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Introduction

The morphology of the supporting elements of the caudal skeleton is considered by most fish systematists to provide important taxonomic and phylogenetic information (Gosline, 1961; Nybelin, 1963; Patterson, 1968). The principal and procurrent rays associated with these elements however, are often not illustrated or described in studies of caudal osteology, and where they are, details of their morphology are usually not considered. In consequence, a phylogenetically significant character within the Perciformes is to date undescribed. This character, involving a unique configuration of the two posteriormost ventral procurrent

rays (fig. 2), was first observed during the course of an investigation into the interrelationships of several percoid families. It was originally taken as a condition unique to the Haemulidae, but further exploration has shown it to be present with surprising consistency in other percoid families. The purpose of this paper is to describe the character, present a synoptic survey of its distribution within the Perciformes, and discuss some of its phylogenetic implications.

Material and Methods

Both cleared and stained and alcoholic specimens were examined. In the latter, the morphology of the caudal ray bases could be clearly determined by examination with transmitted light under a dissecting microscope after minor dissection and folding back of the skin and flesh in this region.

The majority of the specimens examined are in the collections of the Scripps Institution of Oceanography (SIO) and the California Academy of Sciences (CAS). A few specimens are part of a cleared and stained collection housed at the Southwest Fisheries Center, National Marine Fisheries Service (NMFS). In order to shorten table I, catalogue numbers are not included. However, a complete listing of all specimens examined and their catalogue numbers is on file with the California Academy of Sciences.

Description

The usual number of principal rays in the perciform caudal is 17, consisting of 15 branched and 2 unbranched rays (Regan, 1913). These 17 rays support the major surface of the caudal fin. Anterior to these principal rays, dorsally and ventrally, are the procurrent rays, a series of much shorter rays not typically included in the posterior margin of the fin.

Figure 1 shows the usual arrangement of principal and procurrent caudal rays. There is no modification of the proximal ends of the procurrent rays, and the ventral series is very nearly a mirror image of the dorsal one. This is the situation in the majority of teleosts. However, in a group of about 30 percoid families and the Polynemidae, Sphyraenidae, and Stromateoidei, there is a unique specialization of the ventral series. The posteriormost procurrent ray bears a spur that projects ventrally to overlap the preceding ray (fig. 2). Ordinarily, in fishes with a spur the preceding ray does not extend forward proximally to meet the bases of the remaining procurrent rays, but is basally shortened, often originating just anterior to the overlapping spur. The presence or absence of the spur and the shortening of the preceding ray are indicated for the species examined

(arranged by family) in table I. Not shown in table I are those species observed in a cursory search for the spur or shortening in various non-acanthopterygian orders; this search failed to reveal any trace of either condition.

Shortening of the preceding ray does not always accompany the development of the spur, but this is by far the more frequent condition. In some genera, particularly within the Sciaenidae and the Stromateoidei, the spur is well developed, but the preceding ray extends forward normally. A condition which may or may not be homologous with that shown in figure 2 is found in the Beryciformes and in the genus *Symphysanodon*; the preceding ray is shortened with no trace of spur development. This condition is also evident in two genera of Polynemidae, but the presence of the spur in other members of that family possibly indicates a secondary reduction. A few species, as in the genera *Siniperca* and *Scombrolabrax*, have no typically developed spur but do have a small projection interpretable as a remnant of the spur. This condition is indicated by "r" in table I. Although usually the preceding ray base is obviously either shortened or not, the situation has proved to be difficult to interpret in a few species. A very slight basal shortening is indicated by ^{1} in the table. In the text it is assumed that the spur is accompanied by shortening of the preceding ray except where otherwise indicated.

The caudal musculature was compared in genera with and genera without the spur. All muscle bundles described and illustrated by Nursall (1963) occur in each group and exhibit similar origins and insertions. The ventral bundle of the main body of the deep ventral flexor inserts on the last ventral procurrent ray, which is the one that bears the spur. The spur, when present, forms the point of insertion. In its absence, insertion is directly on the ray axis. No difference was noted in the insertion of the remaining tendons of the ventral bundle.

Discussion

The presence of such a character as the procurrent spur in a large number of fairly diverse families leads to two possible conclusions. Either it has been evolved independently in several separate lineages and fixed by strong selection pressures resulting from its functional importance, or it has been evolved only once and thus indicates relationship by common ancestry of all those groups possessing it.

