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SOME NERVE PATTERNS AND THEIR  
SYSTEMATIC SIGNIFICANCE IN PARACAN-  
THOPTERYGIAN, SALMONIFORM, GOBIOID,  
AND APOGONID FISHES<sup>1,2,3</sup>

By

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Some time ago while examining the salmopercooid genera *Percopsis* and *Aphredoderus* for the ramus lateralis accessorius, I noticed from superficial dissections on the head that these fishes had some strikingly interesting nerves emanating from one main point in the upper cheek region next to the preopercle (Frehofer, 1960). The nerves came up to the skin from their source below on the truncus hyomandibularis. There were four main nerves, one to each of the roofing membranes of the supraorbital, infraorbital, preopercular, and mandibular canals. In 1950 Ray had reported similar nerves for the lantern fish *Lampanyctus leucopsarus* and recognized them to constitute a group of nerves which she called the ramus canalis lateralis facialis system. The statement by Frost (1926) that the otoliths of *Apogon* and of the salmopercooid fishes strongly resembled each other led me to examine apogonids for these ramus canalis nerves. They were found to have these nerves in similar pattern. These facts suggested that there might be a relationship between lantern fishes, salmopercooid (or percopsiform fishes, as they are now called), and the supposedly percooid apogonids.

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<sup>2</sup> A summary of results was kindly read for me by Dr. G. S. Myers at the New York City meetings of the American Society of Ichthyologists and Herpetologists in June, 1969.

<sup>3</sup> Submitted for publication February 2, 1969.

The salmopercoïd fishes are especially intriguing since they obviously appear to combine features of both salmonids and percoïds. Detailed studies of the nervous and skeletal systems of salmopercoïds were begun as well as a survey of many fish groups for the ramus canalis lateralis system and the ramus lateralis accessorius. Two events influenced the survey. One was the publication in 1966 by Greenwood, Rosen, Weitzman, and Myers of a classification in which a new superorder of fishes, the Paracanthopterygii, was proposed which brought together six orders or parts of orders, some for the first time. The survey was directed to include all these groups. Its success was furthered by a second event, my fortuitously being present on cruise 16 of the *R/V Anton Bruun*. Bottom hauls frequently brought up large numbers of most major groups of paracanthopterygian fishes, thus affording material that could be processed in the Sihler technique. Preliminary observations of the nerves of all these paracanthopterygian fishes might, I thought, reveal nerve features that would test the validity of this new superorder as well as help in the question of codfish and brotulid relationships, fishes which looked much alike as they lay together on the ship's deck. A simple soul, but not perhaps an "educated" one, would think these latter two groups must be related. To suppose that the percopsids, batrachoidids, ogocephalids, gobiocids, lophiids, and their related families, had a relationship to each other let alone to the codfishes, hakes, ophidioids, and zoarcids would have and apparently still does strain beyond the bounds of belief the minds of most ichthyologists. The results of the nerve survey should lessen doubts now generally held about the Paracanthopterygii.

There is enough detail in the descriptive section of patterns of the ramus lateralis accessorius (RLA) to show how similar these are in brotulid, ophidiid, and gadiform fishes. Preliminary information is given on a special enlarged lateral-line branch (or several branches) which supply the pectoral-pelvic area in percopsiform, brotulid, batrachoid, and gobioid fishes and which is part of a segmental series of lateral-line nerves. This nerve and the segmental series of which it is a part may be a primitive paracanthopterygian feature inherited from lower fishes. A preliminary account is given of the manner in which the fin-ray nerves course in paracanthopterygian fishes in contrast to the way they do in acanthopterygian and numerous other fishes. It is a feature that appears characteristic but not unique to the Paracanthopterygii.

Brief, preliminary, comparative studies of the ramus canalis lateralis system of nerves are given for a number of families. A much fuller treatment is planned for a future paper.

One of the purposes of the present paper is to report some features of nerves which bear on the systematic validity of the Paracanthopterygii. Other main systematic questions to which the results presented are relevant are: (1) relationships of the salmopercoïd fishes to other paracanthopterygian fishes; (2) the re-

relationships of salmopercoïd fishes to acanthopterygian fishes; (3) the origin of the salmopercoïd fishes and of gadoid, ophidioid and batrachoid fishes; (4) the interrelationships of the gadoid and ophidioid fishes; (5) the relationships and reclassification of the gobioid fishes; (6) the relationships of the Apogonidae.

A note of explanation on the ramus lateralis accessorius. It supplies taste buds on the body and or fins. It is not a lateral-line nerve. The name ramus recurrens facialis is more descriptive and can be shortened to "recurrent facial," but the abbreviation "RLA" for the former term is used here.

### MATERIALS AND METHODS

Specimens of *Merluccius gayi*, *Brotula clarkae*, *Physiculus talarae*, *Lepophidium prorates*, *Porichthys margaritatus*, *Bathygobius lineatus*, *Hoplostethus pacificus*, *Melamphaes* species, *Apogon astradorsatus*, *Scopelengys tristis*, and *Zalilutes elater* were collected on cruise 16 of the R/V *Anton Bruun* and specimens of *Brotuloides emmalas* by Margaret Bradbury on cruise 19 of the R/V *Te Vega*. All were kept in formalin until processed for the nerves by the Sihler technique (Freihofer, 1966), in which the stained nerves stand out in transparent whole specimens. Alizarin specimens were also prepared for examination of the skeleton. Both Sihler and alizarin preparations were also made of *Percopsis omiscomaycus*, *Percopsis transmontana*, *Aphredoderus sayanus*, *Hypomesus pretiosus*, *H. olidus*, *Dicrolene intronigra*. The following specimens were also examined by dissection under the microscope: *Chologaster papilliferus* and *Dicrolene kanazawi*, uncatalogued; *Lamprogrammis niger*, LACM (Los Angeles County Museum) 9708-5, *Watasea sivicola*, 26797; *Monomerepus* species, 57024; *Dinematichthys ilucoeteoides*, uncatalogued; *Eutyx diagrammus* uncatalogued; *Merluccius productus*, LACM 9815-8; *Eleginus gracilis*, 49233; *Microgadus proximus*, 49237; *Boreogadus saida*, 48810; *Urophycis floridanus*, 50878; *Laemonema barbatulum*, 63261; *Coelorhynchus scaphopsis*, 179; *Eleotris fuscus*, uncatalogued. Numerous other species of various families and orders were examined but are not listed. All catalogue numbers are from the Stanford University fish collections unless otherwise noted.

Many of the families and genera mentioned in the text were also examined from specimens in the Starks skeletal collection at Stanford University.

