

**Relationships of sauries and needlefishes
(Teleostei: Scomberesocoeida) to the internally fertilizing
halfbeaks (Zenarchopteridae) based on the pharyngeal
jaw apparatus**

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Abstract.—The 40 life history, myological, and osteological characters that Tibbetts (1992) used in his study of the hemiramphids are evaluated for both saury genera (*Cololabis* and *Scomberesox*) to determine if the Scomberesocidae are more closely related to the Zenarchopteridae, to the needlefishes (Belonidae), or to the halfbeaks (Hemiramphidae) and flyingfishes (Exocoetidae). Data were analyzed using PAUP*, and eight equally parsimonious trees were found (70 steps, CI 0.814, RI 0.938). This analysis indicates that sauries are most closely related to needlefishes, supporting the historical concept of the superfamily Scomberesocoeida as a monophyletic assemblage. A caudal displacement of the origin of the retractor dorsalis muscle is a tentative additional synapomorphy for all four saury species. Zenarchopteridae is strongly supported as a valid family sister to the Scomberesocoeida (decay index = 19, bootstrap = 100). Resolution of the internal structure of the Belonidae and the Hemiramphidae requires the identification of additional characters and examination of a greater number of taxa.

The teleostean order Beloniformes is composed of the needlefishes (family Belonidae), sauries (Scomberesocidae), halfbeaks (Hemiramphidae), flyingfishes (Exocoetidae), and rice fishes (Adrianichthyidae). Schlesinger (1909) and Regan (1911) recognized two superfamilies, the Scomberesocoeida (sauries + needlefishes) and Exocoetoidea (halfbeaks + flyingfishes). Rosen & Parenti (1981) later added the rice fishes to the order as a separate suborder. Collette et al. (1984) identified two synapomorphies that unite the Scomberesocoeida: presence of a premaxillary lateral line

canal, and a slightly or very elongate upper jaw.

Collette et al. (1984) also reaffirmed the monophyly of halfbeaks by identifying eight synapomorphic morphological characters, but Tibbetts' (1992) extensive investigation of the pharyngeal jaw apparatus (PJA) suggested that the family is paraphyletic. A subsequent total evidence analysis including nuclear and mitochondrial genes (Lovejoy 2000, Lovejoy et al. 2004) strongly indicated a paraphyletic Hemiramphidae basal to the needlefish and saury clade. Both of these studies (Tibbetts 1992, Lovejoy 2000) suggested that the five genera of internally fertilizing Indo-West Pacific halfbeaks (Zenarchopteridae) are more closely

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related to the Scomberesocidea than to the Exocoetoidea. Additional comparisons between the herbivorous Hemiramphidae and the carnivorous zenarchopterid genus *Zenarchopterus* revealed differences in the PJA (Tibbetts & Carseldine 2003).

Fowler (1934) described four subfamilies within the family Hemiramphidae. His Zenarchopterinae contained *Zenarchopterus*, *Hemirhamphodon*, *Arrhamphus*, and *Melapedalion* and his Dermogenyinae contained *Dermogenys* and *Nomorhamphus*. Monophyly of the group containing four of these genera, *Zenarchopterus*, *Hemirhamphodon*, *Dermogenys*, and *Nomorhamphus* was proposed as the subfamily Zenarchopterinae by Anderson & Collette (1991) based on five synapomorphies. Based on internal fertilization, several characters of sperm morphology, and Tibbetts' (1992) unpublished doctoral dissertation, Jamieson & Grier (1993) recognized the internally-fertilizing halfbeaks as the family Zenarchopteridae. Collette (1995), Meisner & Collette (1999), Meisner (2001), and Collette (2004b) continued to recognize the group at the subfamily level and added a fifth genus, *Tondanichthys*. Based on molecular data, Lovejoy (2000) and Lovejoy et al. (2004) recognized a monophyletic unit as the Indo-West Pacific ("IWP") halfbeaks containing four genera of Zenarchopterinae (all except *Tondanichthys*) that was more closely related to sauries (Scomberesocidae) and needlefishes (Belonidae) than to other halfbeaks (Hemiramphidae) and flyingfishes (Exocoetidae).

Lovejoy's (2000) consensus tree shows a robust relationship between the sauries and the needlefish genus *Belone*, suggesting a paraphyletic Belonidae, but the position of this clade within the Scomberesocidea is uncertain. Lovejoy (2000) noted that his morphological data set was relatively small, and inclusion of additional characters could yield a better-resolved phylogenetic tree.

Monophyly has been hypothesized for the sauries, flyingfishes (Lovejoy 2000, Lovejoy et al. 2004), and Zenarchopterinae (Meisner 2001), but no sauries were includ-

ed in Tibbetts' (1992) analysis of the PJA. Sauries are valuable commercial fishes in some areas such as the Mediterranean and are important links in the epipelagic food chain (Hardy & Collette 2003). The family has been diagnosed by one synapomorphy: a series of four to seven finlets posterior to the dorsal and anal fins. There are four recognized extant species in two genera, *Cololabis* and *Scomberesox*, each comprising a large and a dwarf species (Hubbs & Wisner 1980, Collette et al. 1984, Collette 2004a).

The pharyngeal region of the two large saury species was examined to expand Tibbetts' (1992) 40-character data matrix. The Pacific saury, *Cololabis saira* (Brevoort, 1856), and the Atlantic saury, *Scomberesox saurus* (Walbaum, 1792), were studied to determine if sauries are more closely related to the Belonidae, to the Zenarchopteridae, or to the Hemiramphidae and Exocoetidae.

