that includes the aforementioned families on the basis of the following three synapomorphies, two of which we newly propose:

Branchiostegal rays five. All Recent non-gobiid gobioids normally have six branchiostegal rays, the anteriormost two of which are positioned on the narrow, anterior edge of the anterior ceratohyal (e.g., Akihito 1969: fig. 3a; Springer 1983: figs 9–10; Hoese & Gill 1993: fig. 6). In gobiids there are only five branchiostegal rays, usually with only a single ray on the narrow anterior portion of the anterior ceratohyal (e.g., Akihito 1969: fig. 3b; Murdy 1985: fig. 7; Wang & Winterbottom 2006: fig. 6). The only exception is the highly paedomorphic genus *Schindleria* Giltay, which has five branchiostegal rays, but with two (rather than one) rays on the narrow anterior portion of the ceratohyal (Johnson & Brothers 1993: fig. 8). V.G. Springer (in Johnson & Brothers 1993) suggested that this represents a non-homologous count in *Schindleria,* that the low count in the genus was due to an absence of one of the more posterior rays, whereas in other gobiids an anterior ray was absent. We agree with Johnson & Brothers that this evidence is ambiguous, owing to the modified configuration and shape of the hyoid apparatus in *Schindleria*. Moreover, recent phyologenies nest the genus within the Gobiidae as here circumscribed (see Gill & Mooi 2010), indicating an unlikely independent origin of five branchiostegal rays. Akihito (1969) noted slight individual variation in branchiostegal ray numbers in gobioids, although this does not change our general conclusions regarding the distribution of this character. The Upper Oligocene fossil genus *Pirskenius* Obrhelová, a purported gobioid relative from freshwater deposits of Bohemia, reportedly has seven branchiostegal rays (discussed by Springer 1983: 37), but is in need of phylogenetic and anatomical re-evaluation. Miller (1973) classified the genus in its own subfamily (Pirskeninae) within his Gobiidae, which included all non-rhyacichthyid gobioids known at the time.

Expanded and medially-placed ventral processes on ceratobranchial 5. Gobiids have a distinct plate-like or pointed ventral process projecting from each ceratobranchial 5 (Fig. 1D). Other gobioids lack similar ventral processes on ceratobranchial 5, although variously developed lateral, low ridges or lamina may be present (Fig. 1A–C). The gobiid process is oriented anteriorly to posteriorly and may be concave on its medial face. The processes appear to be solely for insertion of the *transverses ventralis V*, a muscle that in gobiids tends to be almost circular in transverse section; in basal gobioids the muscle has a much lower profile (almost flattened). There are several noteworthy exceptions among gobiids, all involving taxa that have highly reduced gill arch structures. The processes are absent in the paedomorphic *Schindleria*, in which the 5th ceratobranchials are reduced to simple rod-like bones. They are also absent in at least some members of Birdsong *et al.*'s (1988) *Astrabe* group (*Clariger* Jordan & Snyder and *Luciogobius* Gill), though they are present in at least one genus (*Leucopsarion* Hilgendorf). Typical gobiid processes are exhibited by kraemeriines, ptereleotrines,and microdesmines, and even by small taxa such as *Trimma* Jordan & Seale, *Risor* Ginsburg, *Pandaka* Herre and others. Among taxa that have highly modified and closely associated 5th ceratobranchials, there is retained a medially-ridged socket that we recognize as homologous to the condition found in other gobiids. This interpretation is supported, for example, in oxudercines, where *Periophthalmus* Bloch & Schneider has a typical gobiid condition. Some sicydiines (*Sicyopterus* Gill) have reduced medial processes, but they are present in *Sicydium* Valenciennes in Cuvier & Valenciennes. Similarly, various gobionellines show the typical form, whereas others exhibit the ridge socket.

Complex base on dorsal hemitrich of pelvic-fin rays. All gobiids have a remarkably complex proximal base on the dorsal hemitrichs for attachment of pelvic muscles and ligaments between rays. It is a three-part structure that is composed of a medially directed tapering blade, an anteriorly directed articular process and a laterally directed triangular process (Fig. 2G–K). This structure is evident even in those taxa with reduced pelvic fins such as the members of the *Astrabe* group of Birdsong *et al.* (1988) (Fig. 2K), ptereleotrines (Fig. 2J)), and various *Eviota* species, among others. The fifth (medial) ray, present in most gobiids, is modified from this arrangement to accept the insertion of the *extensor proprius* muscle. No non-gobiid gobioids exhibit the three-part structure of the dorsal pelvic-ray hemitrichs (e.g. Fig. 2A–F).

The bases of the ventral hemitrichs of gobiids are simpler in structure, but are blade-like (Fig. 2G–K). However, the blade-like ventral hemitrich is present in several non-gobiid gobioids and differences among these structures are subtle and inconsistent (Fig. 2A, D–F).

Remarks. The Gobiidae of previous authors differs substantially in content from the taxa we include here. Miller's (1973) concept of the family is also demonstrably monophyletic, but has little explanatory power since it contains all gobioids except *Rhyacichthys* Boulenger, and includes a subfamilial and tribal classification that is not cladistically defensible. Akihito (1986) used the same two-family classification for gobioids (i.e., Rhyacichthyidae and Gobiidae), but recognised only two gobiid subfamilies (Eleotridinae and Gobiinae). The current definition of the Gobiidae is essentially equivalent to Akihito's Gobiinae and is based on one of his synapomorphies (five branchiostegal rays). Hoese & Gill (1993) also advanced a relatively inclusive concept of the Gobiidae; they allocated six-branchiostegal-rayed genera assigned by Akihito to the Eleotridinae to a new family (Odontobutidae) and two gobiid subfamilies (Butinae and Eleotridinae), with more typical gobiids assigned to a third gobiid subfamily (Gobiinae). However, because their Gobiinae did not include microdesmines, ptereleotrines or kraemeriines, their concept of the subfamily differs from that of Akihito (1986), and is not demonstrably monophyletic.

Thacker (2009) divided taxa we place in the Gobiidae among two families, Gobiidae and Gobionellidae. We feel this division is unwarranted for several reasons: 1) the classification is based on the results of an analysis of mitochondrial sequences, and previous analyses of such sequences (e.g., Wang *et al*. 2001; Thacker & Hardman 2005; Thacker 2003) have yielded vastly different relationships among gobioid genera, suggesting either inadequate methodology or incorrect (fluid) assumptions about character homology (see also Mooi & Gill 2010, Mooi *et a*l. 2011); 2) no morphological characters are available to diagnose the two taxa as monophyletic; 3) taxon sampling was very limited, and, in particular, type genera of neither family group was included (i.e., *Gobius* Linnaeus and *Gobionellus* Girard); 4) nomenclatural considerations were generally ignored. In particular, Thacker's use of the name Gobionellidae (which apparently dates to Bleeker 1874, although Miller, 1973, called it his new subfamily) is predated by at least three family-group names: Oxudercidae, Amblyopina and Trypauchenina, all of which date to Günther (1861). The first two names are in current use (as Oxudercinae and Amblyopinae), and thus can not be rejected as unused senior synonyms of Gobionellidae (see ICZN, 1999: article 35.5).