### ACKNOWLEDGMENTS

I would like to express my appreciation for the generous and essential help the following people gave in sending specimens kept specially in formalin or who helped in the field: Carl Bond, Oregon State University; Margaret Bradbury, San Francisco State College; Daniel M. Cohen, Systematics Laboratory, U. S. Fish and Wildlife Service; E. J. Crossman, Royal Ontario Museum; William Eschmeyer, California Academy of Sciences; Carter Gilbert, Florida State Mu-

seum; Shelly Johnson, University of Southern California; Robert Lea, California Division of Fish and Game; the late Fr. Romeo O. Legault, University of Ottawa; Donald McPhail, University of British Columbia, John Massie, California Aqueduct Facility; William Weaver, Florida State Museum; James Davis, North Carolina, State Fish and Game.

Observations on osmerids are from Sihler preparations and serial sections made by Craig Findly as part of a special problems study he was doing at Stanford University.

Dr. Daniel Cohen identified the gadoid and ophidioid fishes collected on the R/V *Anton Bruun* except for *Lepophidium prorates* identified by Dr. C. Richard Robins; Dr. Ernest Lachner identified the apogonid and Doug Hoese the goby.

My special thanks are due Adair Fehlmann, Smithsonian Oceanographic Sorting Center, for arranging my participation on cruise 16 of the R/V *Anton Bruun* and for much additional help in procuring specimens. Leonard Compagno was a patient listener and excellent discussant while the work was in progress. Max Millsap, Stanford Anatomy Department, took all photographs except that in figure 17 which was taken by the author.

## RAMUS LATERALIS ACCESSORIUS

### DESCRIPTION OF RAMUS LATERALIS ACCESSORIUS IN THE OPHIDIIDAE

In *Lepophidium prorates* an enormous ramus lateralis accessorius (RLA) arises from the geniculate ganglion (fig. 1), passes dorsolaterally and posteriorly up to the cranial roof where it bifurcates into a large branch (RLA-PP) going to the pectoral and pelvic fins and a small branch (RLA-PDA), about  $\frac{1}{3}$  the size of the other, which goes to the dorsal and anal fins. The pectoral-pelvic branch turns posterolaterally beneath the cranial roof, enters an intraosseous passageway in the parietal, leaving it at its posterolateral corner by a large foramen.

The dorsal-anal branch, RLA-PDA, after leaving the parietal, passes posteriorly near the middorsal line, beneath skin back to the dorsal fin where it dips ventrally and passes posteriorly alongside the pterygiophores about  $\frac{1}{2}$  of their length below their outer distal ends. It forms a longitudinal plexus with crossing branches of the dorsal rami of the spinal nerves supplying the fin rays and membrane. At the seventh and eighth dorsal crossing segmental rami, 2 large branches are given off, one at each of these segments, which pass beneath the skin posteroventrally towards the origin of the anal fin. These 2 branches of RLA-PDA join at the second segment from the anal origin and pass inwardly and run posteriorly alongside the pterygiophores forming a longitudinal plexus with branches of the crossing ventral spinal rami supplying the fin rays and membrane. On their course from the dorsal to the anal fins the 2 branches of RLA-A cross numerous branches of the lateral line and segmental rami going to the skin and also exchange a few branches between each other. The nerves from the longitudinal plexi of

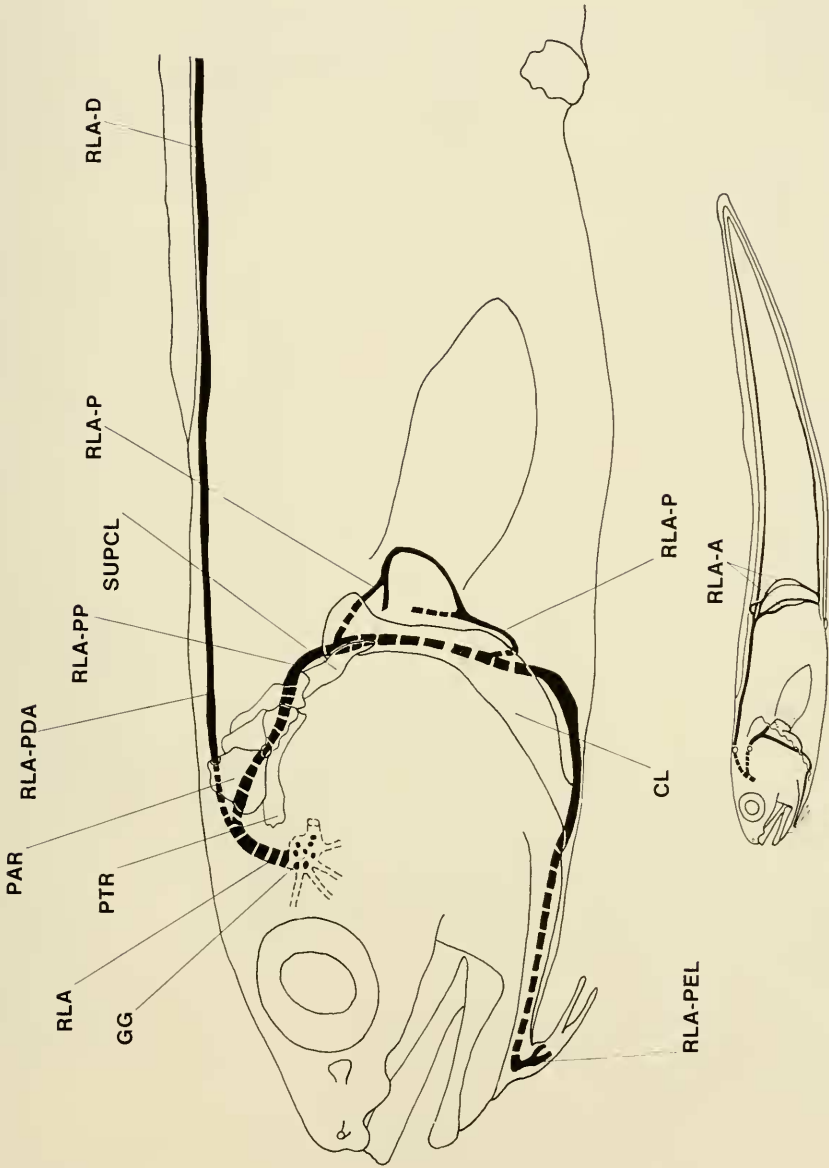


FIGURE 1. Pattern of ramus lateralis accessorius (recurrent facial nerve) in *Lepophidium prorates* (Ophiidae). See list of abbreviations.

the dorsal and anal fins enter the fin rays and membrane in a characteristic way. For each segment, a branch of RLA serves the half fin ray of its side and its half membrane lying posterior to the half ray. In doing so, the fin-ray nerve passes inward towards the opening in the base of the ray and gives off a branch which runs distally in the fin membrane of its side of the body. The rest of the fin-ray nerve passes forward into and through the split base of the fin ray and then onto the outer, external surface of the half of the ray of its side and along the half fin ray to its distal end. The longitudinal plexus of each side of the dorsal fin continues posteriorly and meets its counterpart from the anal fin at the mid point of the tip of the hypural fan.