Materials and Methods

Character analysis.—Investigations were limited to assessing Tibbetts' (1992) 40 morphological and life history characters (Appendix I) in *C. saira* and *S. saurus*. The dwarf species were not comprehensively examined due to difficulty in unambiguously resolving character states in these small fishes. While examining sauries, it became apparent that several of the character states in Tibbetts (1992) were not defined rigorously. We decided to include the sauries and will clarify the character states in a later paper by Collette & Tibbetts. All morphological character states for a needlefish (*Belone belone*), a halfbeak (*Arrhamphus sclerolepis*), and a zenarchopterid (*Zenarchopterus buffonis*), as described by Tibbetts (1992), were confirmed. Specimens of additional species such as a flyingfish (*Fodiator acutus*) and the two dwarf sauries were examined to resolve character states as necessary.

Tibbetts' (1992) coding of the association of the third pharyngobranchials (Appendix I, character 15) as fused in *Hemi-*

ramphus was found to be inaccurate. The genus exhibits suturally united third pharyngobranchials. This character state in *Hemiramphus* was updated in the data matrix. States for all taxa described in Tibbetts (1992) as having fused third pharyngobranchials were changed to “?” until the bones can be further examined in cross section. The fused condition was confirmed in *Arrhamphus*, and coding was unaltered.

Pharyngeal dissection.—All studied specimens (Appendix II) were obtained from the National Museum of Natural History (USNM). The standard length of each specimen was measured (± 0.1 mm) with Scherr-Tumico, Inc. calipers. After external examination, specimens were placed in a 95% ethanol plus alizarin red S solution until the bones were stained red. Line illustrations of pharyngeal bones were prepared for *C. saira* and *S. saurus* using a Wild Heerbrugg binocular dissecting microscope and camera lucida.

Dissection procedure followed Tibbetts (1992). Following examination of the distal musculature, the branchial arches were removed to expose the proximal muscles and bones. The first through fourth epibranchials, fifth ceratobranchial, and second and third pharyngobranchials were removed. Cleared and stained specimens were not dissected, but were examined by light microscopy. Photographs were taken with a Nikon D100 6.1 megapixel camera and a 105 mm macro lens.

Electron microscopy.—Scanning electron microscopy (SEM) was used to investigate pharyngeal tooth plate characters in finer detail. The fifth ceratobranchial and second and third pharyngobranchials were placed in trypsin solution (30 ml saturated aqueous sodium borate, 70 ml distilled water, and 1 g trypsin) following Dingerkus & Uhler (1977) at room temperature for 72 h to macerate adherent tissues. The bones were de-tissued using forceps, rinsed in tap water, subjected to an ultrasonic bath, and then rinsed again. After dehydration in absolute ethanol, bones were air-dried. Spec-

imens were mounted on 10 mm diameter aluminum stubs, sputter coated with 25 nm of gold, and examined under a Leica Stereoscan 440 or an Amray 1810 scanning electron microscope with LaB₆ sources.

Phylogenetic analysis.—As one pair of taxa, *Hyporhamphus* and *Reporhamphus*, had identical sets of character states, the latter was excluded from the analysis. Tibbetts (1992) similarly discarded *Melapedalion* because of its identical coding to *Arrhamphus*, which was again here removed because the only potential coding difference between the two is the ambiguous degree of third pharyngobranchial association.

A matrix of the 40 characters and 17 remaining taxa was analyzed with PAUP* version 4.0b10 for the Macintosh (Swofford 2003). The heuristic search algorithm (100 replicates of random taxon additions, TBR branch swapping, seed = 2132174257) was used to search for the most parsimonious trees (Lovejoy 2000). All characters were unweighted and unordered. *Parexocoetus* was used as a root for the ingroup analysis because of its strongly supported basal position within the Beloniformes (Lovejoy 2000). Bootstrap values were calculated using PAUP* (100 replicates, seed = 1865323342), and decay indices for nodes were obtained using TreeRot version 2 (Sorensen 1999).

Results

Phylogenetic analysis.—PAUP* yielded eight equally parsimonious trees (70 steps, consistency index = 0.814, retention index = 0.938). A strict consensus of these trees (Fig. 1) contains a large polytomy obscuring the structure of the externally fertilizing halfbeak group.

The sauries and needlefishes are sister clades most closely related to a monophyletic Zenarchopteridae. The pairing of the saury + needlefish clade and the Zenarchopteridae is strongly supported (decay index = 19, bootstrap = 100). The remaining halfbeaks form an unresolved assemblage

