

A phylogeny of sparoid fishes (Perciformes, Percoidei) based on morphology

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Abstract The putative percoid superfamily Sparoidea includes the Nemipteridae, Lethrinidae, Sparidae, and Centranchidae. Although a rigorous cladistic analysis has never been attempted, two hypotheses regarding relationships among these families have been proposed. One early noncladistic hypothesis considered the Sparidae to be intermediate between the more primitive Nemipteridae and the more derived Lethrinidae. A later nonformal phylogenetic treatment provided evidence for a close relationship between Sparidae and Centranchidae and suggested a closer affinity between the Nemipteridae and Lethrinidae. We examine 54 osteological, ligament, and squamation characters in representatives of all 45 genera of these families and 4 outgroup taxa. The results of our cladistic analysis are congruent with a cladistic interpretation of the earlier hypothesis, with strong support for the phyletic sequence Nemipteridae, Lethrinidae, Sparidae plus Centranchidae, with placement of centranchids unresolved with respect to sparid genera.

Key words Nemipteridae · Lethrinidae · Sparidae · Phylogeny · Osteology

The percoid superfamily Sparoidea, as currently recognized, comprises four families of marine fishes. Akazaki (1962) was the first to recognize a close relationship among the Nemipteridae, Lethrinidae, and Sparidae, his “spariform” fishes. Johnson (1980) expanded Akazaki’s spariforms to include the family Centranchidae based on a specialization they share with the Sparidae, and he erected the superfamily Sparoidea for the group. The Nemipteridae are restricted to the Indo-West Pacific and include 62 species among 5 genera of threadfin breams, whiptail breams, monocle breams, and coral breams (Russell, 1990). The Lethrinidae include 28 species in 5 genera of emperors and large-eye breams; 1 of these species is found in the eastern Atlantic, and all others are restricted to the Indo-West Pacific (Carpenter and Allen, 1989). Lethrinids comprise two subfamilies, the Monotaxinae with *Gnathodentex*, *Gymnocranius*, *Monotaxis*, and *Wattsia*, and the Lethrininae with *Lethrinus*. The Sparidae (porgies, seabreams, and dentexes) comprise more than 110 species in 33 genera and are found in all tropical and temperate seas. The Centranchidae, with 1 monotypic genus and 1 genus with 8 species, are restricted to the Mediterranean, eastern Atlantic, and South Africa. Sparoid fishes encompass a range of trophic types including piscivores, benthic invertebrate carnivores, zooplanktivores, and herbivores. They are predominantly neritic and are common and conspicuous components of hard-bottom demersal fish communities, although the nemipterid, *Nemipterus*, is often a dominant component of soft bottom demersal neritic communities in the tropical Indo-West Pacific.

Families of the Sparoidea traditionally have been placed centrally among the 71 families of percoid fishes (Nelson, 1994; Eschmeyer, 1998), but, in general, phyletic placement of families within the Percoidei remains uncertain, and there have been no serious attempts to diagnose a monophyletic Percoidei (Johnson, 1993). Johnson (1980) considered the higher-order relationships within three central percoid subfamilies, the Lutjanoidea, Sparoidea, and Haemuloidea. However, he found no evidence that any two of them are more closely related to one another than to other percoid families. Nelson (1994) placed 65 of 71 families of his suborder Percoidei in the superfamily Percoidea (including lutjanoid, haemuloid, and sparoid families), but recognized that neither group is likely to be monophyletic. We retain the superfamily Sparoidea as a taxonomic convenience but recognize that, when phylogenetic relationships within the suborder Percoidei are better understood, its hierarchical status may change.

Akazaki’s (1962) traditional hypothesis of evolutionary relationships among sparoid families placed the Nemipteridae as the most primitive, with the Sparidae intermediate and the Lethrinidae the most derived (Fig. 1A). Johnson (1980) found additional evidence to support the integrity of Akazaki’s (1962) families. However, he questioned Akazaki’s (1962) proposed phylogeny and suggested, based on preliminary evidence, that the Lethrinidae may be the sister-group of the Nemipteridae, these two together forming the sister-group of the Sparidae plus Centranchidae (Fig. 1B). Johnson (1993) suggested that either or both the Nemipteridae and Lethrinidae may be

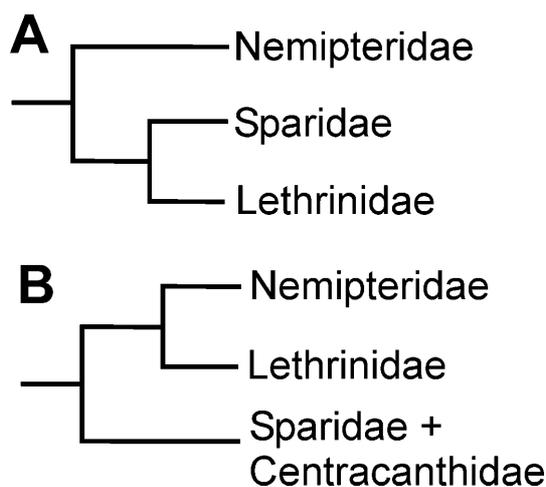


Fig. 1. Hypotheses of phylogenetic placement of **A** “Spariform” families according to our cladistic interpretation of Akazaki’s (1962) traditional evolutionary hypothesis and **B** the Sparoidea of Johnson (1980)

paraphyletic based on specializations shared between certain genera of the two families. Our purpose here is to rigorously test the phylogenetic relationships among sparoid families. We conclude that both Akazaki’s (1962) phyletic sequence and Johnson’s (1980, 1993) preliminary counterproposal should be supplanted by a third hypothesis, one that is in closer agreement with that of Akazaki (1962), were it to be interpreted cladistically. We examined representatives of all sparoid genera and erect tentative hypotheses regarding relationships among these genera. However, a rigorous treatment of generic relationships within any of the families is beyond the scope of this study.

Materials and Methods

Morphological preparations.—Osteological examinations were done primarily on specimens cleared and counterstained for bone and cartilage following the method of Dingerkus and Uhler (1977). In all cleared and stained lots, at least one specimen was dissected to remove the suspensorium and lower jaw on the right side and the gill arches. To supplement cleared and stained specimens, certain species were also X-ray radiographed or examined as dry skeletal preparations. Ligaments were viewed directly on cleared and stained specimens, sometimes with these specimens soaked for a short time in ethanol to improve visibility of this tissue. Alternatively, rostral ligaments were exposed on preserved whole specimens using the dissection method outlined in Johnson (1980). Lateral line scales were extracted from the right side above the middle part of the pectoral fin from whole preserved specimens or from cleared and stained specimens when scales still remained.

Phylogenetic analysis.—Maximum-parsimony analysis was performed using PAUP (Swofford, 2001). Equally parsimonious trees were obtained using the heuristic search algorithm with sequences added randomly ($n = 1$; 100 repli-

cates with 100 trees held per replicate) and tree-bisection-reconnection (TBR) branch swapping. SEPAL (Salisbury, 2000) was used to calculate Bremer decay values (Bremer, 1988). Bootstrap values were obtained from PAUP at 100 replicates. To avoid potentially unfounded evolutionary assumptions, all multistate characters were treated as unordered. For binary characters, whenever two character states occur in the outgroups, the character was left unpolarized. As outgroups to sparoids we chose a “basal” percoid, *Morone*, and representatives of lutjanoids and haemuloids based on the traditional placement of these groups within the Percoidei.

Material examined. Outgroup families are listed first, followed by sparoid families. Taxa are listed alphabetically within family. All materials examined were cleared and stained except whole specimens that are listed with an asterisk (*), X-ray radiographed material listed with an “X” superscript (X), or dry skeletal material marked with an “S” superscript (S). Institutional acronyms follow Leviton et al. (1985).

Outgroups.—Moronidae: *Morone americana* ODU 2872 (7). Lutjanidae: *Lutjanus griseus* ODU 2869 (2), ODU 2905 (1)*. Haemulidae: *Haemulon plumieri* ODU 2870 (1); *Pomadysys kaakan* ODU 2868 (1).