Emerging from the posterolateral corner of the parietal, the pectoral-pelvic branch, RLA-PP, passes across the medial surfaces of the supratemporal canal bone and the epiotic arm of the posttemporal and ventrally beneath skin along the posterior edge of the supracleithrum and cleithrum en route to the pectoral and pelvic fins. A short distance above the pectoral fin a branch is detached which passes along the dorsal edge of the muscular base of the pectoral fin. A branch from the branchial plexus joins the pectoral branch of RLA and the compound nerve enters the bases of the fin rays ventrally, giving off branches to the half rays and membrane. As for the fin rays of the other fins, the nerves to each half ray course on the outside surface of the rays, not internally between each of the halves of each fin ray as is characteristic of percoid and most other fishes. As RLA-PP passes the ventral edge of the pectoral fin a branch is detached which joins a nerve from the brachial plexus which enters the ventral base of the pectoral fin and passes dorsally up through the pectoral fin giving off branches to each fin ray as described for the dorsal base of the pectoral fin.

The enormous remainder of RLA-PP passes anteroventrally beyond the pectoral fin to enter the pelvic fin. At the posterior end of the fleshy isthmus between the two gill openings, the large trunk of RLA-PP of each side of the body join in the midventral line and continue anteriorly as one trunk. Next, the common trunk is joined by a large spinal ramus of each side that comes to the surface at the midventral line after having passed down the medial side of the body wall. The resulting huge common spinal and recurrent facial trunk divides at the base of the pelvic fin. A branch is given to each of the two pelvic fin-ray bases. Each pelvic fin ray has the fin-ray nerve coursing on its external surface as in the other fins, a pattern which, as has been mentioned, is significantly different from that for percoid and many other fishes.

#### DESCRIPTION OF THE RAMUS LATERALIS ACCESSORIUS IN THE BROTLIDAE

In *Ogilbia ventralis*, studied from a dissected alcoholic specimen only, a very large RLA arises from the geniculate ganglion (fig. 2) and passes a rather long

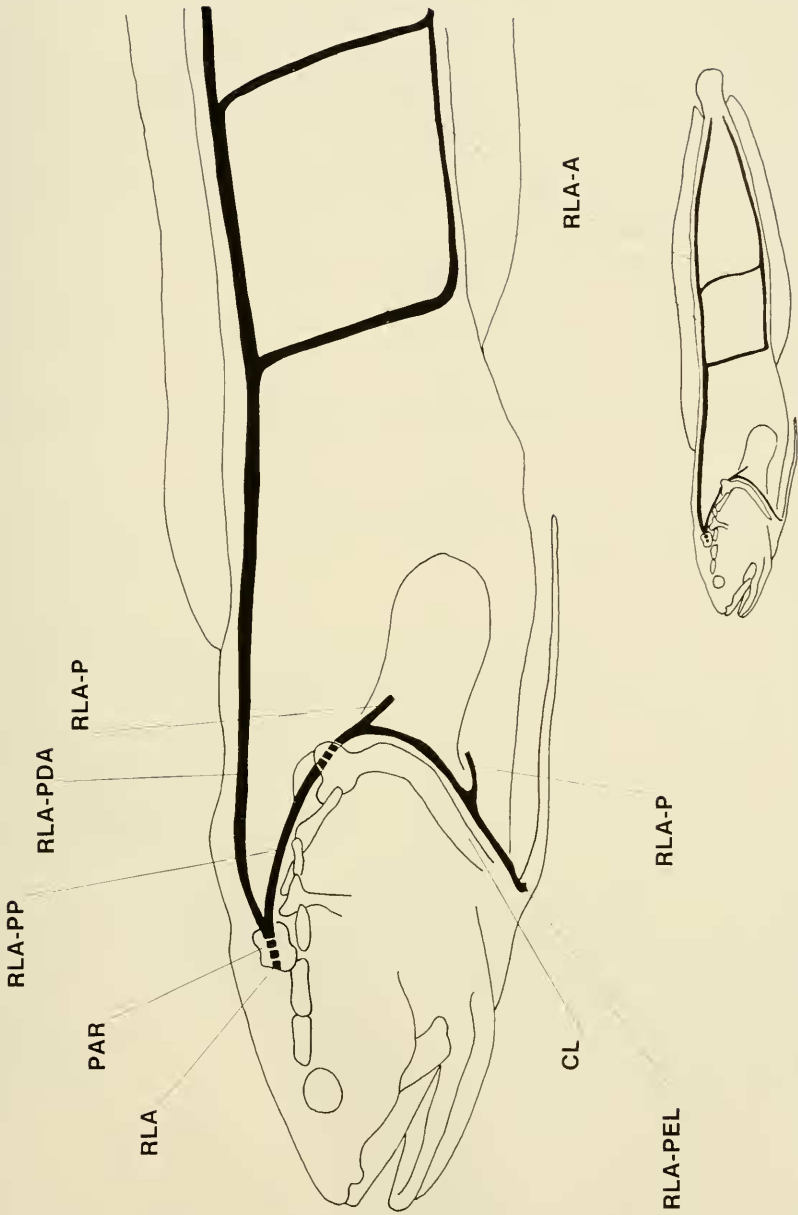


FIGURE 2. Pattern of ramus lateralis accessorius in *Ogilbia ventralis* (Brotulidae). See list of abbreviations.

distance posterodorsally up to the cranial roof where it is met by an extremely thin vagal ramus just before cranial exit through the parietal near its posteromedial corner. Immediately outside the cranium on the nape it divides into almost equal sized branches, RLA-PDA to the dorsal and anal fins, and RLA-PP to the pectoral and pelvic fins. Branch RLA-PP to the pectoral and pelvic fins passes posteroventrally following the posterior edges of the posttemporal, supra-cleithrum and cleithrum directly beneath skin. It passes medially behind the dorsoposterior end of the cleithrum and, upon emerging from its posterior edge, it detaches a large branch along the dorsal edge of the muscular base of the pectoral fin. This branch is joined by a large spinal nerve branch of the brachial plexus just before entering the upper end of the base of the pectoral fin. The remainder continues ventrally posterior to the cleithrum and beneath skin on its way to the pelvic fin where it is met at the midventral line by a large branch of a spinal nerve. In passing the ventral end of the pectoral fin, a small branch of RLA passes dorsoposteriorly to the ventral end of the pectoral fin base where it joins a branch of the brachial plexus that enters the ventral end of pectoral fin base.