The association of the procurrent spur with the caudal musculature suggests a possible function. Nursall (1963) pointed out that, in *Hoplopagrus*, the chief action of the deep ventral flexor "is flexion with abduction also being applied owing to the form of the heads of the fin rays and sites of attachment." If any functional significance for the procurrent spur is to be inferred, it must surely involve an increased ability to abduct the last procurrent ray

(and through their connective association, all ventral rays of the caudal). A shift in insertion of the uppermost tendon of the ventral bundle from a point on the lateral surface of the ray to a ventrolateral projection (procurrent spur) could alter the forces acting on the ray when the muscle contracts in such a way as to increase the abduction vector. Increase in size of the spur would increase abduction leverage. The associated shortening of the base of the preceding ray might prevent its interference with full abduction, allowing the base of the next preceding ray to project up into the resulting space as its posterior part is pushed downward. In essence, this may mean that those fishes possessing a procurrent spur have a greater ability to spread the ventral rays of the caudal fin or at least a more efficient way of spreading them to the same degree.

The establishment of this rather speculative possible function for the procurrent spur does not necessarily lead to the acceptance of the alternative multiple-origin hypothesis. It is not the existence of the function itself but its adaptive value that is crucial to the concept of convergence. Any functional advantage in this case would surely be associated with the operation of the caudal fin and locomotion. Yet a quick survey of table I shows that there is no obvious correlation between the presence or absence of the spur and caudal fin structure, swimming type, or life style. The spur is present in such diverse swimming and feeding types as *Stereolepis* and *Emmelichthys* and yet absent in *Epinephelus* and *Pterocaesio*, two forms representing a similar ecological range. It is absent in the fast swimming Carangidae and yet present in *Pomatomus*, also a powerful swimmer. Its presence or absence within families is very consistent, despite variation therein in swimming and feeding types, and where a few members of a family have lost the spur, no unifying pattern is apparent. The procurrent spur appears to be associated in no obvious way with adaptive radiation.

Ventral spurs are developed on one or more of the principal caudal ray bases in certain groups with a reduced number of rays, most notably in the Scorpaeniformes, Blennioidei, and Gobioidei. These spurs would probably facilitate abduction of the rays as is hypothesized for the procurrent spur. However, the procurrent spur has not been found in any members of these groups. Its absence, in spite of the apparent importance of abduction in these fishes as evidenced by spurs on the principal rays, strengthens the concept of the procurrent spur as a specialization of unique origin.

Several facts point to the primitiveness of the procurrent spur within the percoids. The Beryciformes exhibit a basal shortening of the next to last procurrent ray which might be interpreted as a foreshadowing of the percoid condition. The spur and the associated shortening characterize the Polynemidae and Sphyraenidae, two groups often placed at the pre-perciform or basal perciform level.

Finally, the presence of the spur in the lower percoid families Percichthyidae, Kuhliidae, Centropomidae, Scorpididae, Kyphosidae, and Monodactylidae directly demonstrates its early occurrence within the percoids.

These facts, and the fact that the presence or absence of the procurrent spur agrees for the most part with well known and accepted taxonomic groupings, particularly families, support the interpretation that the presence of the spur is a primitive perciform character, uniquely derived and thus indicative of phylogenetic relationship, i.e. all groups possessing it were derived from a common ancestor. The relationship of those groups lacking the spur is less clear. It is evident that the spur and associated shortening can be lost with no trace (essentially a reversion to the generalized teleost condition), as this has apparently occurred independently within the Sciaenidae and the Stromateoidei. It cannot be argued therefore, that other families without a spur represent a single lineage within the percoids. However, it does seem likely that many if not all of these families were derived from ancestors possessing the spur.

The value of the procurrent spur as a taxonomic and phylogenetic indicator can perhaps best be illustrated by considering its occurrence in relation to some current concepts of familial relationships and generic placements within the Perciformes:

Axillary process. The presence or absence of the scaly process in the axil of the pelvic fin was used by Regan (1913) and Gosline (1966) to suggest an arrangement of percoid families, the general phylogenetic validity of which is still uncertain. A comparison of the distribution of the procurrent spur with that of the axillary process shows only that the spur occurs more frequently in those families with the axillary process than in those without it (of 35 families, excluding beryciforms, listed by Gosline as having an axillary process, 15 have the spur; of 36 listed as not having the axillary process, only 8 have the spur). This higher frequency of coincidence of the two characters is probably a reflection of the fact that they are both primitive at the percoid level.