We reserve judgment on the subfamilial classification of the Gobiidae pending a better understanding of relationships within the family. However, we advocate the informal use of vernacular names derived from the existing subfamilies and those families here subsumed into the Gobiidae (thus "gobiine," "gobionelline," "kraemeriine," "ptereleotrine," "microdesmine," etc.; see also Gill & Mooi, 2010). We suggest this from a pragmatic standpoint, as it allows continued discussion of collectives of genera, even though not all of these collectives have been cladistically diagnosed.

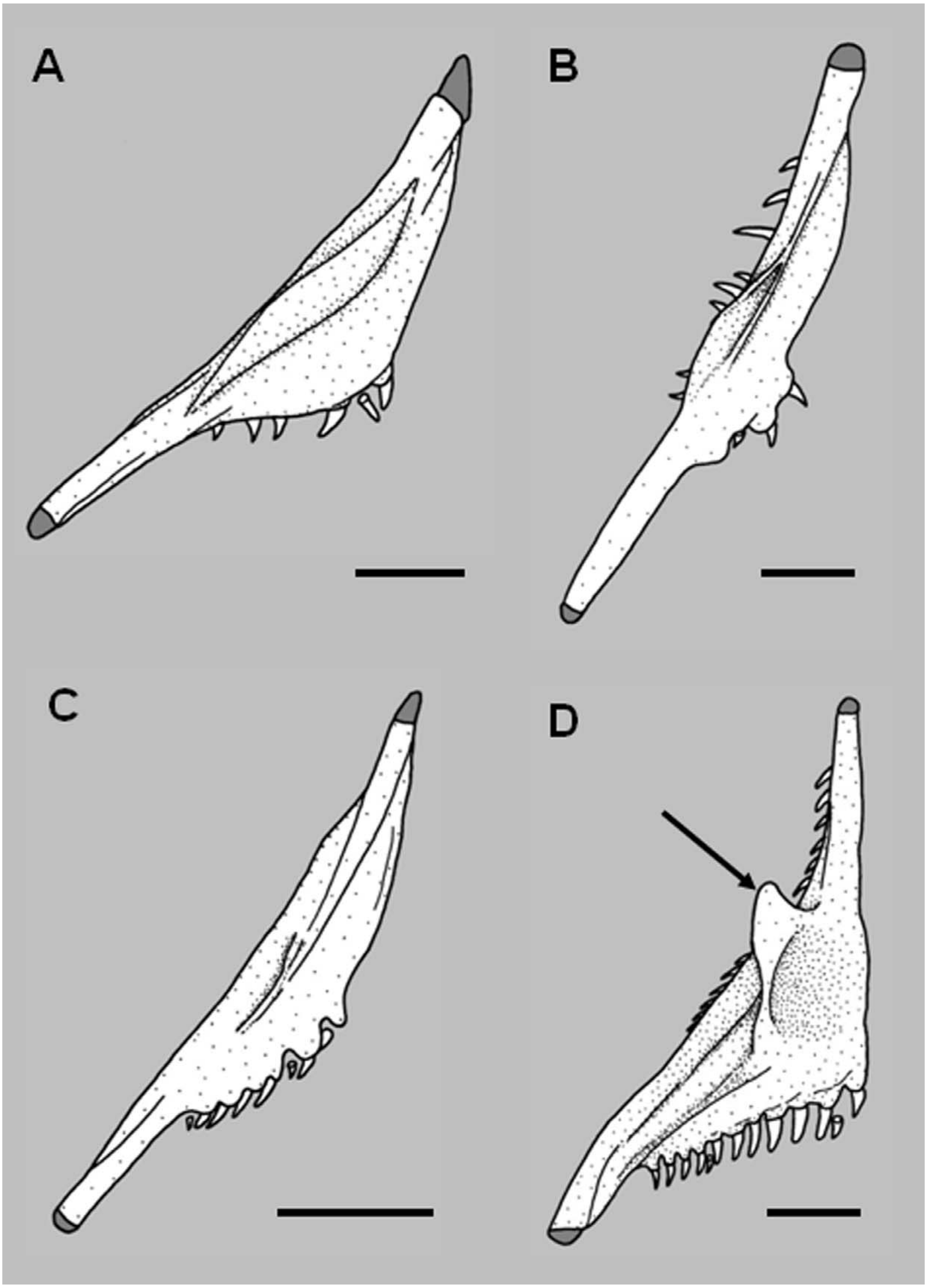

FIGURE 1. Ventral view of right ceratobranchial 5 of: A) the odontobutid *Micropercops swinhonis* (Günther), AMS I.27275, 42 mm SL; B) the thalasseleotridid *Grahamichthys radiatus*, AMS I.41350-001, 51.8 mm SL; C) the thalasseleotridid *Thalasseleotris adela*, AMS I.18241-035, 27.1 mm SL; D) the gobiine gobiid *Lophogobius cyprinoides* (Pallas), AMS uncat., 41 mm SL. Arrow in D points to ventral process; scale bars = 0.5 mm.