Branch RLA-PDA runs along the base of the dorsal fin as in other brotulids. A large branch detaches from the dorsal fin branch at about the eleventh segment back from the anterior end of the dorsal fin. A second fair-sized branch arises at about segment 22.

With its 2 main branches arising from the main trunk of RLA outside of the parietal, the pattern in *Ogilbia* is basically like that in the gadiform fishes.

The same pattern was found in *Dinematichthys iluocoetoides*.

In *Brotula clarkae* (fig. 3), the pattern of RLA is the same as that described for *Brotula multibarbata* from a dissection of an alcoholic specimen (Freihofer, 1963). An anal branch was not noted at that time. A Sihler preparation of *Brotula clarkae* shows that there is an anal branch similar to that in the ophidiid *Lepophidium* and the morid, *Physiculus*.

The branch to the dorsal and anal fins, RLA-PDA, passes into the trigeminal foramen with the supra- and infraorbital trunks, but inside the foraminal passageway of the prootic bone RLA-PDA departs and passes dorsoposteriorly through the body of the sphenotic and re-enters the cranium where it continues dorsoposteriorly over the cranial ceiling up to its exit via an osseous passageway in the parietal at its posteromedial corner next to the base of the supraoccipital spine. On one Sihler preparation 5 anal branches are detached from RLA-PDA. The first two, which join and separate again on their way to the anal fin, come off at segments 9 and 10 counting from the origin of the dorsal fin. The next three come off at segments 13, 14, and 19. These branches enter the anal fin respectively at 2, 7, 9, 10, and 19 segments from its origin. Four similar branches occur on the other side. Two other specimens had 4 anal branches similarly spaced. Fi-



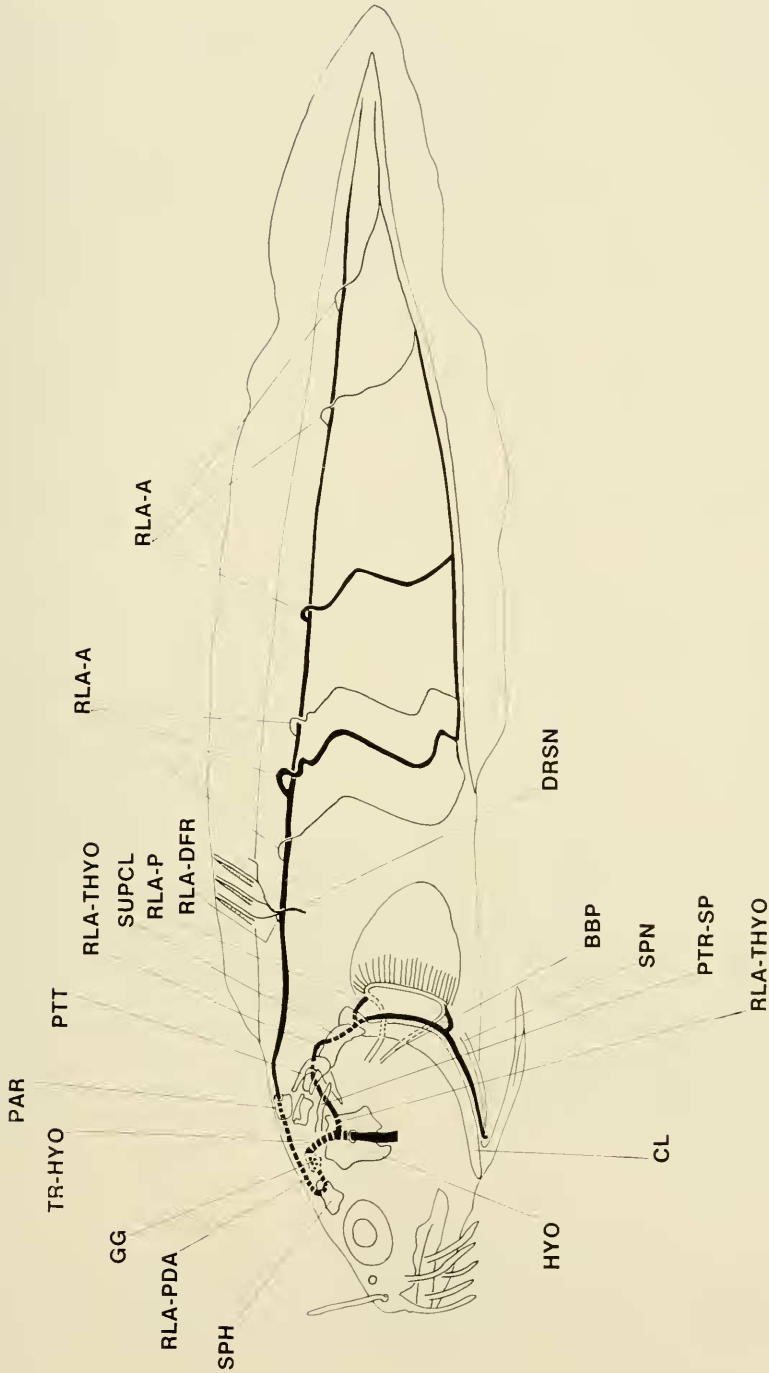


FIGURE 3. Pattern of ramus lateralis accessorius in *Brotula clarkae* (Brotulidae). See list of abbreviations.

nally, a fourth specimen had 1 large anterior anal branch entering the anal fin at the twentieth ray with no RLA innervation going to these first 20 rays, apparently, and with a second anal branch in the position of the last branch on the other specimens.