Ingroup.—Nemipteridae: *Nemipterus celebicus* NTM S. 11333-001 (2); *Nemipterus marginatus* NTM-S. 12898-006 (1); *Nemipterus japonicus* USNM 345201 (2); *Nemipterus virgatus* ODU 2934 (1)*; *Parascalopsis tanyactis* NTM S. 13567-005 (2); *Pentapodus porosus* NTM S. 12954-004 (1); *Scaevius milli* USNM 325885 (2); *Scolopsis bilineatus* USNM 290482 (1); *Scolopsis ciliatus* USNM 264481 (2); *Scolopsis taeniopterus* NTM S. 10124-001 (2). Lethrinidae: *Gnathodentex aurolineatus* ODU 2857 (1), ODU 2926 (2)*; *Gymnocranius griseus* USNM 356860 (2); *Lethrinus atkinsoni* USNM 258528 (5), ODU 2927 (6)*; *Lethrinus borbonicus* ODU 2862 (1), ODU 2860 (1), ODU 2859 (1), ODU 2861 (1); *Lethrinus harak* USNM 290483 (1); *Lethrinus ornatus* USNM 345260 (3); *Lethrinus nebulosus* USNM 212211 (3), ODU 2978 (1)^S, ODU 2904 (1)*; *Lethrinus xanthochilus* USNM 349306 (2); *Monotaxis grandoculis* ODU 2858 (1), ODU 2937 (1)^S, ODU 2915 (1)*; *Wattsia mossambica* AMS I.36447-005 (1)^{S,X}. Sparidae: *Acanthopagrus berda* ODU 2831 (3), ODU 2849 (1), ODU 2921 (1)*; *Acanthopagrus bifasciatus* ODU 2834 (1), ODU 2918 (2)*; *Acanthopagrus latus* ODU 2833 (1), AMS Uncat (1)^S, ODU 2907 (1)*; *Archosargus probatocephalus* ODU 2816 (1), ODU 2846 (1); *Argyrops spinifer* ODU 2814 (3), ODU 2850 (1), ODU 2851 (1), ODU 2852 (1), ODU 2922 (5)*; *Argyrozona argyrozona* USNM 325743 (1), ODU uncatalogued (3)^X; *Boops boops* ODU 2825 (2), ODU 2912 (3)*; *Boopsoida inornata* RUSI 15892 (1), ODU 2908 (1)*; *Crenidens crenidens* USNM 147482 (2); *Calamus arcifrons* VIMS 05696 (1); *Calamus pennatula* ODU 2923 (1)*; *Calamus providens* USNM 188836 (1); *Cheimierius nufar* ODU 2933 (1); *Chrysoblephus cristiceps* ODU 2828 (2); *Cymatoceps nasatus* RUSI 22456 (1), ODU uncatalogued (1)^X; *Dentex barnardi* ODU 2883 (1), ODU 2823 (1); *Dentex congoensis* ODU 2821 (1), ODU 2842 (3), ODU 2911 (13)*; *Dentex tumifrons* AMS I.20319-009 (2), NSMT P-47490 (1), NMST-P 47491 (1); *Dentex macrophthalmus* ODU 2822 (2), ODU 2928 (1)*; *Diplodus bermudensis* ODU 2815 (2); *Diplodus cervinus* RUSI 014970 (1), ODU 2854 (1), ODU 2931 (2)*; *Diplodus holbrooki* ODU 2819 (1); *Evyynniss japonica* NSMT-P 47493 (1), NSMT-P 47497 (1), NSMT-P 21067 (1), NSMT-P 21067 (1); *Gymnocrotaphus curvidens* RUSI 55170 (1); *Lagodon rhomboides* ODU 2817 (1), ODU 2820 (1), ODU 2838 (1), ODU 2818 (2), ODU 2917 (1)*; *Lithognathus lithognathus* RUSI 014261 (1), RUSI 14261 (1), ODU 2929 (1)*; *Lithognathus mormyrus* RUSI 008375 (3);

Oblada melanura USNM 276287 (2); *Pachymetopon blochii* RUSI 038734 (1); *Pachymetopon grande* RUSI 051270 (1), ODU 2909 (1)*; *Pagellus acarne* ODU 2824 (1), ODU 2826 (1); *Pagellus bellotti* RUSI 49924 (2); *Pagellus bogaraveo* ODU 2840 (1); *Pagrus auratus* UMMZ 183572 (1), AMS I.18234001 (2), UMMZ 183558 (1), AMS I.17058.002 (1); *Pagrus ehrenbergi* USNM 350949 (4); *Pagrus pagrus* ODU 2993 (2), ODU 2992 (1), ODU 2924 (3)*; *Petrus rupestris* RUSI 13653 (1); *Polyamblyodon germanum* RUSI 53544 (1); *Polysteganus caeruleopunctatus* ODU 2936 (1)*; *Polysteganus undulosus* RUSI 011708 (2); *Porcostoma dentata* ODU 2835 (2), ODU 2910 (2)*; *Pterogymnus laniarius* RUSI 51270 (1), ODU 2906 (1)*, ODU 2920 (1)*; *Rhabdosargus haffara* ODU 2830 (2), ODU 2913 (1)*; *Sarpa salpa* RUSI 050293 (2); *Sparodon durbanensis* RUSI 050274 (2), ODU 2932 (1)*; *Sparidentex hasta* ODU 2829 (1); *Sparus auratus* USNM 350948 (2); *Spondyliosoma cantharus* ODU 2782 (1), ODU 2919 (1)*; *Spondyliosoma emarginatum* RUSI 012187 (2); *Stenotomus chrysops* ODU 2832 (1), ODU 2836 (1), ODU 2837 (2), ODU 2925 (2)*; Centracanthidae: *Centracanthus cirrus* BMNH uncatalogued (1); *Spicara alta* ODU 2794 (1), ODU 2811 (1); *Spicara maena* ODU 2812 (2), USNM 356859 (2).

Results

Characters are grouped according to anatomical complex: braincase (characters 1–6), suspensorium and operculum (7–13), jaws (14–24), infraorbital bones (25–28), gill and hyoid arches (29–40), axial skeleton (41–46), pectoral, pelvic, and median fins (47–51), and squamation (52–54). The consistency and retention indices are listed as real numbers with each character title in the format (CI, RI), with only one number given when they are equivalent. The character state (0–8) is listed as an integer in parentheses after each respective character state description.

1. External openings in lateral wall of pars jugularis (1.00). In the outgroups, Nemipteridae, and Lethrinidae there are two external openings in the lateral wall of the pars jugularis (0) (e.g., Patterson, 1964: fig. 96). In Sparidae and Centracanthidae, there are three (1).

2. Processes on epioccipital (0.50, 0.94). In *Morone*, Nemipteridae, and Lethrinidae a single arm of this caudally directed process on the epioccipital articulates with the posttemporal (0). In Sparidae, Centracanthidae, and remaining outgroup taxa this process has two arms (1).

3. Posterodorsal opening of pterotic sensory canal (1.00). The posterodorsal opening of the pterotic sensory canal communicates with the posttemporal canal through the lateral extrascapular. In the outgroups and all Sparoidea except Nemipteridae, the opening is close to and approximately in line with the bony ridge bearing the sensory canal of the pterotic (0) (Fig. 2B,C). In Nemipteridae, the opening is notably elevated on a columnar extension above the bony ridge bearing the sensory canal (1) (Fig. 2A).

4. Sensory canal of pterotic (0.75, 0.94). In *Morone* and Lethrinidae the pterotic sensory canal is wide and open dorsally along its entire length (0) (Fig. 2B). In *Lutjanus*, Sparidae, and Centracanthidae it is wide and closed dorsally except for three to five openings (1) (Fig. 2C). In Nemipteridae, this canal is laterally pinched, and closed dorsally with typically five more restricted oblong openings

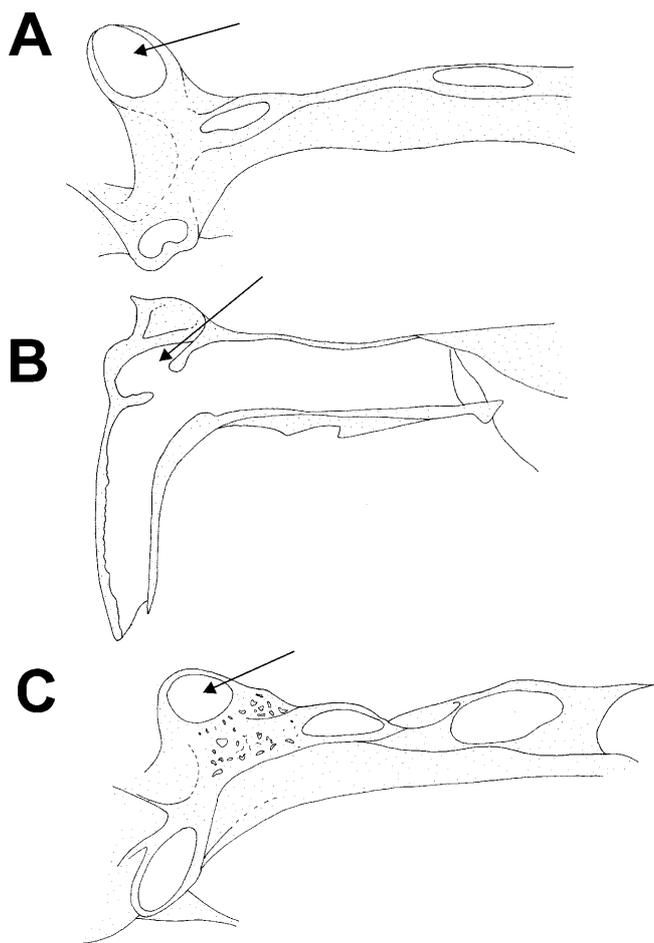


Fig. 2. Right-side lateral view of pterotic sensory canal opening configurations for **A** *Nemipterus virgatus* (215 mm SL), **B** *Lethrinus nebulosus* (214 mm SL), and **C** *Polysteganus caeruleopunctatus* (251 mm SL). Arrows show the upper posterior opening of the pterotic sensory canal that communicates with the posttemporal canal through an extrascapular bone

(2) (Fig. 2A). In Haemulidae, the canal is wide with characteristic quadrangular openings (3).