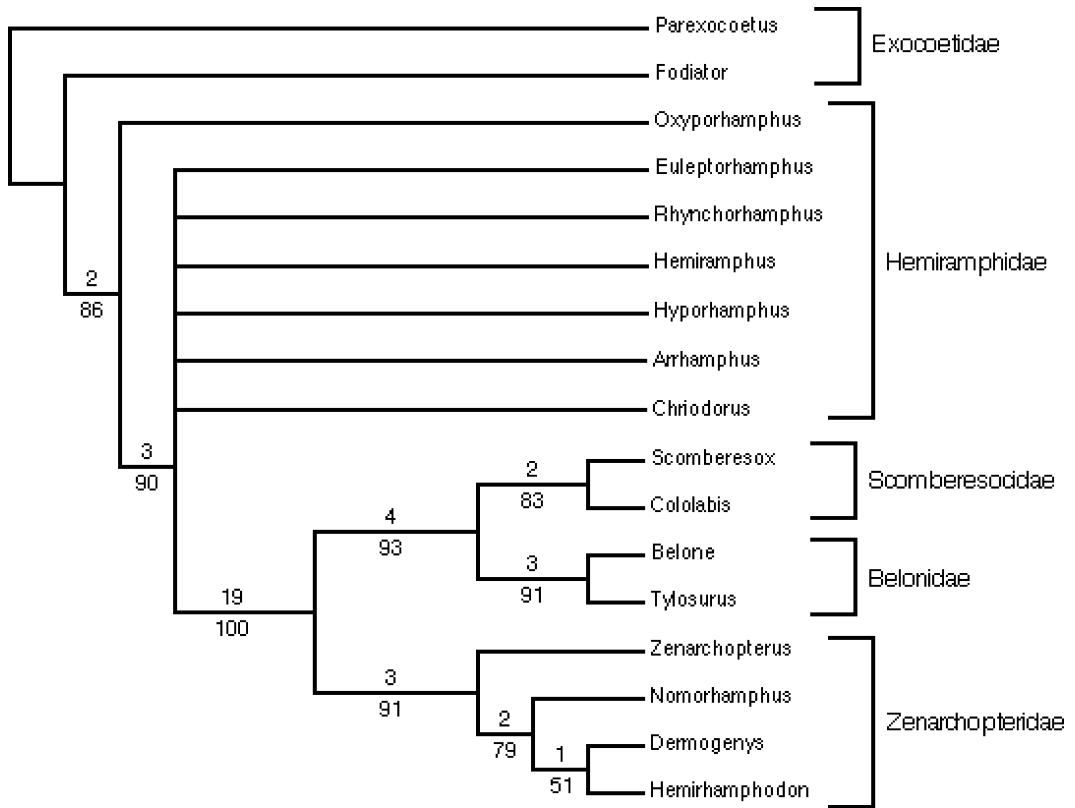


Fig. 1. Strict consensus of eight most parsimonious trees produced by unweighted and unordered data analysis, CI 0.814, RI 0.938. Numbers above nodes are decay indices. Numbers below nodes are bootstrap proportions.

with a strong basal relationship to the saury, needlefish, and Zenarchopteridae clade.

Morphological examination.—Several characters in the matrix (Appendix III) warranted comparison between the large and dwarf saury species. The presence of a fourth pharyngobranchial tooth plate (Appendix I, character 17) in the Belonidae (Tibbetts 1992) was confirmed in *Belone*. A very small plate bearing a single row of teeth was observed in both of the large saury species (Fig. 2) and was absent in the dwarf species.

The retractor dorsalis is a bilaterally paired muscle that connects the posterior pharyngobranchials to the vertebral column (Winterbottom 1974). Tibbetts (1992) described two states for the origin of the retractor dorsalis (Appendix I, character 29):

the anterior margin of the origin is on the third vertebra, as in *Tylosurus*, *Dermogenys*, the hemiramphid halfbeaks, and *Fodiator*; or the second vertebra, as in *Belone*, the other Zenarchopteridae, and *Parexocoetus*. Because the origin of the retractor dorsalis in both *C. saira* (Fig. 3) and *S. saurus* extends from the sixth to the eighth vertebrae, a new state for this character was herein defined. The retractor dorsalis is similarly modified in both of the dwarf species, originating on vertebrae four through six in *Cololabis adocetus* (Böhlke, 1951) and five through seven in *Scomberesox simulans* (Hubbs & Wisner, 1980).

Tibbetts (1992) described the orientation of teeth on the fifth ceratobranchial (Appendix I, character 37) in *Belone* and the Zenarchopteridae as hooked or directed

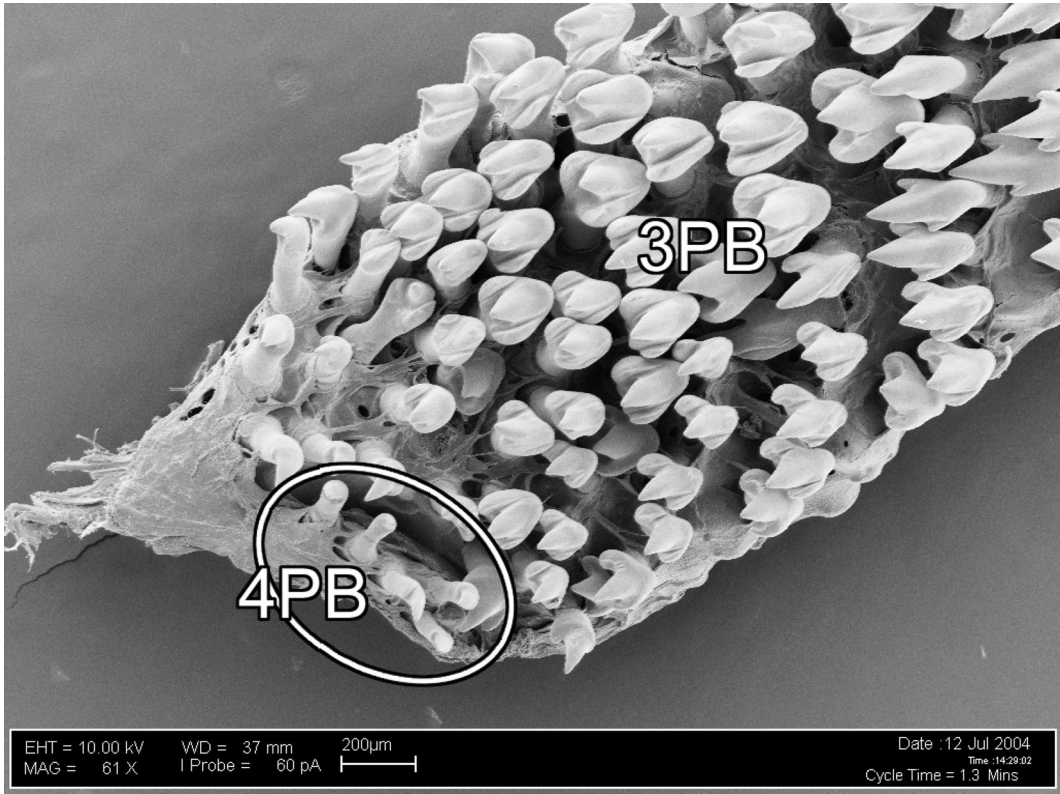


Fig. 2. Scanning electron micrograph of the left third pharyngobranchial of *Scomberesox saurus*, USNM 299755; 275 mm SL, SEM $\times 61$. Scale equals 200 μm . 4PB is circled. Anterior is to the upper right. Abbreviations.—3PB, third pharyngobranchial tooth plate; 4PB, fourth pharyngobranchial tooth plate.

posteriorly in all but the most caudal row, which faces anteriorly. The condition of only posteriorly directed teeth was identified as autapomorphic for *Tylosurus gaviatoides* (Tibbetts 1992). While a row of anteriorly hooked teeth similar to that in *Belone* was observed in *C. saira*, the posterior row in *S. saurus* is distinctly hooked posteriorly. The character was subsequently evaluated in the two dwarf saury species, both of which exhibited the anteriorly hooked state as in *Belone*.