The pectoral-pelvic branch, RLA-THYO, leaves the cranium on the postero-medial surface of the truncus hyomandibularis, turns abruptly posteriorly, and runs along the medial side of the hyomandibular bone (fig. 3). Emerging from behind the posterior end of the hyomandibular, it passes dorsal to a large opercular muscle, then under the long pterotic spine, and onto the medial surface of the posttemporal. It runs for a short distance beneath skin between the posttemporal-supracleithral articulation then medially again behind the cleithrum, coming from behind this bone above the dorsal end of the muscular base of the pectoral fin where a fair-sized branch is detached which runs out the dorsal edge of the muscular pectoral base, being joined en route by a larger branch from the brachial plexus. The dorsal pectoral branch of RLA-THYO detaches 2 small nerves before joining the brachial branch. One of these goes to skin near the base of the fin rays on the medial side of the fin. The other goes to skin on the lateral side. Another branch to the lateral surface of the fin base is detached halfway down the fin. As RLA-THYO passes beneath skin near the ventral end, a large branch is detached which, together with a large branch from the brachial plexus, enters the ventral base of the fin rays. The dorsal and ventral fin-ray nerves become smaller as they approach each other as they pass through the bases of the fin rays giving off a branch between each 2 succeeding rays, the fin-ray branch of each side of the fin coursing distally in the membrane between each succeeding whole ray. The main trunk of RLA-THYO passes anteriorly beneath the skin paralleling the cleithrum. Near the base of the pelvic fin it joins with a large branch of a ventral spinal nerve, which, before joining RLA-THYO, gives off a branch to the pelvic muscles. Before joining with the branch from the brachial plexus, RLA-THYO detaches a branch which goes to the anterior surface of the first ray. It is joined by a branch from the ventral spinal ramus. The posterior external surface of the first ray plus the anterior and posterior surfaces of the second pelvic ray are innervated by 2 compound branches from RLA-THYO and spinal nerve trunk. In reaching the pelvic fin the ventral spinal nerve has passed down the wall of the body cavity medial to the pectoral girdle and comes to the surface at the midventral line near the base of the pelvic fins.

#### DESCRIPTION OF RLA IN GADIFORM FISHES

In the morid *Physiculus talarac* a large RLA leaves the geniculate ganglion, courses dorsally in an open groove on the inner surface of the parietal, exits through a large foramen in this bone near its center and passes posterolaterally beneath the large muscle mass on top of the head and then dorsally between the

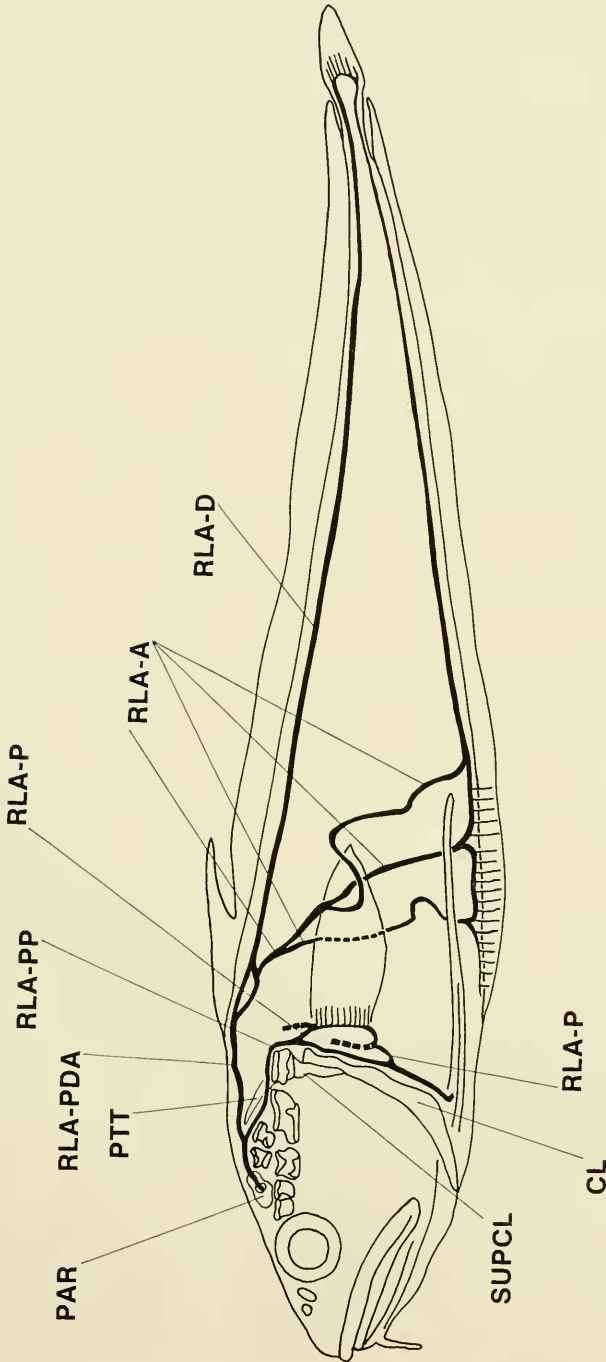


FIGURE 4. Pattern of ramus lateralis accessorius in *Physiculus talarac* (Moridae). See list for abbreviations.

side of the muscle mass and the medial surface of the supratemporal canal bone. A thin vagal ramus joins RLA at its exit through the parietal. Medial to the supratemporal canal RLA bifurcates into RLA-PDA, the dorsal-anal branch, and RLA-PP, the pectoral-pelvic branch. RLA-PDA curves medially beneath the skin on its course to the dorsal fin at the anterior end of which it detaches an anal fin branch, RLA-A, which on one specimen parallels the course of RLA-D for 3 segments and then curves ventroposteriorly under the skin. On another specimen the dorsal branch did not detach the first anal branch, a small one to the anterior part of the anal fin, until the ninth segment from the origin of the dorsal fin. The main large anal branch detaches on this specimen at the twelfth segment. On the specimen illustrated, the anal branch passes beneath the skin and divides en route into 3 parts (fig. 4), a smaller anterior branch which reaches the anal fin at the sixth segment from its origin and forms an anteriorly coursing longitudinal plexus with crossing ramuli of the segmental ventral spinal nerves. The second or main part of the three reaches the base of the anal fin at its fifteenth ray and forms a posteriorly coursing longitudinal plexus. The third branch joins the longitudinal plexus at the twenty-first ray. The plexus continues all the way to the caudal fin. On the other side of the specimen 2 anal branches course beneath the skin paralleling each other and joining at the base of the anal at about its fifteenth ray.

The branches of the longitudinal plexus that enter the fin rays do so in nearly the same way that they do in the ophidiid, *Lepophidium*. In *Physiculus* a fin-ray nerve passes to the posterior side of the base of each half fin ray of its side of the body. Before passing anteriorly through the opening between the two diverging bases of the half fin rays each fin-ray nerve of each side detaches a branch that runs distally out the posterior external surface of the fin ray. The remainder of the fin-ray nerve of each side passes through the opening between the base of the half fin rays and passes distally on the external anterior surface of the half fin ray. As was mentioned for the ophidiid *Lepophidium*, this is drastically different from the pattern shown in most other fishes, for which *Aphredoderus* (fig. 13) is an example, where the fin-ray nerves course in the hollow internal tube formed by the two concave half rays of each side meeting.