5. Vertical flange of sphenotic (0.38, 0.83). In *Morone*, *Lutjanus*, *Lethrinus*, *Spicara alta*, and some sparid genera, the vertical flange of the sphenotic is entire and joins with a similar flangelike extension of the frontal to form the dorsoposterolateral boundary of the orbit (0) (Fig. 3A). In *Pomadasys*, Monotaxinae, and a few Sparidae, the flange is interrupted by a foramen that partially separates the sphenotic from the frontal, and the frontal broadly extends to and articulates with the sphenotic laterally (1) (Fig. 3B). In Nemipteridae, the sphenotic flange has a foramen centrally and the flange is separated from the frontal by another larger foramen that is bordered laterally by a thin arm of the frontal that articulates with the sphenotic (2) (Fig. 3C). In *Haemulon*, the remaining Centracanthidae, and most Sparidae the sphenotic flange is eroded dorsally and laterally so that there is a large lateral gap between the sphenotic and frontal flanges (3) (Fig. 3D).

6. Intercalar (1.00). Johnson (1980) found the intercalar (referred to as the opisthotic) to be present in

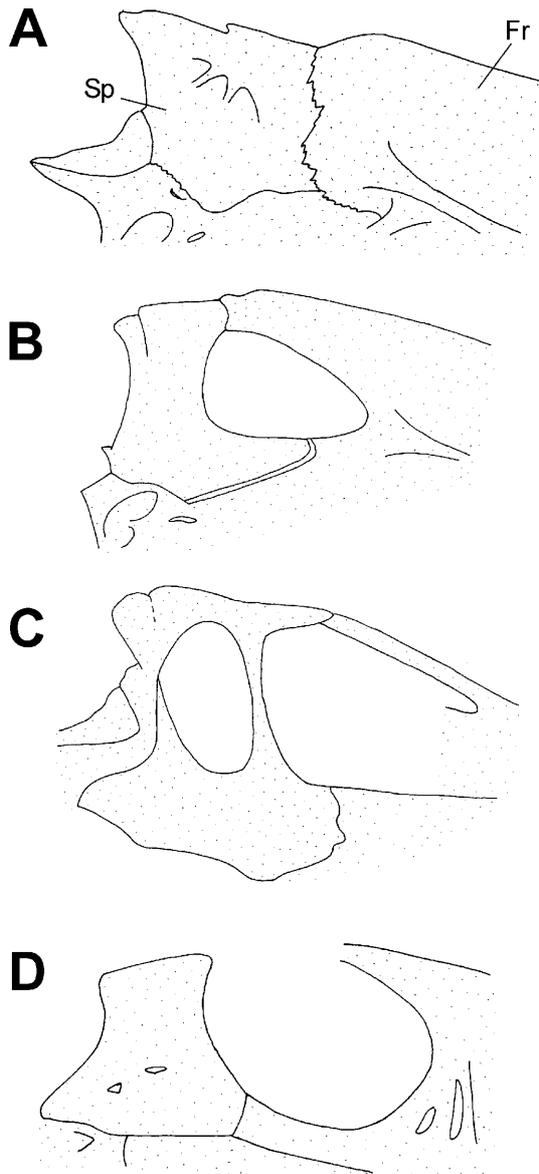


Fig. 3. Anterior view of right-side vertical flange of sphenotic (*Sp*) and frontal (*Fr*) forming the dorsoposterolateral boundary of the orbit for **A** *Lethrinus nebulosus* (378 mm SL), **B** *Wattisia mossambica* (290 mm SL), **C** *Nemipterus virgatus* (215 mm SL), and **D** *Acanthopagrus latus* (228 mm SL). Discontinuities in bone shown in **C** and **D** are portions of the frontal that continue posteriorly away from the plane of the vertical flange

Lutjanidae, Haemulidae, and Nemipteridae (0) and absent in Lethrinidae, Sparidae, and Centranchidae (1).

7. Articulation of palatine and ectopterygoid (1.00). In outgroups and all sparoids examined except the Lethrinidae, the palatine embraces the anterior end of the ectopterygoid broadly in front so that there is a pronounced arm of the palatine projecting ventrally (e.g., Johnson, 1980: figs. 21–26, 28–34). In this condition, the ectopterygoid is more or less triangular in shape with apices pointing roughly dorsally, ventrally, and caudally (0). In the Lethrinidae, the ventral arm of the palatine is reduced and

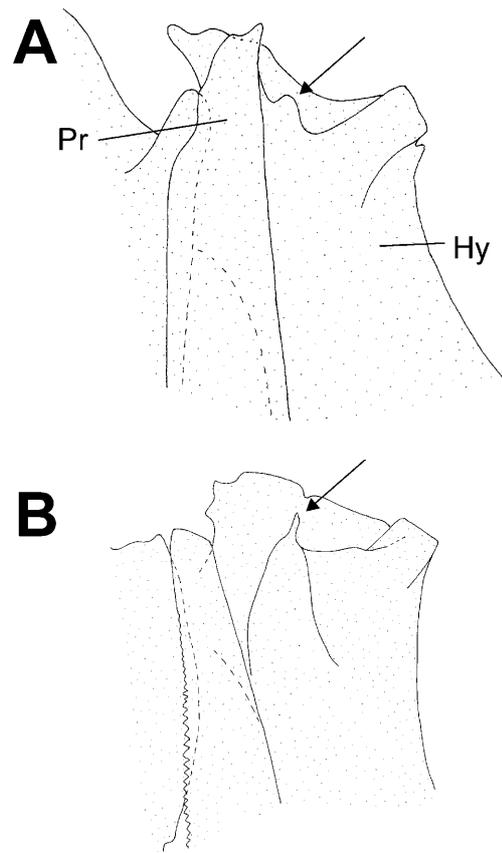


Fig. 4. Right-side lateral view of upper part of hyomandibular (*Hy*) that articulates with the preopercular (*Pr*) sensory canal for **A** *Lethrinus nebulosus* (89 mm SL) and **B** *Parascalopsis tanyactis* (87 mm SL). Arrows indicate position of dorsolateral process on hyomandibular

articulation with the ectopterygoid is more pronounced dorsally than anteriorly (Johnson, 1980: fig. 21). In this case the ectopterygoid is more quadrangular with, roughly, two apices dorsally, one ventrally, and one caudally (1).

8. Symplectic shape (1.00). In all sparoid genera the symplectic has laminar extensions dorsally and ventrally that overlap the metapterygoid and preopercle, respectively (1) (Johnson, 1980: figs. 25–28). In the outgroups, the symplectic is a simple rodlike structure (0) (e.g., Johnson, 1980: figs. 21–24, 29–34).

9. Hyomandibular-metapterygoid articulation (1.00). In all sparoid genera the hyomandibular articulates with the metapterygoid broadly, without an interosseous space (1) (Johnson, 1980: figs. 25–28). In the outgroups and all other percoid groups examined to date, the horizontal arm of this articulation is interrupted by a conspicuous interosseous space (0).

10. Dorsolateral process on hyomandibular (1.00). Near the dorsal edge of the hyomandibular there is a process on the lateral surface near the vertical arm of the preopercle. In all outgroups, Lethrinidae, Sparidae, and Centranchidae this process is adjacent to the vertical arm of the preopercle (0) (Fig. 4A). In Nemipteridae this process

extends rostrally and the vertical arm of the preopercle is displaced posteriorly and separated from this process (1) (Fig. 4B).

11. Openings to sensory canal on vertical arm of preopercle (1.00). There is a single, continuous posterior opening to the sensory canal on the vertical arm of the preopercle in *Morone* (0). In *Lutjanus*, Lethrinidae, Sparidae, and Centranchidae there are several elongate, wide posterior openings (1). Haemulidae have distinctive wide openings that extend both posteriorly and laterally (2). The openings in Nemipteridae are narrow (3).

12. Lateral ethmoid articular surface on palatine (1.00). In the outgroups and Nemipteridae, the facet on the palatine that articulates with the lateral ethmoid is directed medially (0). In Lethrinidae, Sparidae, and Centranchidae this facet is directed mostly caudally (1).

13. Serrations on preopercle (1.00). The outgroups and Nemipteridae have distinctly developed serrations on the vertical posterior edge of the preopercle (0). In Lethrinidae, Sparidae, and Centranchidae these are absent or very poorly developed (1).