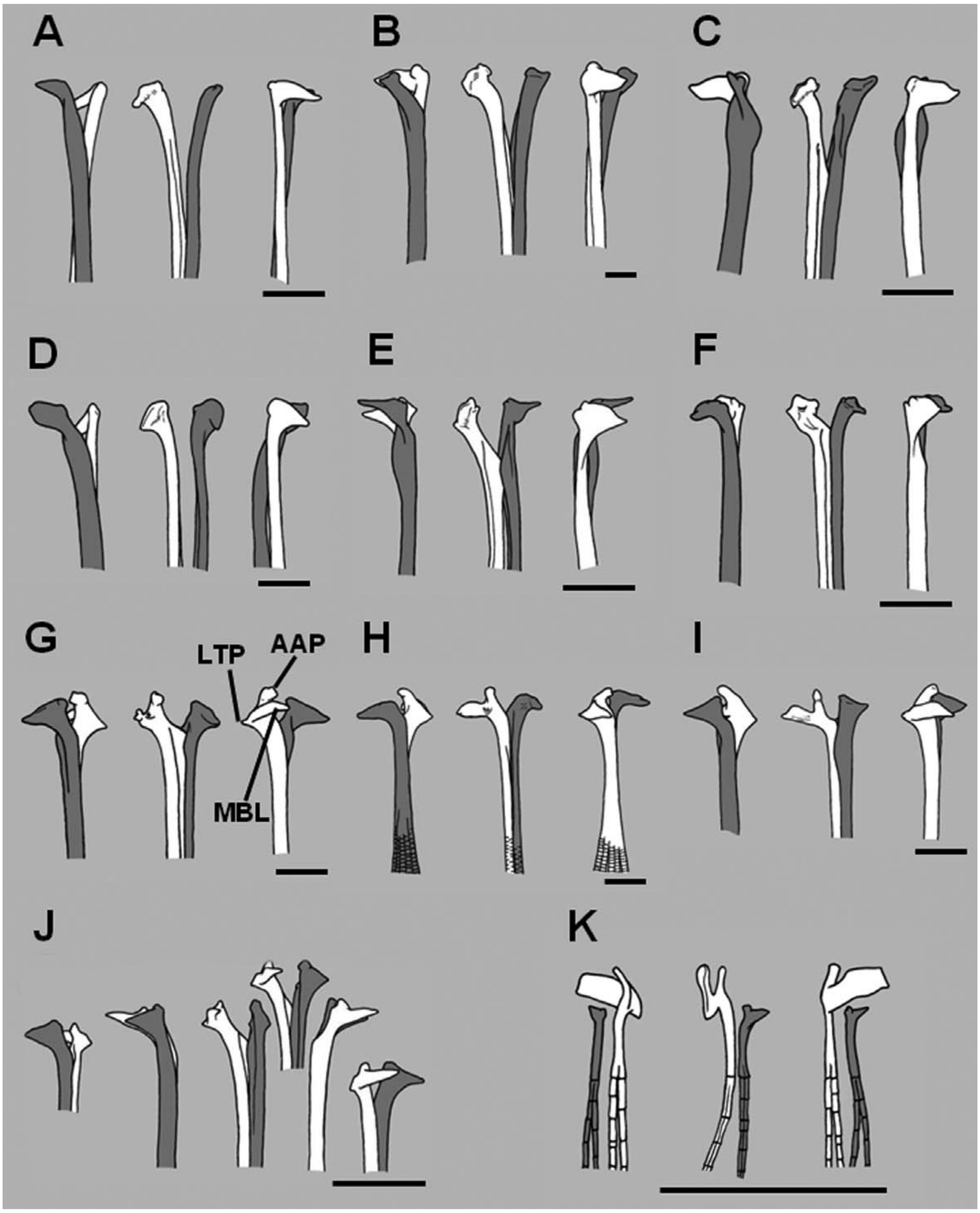

FIGURE 2. Proximal articular head of left 2nd segmented pelvic-fin ray in ventral, medial and dorsal view (from left to right) of: A) the odontobutid *Perccottus glenii* Dybowski, MPM 43268, 52.4 mm SL; B) the eleotridid *Gobiomorus dormitor* Lacepède, MPM 13786, 77.6 mm SL; C) the eleotridid *Guavina micropus* Ginsburg, uncat., 54.1 mm SL, right ray reversed; D) the eleotridid *Eleotris melanosoma* Bleeker, MPM 43115, 61.0 mm SL; E) the thalasseleotridid *Grahamichthys radiata*, MPM 43073, 51.3 mm SL; F) the thalasseleotridid *Thalasseleotris adela*, NMV A.17805, 28.0 mm SL, right ray reversed; G) the gobiine gobiid *Gobius niger* Linnaeus, USNM 298541, 58.2 mm SL, right ray reversed; H) the gobionelline gobiid *Awaous tajasica (*Lichtenstein), MPM 45635, 80.5 mm SL; I) the gobiine gobiid *Acentrogobius viridipunctatus* (Valenciennes in Cuvier & Valenciennes), MPM 32579, 55.8 mm SL; J) the ptereleotrine gobiid *Ptereleotris evides* (Jordan & Hubbs), MPM 40293, 37.8 mm SL, shorter-shafted images show gobiid processes on dorsal hemitrich to better effect and are, left to right, ventral view rotated slightly laterally, medial view rotated slightly dorsally, and dorsal view rotated slightly medially; K) the gobionelline gobiid *Luciogobius* sp., uncat., 62.5 mm SL, right ray reversed, hemitrichs disarticulated and drawn individually. Ventral hemitrich shown dark grey. Labels in G indicate unique gobiid features of dorsal hemitrich: AAP, anterior articular process; LTP, lateral triangular process; MBL, medial blade. Scale bars = 0.5 mm.

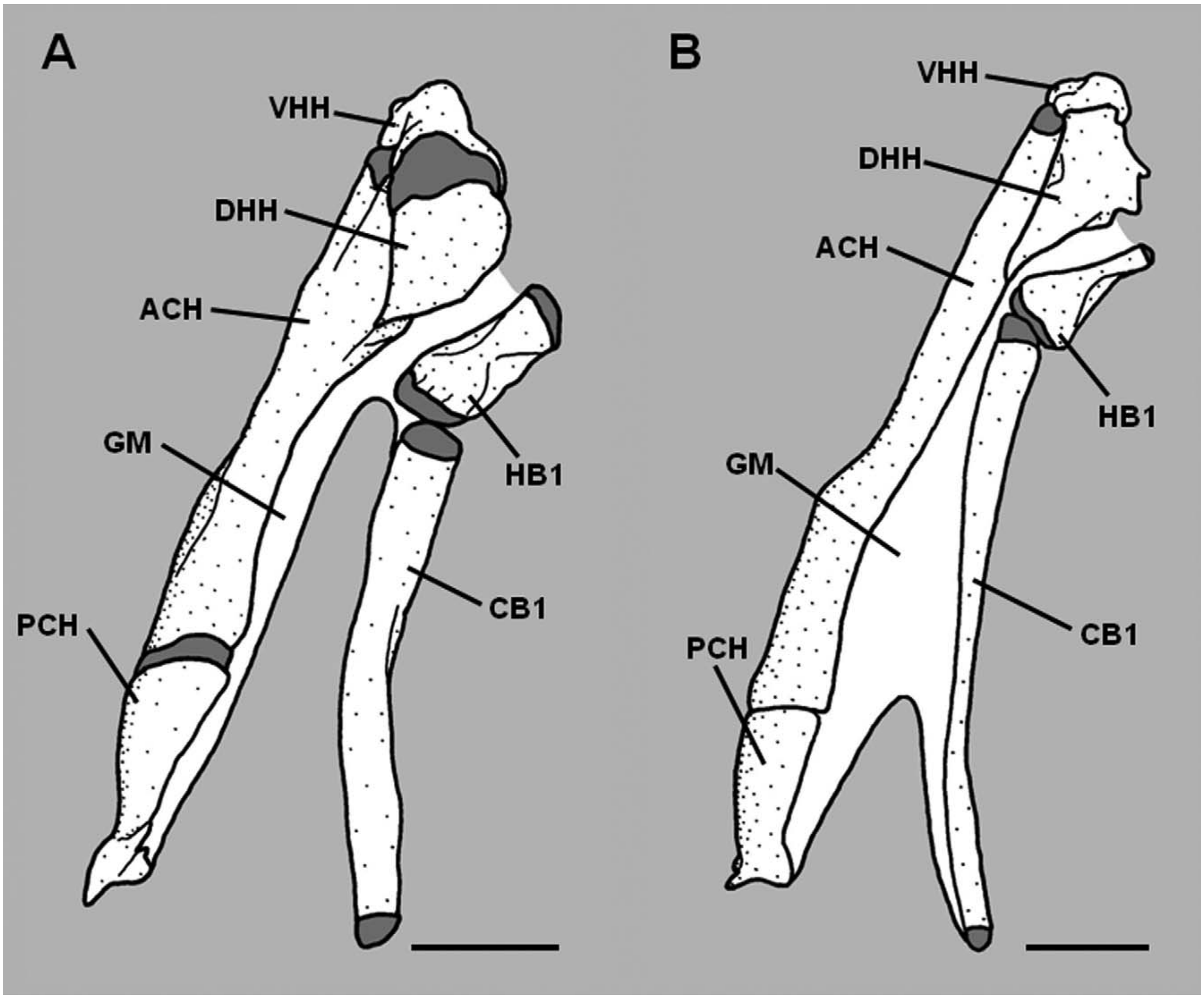

FIGURE 3. Lower part of left side first branchial arch and hyoid arch in dorsal view showing degree of development of gill membrane (white) in: A) the odontobutid *Micropercops swinhonis*, same specimen as in Fig. 1; B) the thalasseleotridid *Grahamichthys radiatus*, same specimen as in Fig. 1. Abbreviations: ACH, anterior ceratohyal; CB1, ceratobranchial 1; DHH, dorsal hypohyal; GM, gill membrane; HB1, hypobranchial 1; PCH, posterior ceratohyal; VHH, ventral hypohyal. Gill rakers not illustrated. Scale bars = 1 mm.