From its origin from the main trunk of RLA, the pectoral-pelvic branch, RLA-PP, passes posterolaterally on the medial surface of the supratemporal canal, crosses laterally over the epiotic arm of the posttemporal and ventrally beneath the skin slightly posterior to the supracleithrum and cleithrum but anterior to the pectoral fin and lateral to the base of the fin. Dorsal to the pectoral fin base a branch is detached from RLA-PP which joins with a large branch from the brachial plexus which together enter as one nerve the dorsal base of the pectoral fin and pass down through the basal opening between the fin-ray halves giving off a branch to each half fin ray as already described for the dorsal and anal fins. Further on its course ventrally over the lateral surface of the muscular

base of the pectoral fin, a smaller branch detaches from RLA-PP and passes over towards the ventral end of the pectoral fin base where it is met by a large nerve from the brachial plexus. The compound nerve enters the ventral end of the base of the pectoral fin and passes dorsally through successive rays until it meets with the branch coming from the dorsal end of the pectoral base.

The very large remainder of RLA-PP passes ventrally beneath the skin to the slightly jugular pelvic fin where it is met by a large branch from the first ventral spinal nerve posterior to the occipito-spinal complex. The fin-ray nerves run distally on the external surface of the fin rays as already described for the other fins.

In the Merlucciidae, no RLA was found in a Sihler nerve preparation of *Merluccius productus*.

The pattern in the Gadidae as represented by *Microgadus* (fig. 5) differs significantly from that in the Moridae in that the anal-fin branch in the Gadidae detaches from the pectoral-pelvic branch not far above the base of the pectoral fin, whereas in the Moridae the anal branch detaches from the dorsal fin branch about a dozen segments back from the origin of the dorsal fin or by one or two additional branches more posteriorly.

Other gadid genera examined showing the same pattern as *Microgadus* are *Gadus*, *Boreogadus*, and *Eleginus*.

In the Macruridae the dorsal-anal branch detaches after the main trunk of RLA passes the epiotic arm of the posttemporal. This pattern bears a small resemblance to the gadid pattern but a larger one to the morid pattern. In *Macrurus* RLA crosses laterally the posttemporal bone and divides, one branch passing down the posterior edge of the supracleithrum and cleithrum to supply the pectoral and pelvic fins, and the other arching dorsally then straightening out, crossing several septa and then sending one branch up to the overlying dorsal fin and one ventroposteriorly to the anal fin.

A branch of a dorsal ramus to the first elongated spine of the dorsal fin was found which is of unusual interest for the speculation that it arouses as to its use in the life of macrurids. All the numerous species examined had it well developed but not as conspicuously developed as in *Lionurus gibber*. In this species a relatively enormous nerve extends out in the posterior groove of the elongated anterior dorsal spine and out beyond the spine in the protective sheath that is more than once again as long as the spine. This projection appears to be largely nerve. No enlarged nerve was observed in any of the other fins. For a supposedly deep-sea bottom swimming fish, this great dorsally directed tactile and taste feeler is surprising. As was mentioned, this development is much greater than anything seen on the ventral or lateral fins. Some important stimuli from above the fish must be perceived. It suggests that the elongated nerve-filled spine is a contact organ for use in touching other individuals swimming directly above in schooling.

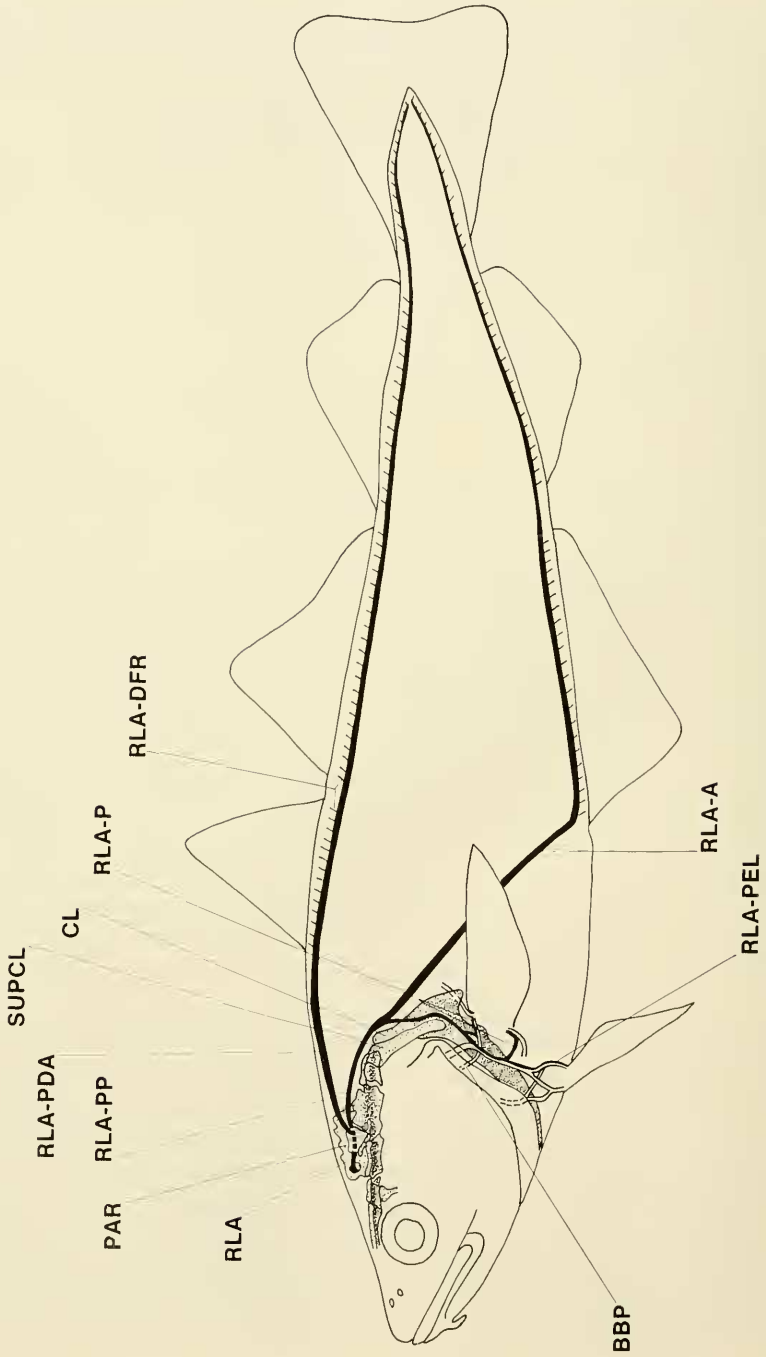


FIGURE 5. Pattern of ramus lateralis accessorius in *Microgadus proximus* (Gadidae). See list for abbreviations.