Ramus lateralis accessorius. Freihofer (1963) described various patterns of the ramus lateralis accessorius nerve (RLA) in the Perciformes and discussed their possible phylogenetic importance. There is a striking correlation between the occurrence of Freihofer's pattern 10 and the presence of the procurrent spur. The following are pattern-10 families: Arripidae, Theraponidae, Pomatomidae, Kuhliidae, Scorpididae, Kyphosidae, Girellidae, Nematistiidae, Centrolophidae, Nomeidae, Stromateidae (Freihofer, 1963), and Oplegnathidae (Freihofer, pers. comm.). Of these, only the Girellidae and Nematistiidae lack the spur. In the

Girellidae, the probably primitive genus *Graus*[1] retains a remnant of the spur, indicating that the absence of the spur in the other members of this family is secondary. *Nematistius* was described by Freihofer as having a "reduced pattern 10" which he considered homologous to the typical pattern 10. The absence of the spur then could be explained as a secondary loss, perhaps resulting from the modified caudal fin structure (deeply cleft fin ray bases, overlapping and closely applied to the hypurals). The possibility also exists that the "reduced pattern 10" is not homologous to the typical pattern 10 and that the usual placement of *Nematistius* in or near the Carangidae is correct. Interestingly, of the eleven pattern-10 families listed in table I of Haedrich (1967), only two, Girellidae and Nematistiidae, lack a bony bridge over the anterior vertical canal of the inner ear (AVC bridge), and these are the same two that lack the procurrent spur.

Percichthyidae. Gosline (1966) removed several genera from the Serranidae and placed them in the somewhat heterogeneous family Percichthyidae. The presence of the procurrent spur in all these genera (except *Niphon* and *Maccullochella*, of questionable pertinence to the group on other grounds) supports their exclusion from the Serranidae, in which the spur is consistently absent.

Symphysanodon. On the basis of an osteological study, Katayama (1968) agreed with previous authors in placing *Symphysanodon* in the Lutjanidae. Anderson (1970), while presenting no new anatomical evidence, concurred with Katayama. As part of an ongoing study on the limits and relationships of the lutjanids and some associated groups, I have recently examined the osteology and cheek myology of *Symphysanodon* and am unable to find any sound evidence for relating it to the Lutjanidae. It appears to be more primitive than the lutjanids in several respects and resembles most closely the Percichthyidae (sensu Gosline) except that it has an axillary process. The larva of *Symphysanodon* is distinctive and resembles no known percoid larva (E. H. Ahlstrom, pers. comm.). The presence of a marked shortening of the next to last ventral procurrent ray supports the removal of this genus from the Lutjanidae. The absence of the spur can be interpreted as a secondary loss or as a condition homologous to that seen in the beryciforms, suggesting that *Symphysanodon* may occupy a very primitive position within the percoids.

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[1] The monotypic *Graus nigra* (=*Pinguilabrum punctatum*) was originally described as a labrid by R. A. Philippi in 1887. However examination by the author and R. A. Fritzsche of several specimens of this fish from Chile indicates that it is a primitive girellid (to be reported on further).

Verilus. Most previous authors have treated this genus as a lutjanid closely allied to *Etelis*. However, on the basis of both external and internal morphology, I find no evidence of a lutjanid affinity, but instead a striking resemblance to the genera *Acropoma*, *Doderleinia*, and *Malakichthys*, which Gosline placed in the Percichthyidae. The presence of the procurrent spur in *Verilus* and its total absence in all lutjanid genera support the new placement of this genus.

Apogonidae. The procurrent spur is absent in all apogonid genera examined. Fraser (1972) was uncertain as to the placement of the genus *Brinkmanella*, and the presence of the spur in this genus indicates that it is probably not closely related, unless antecedently, to the Apogonidae. The absence of the spur in *Howella* and *Bathysphyraenops* provides no support for the placement of these genera in the Percichthyidae as was done by Fraser.