Thalasseleotrididae new family

Type genus. *Thalasseleotris* Hoese & Larson, 1987: 44 (feminine; type species *Thalasseleotris adela* Hoese & Larson 1987 by original designation and monotypy).

Diagnosis. Monophyly of the Thalasseleotrididae is supported by a single synapomorphy: membrane connecting the hyoid arch to ceratobranchial 1 broad, extending most of the length of ceratobranchial 1 (= first gill slit restricted or closed) (Fig. 3B). Among basal gobioids, only certain *Eleotris* Bloch & Schneider species (but not others) are known to have expansion of this membrane with some closure of the first gill slit, although not approaching the extent found in thalasseleotridids (Akihito 1967: figs 18–21). The membrane is, however, similarly developed in members of the gobiid genus *Hetereleotris* Bleeker (Hoese & Larson 2005), and in certain *Eviota* Jenkins species. Because none of these taxa is closely related to thalasseleotridids, we treat the occurrence of restricted or closed gill slits as homoplastic. Other gobioids either have the membrane confined to the extreme base of the first arch (near hypobranchial 1), or only extending to about one third of the length of certatobranchial 1 (Fig. 3A). In addition to this synapomorphy, the two included genera share a range of derived characters that are more broadly distributed among gobioid fishes, including: single epural; no mesopterygoid (= endopterygoid); vertebrae

10 + 15–17 (usually 10 + 16–17; note that McDowall's 1965 counts for *Grahamichthys* exclude the urostylar complex, and thus are one fewer than reported here); first dorsal pterygiophore pattern 3-22110 or 3-22101 (formula follows Birdsong *et al*. 1988); anterior four middle + proximal pterygiophores of first dorsal fin closely applied to each other and tipped distally with cartilage; no bony trough in preopercle for support of laterosensory canal; head and anterior body naked (without scales).

Composition. *Thalasseleotris* Hoese & Larson 1987 (with two species, *T. adela* Hoese & Larson 1987 from temperate Australia, and *T. iota* Hoese & Roberts 2005 from New Zealand); *Grahamichthys* Whitley 1956 (with one species, *G. radiata* (Valenciennes in Cuvier & Valenciennes 1837), from New Zealand).

Remarks. A close relationship between *Grahamichthys* and *Thalasseleotris* was first noted by Hoese and Gill (1993), who suggested that the two genera form the sister group of the Microdesmidae (at that time defined to include the Ptereleotrinae; we include both taxa in the Gobiidae), although they retained them within their Eleotridinae. Earlier, in describing *Thalasseleotris*, Hoese and Larson (1987) noted similarity with the gobiid genus *Hetereleotris*, with which it shares 10 + 17 vertebrae and the first gill slit closed (see above). However, they recognized that it otherwise lacks gobiid specializations, and instead suggested a possible relationship with the Australian eleotridid genus *Philypnodon* Bleeker and the Australian-New Zealand genus *Gobiomorphus* Gill. Our studies do not support a close relationship between these two genera and thalasseleotridids.

We acknowledge that as an alternative to describing the Thalasseleotrididae, we could have simply classified the two included genera in the Gobiidae, which—given the sister relationship noted below—would have not affected the monophyletic status of the Gobiidae *sensu lato*. We have three primary reasons for not choosing this option. Firstly, such action would leave the Gobiidae (an important taxon in various biological and ecological studies) undiagnosed by external characters; in contrast, under our chosen option specimens can be identified to that family on the basis of one readily observed external character (number of branchiostegal rays). Secondly, inclusion of *Thalasseleotris* and *Grahamichthys* in the Gobiidae would have thrown the two genera into the morass that is the suprageneric classification of gobiids. This in turn would have ignored the sister-group relationship between the two genera and the Gobiidae. Thirdly, in order to reflect these relationships, it would ultimately be necessary to erect a family-group name for the two genera anyway (even if only at the subfamilial level).

Sister–group relationship between the Gobiidae and Thalasseleotrididae

A sister-group relationship between the two families is supported by the following synapomorphies.

Interhyal with cup-shaped lateral structure for articulation with preopercle. All examined gobiids and thalasseleotridids have small processes on the lateral surface of the interhyal (though sometimes indistinctly developed in *Grahamichthys*), which usually form a disc- or cup-shaped structure that embraces a small plug of connective tissue and articulate with the medial surface of the preopercle (Fig. 4E–I). The articular surface of the preopercle is also modified for this articulation, but is often more subtle and was not thoroughly surveyed in this study. All other gobioids lack similar lateral structures on the interhyal, although processes are usually present medially on the posterior and anterior edges of the bone (Fig. 4A–D). The noteworthy exception among gobiids is the highly paedomorphic *Schindleria*, in which the preopercle does not develop, and the interhyal is present as a simple, short rod of cartilage (Johnson & Brothers 1993: figs. 6c, 8b).

Posterior ceratohyal with laterally-directed process to support a posteriorly-positioned interhyal. In all basal gobioids, the posterior ceratohyal has a dorsal articulation with the interhyal, composed of a short medial shelf with a socket for the cartilaginous tip of the interhyal followed by a posteriorly-directed extension (Fig. 3A; Fig. 5A–D). The interhyal of gobiids and thalasseleotridids shares an extreme posterior articulation with the ceratohyal (Fig. 5E–I) that is distinctive relative to most basal gobioids. In this arrangement, the medial shelf of the posterior ceratohyal is retained, but the posterior articulation is laterally positioned (rather than posteriorly) and modified in such a way as to form an angled T-shaped support for the interhyal in dorsal view (Fig. 3B; Fig. 5E–I). In *Dormitator*, the one eleotridid taxon that superficially resembles the derived condition in having a posteriorly-positioned interhyal, a dorsal view of the posterior ceratohyal shows that it does not exhibit the laterally displaced posterior process found in Thalasseleotrididae and Gobiidae. Rather, the posteriorly directed posterior ceratohyal process is present, but reduced in *Dormitator* (Fig. 5D).