14. Maxillary-premaxillary distal articulation (1.00). In Sparidae and Centranchidae the distal end of the alveolar ramus of the premaxilla is modified to articulate with the distal ventral edge of the maxilla (1) (e.g., Johnson, 1980: figs. 7, 8). Carpenter (unpublished data) has identified five distinct character states of this articulation. However, these elucidate relationships among genera of Sparidae and are not presented here. In other sparoids and the outgroups, the premaxilla is not modified for articulation with the distal end of the maxilla (0). In *Scaevius*, however, there is a notch on the upper edge of the distal tip of the alveolar ramus that articulates near the midpoint of the ventral edge of the maxilla. We consider this an autapomorphic condition, morphologically and functionally distinct from that found in the Sparidae.

15. Fusion of articular and ascending processes of premaxilla (1.00). The articular process of the premaxilla is not fused proximally with the ascending process in the Nemipteridae (Akazaki, 1962: fig. 9) or the outgroups (e.g., Johnson, 1980: figs. 2–4) (0). In Lethrinidae (Johnson, 1980: figs. 11, 12) and Sparidae (Johnson, 1980: fig. 7), these processes are continuous (1). In both centranchid genera, there is no articular process (2) (Johnson, 1980: fig. 8).

16. Molariform teeth in jaws (0.17, 0.84). In *Lethrinus atkinsoni*, *L. ornatus*, *L. nebulosus*, *Monotaxis*, and all sparid genera except *Boops*, *Gymnocrotophus*, *Oblada*, *Pachymetapon*, *Polyamblydon*, *Sarpa*, *Spondylisoma*, *Argyrozona*, *Cheimerius*, *Dentex*, *Petrus*, *Polysteganus*, and *Sparidentex*, molariform teeth are present (1). In the Nemipteridae, Centranchidae, outgroups, and *Lethrinus xanthochilus* only distinctly conical teeth are present (0).

17. Maxilla with longitudinal denticulated ridge on lateral surface (0.50, 0.67). In *Gnathodentex*, *Monotaxis*, *Wattisia*, and certain species of *Scolopsis* there is a denticulated ridge on the lateral surface of the maxilla (1) (Russell, 1990: fig. 116). The lateral surface of the maxilla lacks such a ridge in all other taxa (0).

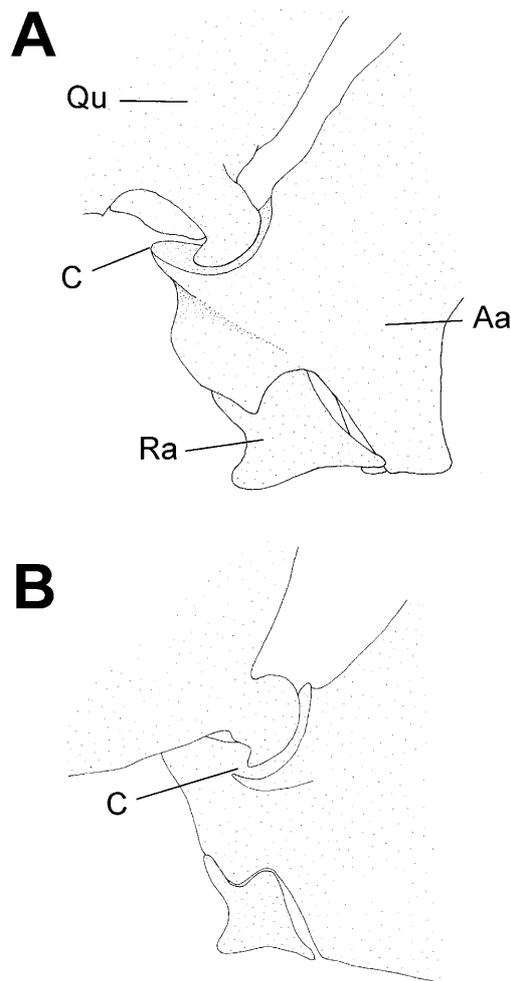


Fig. 5. Right-side lateral view of articular condyle C of anguloarticular (Aa) relative to the quadrate (Qu) and retroarticular (Ra) for **A** *Scolopsis taeniopterus* (94 mm SL) and **B** *Dentex barnardi* (120 mm SL)

18. Proximity of ascending processes of dentary and anguloarticular (0.33, 0.86). In the outgroups, Nemipteridae, *Spicara*, and *Oblada*, the ascending processes of the dentary and anguloarticular are well separated (0) (Akazaki, 1962: fig. 9). In Lethrinidae, all Sparidae except *Oblada*, and *Centranchus*, these processes are closely approximated (1).

19. Articular condyle of anguloarticular (1.00). In the outgroups and Nemipteridae, the articular condyle of the anguloarticular (sometimes referred to as angular) is posterolaterally expanded to the posteriormost edge of that bone, and the proximal portion of the condyle is not well developed (0) (Fig. 5A). In Haemulidae, Lethrinidae, Sparidae, and Centranchidae the condyle is not expanded posterolaterally to the edge of the anguloarticular and the proximal part of the condyle is well developed (1) (Fig. 5B).

20. Articulation of ascending processes of premaxillae (0.50, 0.90). In Nemipteridae and all outgroups except *Haemulon*, the ascending processes of the premaxillae are closest along their ventral edges and farthest apart along their dorsal edges (0). In Lethrinidae, Sparidae, and

Centracanthidae they are closest along the dorsal edges and farthest apart along their ventral edges (1).

21. Premaxilla with postmaxillary process (0.50, 0.80). A broad-based postmaxillary process is present in *Morone*, *Lutjanus*, and Nemipteridae (0) (Akazaki, 1962: fig. 9). In *Centracanthus* and *Spicara alta* the tip of this process is slender and curved posteriorly (1). In Haemulidae, Lethrinidae, Sparidae, and *Spicara maena*, it is absent (2).

22. Length of ascending process of premaxilla (1.00). In all taxa examined except Centracanthidae, the ascending process of the premaxilla extends posterodorsally over the ethmoid (0). In Centracanthidae the ascending process extends posterodorsally well beyond the ethmoid where it fits into a groove in the frontal that nearly reaches the supraoccipital (1).

23. Palatopremaxillary ligament (1.00). In all taxa examined except Centracanthidae, a broad ligament extends from the palatine to the ascending process of the premaxilla and continues to the contralateral palatine (0) (Johnson, 1980: figs. 4, 7, 9–12). In Centracanthidae it is absent (1) (Johnson, 1980: fig. 8).

24. Ethmomaxillary ligament (0.29, 0.75). A well-developed ligament extends unbranched from the ethmoid to the articular head of the maxilla in the outgroup taxa and a number of sparid and centracanthid genera (0) (Johnson, 1980: figs. 4, 7, 8). In the Nemipteridae it bifurcates to send a short branch to the palatine (1) (Johnson, 1980: figs. 9, 10). This ligament is absent in Lethrinidae, *Spicara alta*, and most sparid genera (2) (Johnson, 1980: figs. 11, 12).

25. Shape of suborbital shelf (0.90, 0.97). The suborbital shelf projects from the medial margin of the third infraorbital and exhibits a number of distinct shapes, most of which are illustrated for sparoids by Akazaki (1962: fig. 6). In Haemulidae there is no suborbital shelf (0). In *Morone* and *Lutjanus* the suborbital shelf is nearly quadrangular (1). In the nemipterid genera *Nemipterus*, *Parascolopsis*, and *Pentapodus* the shelf is ovoid (2). In the nemipterid genera *Scolopsis* and *Scaevius*, the shape is roughly trapezoidal with the widest base proximally and with sharp apices both anteriorly and posteriorly (3). In the lethrinids *Gnathodentex*, *Gymnocranius*, *Monotaxis*, and in Centracanthidae the shelf is reduced to an L-shaped strut (4). In *Lethrinus* this L-shaped strut is further reduced to a tiny projection (5). In many Sparidae the shelf is roughly trapezoidal, the widest base proximally with the anterior apex pointed with a ventrally directed laminar extension, and the posterior apex is rounded (6). In other sparids the shelf is roughly trapezoidal, the widest base proximally with a rounded apex posteriorly and without a ventrally directed laminar extension on the anterior apex (7). In the sparid genera *Acanthopagrus*, *Rhabdosargus*, and *Sparidentex* the shelf is roughly a parallelogram, wider in lateral rather than a rostral-caudal plane (8). In the lethrinid *Wattsia*, there is a unique roughly trapezoidal shape with the widest base proximally with the anterior apex rounded and the posterior apex pointed (9).

26. Shape of first two infraorbital bones (0.20, 0.86). The first two infraorbitals are wider than deep in the outgroups, Nemipteridae, Centracanthidae, and certain

Sparidae (0) (Akazaki, 1962: fig. 6). In Lethrinidae and most Sparidae, one or both of these bones are deeper than wide (1).