An additional state was described for the orientation of dentition on the second pharyngobranchial tooth plate (Appendix I, character 38). The medial series of teeth in *C. saira* is strongly directed antero-medially (Fig. 4), while more distal series face posteriorly. A similar antero-medial direc-

tion of this tooth plate's dentition, differing only in that some rostral rows of teeth are even more medially directed, is found in *S. saurus*. These patterns sufficiently differed from the medial direction of almost all second pharyngobranchial teeth, as in *Fodiator*, to support defining another state. The dwarf *S. simulans* resembled its larger sister species in this character, but *C. adocoetus* exhibited a needlefish-like posterior orientation.

Discussion

Monophyly of the Beloniformes, excluding rice fishes, has long been recognized (Gill 1896) and is well-supported by morphological characters (Schlesinger 1909, Regan 1911, Nichols & Breder 1928, Col-

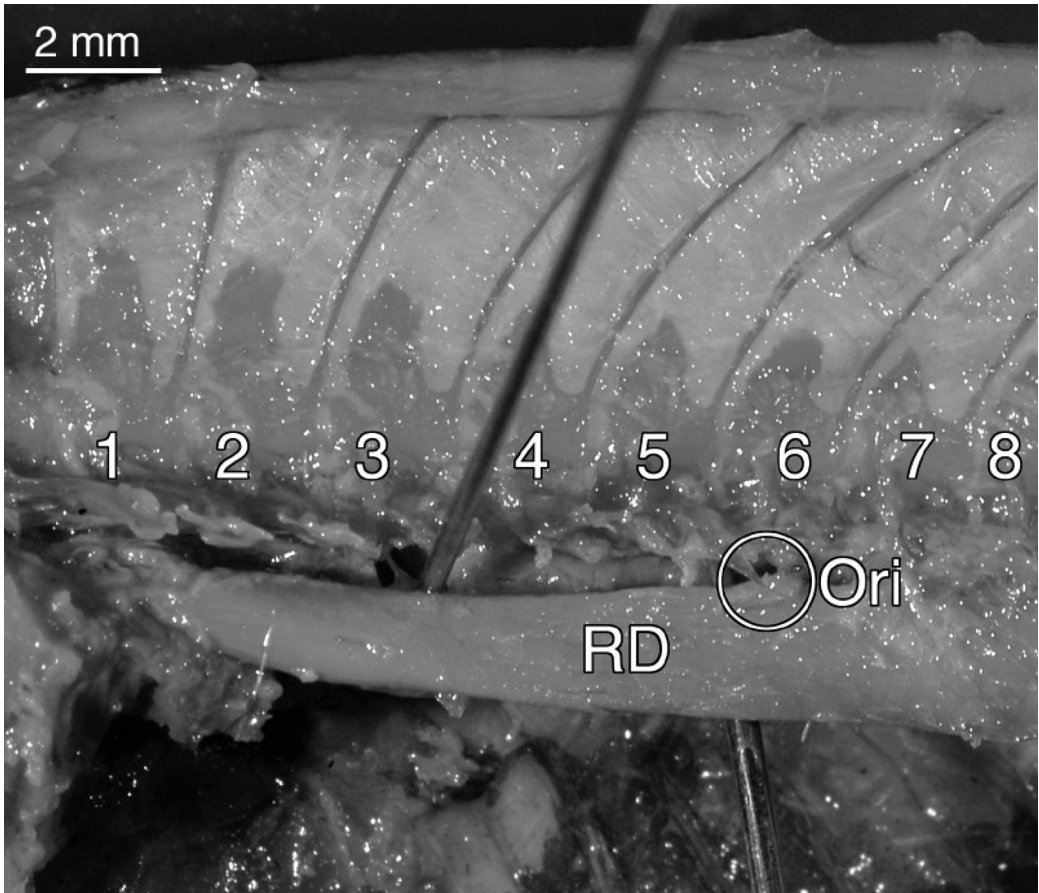


Fig. 3. Photograph of left retractor dorsalis in *Cololabis saira*, USNM 320999. Anterior is to the left. The anterior margin of the origin, on vertebra six, is circled. Vertebrae are numbered. Scale equals 2 mm. Abbreviations.—Ori, anterior extent of origin; RD, retractor dorsalis.

lette et al. 1984), including those derived from the lateral line system (Parin & Astakhov 1982) and PJA (Rosen 1964, Collette 1966, Rosen & Parenti 1981, Collette et al. 1984). The dichotomy of this clade into historical needlefish + saury and halfbeak + flyingfish groups is poorly supported by data from Tibbetts' (1992) PJA characters. The analysis (Springer & Orrell 2004) of a recent survey of the dorsal gill arch musculature across 147 families of acanthomorph fishes (Springer & Johnson 2004) supports such a phylogeny but used few representative taxa, many alternative characters, and excluded Zenarchopteridae. Springer & Johnson (2004) identified the

presence of a muscularis pharyngobranchialis 3 posterior as a notable shared character of the halfbeaks and flyingfishes.