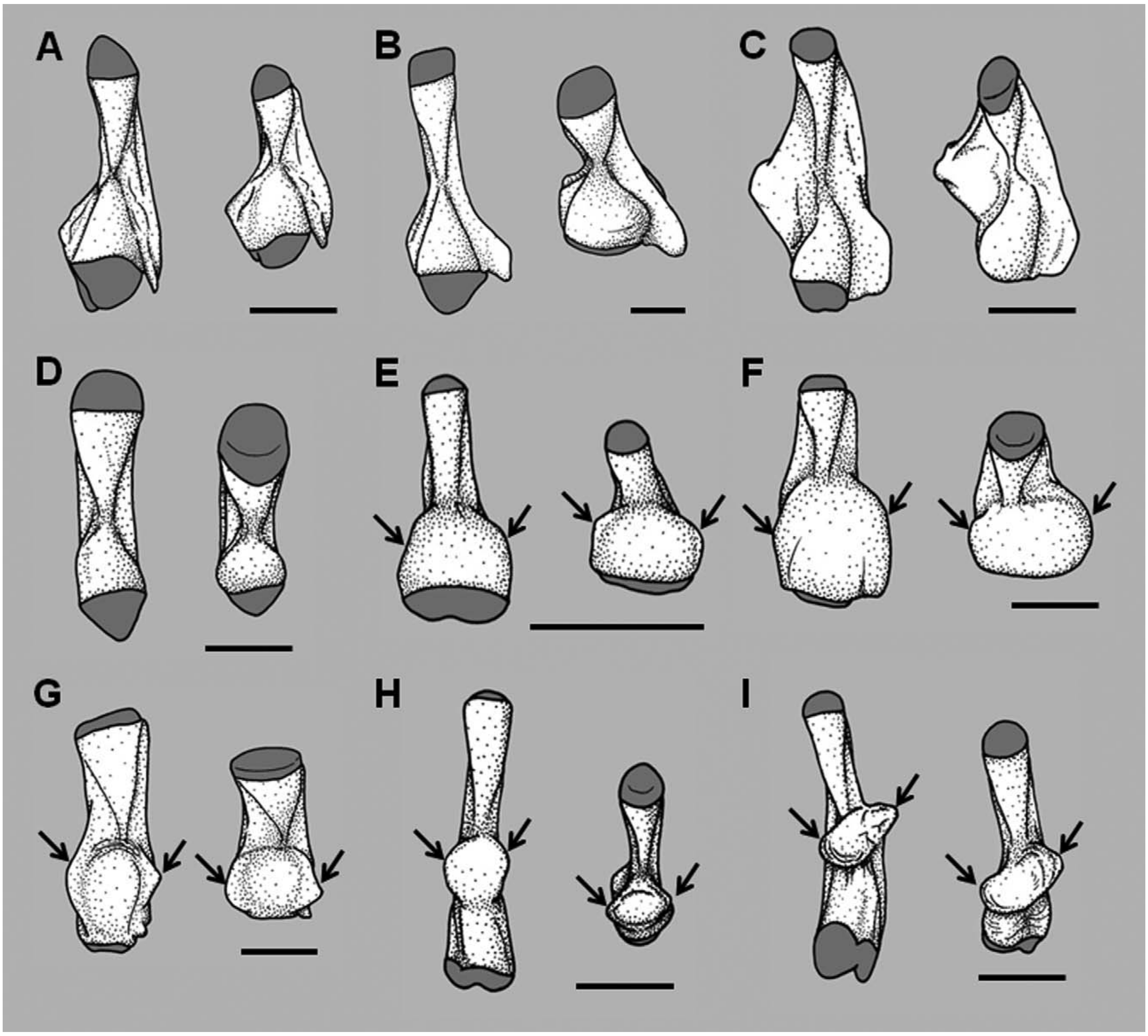

FIGURE 4. Lateral (left) and dorso-lateral (right) views of left interhyal of: A) the odontobutid *Perccottus glenii*, same specimen as in Fig. 2; B) the eleotridid *Gobiomorus dormitor*, same specimen as in Fig. 2; C) the eleotridid *Eleotris melanosoma*, same specimen as in Fig. 2; D) the eleotridid *Dormitator latrifrons* (Richardson), ANSP 140703, 53.1 mm SL ; E) the thalasseleotridid *Thalasseleotris adela*, same specimen as in Fig. 2; F) the thalasseleotridid *Grahamichthys radiata*, same specimen as in Fig. 2; G) the gobiine gobiid *Gobius niger*, same specimen as in Fig. 2; H) the gobionelline gobiid *Stenogobius zurstrasseni* (Popta), USNM 264770, 45.9 mm SL (right side reversed); I) the gobiine gobiid *Valenciennea sexguttata* (Valenciennes in Cuvier & Valenciennes), MPM 43110, 55.5 mm SL. Arrows in E–I indicate cup-shaped process. Scale bars = 0.5 mm.

Pharyngobranchial 4 absent, epibranchial 4 directly articulating with pharyngobranchial 3. A cartilaginous pharyngobranchial 4 is present in all basal gobioids except derived xenisthmids (Gill & Hoese 1993; Fig 6A). The structure is absent in gobiids, *Thalasseleotris* and *Grahamichthys* (Fig. 6B–D). Springer & Johnson (2004: table 11) indicated that PB4 is present in the ptereleotrine gobiid *Nemateleotris* Fowler, but our examination of their and other specimens of the genus failed to reveal this structure. Along with the loss of the cartilaginous pharyngobranchial 4 is a concomitant shift of the articulation of the medial head of epibranchial 4 directly to pharyngobranchial 3. Wang & Winterbottom (2006: fig. 7) illustrated the gill arches of the ptereleotrine *Parioglossus raoi* (Herre) with epibranchial 4 in a relatively posterior and lateral position, and articulating medially with the pharyngobranchial 4 toothplate, rather than with pharyngobranchial 3. However, as noted in their figure caption and description, the depiction is inaccurate, and epibranchial 4 should be positioned more medially and anteriorly. In our material of the genus (e.g., *P. philippinus* (Herre), AMS uncat.; *P. raoi*, MPM 43121), the medial tip of epibranchial 4 articulates solely with pharyngobranchial 3.