27. Suborbital shelf anterior extension (1.00). In all outgroup taxa with a suborbital shelf, the shelf occurs on the third infraorbital and does not extend anteriorly behind the second infraorbital (0). In all sparoid taxa examined, there is a suborbital shelf on the third infraorbital that extends anteriorly behind the second infraorbital (1). A similar condition was described and illustrated for other percoids by Smith and Bailey (1962) and Baldwin and Johnson (1993).

28. Extent of suborbital shelf origin on third infraorbital (1.00). In Haemulidae there is no suborbital shelf (0). In *Morone*, *Lutjanus*, and Nemipteridae the suborbital shelf originates along the entire length of the third infraorbital (1). In the Lethrinidae, Sparidae, and Centracanthidae, the suborbital shelf originates only on the anterior part of the third infraorbital (2).

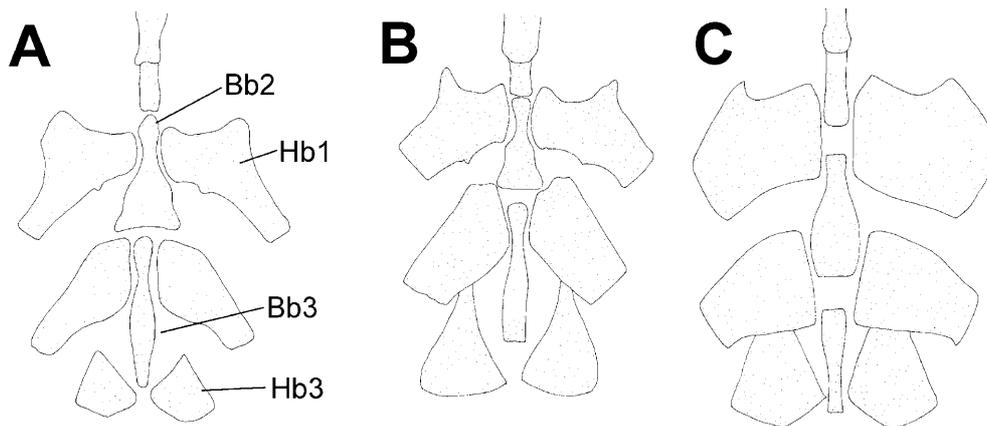
29. Shape of gill rakers (0.67, 0.92). In the outgroups, Sparidae, and *Nemipterus japonicus*, the anterior row of gill rakers on the first arch are “lathelike,” flattened, elongate, sharp-tipped, and higher than wide (0) (Akazaki, 1962: fig. 4). In lethrinids and most nemipterids, these gill rakers are more “clublike,” flattened, round-tipped, and typically wider than high (1). In two Nemipteridae, *Scaevius milli* and *Scolopsis ciliatus*, they are rounded and the anterior faces are concave, so that they are cupped (2).

30. Teeth on gill rakers (0.40, 0.79). In the outgroups and all sparid genera except *Petrus*, the anterior row of gill rakers on the first arch bear teeth more or less linearly arranged along the length of the medial edges (0). In the nemipterids *Nemipterus*, *Parascolopsis*, *Pentapodus*, and all species of *Scolopsis* except *S. ciliatus*, all lethrinids, and the sparid *Petrus*, all gill rakers are short and blunt with teeth arranged in a cluster at the tips (1). In *Scaevius milli* and *Scolopsis ciliatus*, teeth are lacking on some or all the rakers of the first arch (2). This character is partially correlated with character 29.

31. Position and shape of third basibranchial (1.00). In the outgroups, Nemipteridae, and Sparidae, the third basibranchial is robust and elongate (typically longer than the second basibranchial) and the posterior tip extends to a point just anterior to or near the point where the third hypobranchials most closely approach one another in the middle (0) (Fig. 6A). In centracanthids the basibranchial is also robust and elongate (much longer than the second basibranchial) and the posterior tip extends to a point notably anterior to the point where the third hypobranchials approach the midline (1) (Fig. 6B). In Lethrinidae the third basibranchial is less robust and shorter than the second basibranchial and its posterior tip turns down posteriorly to extend below and beyond the point where both third hypobranchials approach the midline (2) (Fig. 6C).

32. Insertion of branchiostegals on ceratohyals (1.00). The outgroups examined have seven branchiostegal rays with five inserted on the proximal ceratohyal, and one inserted on the distal ceratohyal (elsewhere referred to as the epihyal, although Goodrich, 1930, pointed out that this terminology is inconsistent with true homology) and one in-

Fig. 6. Dorsal view of second and third basibranchials (*Bb2*, *Bb3*) relative to first and third hypobranchials (*Hb1*, *Hb3*) for **A** *Oblada melanura* (81 mm SL), **B** *Spicara maena* (118 mm SL), and **C** *Monotaxis grandoculis* (73 mm SL)



serted in the space between the proximal ceratohyal and distal ceratohyal in *Morone*, or two inserted on the distal ceratohyal in all other outgroups. Because more numerous branchiostegals are considered the primitive condition in perciform outgroups and both insertion patterns in the outgroups are unique with respect to those in the ingroups, we consider the insertion patterns in the outgroups as a single character state (0). All sparoids have six branchiostegals with insertion patterns all distinct from the outgroups. In the Nemipteridae, five branchiostegals insert on the distal ceratohyal and one inserts in the space between the distal and proximal ceratohyal (2). In Lethrinidae, Sparidae, and Centracanthidae, four branchiostegals insert on the distal ceratohyal, one on the proximal ceratohyal, and one in the space between the distal and proximal ceratohyals (1).

33. Dorsal margin of urohyal (1.00). In the outgroups examined and all sparoids except the Lethrinidae, the dorsal margin of the urohyal is not noticeably flared laterally or flared only slightly, so that a dorsal cross section appears in the shape of a "T" (0). In the Lethrinidae, the upper margin of the urohyal is flared dorsolaterally to form a distinct Y shape in dorsal cross section (1) (Akazaki, 1962: fig. 16).

34. Second epibranchial toothplate (0.50, 0.88). In many percoids, including *Lutjanus*, Haemulidae, Lethrinidae, Sparidae, and Centracanthidae, there is an autogenous toothplate closely associated with the posterior end of the large fused toothplate of the second pharyngobranchial (0). Although it has generally been referred to as the second epibranchial toothplate (e.g., Johnson, 1980: fig. 36), its close association with the second pharyngobranchial casts some uncertainty on its origin. In *Morone* and the Nemipteridae it is absent (1).

35. Basihyal ventral keel (0.50, 0.88). In Lethrinidae and *Pentapodus*, there is a well-developed ventral keel on the first basibranchial (1) (Fig. 7A). In the outgroups, Sparidae, Centracanthidae, and all remaining Nemipteridae this keel is weak or absent (0) (Fig. 7B).

36. Uncinate process on fourth epibranchial (1.00). The presence of an uncinate process on the fourth epibranchial characterizes acanthomorphs (Johnson and Patterson, 1996,

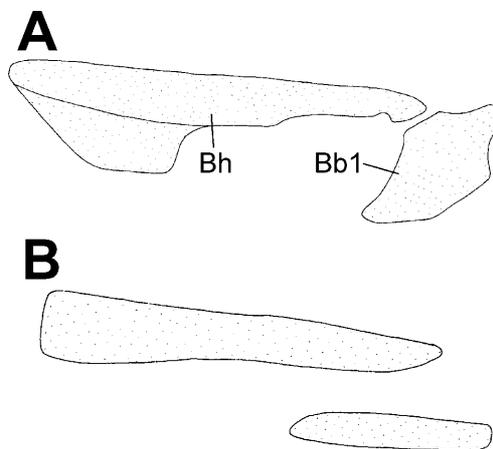


Fig. 7. Left-side lateral view of basihyal (*Bh*) articulation with first basibranchial (*Bb1*) for **A** *Lethrinus ornatus* (109 mm SL) and **B** *Scaevius milli* (74 mm SL). The ventral projection on the anterior part of the basihyal of *Lethrinus ornatus* is the basihyal keel

p. 275). It is present in all outgroups examined and all sparoids (0) except the Nemipteridae (1). Although present, in *Lethrinus* and *Gnathodentex* it is sometimes difficult to see because it has become closely associated with the levator process (present in all taxa examined) and has lost a close association with the uncinate process of the third epibranchial.

37. Basihyal articulation with first basibranchial (0.50, 0.88). In *Morone*, Haemulidae, Lethrinidae, Sparidae, and Centracanthidae, the posterior tip of the basihyal is in close proximity to and articulates with a specialized flattened articular surface on the dorsal edge of the first basibranchial (0) (Fig. 7A). In *Lutjanus* and Nemipteridae, the posterior tip of the basihyal is not in close proximity to and does not articulate with a specialized surface of the first basibranchial (1) (Fig. 7B).