## PATTERN OF RLA IN PERCOPSIFORMES

In *Percopsis* (fig. 6) the sympathetic chain and RLA course bound together, the two forming a common trunk. All the branches that are given off from this common trunk may contain fibers from both these nerve trunks. The RLA-sympathetic common trunk is very large, 4 times the size of the ninth cranial nerve. The sympathetic chain alone in most fishes is usually less than  $\frac{1}{2}$  the size of the ninth cranial nerve.

The RLA part of the common trunk arises from the geniculate ganglion. What evidently is a sympathetic trunk, and which is about  $\frac{1}{20}$  the size of the RLA-sympathetic common trunk, curves anteromedially around the root of the truncus hyomandibularis. It was not followed further on the surface of the truncus hyomandibularis as this truncus and the truncus infraorbitalis come together as they pass medially towards the fifth-seventh complex. The common trunk of RLA + sympathetic chain leaves the truncus hyomandibularis shortly outside the cranium and passes posteromedially across the wall of the otic bulla, crossing the ninth cranial nerve en route to which it is connected by a thin branch which evidently is sympathetic. The common trunk passes onto the ventral side of the vertebral column and then along it to the caudal fin. As the common trunk passes the pharyngo-branchial roots of the vagus, 2 sympathetic branches leave from 2 ganglia located on the surface of the common trunk. One of the branches is about  $\frac{1}{40}$  the size of the common trunk; the other is about  $\frac{1}{20}$  its size. At the same point a large branch, about  $\frac{1}{4}$  the size of the common trunk leaves from a bundle of fibers already formed anterior to the 2 sympathetic ganglia. This large branch must be mostly RLA fibers. It does not come from these 2 ganglia. This large branch passes to the base of the first and second ventral spinal rami of the occipito-spinal nerves. Opposite Baudelot's ligament a small branch detaches from the common trunk, runs parallel to the ligament, and then joins the third ventral occipito-spinal ramus. The next branch is a large one, about  $\frac{1}{4}$  the size of the first large trunk branch. It goes to the fourth ventral spinal ramus. The next branch is about  $\frac{1}{2}$  as large as this one and each succeeding branch going to each ventral spinal ramus is small. The specimen illustrated in figure 6 is different from the specimen described in the text.

The Amblyopsidae have the same pattern as *Percopsis*, not as in *Aphredoderus*. In *Chologaster papilliferus* RLA appears even larger.

In *Aphredoderus sayanus* (fig. 7) the pattern is quite different from that in *Percopsis*, but one basic similarity remains, that of having the fibers of RLA destined for the pectoral fins, and perhaps for the pelvics also, distributed via the occipito-spinal complex.

In *Aphredoderus* a sizable RLA leaves the cranium through the parietal and courses beneath the skin towards the dorsal fin. Directly outside the cranium RLA detaches a branch down the posterior surface of the cranium that joins the

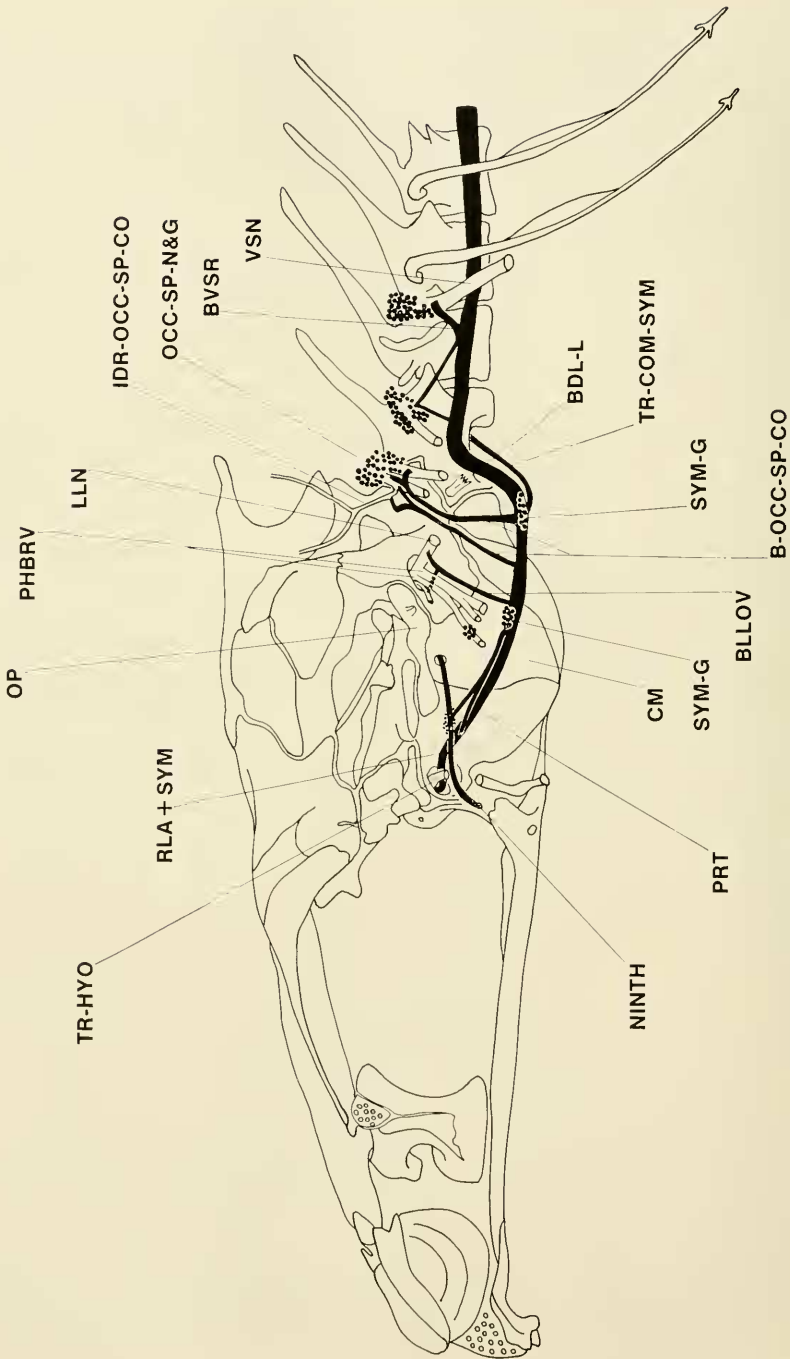


FIGURE 6. Pattern of ramus lateralis accessorius coursing with sympathetic system in *Percopsis omiscomaycus* (Percopsidae). See list for abbreviations.