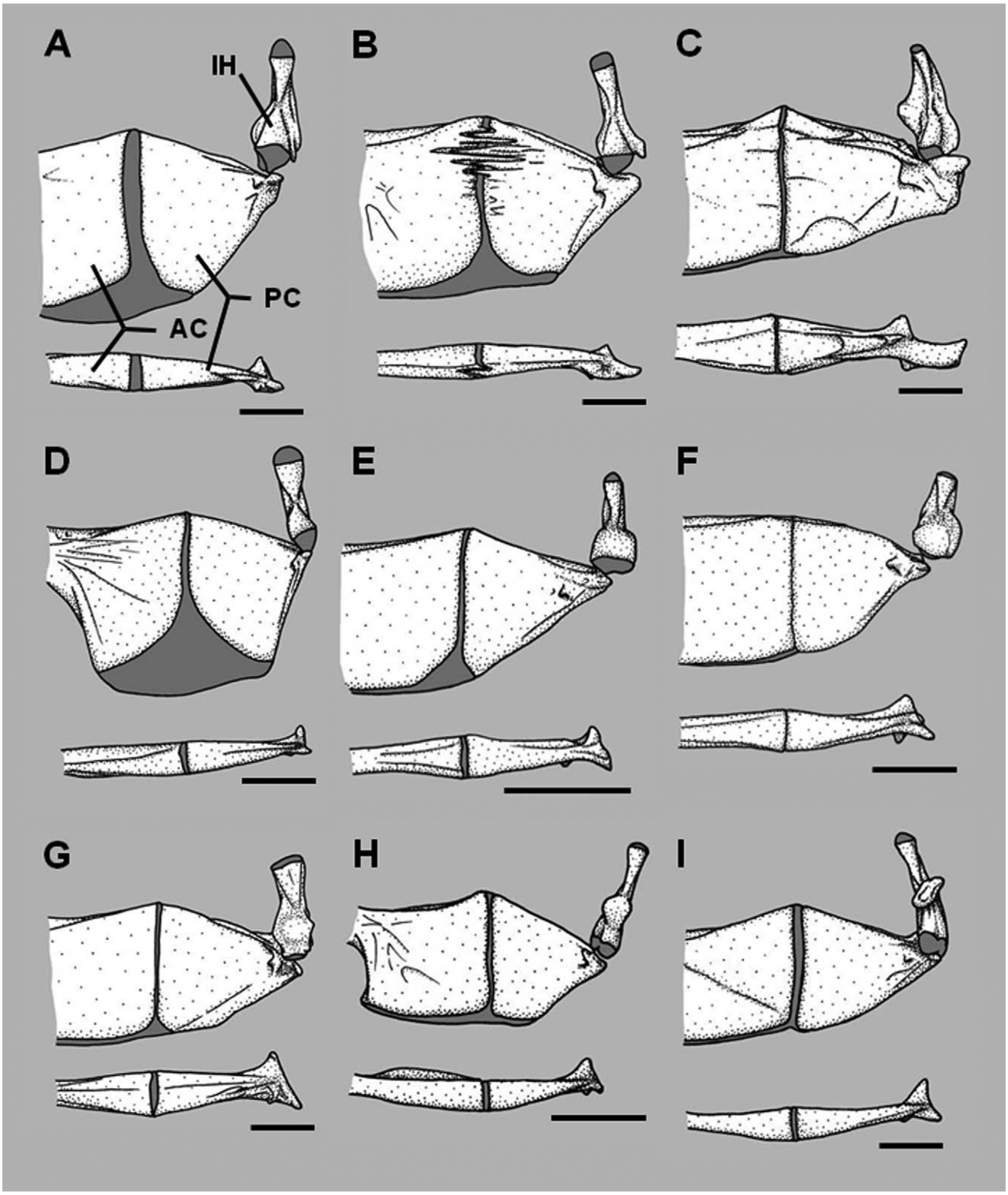

FIGURE 5. Lateral view of left posterior ceratohyal and interhyal, and dorsal view of posterior ceratohyal with interhyal removed of: A) the odontobutid *Perccottus glenii*; B) the eleotridid *Gobiomorus dormitor*; C) the eleotridid *Eleotris melanosoma*; D) the eleotridid *Dormitator latrifrons*; E) the thalasseleotridid *Thalasseleotris adela*; F) the thalasseleotridid *Grahamichthys radiata*; G) the gobiine gobiid *Gobius niger*; H) the gobionelline gobiid *Stenogobius zurstrasseni*; I) the gobiine gobiid *Valenciennea sexguttata*. All specimens as in Fig. 4. Scale bars = 1 mm. AC, anterior ceratohyal; PC, posterior ceratohyal; IH, interhyal.

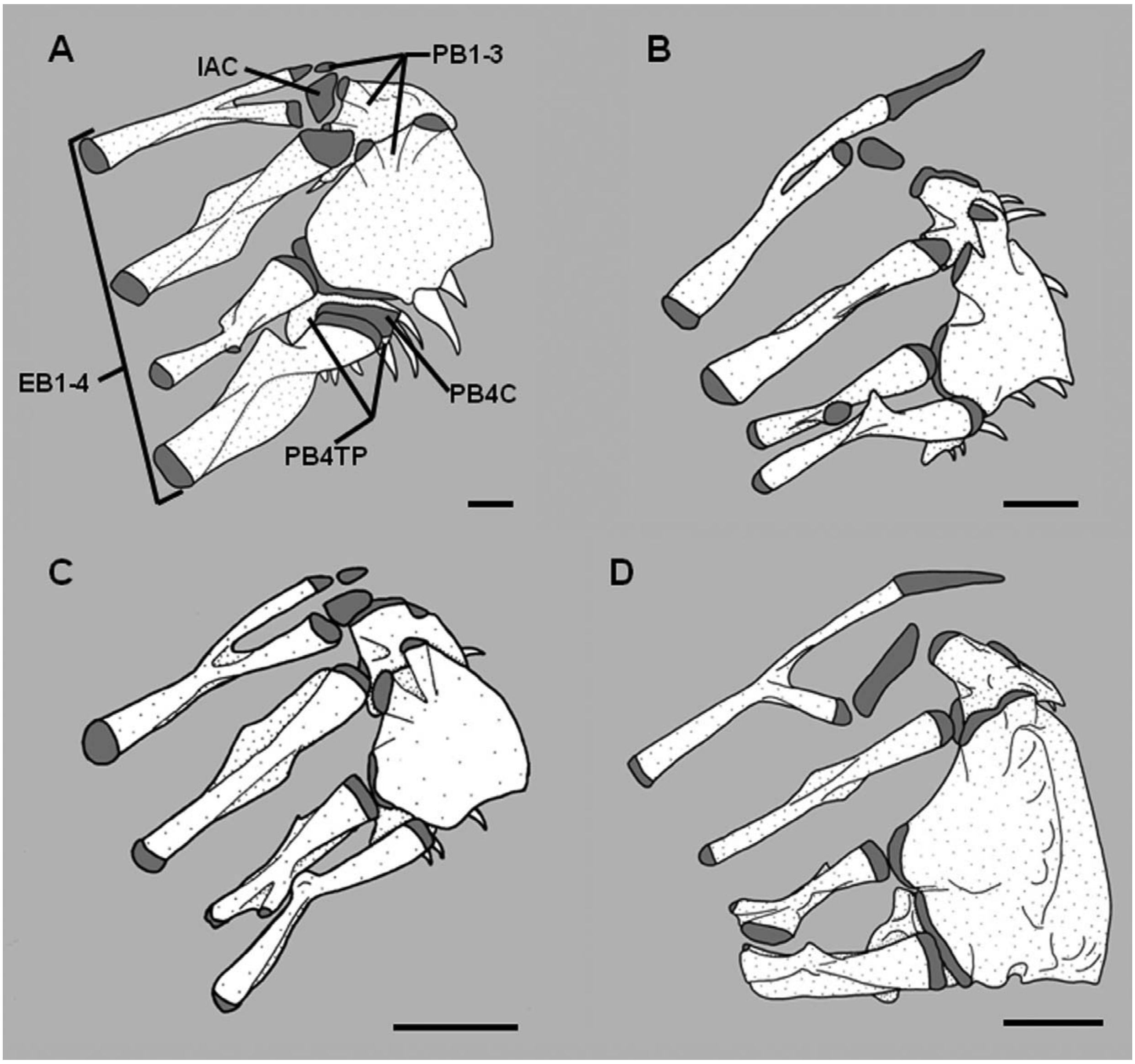

FIGURE 6. Dorsal view of left dorsal gill arches of: A) the odontobutid *Perccottus glenii*, same specimen as in Fig. 2; B) the thalasseleotridid *Grahamichthys radiatus*, same specimen as in Fig. 1; C) the thalasseleotridid *Thalasseleotris adela*, same specimen as in Fig. 1; D) the gobiine gobiid *Callogobius maculipinnis* (Fowler), MPM 45773, 31.6 mm SL. Abbreviations: IAC – interarcual cartilage; EB1–4, epibranchials 1–4; PB1–3, pharyngobranchials 1–3; PB4C, pharyngobranchial 4 cartilage; PB4TP, pharyngobranchial 4 toothplate. Gill rakers not illustrated. Scale bars = 0.5 mm.