38. Second and third pharyngobranchials articulate at site where both articulate with the second epibranchial (1.00). In Lethrinidae, Sparidae, and Centracanthidae the second pharyngobranchial bears one elongate or two lateral

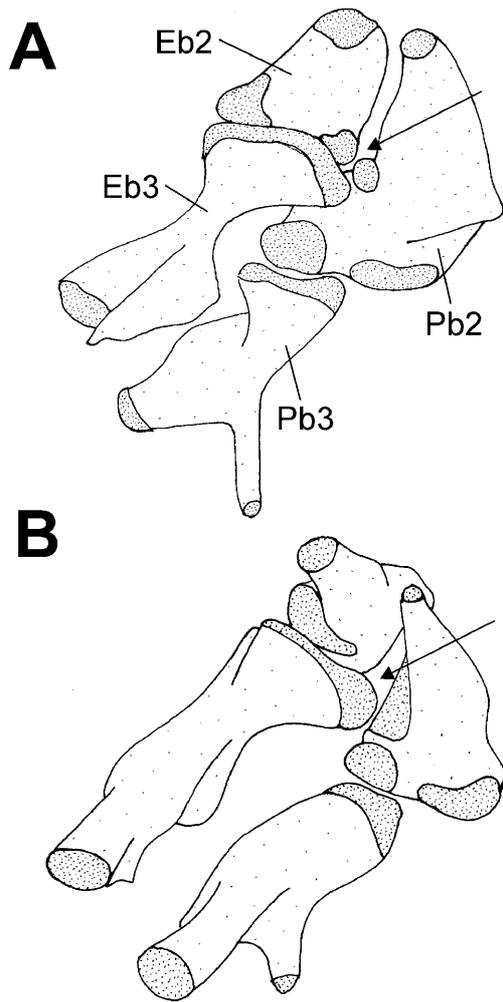


Fig. 8. Dorsal view of left second epibranchial (*Eb2*), second pharyngobranchial (*Pb2*), third epibranchial (*Eb3*), and third pharyngobranchial (*Pb3*) of **A** *Lethrinus harak* (98mm SL) and **B** *Scolopsis bilineatus* (114mm SL). Heavily stippled areas are cartilage. Arrows indicate where opposing condyles on *Pb2* and *Pb3* either do **A** or do not **B** articulate. Pharyngeal teeth are not shown

condyles, the posteriormost of which articulates with or near a cartilaginous condyle on the anterolateral corner of the third pharyngobranchial; the broad medial cartilaginous tip of the second epibranchial articulates with all three of these condyles (1) (Fig. 8A). In the outgroups and Nemipteridae, the second pharyngobranchial also bears one or two lateral condyles and one on the anterolateral corner of the third pharyngobranchial; the second epibranchial articulates with both of these but the edges of the two pharyngobranchials are well separated in this area, with no condylar articulation (0) (Fig. 8B).

39. Interarcual cartilage and associated uncinate process on first epibranchial (0.50, 0.89). In the outgroups, Lethrinidae, Centracanthidae, and Sparidae there is a cartilage-tipped uncinate process on the first epibranchial and a variously developed interarcual cartilage extending part-way or completely between its tip and a cartilaginous

condyle of the second pharyngobranchial (0) (e.g., Johnson, 1980: fig. 36). Nemipteridae lack a cartilage-tipped uncinate process on the first epibranchial and an interarcual cartilage (1).

40. Cartilaginous articulation of first pharyngobranchial and first epibranchial (1.00). In the outgroups, Lethrinidae, Sparidae, and Centracanthidae the proximal-dorsal cartilaginous tip of the first epibranchial loosely articulates with the cartilaginous tip of the first pharyngobranchial (0). In Nemipteridae, the lateral distal cartilaginous tip of the first pharyngobranchial is cupped and strongly embraces and envelops the entire proximal cartilaginous tip of the first epibranchial (1).

41. Supraneural and dorsal pterygiophore insertion (0.67, 0.80). Following the formula used by Ahlstrom et al. (1976), four supraneural and dorsal pterygiophore insertion patterns exist: 0/0/0 + 2/1 + 1/ in *Morone*, *Lutjanus*, and *Sarpa* (0); 0/0 + 0/2 + 1/1/ in Haemulidae, Lethrinidae, *Spicara*, and most Sparidae (1); 0/0/2 + 1/1/ in Nemipteridae (2); 0/0 + 0/2/1 + 1/ in *Oblada* (3); and 0/0/0 + 2/1/ in *Centracanthus* and *Boops* (4).

42. Shape of distal tips of supraneurals (0.67, 0.94). In Haemulidae and Nemipteridae, the distal tips of the supraneurals are roundish or oblong (0) (Akazaki, 1962: fig. 19). In *Morone*, *Lutjanus*, and all sparids and centracanthids they are wedge shaped in dorsal view (1). In Lethrinidae they are roughly star- or chevron shaped in dorsal view (2).

43. Anterior laminar expansion on first dorsal pterygiophore (1.00). In Nemipteridae the anterior lamina of the first pterygiophore is greatly expanded (1) (Akazaki, 1962: fig. 19) relative to its condition in the outgroups and all other sparoids (0).

44. Overlap of bases of first hypural and parhypural with urostyle (1.00). In all Sparidae and Centracanthidae, the proximal tips of the first hypural and parhypural have a laminar extension, terminating in a point that broadly overlaps and embraces the urostyle (1) (Fujita, 1990: figs. 320, 322, 323). In the outgroups, Lethrinidae, and Nemipteridae the first hypural and parhypural articulate with but do not broadly overlap the urostyle (0) (Fujita, 1990: fig. 324). In Haemulidae there is a small laminar extension of the proximal tips of the first hypural and parhypural but these do not embrace the urostyle.

45. Neural pre- and postzygopophyses of caudal vertebrae (1.00). In the outgroups, Nemipteridae, Sparidae, and Centracanthidae, most caudal vertebrae bear neural prezygopophyses that are directed anteriorly and intrude over the postzygopophyses of the preceding vertebra (0). In Lethrinidae most caudal vertebrae bear neural prezygopophyses that are directed upward and the postzygopophyses of the preceding vertebrae are also directed upward and nearly equal in height to the prezygopophyses (1).

46. Neural prezygopophyses of precaudal vertebrae (0.50, 0.90). In *Lutjanus*, Haemulidae, and Nemipteridae, most of the neural prezygopophyses of precaudal vertebrae are pointed primarily in a rostral direction (0) (Fig. 9A). In *Morone*, Lethrinidae, Sparidae, and Centracanthidae they are pointed dorsorostrally (1) (Fig. 9B).

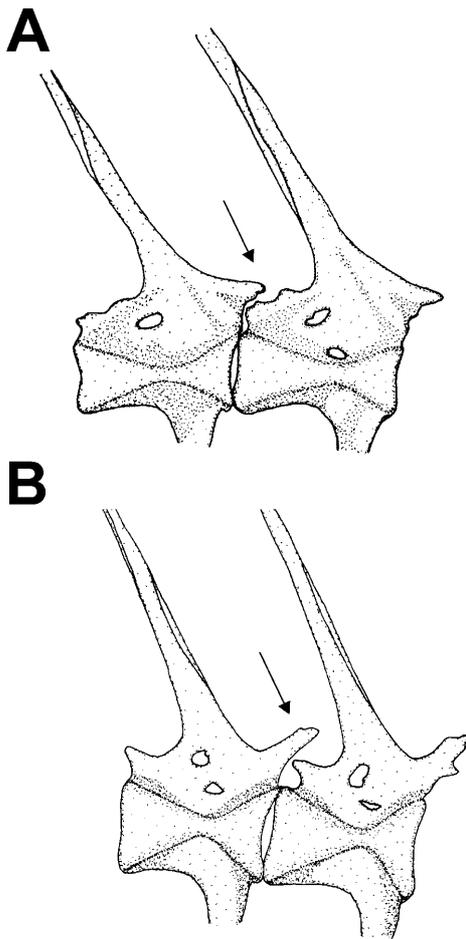


Fig. 9. Right-side lateral view of shape of prezygopophyses (arrows) of fifth and sixth precaudal vertebrae of **A** *Nemipterus celebicus* (98 mm SL) and **B** *Monotaxis grandoculis* (73 mm SL)

47. Accessory subpelvic keel (0.50, 0.88). In *Morone* and all Nemipteridae there is a long laminar ridge (accessory subpelvic keel, sensu Katayama, 1959) on the ventral surface of each pelvic bone, medial to the ventrolateral ridge (main subpelvic keel) (1). In the other outgroups examined and all other sparoids, there is no accessory subpelvic keel (0).

48. Subpelvic and postpelvic processes (1.00). In Lethrinidae the subpelvic and postpelvic processes are about equal in length or the postpelvic process is longer, and the subpelvic processes are directed ventrally as well as rostrally (1) (Fig. 10B). In the outgroups, Nemipteridae, Sparidae, and Centracanthidae the subpelvic process is typically much longer than the postpelvic process and it is directed mostly rostrally rather than ventrally (0) (Fig. 10A). In *Morone* these processes are equal in length and in *Lutjanus* the postpelvic process is longer but the subpelvic processes are directed rostrally, not ventrally.