Scombrolabrax. Gosline (1968) stated that "except in a few characters, the genus *Scombrolabrax* could serve morphologically as an ancestral form for the trichiuroids and, in most respects, for the Scombridae as well." The presence of a remnant of the spur and shortening of the preceding ray suggest that if this genus does share any close relationship with the Scombroidei, it must indeed be a primitive one. If we accept *Scombrolabrax* as a basal scombroid, the presence of the spur supports Gosline's objection to the postulation of Starks (1911) that scombroid origins probably lie in the area of the carangids, and his suggestion, instead, of a pomatomid origin.

The above discussion and specific examples demonstrate the value of the procurrent spur in perciform systematics. It appears to be a phylogenetically significant character and one which should be considered in any systematic investigation of the perciform fishes, particularly the Percoidei. Because there are clear indications that the spur has been lost independently several times, it is not possible to draw any broad inferences concerning familial relationships solely from the distribution of the spur. Only a more comprehensive knowledge and understanding of all aspects of perciform morphology will eventually allow us to elucidate the complex evolutionary relationships of this diverse group of fishes.

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Literature Cited

ANDERSON, WILLIAM D., JR.
1970. Revision of the genus *Symphysanodon* (Pisces: Lutjanidae) with descriptions of four new species. Fishery Bulletin, vol. 68, no. 2, pp. 325-346, 5 figs., 3 tables.

FRASER, THOMAS H.
1972. Comparative osteology of the shallow water cardinal fishes (Perciformes: Apogonidae) with reference to the systematics and evolution of the family. Ichthyological Bulletin of the Rhodes University, no. 34, pp. 1-105, 44 pls., 6 tables.

FREIHOFER, WARREN C.
1963. Patterns of the ramus lateralis accessorius and their systematic significance in teleostean fishes. Stanford Ichthyological Bulletin, vol. 8, no. 2, pp. 79-189, 29 figs., 2 tables.

GOSLINE, W. A.
1961. The perciform caudal skeleton. Copeia, no. 3, pp. 265-270, 3 figs.
1966. The limits of the fish family Serranidae, with notes on other lower percoids. Proceedings of the California Academy of Sciences, ser. 4, vol. 33, no. 6, pp. 91-112, 10 figs., 1 table.
1968. The suborders of perciform fishes. Proceedings of the United States National Museum, vol. 124, no. 3647, 78 pp., 12 figs., 3 tables.

HAEDRICH, RICHARD L.
1967. The stromateoid fishes: systematics and a classification. Bulletin of the Museum of Comparative Zoology, vol. 135, no. 2, 56 figs., 2 tables.

KATAYAMA, MASAO
1968. Notes on the osteology and systematic position of *Symphysanodon typus* Bleeker. Bulletin of the Faculty of Education, Yamaguchi University, vol. 17, pt. 2, pp. 105-111, 3 figs.

NURSALL, J. R.
1963. The caudal musculature of *Hoplopagrus guntheri* Gill (Perciformes: Lutjanidae). Canadian Journal of Zoology, vol. 41, pp. 865-880, 6 figs.

NYBELIN, O.
1963. Zur Morphologie und Terminologie des Schwanskelettes der Actinopterygier. Arkiv för Zoologie, ser. 2, vol. 15, pp. 485-516, 22 figs.
PATTERSON, C.
1968. The caudal skeleton in Mesozoic acanthopterygian fishes. Bulletin of the British Museum (Natural History), Geology, vol. 17, pp. 47-102, 28 figs.
PHILIPPI, R. A.
1887. Sobre los tiburones y algunos otros peces de Chile. Universidad de Chile, Anales, vol. 71, pp. 1-42, 8 pls.
REGAN, C. T.
1913. The classification of the percoid fishes. Annals and Magazine of Natural History, ser. 8, vol. 12, pp. 111-145.
STARKS, E. C.
1911. Osteology of certain scombroid fishes. Leland Stanford Junior University Publications, University Series, no. 5, 49 pp., 2 pls., 1 fig.