Monophyly of the superfamily Scomberesocidae is corroborated by this analysis. The monophyly of each of the two component families is supported by modest decay indices and bootstrap proportions. The *Belone* + saury group identified by Lovejoy (2000) and Lovejoy et al. (2004) was not supported by pharyngeal characters. All belonid genera should be investigated and additional characters identified to resolve this question.

Zenarchopteridae is a well-supported clade, but the internal structure is not en-

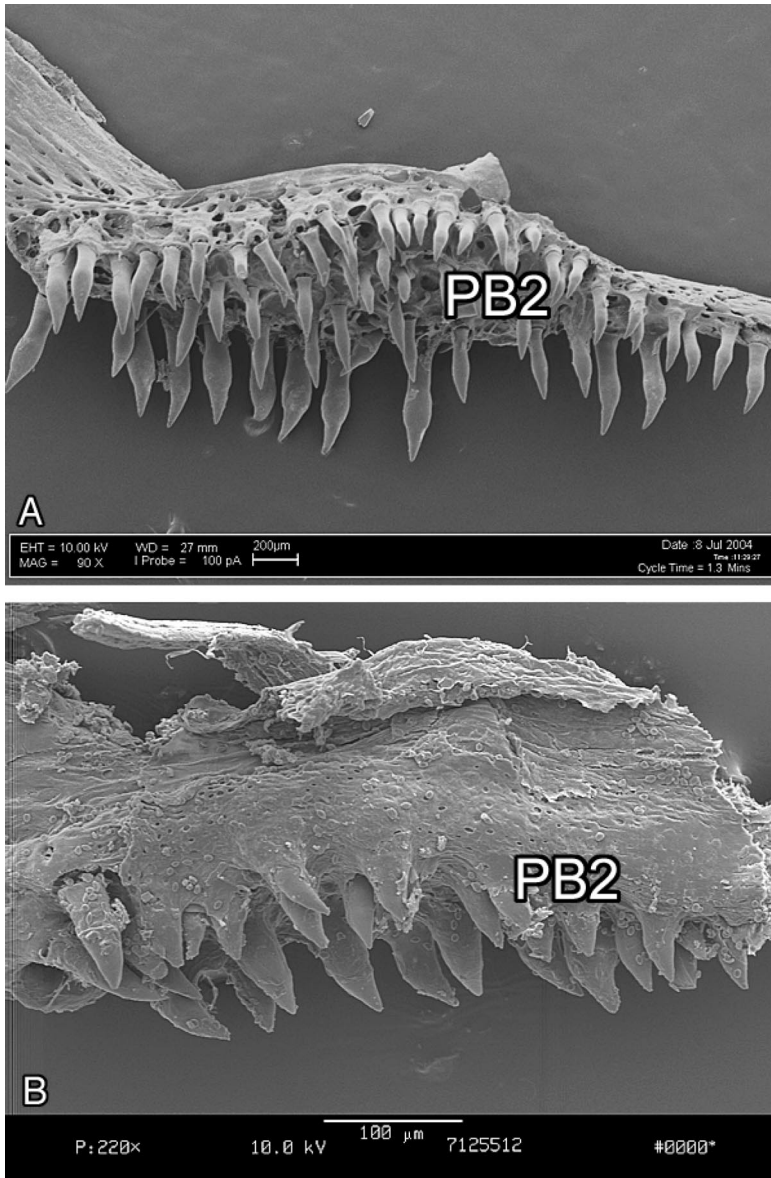


Fig. 4. Scanning electron micrographs of the left second pharyngobranchial of (A) *Cololabis saira*, USNM 320999; 211 mm SL, SEM $\times 90$, scale equals 200 μm ; (B) *C. adocoetus*, USNM 258831; 55.7 mm SL, SEM $\times 220$, scale equals 100 μm . Anterior is to the left.

tirely resolved. The pairing of *Dermogenys* and *Hemirhamphodon* is not well supported (decay index = 1, bootstrap = 51). The identification of Zenarchopteridae as sister to the Scomberesocidae is strongly supported, corroborating the previously proposed paraphyly of the Hemiramphidae

sensu Collette et al. (1984). The rest of the halfbeaks are an unresolved assemblage defined by bootstrap proportions of less than 50 and decay indices of 1. These observations do not preclude the proposed basal position of the externally fertilizing halfbeaks and flyingfishes in the Beloni-