49. Ventral tip of cleithrum (1.00). In Nemipteridae the ventral tip of the cleithrum is extended posteriorly (1) (Fig. 11A). In all other taxa examined this tip is not extended posteriorly (0) (Fig. 11B).

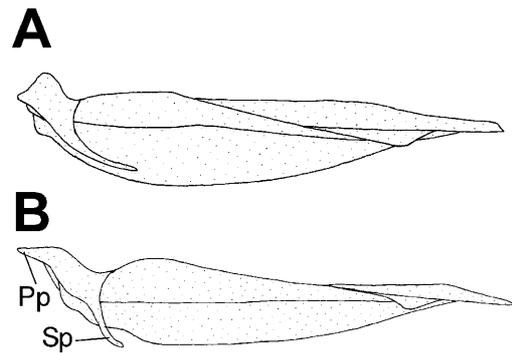


Fig. 10. Medial view of left pelvic bone and subpelvic (*Sp*) and postpelvic (*Pp*) processes for **A** *Polysteganus caeruleopunctatus* (251 mm SL) and **B** *Lethrinus nebulosus* (214 mm SL)

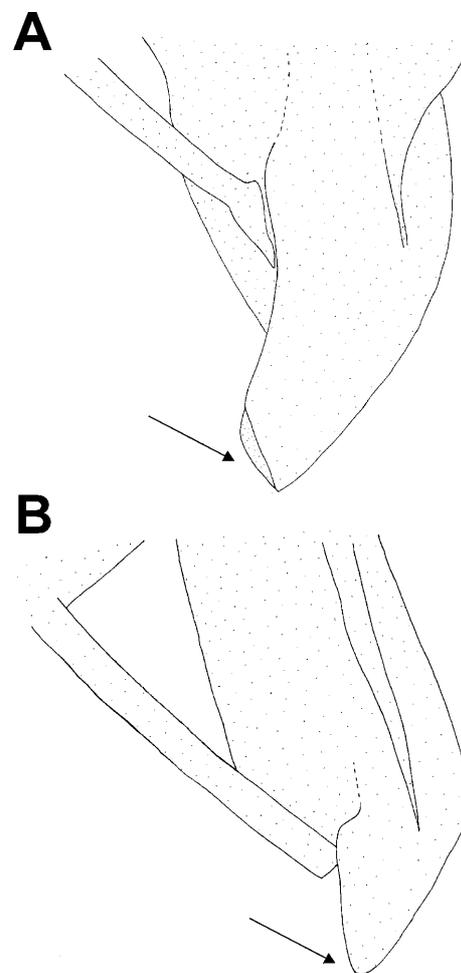


Fig. 11. Lateral view of right ventral tip of cleithrum (arrows) and coracoid for **A** *Nemipterus celebicus* (98 mm SL) and **B** *Dentex barnadi* (120 mm SL)

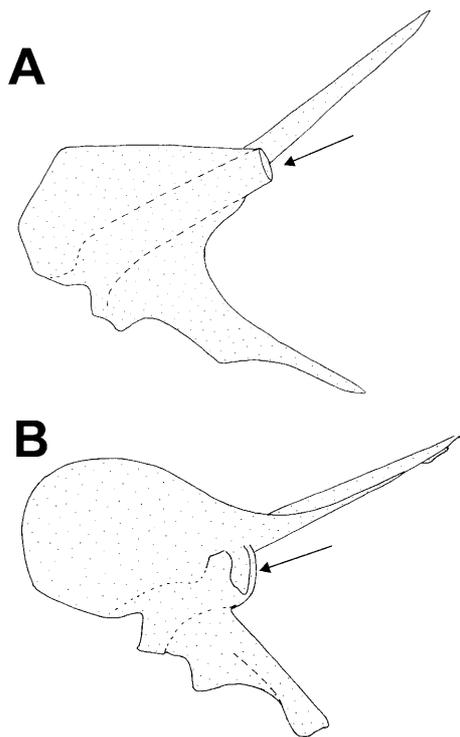


Fig. 12. Right-side lateral view of configuration of sensory canal (arrows) of posttemporal for **A** *Nemipterus marginatus* (83 mm SL) and **B** *Polysteganus caeruleopunctatus* (251 mm SL)

50. Articulation of ventralmost proximal radial of pectoral girdle (1.00). In Nemipteridae this ventralmost proximal radial of the pectoral girdle articulates entirely with the coracoid (1). In the outgroups examined and all other sparoids, it articulates with the scapula or the coracoid but partially extends into the gap between the coracoid and the scapula (0).

51. Sensory canal opening on posttemporal (0.50, 0.88). In Nemipteridae and *Spicara alta* this opening is over and adjacent to the upper arm of the posttemporal (1) (Fig. 12A). In the outgroups, Lethrinidae, Sparidae, and remaining Centracanthidae species, the anterior opening of the sensory canal is below and separated from the upper arm of the posttemporal (0) (Fig. 12B).

52. Denuded area anterior to lateral line tube of lateral line scales (0.50, 0.90). In Nemipteridae and all outgroups examined except *Morone*, there is a distinct area anterior to the lateral line tube of lateral line scales that does not have circuli (0). In *Morone*, Lethrinidae, Sparidae, and Centracanthidae this area is completely or mostly populated with circuli (1).

53. Apical pore in lateral line scale (1.00). There is an apical pore in each lateral line scale of Sparidae and Centracanthidae (1) that is lacking in the outgroups, Nemipteridae, and Lethrinidae (0).

54. Direction of circuli in posterior field of lateral line scales (0.25, 0.77). In the outgroups, most Lethrinidae, and all Nemipteridae except *Nemipterus*, the circuli in the posterior field of lateral line scales are directed caudally (0). In

Nemipterus, some *Lethrinus*, and all Centracanthidae and Sparidae, the circuli flare dorsally and ventrally to the edge of the scale (1).

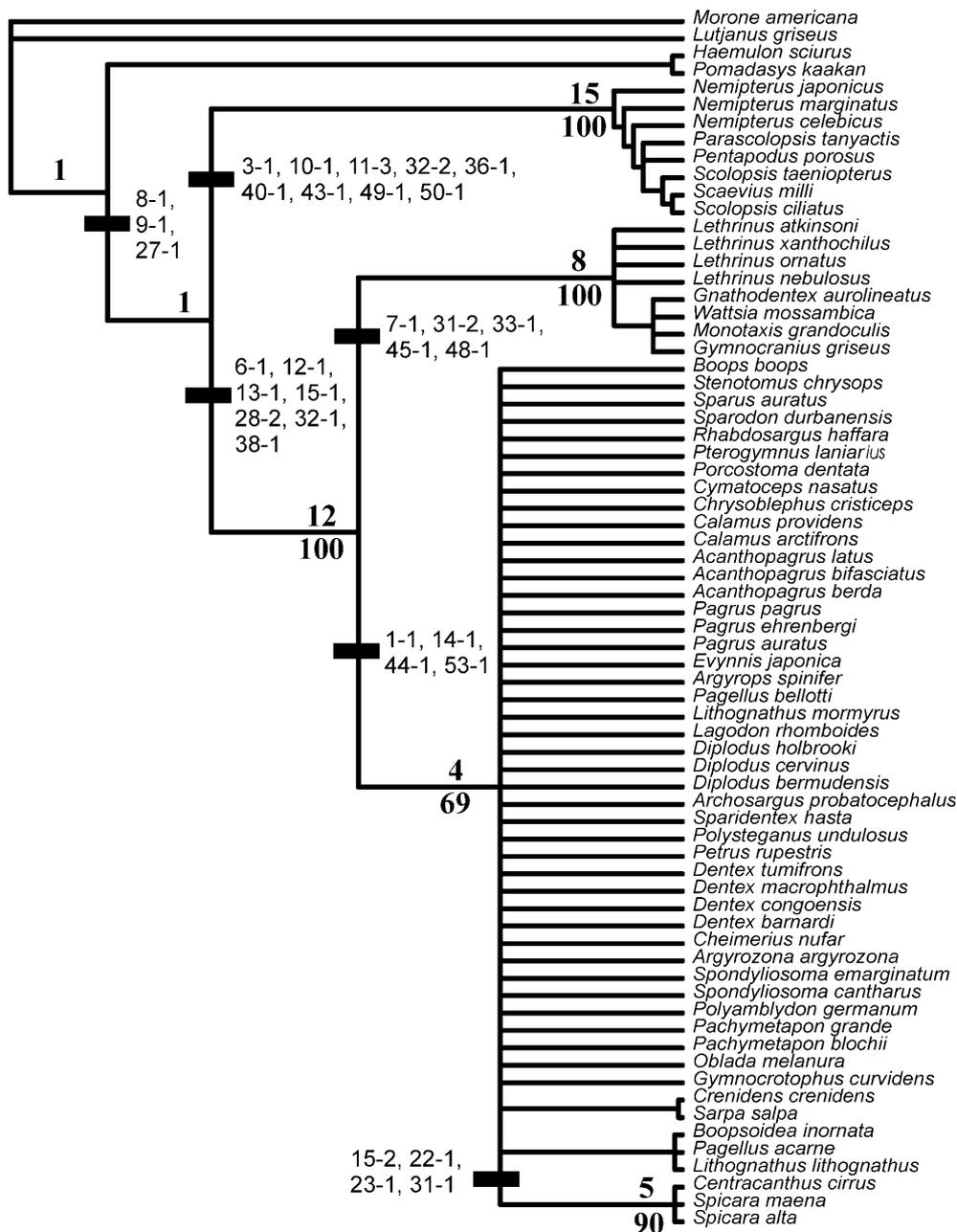
A matrix of character states for all taxa is summarized in Table 1. A strict consensus of 45 most parsimonious trees obtained from an analysis of this matrix is given in Fig. 13. The consistency index is 0.635 and retention index is 0.926. The total number of steps is 126.