TABLE 1. *The list below follows the classification of Greenwood* et al. *(1966) with certain modifications. The procurrent spur is present (+), absent (-), or a remnant (r). The preceding ray base is shortened (+), not shortened (-), or slightly shortened (1).*

	Procurrent Spur	Preceding Ray Base Shortened
BERYCIFORMES		
Polymixoidei		
Polymixiidae		
Polymixia lowei	-	-
Berycoidei		
Trachichthyidae		
Gephyroberyx japonicus, *Hoplostethus japonicus*, *Paratrachichthys fernandezianus*	-	+
Anomalopidae		
Anomalops katoptron, *Photoblepharon palpebratus*	-	+
Berycidae		
Beryx affinis	-	+
Holocentridae		
Myripristis leiognathus, *Adioryx suborbitalis*	-	1
Anoplogasteroidei		
Anoplogasteridae		
Anoplogaster cornuta	-	+
STEPHANOBERYCIFORMES		
Stephanoberycoidei		
Melamphaeidae		
Poromitra crassiceps, *Poromitra capito*, *Melamphaes spinifer*, *Melamphaes macrocephalus*	-	+
PERCIFORMES		
Mugiloidei		
Mugilidae		
Mugil cephalus, *Agonostomus monticola*	-	-

Sphyraenoidei		
Sphyraenidae		
Sphyraena barracuda, *Sphyraena lucasana*	+	+
Polynemoidei		
Polynemidae		
Polydactylus approximans, *Galeoides polydactylus*	+	+
Pentanemus quinquarius, *Eleutheronema tetradactylus*	-	+
Percoidei		
Percichthyidae		
Verilus sordidus, *Acropoma japonicum*, *Doderleinia berycoides*, *Malakichthys wakiyae*, *Synagrops bella*, *Stereolepis gigas*, *Morone saxatilis*, *Lateolabrax japonicus*, *Dicentrarchus punctatus*, *Percichthys trucha*, *Macquaria australasica*, *Percilia gillissi*	+	+
Siniperca chuatsi	r	+
Niphon spinosus, *Maccullochella macquariensis*	-	-
Incertae sedis		
Symphysanodon berryi	-	+
Kuhliidae		
Kuhlia marginata, *Kuhlia arge*	+	+
Labracoglossidae		
Labracoglossa argentiventris	+	+
Scorpididae		
Scorpis aequipinnis, *Medialuna californiensis*, *Micracanthus strigatus*	+	+
Kyphosidae		
Kyphosus elegans, *Sectator ocyurus*, *Hermosilla azurea*	+	+
Girellidae		
Graus nigra	r	-
Girella nigricans, *Melambaphes zebra*, *Doydixodon fremenvillii*	-	-

Monodactylidae		
Monodactylus argenteus	+	-
Centropomidae		
Centropomus nigrescens, Lates niloticus, Psammoperca waigiensis	+	+
Ambassidae		
Ambassis interrupta, Ambassis gymnocephala, Priops lungi	-	-
Glaucosomidae		
Glaucosoma burgeri	+	+
Serranidae		
Epinephelus labriformis, Paralabrax maculatofasciatus, Centropristes philadelphicus, Ellerkeldia maccullochi, Cratinus agassizii, Hypoplectrus lamprurus, Variola louti, Hapalogenys mucronatus, Serranus phoebe, Diplectrum pacificum, Schultzea beta, Liopropoma sp., Pikea aurora, Anthias anthias, Callanthias platei, Pseudanthias thompsoni	-	-
Grammistidae		
Rypticus bicolor	-	-
Pseudochromidae		
Pseudochromis fuscus	-	-
Plesiopidae		
Plesiops nigricans	-	-
Acanthoclinidae		
Belonepterygion fasciolatus	-	-
Theraponidae		
Therapon theraps, Pelates quadrilineatus, Datnia plumbea	+	+
Nannopercidae		
Nannoperca australis	-	-

Centrarchidae		
Micropterus salmoides, Lepomis machrochirus, Enneacanthus obesus, Elassoma zonatum, Chaenobryttus gulosus, Pomoxis annularis, Centrarchus macropterus, Acantharchus pomotis, Archoplites interruptus	-	-
Percidae		
Perca flavescens, Percina caprodes, Gymnocephalus cernua, Gymnocephalus schraetzer, Etheostoma nigrum	-	-
Apogonidae		
Apogon retrosella, Fowleria aurita, Archamia bleekeri, Cheilodipterus macrodon, Sphaeramia orbicularis, Rhabdamia gracilis, Pseudamia gelatinosa, Gymnapogon philippinus, Howella sp., Bathysphyraenops simplex	-	-
Incertae sedis		
Brinkmanella elongata	+	+
Priacanthidae		
Priacanthus cruentatus, Cookeolus boops	-	-
Malacanthidae		
Caulolatilus princeps, Malacanthus parvipinnus	-	-
Sillaginidae		
Sillago sp.	-	-
Mullidae		
Pseudupeneus grandisquamis, Mullus auratus, Parupeneus barberinus, Upeneus tragula, Mulloidichthys martinicus	-	-
Rachycentridae		
Rachycentron canadum	-	-
Echeneidae		
Remora remora	-	-