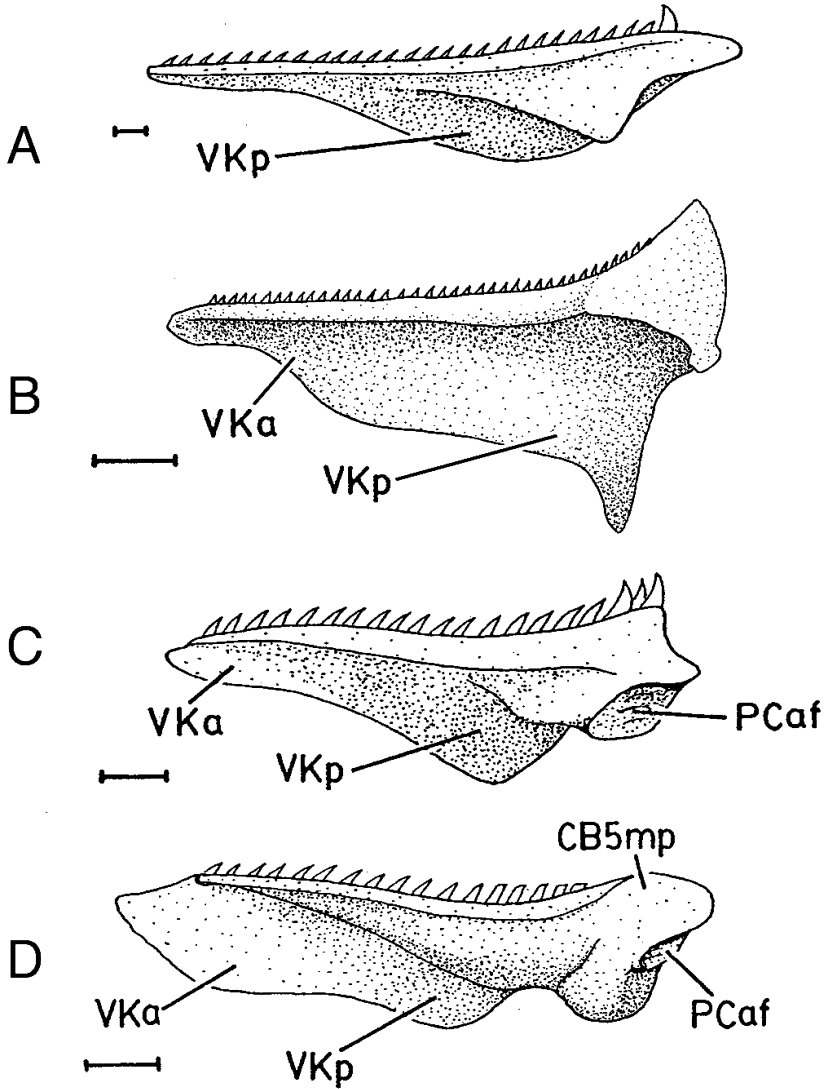


Fig. 5. Lateral view of fifth ceratobranchials of (A) *Belone belone*; (B) *Scomberesox saurus*; (C) *Zenarchopterus buffonis*; (D) *Parexocoetus mento*. Abbreviations.—VKa, anterior ventral keel; VKp, posterior ventral keel; PCaf, cleithral articulation facet; CB5mp, muscular process. Scale equals 1 mm. (A, C, D) are modified from Tibbetts (1992).

formes (Lovejoy 2000, Lovejoy et al. 2004).

Two character state differences between the large and dwarf species in both saury genera may be due to size reduction. The fourth pharyngobranchial tooth plate is reduced to one row of teeth in the large species and may have been lost in the dwarfs as a consequence of a proportional de-

crease in size of the fourth pharyngobranchial cartilage. Further, the caudal displacement of the origin of the retractor dorsalis in all sauries may be due to their terete body plan, although it is observed in neither *B. belone* nor *T. gavioloides*. That the condition is less pronounced in the dwarf species may be due to a reduction in number of vertebrae compared to the

large sauries (Hubbs & Wisner 1980, Collette et al. 1984).

Conclusions

Within the Beloniformes, sauries are hypothesized to be most closely related to needlefishes. Confirmation of this relationship is lacking and additional needlefish taxa and characters should be investigated. For example, caution should be exercised in using the origin of the retractor dorsalis as a synapomorphy for sauries until the character can be evaluated in a more comprehensive sample of the Belonidae. The cause of the displacement of the muscle origin may then also be better understood.

Zenarchopteridae is well-supported as a valid family sister to the Scomberesocoidae. The structure and position of the remaining Hemiramphidae are inadequately resolved by the characters analyzed in this study. Reevaluation of third pharyngobranchial association and identification of additional characters and character states are needed to further evaluate the total evidence hypothesis of Lovejoy (2000) and Lovejoy et al. (2004).

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Literature Cited

- Anderson, W. D., III, & B. B. Collette. 1991. Revision of the freshwater viviparous halfbeaks of the genus *Hemiramphodon* (Teleostei: Hemiramphidae).—*Ichthyological Explorations of Freshwaters* 2:151–176.
- Böhlke, J. E. 1951. A new Pacific saury (genus *Cololabis*) from off the coast of Peru.—*Transactions of the Kansas Academy of Sciences* 54: 83–87.
- Brevoort, J. C. 1856. Notes on some figures of Japanese fish taken from recent specimens by the artists of the U.S. Japan Expedition. Pp. 253–288 in M. C. Perry, *Narrative of the Expedition of an American Squadron to the China Seas and Japan, performed in the years 1852, 1853, and 1854 under the command of Commodore M. C. Perry, United States Navy, by order of the Government of the United States*. U.S. Senate Ex. Doc. No. 79, 33rd Congress, 2nd Session. Beverly Tucker, Washington, D.C. v. 2: 253–288, Pls. 3–12.
- Collette, B. B. 1966. *Belonion*, a new genus of freshwater needlefishes from South America.—*American Museum Novitates* 2274:1–22.
- . 1995. *Tondanichthys kottelati*, a new genus and species of freshwater halfbeak (Teleostei: Hemiramphidae) from Sulawesi.—*Ichthyological Exploration of Freshwaters* 6:171–174.
- . 2004a. Family Scomberesocidae Müller 1843—sauries.—*California Academy of Sciences Annotated Checklists of Fishes* 21:1–6.
- . 2004b. Family Hemiramphidae Gill 1859—halfbeaks.—*California Academy of Sciences Annotated Checklists of Fishes* 22:1–35.
- , G. E. McGowen, N. V. Parin, & S. Mito. 1984. Beloniformes: development and relationships. Pp. 335–354 in H. G. Moser et al., eds, *Ontogeny and systematics of fishes*. American Society of Ichthyologists and Herpetologists Special Publication 1:1–760.
- Dingerkus, G., & L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage.—*Stain Technology* 52:229–232.
- Fowler, H. W. 1934. Descriptions of new fishes obtained from 1907 to 1911, chiefly in the Philippine Islands and adjacent seas.—*Proceedings of the Academy of Natural Sciences, Philadelphia* 85:233–367.
- Gill, T. 1896. The families of synentognathous fishes and their nomenclature.—*Proceedings of the United States National Museum* 18:167–178.
- Hardy, Jr., J. D., & B. B. Collette. 2003. Preliminary guide to the identification of the early life history stages of scomberesocid fishes of the western central North Atlantic.—*NOAA Technical Memorandum NMFS-SEFSC-505:1–4*.