Dorsal postcleithrum absent. Almost all basal gobioids have a dorsal postcleithrum, which is positioned just behind the upper part of the pectoral fin, articulating via connective tissue at its dorsal tip with the posterodorsal corner of the cleithrum and midway along its length with the distal tip of the first epineural. It is absent in *Thalasseleotris*, *Grahamichthys* and all examined gobiids. Among basal gobioids, it is otherwise absent only in derived xenisthmids (Springer 1983, 1988), but is present in the basal genus *Paraxenisthmus* Gill & Hoese (Gill & Hoese 1993: fig. 8). Akihito (1969, 1986) also documented the distribution of this bone in gobioid fishes, noting that it was absent in gobiids (his gobiines), *Xenisthmus* Snyder and *Grahamichthys*.

Urohyal without ventral shelf. Most basal gobioids have a shelf or lamina on the ventral edge of the urohyal. In contrast, gobiids and thalasseleotridids lack this structure. It is also lacking in the Xenisthmidae, suggesting that the three families form a monophyletic group. However, our analyses do not support this relationship and suggest instead that the family is more basally positioned within the Gobioidei. We therefore consider the absence of a ventral shelf on the urohyal in that family as non-homologous with the condition found in gobiids and thalasseleotridids. This character was also discussed and illustrated by Akihito (1986: 636, fig. 8), who reported a similar distribution among gobioids.

Discussion

Perhaps the most important (and common) empirical contribution of cladistics is the reassessment of taxa that are undiagnosed by apomorphic characters (and thus essentially defined by symplesiomorphies), and the subsequent conclusion that such taxa are paraphyletic. As Nelson (1989, p. 276), put it "paraphyly is cladistics' stock in trade." The present study represents a contribution to our ongoing understanding of one such group undiagnosed by apomorphic characters—the Eleotrididae. Traditionally the Eleotrididae has served to accommodate an assemblage of gobioid taxa that are not placed among the more derived taxa (= Gobiidae in our sense). Previous morphology-based contributions to refinement of the Eleotrididae have included the removal of *Rhyacichthys* Boulenger to the Rhyacichthyidae as the sister-group to all other gobioids by Miller (1973) and Springer (1983), and the erection of the Odontobutidae by Hoese and Gill (1993) with concomitant diagnosis of an un-named clade consisting of all gobioids exclusive of rhyacichthyids and odontobutids. In this light, the primary contribution in the present study is not so much the erection of a new family (for which we have only a single synapomorphy), but in further clarifying the Eleotrididae by diagnosing an exclusive relationship between the two included genera and the Gobiidae. Our ongoing morphological studies anticipate that further refinement of the Eleotrididae is needed. Recent molecular studies (e.g., Akihito 2000a; Wang *et al*. 2001; Thacker 2003, 2009; Thacker & Hardman 2005) have also suggested that the traditional Eleotrididae is paraphyletic, though each study differs markedly in the details of paraphyly (see Mooi & Gill 2010). Remarkably, neither *Grahamichthys* nor *Thalasseleotris* have participated in molecular studies to date. Our intention in the present study is, in part, to draw attention to the two genera and their prominent position as sister group to the Gobiidae.

Acknowledgements

We are grateful to D.F. Hoese for his helpful discussions of gobioid systematics and for sharing his unpublished data on thalasseleotridids. We also thank Emperor Akihito and V.G. Springer for helpful discussions on basal gobioid anatomy and relationships. For the loan or gift of specimens used in this study we thank Emperor Akihito, M. Aizawa, D. Bray, B. Brown, O. Crimmen, N. Delventhal, M. Gomon, R. Henderson, D.F. Hoese, Y. Ikeda, C. Johnston, J. Lundberg, J. Maclaine, M. McGrouther, D. Nelson, L. Palmer, C. Rader, C. Roberts, M. Rogers, M. Sabaj, K. Sakamoto, A. Stewart, M. Westneat, J.W. Williams, R. Winterbottom, J. van Tassell and staff of three aquarium stores in Arizona ("About the Reef", Scottsdale, "Pets Inc.", Tempe, and "Aquarium Arts", Mesa). N. Gill assisted with figure preparation. The manuscript was improved by helpful comments from H.K. Larson and an anonymous reviewer. This study was supported by National Science Foundation (USA) awards DEB-0108244 to RDM and DEB-0541914 to ACG, Natural Sciences and Engineering Research Council of Canada Discovery Grant 327844-06 to RDM, and an Australian Museum Visiting Research Fellowship to ACG.

References

Akihito, Prince. (1967) On four species of the gobiid fishes of the genus *Eleotris* found in Japan. *Japanese Journal of Ichthyology*, 14, 135–166.

Akihito, Prince. (1969) A systematic examination of the gobiid fishes based on the mesopterygoid, postcleithra, branchiostegals, pelvic fins, scapula and suborbital. *Japanese Journal of Ichthyology*, 16, 93–114.

Akihito, Prince (1986) Some morphological characters considered to be important in gobioid phylogeny. *In*: Uyeno, T., Arai, R., Taniuchi, T. & Matsuura, K. (Eds), *Indo-Pacific Fish Biology. Proceedings of the Second International Conference on Indo-Pacific Fishes*. The Ichthyological Society of Japan, Tokyo, pp. 629–639.

Akihito, Prince, Hayashi, M., Yoshino, T., Shimada, K., Yamamoto, T., & Senou, H. (1984) Suborder Gobioidei. *In*: Masuda, H., Amaoka, K., Araga, C., Uyeno, T., & Yoshino, T. (Eds), *The Fishes of the Japanese Archipelago.* Tokai University Press, Tokyo, pp. 236–289. English text; plates 235–258 and 353–355.

Akihito, Iwata, A., Kobayashi, T., Ikeo, K., Imanishi, T., Ono, H., Umehara, Y., Hamamatsu, C., Sugiyama, K., Ikeda, Y., Sakamoto, K., Fumihito, A., Ohno, S. & Gojobori, T. (2000a) Evolutionary aspects of gobioid fishes based upon a phylogenetic analysis of mitochondrial cytochrome b genes. *Gene,* 259, 5–15.

Akihito, Sakamoto, K., Ikeda, Y. & Iwata, A. (2000b) Suborder Gobioidei. *In*: Nakabo, T. (Ed.), *Fishes of Japan with Pictorial Keys to the Species*, second edition. Tokai University Press, Tokyo, pp. 1139–1310.