Carangidae		
Hemicaranx zelotes, *Trachinotus falcatus*, *Vomer declivifrons*, *Naucrates ductor*, *Trachurus symmetricus*, *Elegatis bipinnulatus*, *Gnathanodon speciosus*, *Decapterus punctatus*, *Chloroscombrus orqueta*, *Seriola dorsalis*	-	-
Nematistiidae		
Nematistius pectoralis	-	-
Coryphaenidae		
Coryphaena equiselis	-	-
Apolectidae		
Parastromateus niger	-	-
Menidae		
Mene maculata	-	-
Bramidae		
Brama japonica	-	-
Caristiidae		
Caristius maderensis	-	-
Pomatomidae		
Pomatomus saltatrix, *Scombrops boops*	+	+
Lactariidae		
Lactarius lactarius	+	+
Leptobramidae		
Leptobrama mulleri	+	+
Arripidae		
Arripis georgianus	+	+
Emmelichthyidae		
Emmelichthys cyanescens, *Erythrocles schlegeli*, *Plagogenion sp.*	+	+
Banjosidae		
Banjos banjos	+	+

Haemulidae		
Pomadasys panamensis, Orthopristis reddingi, Haemulon sexfasciatum, Lythrulon flaviguttatum, Orthostoechus maculicauda, Anisotremus davidsoni, Conodon serrifer, Microlepidotus inornatus, Xenichthys xanti, Xenistius californiensis, Xenocys jessiae, Isacia conceptionis, Genyatremus luteus, Brachydeuterus auritus, Gaterin chrysotaenia, Parapristipoma trilineatum, Diagramma pictum	+	+
Sciaenidae		
Sciaenops ocellata, Sciaena dussumieri, Otolithes dux, Larimus acclivus, Cynoscion virescens, Micropogon undulatus, Argyrosomus iharae	+	+
Cheilotrema saturnum, Cynoscion regalis, Nebris microps	+	±
Bairdiella icistia, Bairdiella chrysura, Seriphus politus, Pareques viola, Plagioscion sp., Stellifer sp., Corvula macrops, Paralonchurus brasiliensis, Lonchurus lanceolatus, Aplodinotus grunniens, Pachypops furchaeus, Pogonias chromis, Collichthys fragilis	+	-
Pachyurus bonaviensis, Umbrina roncador	r	-
Collichthys niveatus	-	-
Lobotidae		
Lobotes surinamensis	+	-
Datnioides polota	-	-
Gerreidae		
Gerres cinereus, Eugerres brasilianus, Diapterus peruvianus, Eucinostomus dovii, Schizopterus aureolus	+	+

Leiognathidae *Leiognathus splendens, Secutor ruconius*	-	-
Enoplosidae *Enoplosus armatus*	+	+
Pentacerotidae *Histiopterus typus*	+	-
Pentaceros japonicus	+	⊥
Oplegnathidae *Oplegnathus fasciatus*	+	+
Toxotidae *Toxotes insidiator*	+	+
Bathyclupeidae *Bathyclupea argentea*	+	+
Ephippidae *Chaetodipterus zonatus, Platax orbicularis, Drepane punctata*	+	+
Parapsettus panamensis	+	⊥
Scatophagidae *Scatophagus sp.*	-	-
Lutjanidae *Lutjanus argentiventris, Rabirubia inermis, Ocyurus chrysurus, Rhomboplites aurorubens, Hoplopagrus guntheri, Pinjalo pinjalo, Macolor niger, Symphorichthys spilurus, Aprion virescens, Pristipomoides microlepis, Etelis marshi, Aphareus furcatus, Apsilus dentatus*	-	-
Caesionidae *Caesio cuning, Pterocaesio tile, Gymnocaesio argenteus, Dipterygonotus gruvelii*	-	-
Nemipteridae *Nemipterus japonicus, Pentapodus setosus, Scolopsis bilineatus*	-	-