- Hubbs, C. L., & R. L. Wisner. 1980. Revision of the sauries (Pisces, Scomberesocidae) with descriptions of two new genera and one new species.—*Fishery Bulletin* 77:521–566.
- Jamieson, B. G. M., & H. J. Grier. 1993. Influences of phylogenetic position and fertilization biology on spermatozoal ultrastructure exemplified by exocoetoid and poeciliid fish.—*Hydrobiologica* 271:11–25.
- Lovejoy, N. R. 2000. Reinterpreting recapitulation: systematics of needlefishes and their allies (Teleostei: Beloniformes).—*Evolution* 54:1349–1362.
- , M. Iranpour, & B. B. Collette. 2004. Phylogeny and jaw ontogeny of beloniform fishes. *Integrative and Comparative Biology* 44:366–377.
- Meisner, A. D. 2001. Phylogenetic systematics of the viviparous halfbeak genera *Dermogenys* and *Nomorhamphus* (Teleostei: Hemiramphidae: Zenarchopterinae).—*Zoological Journal of the Linnean Society* 133:199–283.
- , & B. B. Collette. 1999. Generic relationships of the internally-fertilized southeast Asian halfbeaks (Hemiramphidae: Zenarchopterinae).—*Proceedings of the 5th Indo-Pacific Fish Conference, Nouméa, 1997, Société Française d'Ichtyologie*:69–76.
- Nichols, J. T., & C. M. Breder, Jr. 1928. An annotated list of the Syntentognathi with remarks on their development and relationships.—*Zoologica* (New York) 8:423–448.
- Parin, N. V., & D. A. Astakhov. 1982. Studies on the acoustico-lateralis system of beloniform fishes in connection with their systematics.—*Copeia* 1982:276–291.
- Regan, C. T. 1911. The classification of the teleostean fishes of the order Syntentognathi.—*Annals and Magazine of Natural History* ser. 8, 7:327–335.
- Rosen, D. E. 1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives.—*Bulletin of the American Museum of Natural History* 127:217–268.
- , & L. R. Parenti. 1981. Relationships of *Oryzias*, and the groups of atherinomorph fishes.—*American Museum Novitates* 2719:1–25.
- Schlesinger, Z. 1909. Zur Phylogenie und Ethologie der Scomberesociden.—*Verhandlungen. Zoologisch—Botanische Gesellschaft in Wien* 59:302–339.
- Sorenson, M. D. 1999. TreeRot, version 2. Boston University, Boston, Massachusetts.
- Springer, V. G., & G. D. Johnson. 2004. Study of the dorsal gill-arch musculature of teleostome fishes, with special reference to the Actinopterygii. *Bulletin of the Biological Society of Washington* 11:1–235.
- , & T. M. Orrell. 2004. Phylogenetic analysis of 147 families of acanthomorph fishes, based primarily on dorsal gill-arch muscles and skeleton. *Bulletin of the Biological Society of Washington* 11:236–254.
- Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.
- Tibbetts, I. R. 1992. The trophic ecology, functional morphology and phylogeny of the Hemiramphidae (Beloniformes). Unpublished Ph.D. dissertation, University of Queensland, Brisbane, 370 pp.
- , & L. Carseldine. 2003. Anatomy of a hemiramphid pharyngeal mill with reference to *Arhamphus sclerolepis krefftii* (Steindachner) (Teleostei: Hemiramphidae).—*Journal of Morphology* 255:228–243.
- Walbaum, J. J. 1792. Petri Arredi sueci genera piscium. In quibus systema totum ichthyologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis. Redactis speciebus 242 ad genera 52. *Ichthyologiae, pars III. Ant. Ferdin. Rose, Grypeswaldiae* [Greifswald]. Pt. 3:1–723, Pls. 1–3.
- Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei.—*Proceedings of the Academy of Natural Sciences of Philadelphia* 125:225–317.

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Appendix I—Morphological characters used for phylogenetic analysis (Tibbetts 1992).