Birdsong, R.S., Murdy, E.O. & Pezold, F.L. (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 système naturel des Gobioïdes. *Archives néerlandaises des sciences exactes et naturelles*, 9, 289–331.

Cuvier, G.L.F.C.D. (1816) *Le Regne Animal.* Volume 2, xviii + 532 pages.

Cuvier, G. & Valenciennes, M.A. (1837) *Histoire de Naturelle Poissons*, 12, i–xxiv + 1–507 + 1 p., pls. 344–368.

Eschmeyer, W.N. (1998a) Introduction. *In*: Eschmeyer, W.N. (Ed.) Catalog of Fishes. *Center for Biodiversity Research and Information, California Academy of Science, Special Publication,* 1, 7–24.

Eschmeyer, W.N. (1998b) Part III. Species in a classification. *In*: Eschmeyer, W.N. (Ed.) Catalog of Fishes. *Center for Biodiversity Research and Information, California Academy of Science, Special Publication,* 1, 2175–2448.

Eschmeyer, W.N. (1998c) Part IV. Genera in a classification. *In*: Eschmeyer, W.N. (Ed.) Catalog of Fishes. *Center for Biodiversity Research and Information, California Academy of Science, Special Publication,* 1, 2449–2499.

Gill, A.C. & Hoese, D.F. (1993) *Paraxenisthmus springeri*, new genus and species of gobioid fish from the West Pacific, and its phylogenetic position within the Xenisthmidae. *Copeia,* 1993, 1049–1057.

Gill, A.C. & Mooi, R.D. (2010) Character evidence for the monophyly of the Microdesminae, with comments on relationships to *Schindleria* (Teleostei: Gobioidei: Gobiidae). *Zootaxa,* 2442, 51–59.

Günther, A. (1861) *Catalogue of the Acanthopterygian Fishes in the Collection of the British Museum. Volume Third.* Trustees of the British Museum, London, xxv + 586 pp.

Hoese, D.F. (1984) Gobioidei: relationships. *In*: Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall, A.W., Jr., & Richardson, S.L. (Eds.). Ontogeny and Systematics of Fishes. *American Society of Ichthyologists and Herpetologists Special Publication*, 1, 588–591.

Hoese, D.F. & Gill, A.C. (1993) Phylogenetic relationships of eleotridid fishes (Perciformes: Gobioidei). *Bulletin of Marine Science,* 52, 415–440.

Hoese, D.F. & Larson, H.K. (1987) New Australian fishes. Part 11. A new genus and species of eleotridid (Gobioidei) from southern Australia with a discussion of relationships. *Memoirs of the Museum of Victoria,* 48, 43–50.

Hoese, D.F. & Larson, H.K. (2005) Description of two new species of *Hetereleotris* (Gobiidae) from the south Pacific, with a revised key to species and synonymization of the genus *Pascua* with *Hetereleotris*. *Zootaxa*, 1096, 1–16.

Hoese, D. F. & Roberts, C.D. (2005) A new species of the eleotrid genus *Thalasseleotris* (Teleostei: Gobioidei) from New Zealand coastal waters. *Journal of the Royal Society of New Zealand*, 35, 417–431.

Johnson, G.D. & Brothers, E.B. (1993) *Schindleria*, a paedomorphic goby (Teleostei: Gobioidei). *Bulletin of Marine Science,* 52, 441–471.

McDowall, R.M. (1965) Descriptive and taxonomic notes on *Grahamichthys radiatus* (Valenciennes), Eleotridae. *Transactions of the Royal Society of New Zealand, Zoology,* 7, 51–56.

Miller, P.J. (1973) The osteology and adaptive features of *Rhyacichthys aspro* (Teleostei: Gobioidei) and the classification of gobioid fishes. *Journal of Zoology, London*, 171, 397–434.

Mooi, R.D. & Gill, A.C. (2010) Phylogenies without synapomorphies—a crisis in fish systematics: time to show some character. *Zootaxa,* 2450, 26–40.

Mooi, R.D., Williams, D.M. & Gill, A.C. (2011) Numerical cladistics, an unintentional refuge for phenetics: a reply to Wiley *et al. Zootaxa*, 2946, 17–28.

Murdy, E.O. (1985) Osteology of *Istigobius ornatus*. *Bulletin of Marine Science*, 36, 124–138.

Nelson, G. (1989) Cladistics and evolutionary models. *Cladistics*, 5, 275–289.

Nelson, J.S. (1984) *Fishes of the World.* Second Edition. New York, John Wiley and Sons, 523 pp.

Nelson, J.S. (1994) *Fishes of the World.* Third Edition. New York, John Wiley and Sons, 600 pp.

Nelson, J.S. (2006) *Fishes of the World.* Fourth Edition. Hoboken, New Jersey, John Wiley and Sons, 601 pp.

Senou, H., Suzuki, T., Shibukawa, K. & Yano, K. (2004) *A Photographic Guide to the Gobioid Fishes of Japan*. Heibonsha, Tokyo, 534 pp.

Springer, V.G. (1983) *Tyson belos*, new genus and species of western Pacific fish (Gobiidae, Xenisthminae), with discussions of gobioid osteology and classification. *Smithsonian Contributions to Zoology*, 390, 1–40.

Springer, V.G. (1988) *Rotuma lewisi*, new genus and species of fish from the southwest Pacific (Gobioidei, Xenisthmidae). *Proceedings of the Biological Society of Washington*, 101, 530–539.

Springer, V.G. & Johnson, G.D. (2004) Study of the dorsal gill-arch musculature of teleostome fishes, with special reference to the Actinopterygii. *Bulletin of the Biological Society of Washington*, 11, 1–260, 205 pls.

Taylor, W.R. & Van Dyke, G.C. (1985) Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9, 107–119.

Thacker, C. (2000) Phylogeny of the wormfishes (Teleostei: Gobioidei: Microdesmidae). *Copeia,* 2000, 940–957.

Thacker, C.E. (2003) Molecular phylogeny of the gobioid fishes (Teleostei: Perciformes: Gobioidei). *Molecular Phylogenetics and Evolution*, 26, 354–368.

Thacker, C.E. (2009) Phylogeny of Gobioidei and placement within Acanthomorpha with a new classification and investigation of diversification and character evolution. *Copeia,* 2009, 93–104.

Thacker, C.E. & Hardman, M.A. (2005) Molecular phylogeny of basal gobioid fishes: Rhyacichthyidae, Odontobutidae, Xenisthmidae, Eleotridae (Teleostei: Perciformes: Gobioidei). *Molecular Phylogenetics and Evolution,* 37, 858–871.

Wang, H.-Y., Tsai, M.-P., Dean, J., & Lee, S.-C. (2001) Molecular phylogeny of gobioid fishes (Perciformes: Gobioidei) based on mitochrondrial 12S rRNA sequences. *Molecular Phylogenetics and Evolution*, 20, 390–408.

Wang, R. & Winterbottom, R. (2006) Osteology and phylogeny of *Parioglossus* (Teleostei, Gobioidei), with a revised key to the species. *Zootaxa*, 1131, 1–32.

Whitley, G. P. (1956) New fishes from Australia and New Zealand. *Proceedings of the Royal Zoological Society of New South Wales*, 1954–55, 34–38.