Lethrinidae		
Lethrinus rhodopterus, *Monotaxis grandoculis*, *Gnathodentex aurolineatus*, *Gymnocranius griseus*	-	-
Sparidae		
Acanthopagrus berda, *Calamus brachysomus*, *Evynnis cardinalis*, *Lagodon rhomboides*, *Lithognathus mormyrus*, *Taius tumifrons*, *Archosargus pourtalesii*, *Boops boops*, *Scatharus graecus*	-	-
Centracanthidae		
Centracanthus cirrus, *Spicara smaris*	-	-
Incertae sedis		
Inermia vittata	+	+
Pempheridae		
Pempheris schomburghi, *Parapriacanthus dispar*	-	-
Embiotocidae		
Cymatogaster aggregata, *Amphistichus argenteus*, *Hyperprosopon argenteum*, *Ditrema temnincki*	-	-
Cichlidae		
Tilapia mossambica, *Geophagus pappaterra*, *Cichlasoma meeki*	-	-
Pomacentridae		
Hypsypops rubicunda, *Microspathodon dorsalis*, *Abudefduf troschelii*, *Chromis punctipinnis*, *Nexillarius declivifrons*, *Eupomacentrus rectifraenum*, *Dascyllus albisella*	-	-

Chaetodontidae		
Forcipiger flavissimus, *Prognathodes aculeatus*, *Heniochus nigrirostris*, *Pomacanthus semicirculatus*, *Holacanthus trimaculatus*, *Centropyge bispinosus*	-	-
Nandidae		
Nandus nandus, *Monocirrhus polyacanthus*, *Polycentrus sp.*	-	-
Badidae		
Badis badis	-	-
Pristolepidae		
Pristolepis sp.	-	-
Gadopsidae		
Gadopsis marmoratus	-	-
Cirrhitidae		
Cirrhitus rivulatus, *Paracirrhites forsteri*, *Oxycirrhites typus*	-	-
Aplodactylidae		
Aplodactylus etheridgi	-	-
Cheilodactylidae		
Cheilodactylus variegatus, *Acantholatris gayi*	-	-
Owstoniidae		
Owstonia sp.	-	-
Cepolidae		
Cepola schlegeli	-	-
Stromateoidei		
Centrolophidae		
Schedophilus maculatus, *Centrolophus japonicus*	+	+
Seriolella crassus	+	-
Icichthys lockingtoni	-	-
Stromateidae		
Stromateus xanthurus, *Peprilus simillimus*, *Peprilus palometa*, *Pampus argenteus*	+	-

Nomeidae		
Nomeus gronovii	+	⊥
Psenes pacificus, *Psenes sio*	+	-
Cubiceps caeruleus, *Cubiceps pauciradiatus*	r	⊥
Tetragonuridae		
Tetragonurus cuvieri	-	-
Ariommidae		
Ariomma melanum, *Ariomma regulus*	-	-
Amarsipidae		
Amarsipus carlsbergi	+	+
Labroidei		
Labridae		
Bodianus diplotaenia, *Halichoeres dispilus*, *Tautoglabrus adspersus*	-	-
Scaridae		
Scarus ghobban, *Nicholsina denticulatus*	-	-
Odacidae		
Neodax balteatus, *Siphonognathus argyrophanes*	-	-
Trachinoidei		
Trichodontidae		
Trichodon trichodon	-	-
Opistognathidae		
Opistognathus punctatus, *Lonchopisthus sp.*	-	-
Bathymasteridae		
Bathymaster caeruleofasciatus	-	-
Mugiloididae		
Parapercis cephalopunctata	-	-
Trachinidae		
Trachinus draco	-	-
Percophididae		
Bembrops gobioides	-	-