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1. Nasal papilla: 0, low and spatulate; 1, elongate and pointed.
 2. Caudal fin: 0, hypocercal; 1, rounded or emarginated caudal, occasionally moderately hypocercal.
 3. Mode of fertilization: 0, external; 1, internal.
 4. Pectoral fin: 0, moderately developed; 1, well-developed; 2, greatly developed.
 5. Premaxillary canal: 0, absent; 1, present.
 6. Fusion between premaxilla and maxilla: 0, bones fused; 1, bones separate.
 7. Upper jaw: 0, short; 1, moderate; 2, long.
 8. Lower jaw: 0, long in juveniles and adults; 1, long in juveniles and moderate in adults; 2, long in juveniles and short in adults.
 9. Oral teeth: 0, small and unicuspid; 1, large and conical; 2, tricuspid.
 10. Scales: 0, small; 1, large.
 11. Caudal extent of swimbladder: 0, limited to visceral cavity; 1, extends into haemal canal.
 12. Basioccipital articulation facet: 0, low-angled basioccipital apophysis; 1, trough-like craniopharyngeal apophysis formed from basioccipital and parasphenoid; 2, ventrally projecting triangular apophysis of basioccipital.
 13. Inferior parasphenoid apophysis: 0, absent; 1, present.
 14. Otic capsules: 0, submerged; 1, prominent and swollen.
 15. Third pharyngobranchials: 0, separate; 1, suturally united or coalescent; 2, fused.
 16. Third pharyngobranchial plate: 0, short, convex posterior margin, narrowly separated anterior processes of moderate length; 1, elongate anterior processes; 2, broad, indented posterior margin, widely spaced anterior processes.
 17. Fourth pharyngobranchial toothplate: 0, present; 1, absent.
 18. Anterior processes of second pharyngobranchial: 0, weak; 1, robust.
 19. Proximal head of fourth epibranchial: 0, broad-based; 1, reduced epibranchial where base lacks abutment with third pharyngobranchial; 2, slot-like process on fourth epibranchial's base mates with a slot in the dorso-lateral surface of third pharyngobranchial.
 20. Uncinate process on fourth epibranchial: 0, absent; 1, present.
 21. Fifth ceratobranchial: 0, equally broad and long; 1, elongate and narrow; 2, broader than long.
 22. Fifth ceratobranchial keel (Fig. 5): 0, anterior keel absent, posterior keel weakly developed; 1, posterior keel developed, slight anterior keel; 2, posterior and anterior keels well-developed.
 23. Shape of fifth ceratobranchial bony process: 0, low and broad; 1, high and narrow.
 24. Anterior division of muscularis cranio-pharyngobranchialis 2: 0, absent; 1, present.
 25. Muscularis cranio-pharyngobranchialis 2 posterior: 0, short; 1, long.
 26. Second levator internus in cross section: 0, strap-like; 1, sub-cylindrical; 2, cylindrical.
 27. Insertion of posterior levator muscles: 0, only on fourth epibranchial; 1, mainly on bony process of fifth ceratobranchial.
 28. Transversus dorsalis posterior: 0, well-developed; 1, weakly developed.
 29. Origin of retractor dorsalis: 0, begins on third vertebra; 1, begins on second vertebra; 2, begins caudal to third vertebra.
 30. Protractor pectoralis: 0, large; 1, small.
 31. Fifth adductor branchialis: 0, large; 1, small.
 32. Pharyngocleithralis externus: 0, undivided muscle; 1, posterior portion overlaps more anterior fibers at origin.
 33. Origin of pharyngocleithralis internus: 0, high; 1, low.
 34. Origin of transversus ventralis: 0, on its contralateral beneath anterior of fifth ceratobranchial; 1, on keel of fifth ceratobranchial.
 35. Pharyngohyoideus: 0, relatively large; 1, relatively small.
 36. Second pharyngobranchial teeth: 0, unicuspid; 1, tricuspid.
 37. Fifth ceratobranchial teeth: 0, all face posteriorly; 1, all but anteriorly hooked posterior row face posteriorly; 2, most face anteriorly.
 38. Second pharyngobranchial teeth: 0, all directed posteriorly; 1, some directed medially; 2, some directed anteriorly; 3, some directed antero-medially.
 39. Wear area of third pharyngobranchial dentition: 0, absent; 1, extreme posterior of tooth field worn; 2, most of field worn.
 40. Wear area of fifth ceratobranchial dentition: 0, absent; 1, extreme posterior of tooth field worn; 2, most of field worn.
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Appendix II—List of specimens used in analysis.

Species	No. specimens	SL range (mm)	Catalog number	Locality
<i>Arrhamphus sclerolepis krefftii</i>	1	212	USNM 206571	Sydney, Australia
<i>Arrhamphus sclerolepis sclerolepis</i>	1	157	USNM 173776	Port Bradshaw, Australia
<i>Belone belone</i>	1	339	USNM 203094	Venice, Italy
<i>Cololabis adocoetus</i>	4	50.0–60.0	USNM 258831	Pacific Peru
<i>Cololabis saira</i>	5	190–217	USNM 320999	Monterey Bay, California
<i>Scomberesox saurus</i>	3	275–328	USNM 299755	Mediterranean
	3	154–172	USNM uncat.	Bear Seamount
<i>Scomberesox simulans</i>	2	50.5–55.6	Paratype, USNM 222664	South Atlantic
<i>Zenarchopterus buffonis</i>	1	159	USNM 294445	New Guinea
Cleared Specimens:				
<i>Arrhamphus sclerolepis</i>	1	39.7	USNM 173771	Australia
<i>Cololabis saira</i>	2	93–126	USNM 050744	Japan
<i>Fodiator acutus</i>	1	104	USNM 054634	Panama

Appendix III—Morphological character matrix.

Species	1	11	21	31
<i>Scomberesox saurus</i>	0000101000	0000010000	0100000020	0000000300
<i>Cololabis saira</i>	0000101200	0000010000	0100000020	0000001300
<i>Belone belone</i>	0000102010	0000010000	0000000010	0000001000
<i>Tylosurus gavioloides</i>	0000102010	0000010000	1000000000	0000000000
<i>Dermogenys pusilla</i>	1110001100	0100121010	2100020100	0100001000
<i>Hemirhamphodon pogonognathus</i>	1110001000	0100121010	2100020110	0100001000
<i>Nomorhamphus</i> sp.	1110001101	0100?21010	0100020110	0100001000
<i>Zenarchopterus buffonis</i>	1110001001	0100121001	0100020010	0100001000
<i>Parexocoetus mento</i>	0002010201	1211101121	0211111011	1011112111
<i>Fodiator acutus rostratus</i>	0002010201	1211101121	0211111001	1011112111
<i>Oxyporhamphus convexus convexus</i>	0001010201	0211101121	0211111001	1011112211
<i>Euleptorhamphus viridis</i>	0001001020	0211?01121	1211111001	1011112211
<i>Rhynchorhamphus georgii</i>	0000001021	0211?01121	0211111001	1011112211
<i>Hemiramphus robustus</i>	0000001021	0211101121	0211111001	1011112221
<i>Hyporamphus regularis ardelio</i>	0000001021	0211?01121	0211111001	1011112222
<i>Hy. (Reporhamphus) balinensis</i>	0000001021	0211?01121	0211111001	1011112222
<i>Arrhamphus sclerolepis krefftii</i>	0000001221	0211201121	0211111001	1011112222
<i>Chriodorus atherinoides</i>	0000001221	0211?01121	0211111001	1011112212
<i>Melapedalion breve</i>	0000001221	0211?01121	0211111001	1011112222