Discussion

The monophyly of the Sparoidea is confirmed but not well supported (Fig. 13). This node had a bootstrap support below 50% and a Bremer support of only one. Three nonhomoplasious characters support this node: symplectic with dorsal and ventral laminar extensions (8-1; numbers given in the discussion after characters refer to the character number followed by the character state as presented in the results and Table 1), broad articulation between hyomandibular and metapterygoid (9-1), and anterior extension of suborbital shelf behind second infraorbital (27-1). The former two of these characters have not been reported elsewhere among the Percoidei (Johnson, 1980), although a complete survey of these characters in all percooid families has not been done. The third character is not unique among percooids (Smith and Bailey, 1962; Baldwin and Johnson, 1993), although an anterior extension of the suborbital shelf does not occur in the outgroups we examined for this study. The Lethrinidae node, the Sparidae plus Centracanthidae node, and the Lethrinidae plus Sparidae plus Centracanthidae nodes are all well supported and therefore weak support for Sparoidea only questions the inclusion of Nemipteridae. In a molecular study, Orrell et al. (in press) failed to find strong support for the inclusion of Nemipteridae in Sparoidea. At present, the most parsimonious solution supports a monophyletic Sparoidea that includes Nemipteridae, Lethrinidae, Sparidae, and Centracanthidae. The Haemulidae are sister to the Sparoidea in our study but there is weak node support with bootstrap values below 50% and a Bremer decay value of one. The phylogenetic relationship of the Haemulidae and Sparoidea cannot be tested until a more comprehensive review of percooid families is accomplished.

The Nemipteridae are monophyletic with 100% bootstrap support and a Bremer support of 15. Nonhomoplasious character states that define the Nemipteridae include posterodorsal opening of pterotic sensory canal on columnar extension (3-1), dorsolateral process on hyomandibular separated from preopercular sensory canal (10-1), narrow sensory canal openings on preopercle (11-3), five branchiostegals inserted on distal ceratohyal and one inserted in space between proximal and distal ceratohyal (32-2), absence of uncinat process on fourth epibranchial (36-1), cuplike cartilaginous articulation between first pharyngo- and epibranchials (40-1), expansion of anterior median dorsal pterygiophore lamina (43-1), posterior extension of ventral tip of cleithrum (49-1), and articulation of ventralmost pectoral radial entirely with coracoid (50-1).

Fig. 13. Strict consensus tree from parsimony analysis of 54 morphological characters for sparoid fishes and four outgroups. The number above the base of a node indicates the Bremer support value and the number below the node indicates bootstrap support for the respective node. Nonhomoplasious characters that support nodes are indicated on branches by their respective character number, followed by the character state



The Lethrinidae are the sister group of the Sparidae plus Centracanthidae. This node is well supported with 100% bootstrap support and a Bremer decay value of 12. A number of nonhomoplasious characters support this relationship: these include absence of intercalar (6-1), caudally directed ethmoid articular surface on palatine (12-1), lack of strong serrations on preopercle (13-1), continuous fusion of articular and ascending process of premaxilla (15-1), suborbital shelf origin restricted to anterior part of third infraorbital (28-2), four branchiostegals inserted on proximal ceratohyal, one on distal ceratohyal, and one in between (32-1), and second and third pharyngobranchials articulate at site where both articulate with second epibranchial (38-1). Most of these are known or likely to be present in other percoids.

Monophyly of the Lethrinidae is supported with 100% bootstrap values and a Bremer decay value of 8. Nonhomoplasious characters that support this node are reduced anterior articulation of the palatine and ectopterygoid (7-1), reduced third basibranchial (31-2), Y-shaped cross section of dorsal margin of urohyal (33-1), dorsally directed prezygopophyses and postzygopophyses of precaudal vertebrae (45-1), postpelvic process longer or about equal in length relative to subpelvic process (48-1). The Monotaxinae are also monophyletic but the monophyly of *Lethrinus* has yet to be confirmed.

The Sparidae plus Centracanthidae are monophyletic with bootstrap support of 69% and Bremer decay value of 4. Nonhomoplasious synapomorphies that support this node are three openings in lateral wall of pars jugularis

Table 1. Continued

Taxon	Character
	111111111122222222223333333333444444444455555 123456789012345678901234567890123456789012345678901234
<i>Eynniss japonica</i>	110101011011111101112002611200010100010011010100000111
<i>Pagrus auratus</i>	110101011011111101112002611200010100010011010100000111
<i>Pagrus ehrenbergi</i>	110131011011111101112002611200010100010011010100000111
<i>Pagrus pagrus</i>	110131011011111101112002611200010100010011010100000111
<i>Acanthopagrus berda</i>	110131011011111101112002811200010100010011010100000111
<i>Acanthopagrus bifasciatus</i>	110131011011111101112002811200010100010011010100000111
<i>Acanthopagrus latus</i>	110131011011111101112002811200010100010011010100000111
<i>Calamus arctifrons</i>	110131011011111101112002711200010100010011010100000111
<i>Calamus providens</i>	110131011011111101112002711200010100010011010100000111
<i>Chrysoblephus cristiceps</i>	110131011011111101112002611200010100010011010100000111
<i>Cymatoceps nasatus</i>	110101011011111101112002711200010100010011010100000111
<i>Porcostoma dentata</i>	110101011011111101112002711200010100010011010100000111
<i>Pterogymnus lanarius</i>	110131011011111101112002711200010100010011010100000111
<i>Rhabdosargus haffara</i>	110131011011111101112002811200010100010011010100000111
<i>Sparodon durbanensis</i>	110131011011111101112002711200010100010011010100000111
<i>Sparus auratus</i>	110131011011111101112002611200010100010011010100000111
<i>Stenotomus chrysops</i>	110131011011111101112002711200010100010011010100000111

(1-1), distal end of alveolar ramus of premaxillary modified to articulate with distal ventral edge of maxilla (14-1), proximal tips of first hypural and parhypural broadly overlap and articulate with urostyle (44-1), and apical pores present in lateral line scales (53-1). The second two characters have not been reported elsewhere among percoids. Monophyly of the species of Centracanthidae included in this study is supported by bootstrap values of 90% and a Bremer decay value of 5. Centracanthids share absence of the articular process of the premaxilla (15-2), ascending process of premaxilla extending posteriorly over frontal (22-1), absence of the palatopremaxillary ligament (23-1), and a robust third basibranchial that extends noticeably anterior to the point where both third hypobranchials approach the midline (31-1). Placement of centracanthids is unresolved with respect to sparid genera. Orrell et al. (in press) found Sparidae to be paraphyletic without inclusion of two species of *Spicara*. However, this molecular evidence also suggests that *Spicara* is nonmonophyletic. Additional molecular and morphological data are needed on all centracanthid species and sparid genera to specifically resolve these relationships.

Our phylogeny of sparoid families, which places Nemipteridae as the sister-group of Lethrinidae plus Sparidae (including centracanthids), is congruent with what we believe to be a cladistic interpretation of Akazaki's (1962) hypothesis (see Fig. 1A). Johnson (1980, 1993), on the other hand, argued that the available evidence pointed to a closer affinity between Nemipteridae and Lethrinidae, but with a broader sampling of taxa we find some characters (e.g., dorsal fin ray formulas and numbers of epineurals, sensu Patterson and Johnson, 1995) are more variable among sparoids than Johnson recognized. Johnson (1980) also suggested that one or both of these families may be

paraphyletic, and believed the strongest evidence for this was found in the similarity of jaw muscles and ligaments in the nemipterid *Scolopsis* and the lethrinid *Gnathodentex*. Our more extensive observations indicate that the size and shape of the adductor mandibulae muscles and ligaments is more variable within lethrinids and that coding of these characters is problematic.

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