Dactyloscopidae		
Dactyloscopus tridigitatus	-	-
Uranoscopidae		
Uranoscopus japonicus	-	-
Champsodontidae		
Champsodon sp.	-	-
Chiasmodontidae		
Chiasmodon niger	-	-
Scombroidei		
Scombrolabracidae		
Scombrolabrax heterolepis	r	+
Gempylidae		
Gempylus serpens, *Nealotus tripes*	-	-
Trichiuridae		
Lepidopus xantusi	-	-
Scombridae		
Scomber japonicus, *Thunnus atlanticus*, *Scomberomorus concolor*	-	-
Istiophoridae		
Istiophorus platyptera	-	-
Notothenoidei		
Nototheneidae		
Trematomus nicolai, *Notothenia longipes*	-	-
Bovichthyidae		
Cottoperca gobio	-	-
Gobeoidei		
Gobiidae		
Eleotris sandwicensis, *Bathygobius ramosus*, *Coryphopterus nicholsi*	-	-
Microdesmidae		
Microdesmus floridanus, *Cerdale ionthas*	-	-
Ammodytoidei		
Ammodytidae		
Ammodytes tobianus	-	-

Blenniodei		
Blenniidae		
Hypsoblennius gilberti	-	-
Clinidae		
Labrisomus multiporosus, *Neoclinus stephensae*	-	-
Chaenopsidae		
Chaenopsis alepidota, *Coralliozetus angelica*	-	-
Tripterygiidae		
Axoclinus carminalis	-	-
Acanthuroidei		
Acanthuridae		
Acanthurus xanthopterus, *Zanclus cornuta*	-	-
Siganidae		
Siganus doliatus	-	-
Anabantoidei		
Anabantidae		
Betta splendens	-	-
Osphronemidae		
Trichogaster leeri	-	-
SCORPAENIFORMES		
Scorpaenoidei		
Scorpaenidae		
Sebastes serriceps, *Scorpaena guttata*, *Pontinus furcirhinus*	-	-
Triglidae		
Prionotus stephanophrys	-	-
Hexagrammoidei		
Hexagrammidae		
Oxylebius pictus	-	-
Anoplopomatidae		
Anoplopoma fimbria	-	-
Zaniolepidae		
Zaniolepis frenata	-	-

Platycephaloidei		
Platycephalidae		
Platycephalus malayanus	-	-
Cottoidei		
Cottidae		
Orthonopias triacis, *Hemilepidotus jordani*	-	-
Agonidae		
Asterotheca pentacantha	-	-

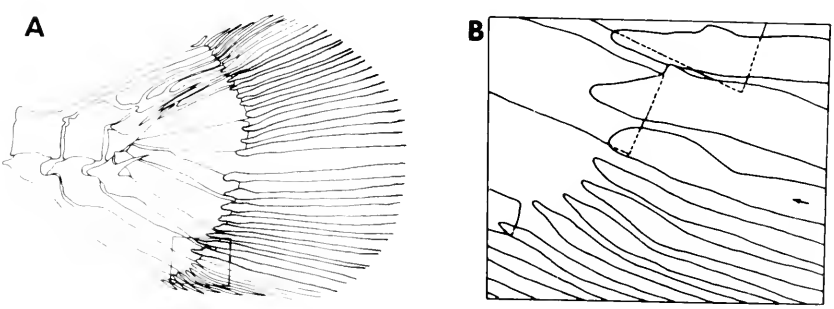

FIGURE 1. Caudal skeleton of *Lutjanus argentiventris*. A. Full view, principal rays shaded, area enlarged in B outlined. B. Enlargement showing typical ventral procurrent ray series, arrow marks posteriormost (last) procurrent ray.

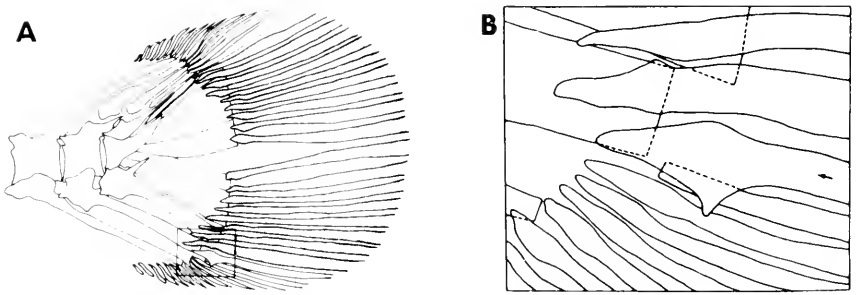

FIGURE 2. Caudal skeleton of *Lythrulon flaviguttatum*. A. Full view, principal rays shaded, area enlarged in B outlined. B. Enlargement showing procurrent spur on posteriormost ventral procurrent ray (marked by arrow) and shortening of preceding ray base.