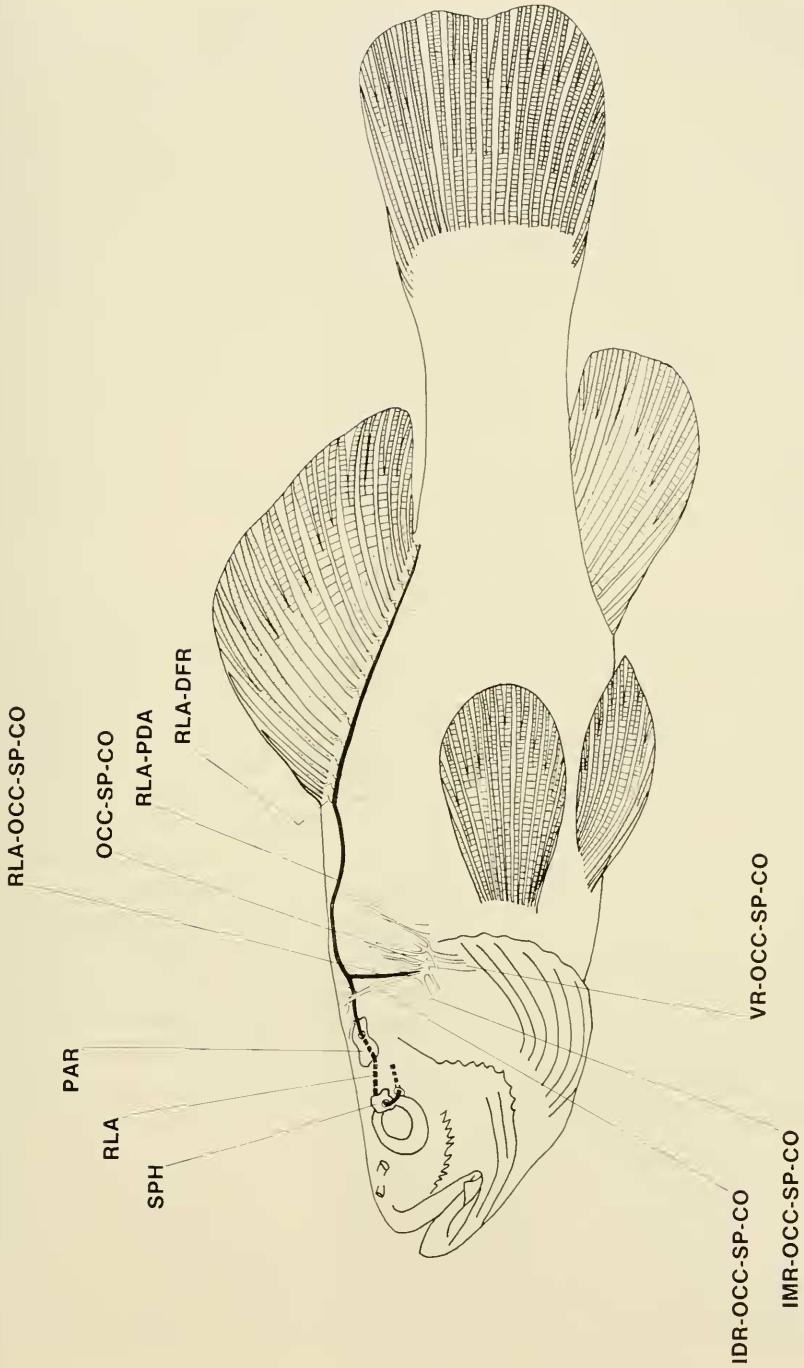


FIGURE 7. Pattern of ramus lateralis accessorius in *Aphredoderus sayanus* (Aphredoderidae). See list for abbreviations.

occipito-spinal complex where the first dorsal ramus leaves its vertebra. Varying with the specimen, this first branch of RLA either courses to the first occipito-spinal nerve independently of the first dorsal ramus which passes up the posterior surface of the cranium and innervates skin overlying the posterolateral area of the cranium; or the two run in common, or part of the way in common, but in opposite directions. As RLA continues towards the dorsal fin other dorsal spinal rami cross it. It appears that a second branch from RLA courses down the posterior edge of the first neural spine to join another part of the occipito-spinal complex. The crossing dorsal rami and RLA form a longitudinal plexus alongside the dorsal pterygiophores. The plexus continues beyond the dorsal fin but in diminished size until it reaches the caudal fin. It could not be determined if any RLA fibers remained in it that far. No branch of RLA to the anal fin was discernible nor was there a pronounced longitudinal plexus along the anal as there is along the dorsal fin.

The common trunk of RLA + sympathetic chain in *Percopsis* is about 20 times the size of the sympathetic trunk in *Aphredoderus* where this trunk crosses the wall of the otic bulla.

#### PATTERN OF RLA IN BATRACHOIDIDAE

In *Porichthys margaritatus* (fig. 8) RLA must be looked for in the same place as in *Percopsis*, that is, issuing from the facial foramen together with the truncus hyomandibularis combined with the sympathetic chain. Shortly outside of the facial foramen the common trunk of RLA + sympathetic chain leaves the truncus hyomandibularis, turns posteriorly and separates, the sympathetic trunk passing posteromedially across the wall of the otic bulla and onto the ventral side of the vertebral column and along it to the caudal fin. The trunk of RLA passes posterolaterally across the wall of the otic bulla, gradually diverging from the sympathetic trunk. RLA crosses the ninth cranial nerve, drops ventrally, is pierced by a branch of the vagal trunk with no exchange of fibers. This vagal branch passes directly laterally, then ventrally across the base of the opercular spine and innervates skin down as far as the branchiostegal rays. As the main trunk of RLA passes posteriorly medial to the cleithrum, the pectoral-dorsal and pelvic-anal branches arise (fig. 8). The pectoral-dorsal branch courses laterally, reaching the skin directly posterior to the cleithrum from which point it arches dorsoposteriorly towards the dorsal fin. A branch is given off which passes to the dorsal end of the pectoral fin base. The pelvic-anal branch crosses the medial side of the cleithrum and passes down the body wall medial to the base of the pectoral fin, dividing shortly beyond the cleithrum into the pelvic and anal branches. The anal branch slants towards the anal fin. The pelvic branch turns anteroventrally at the tip of the postcleithrum and courses beneath skin towards the base of the pelvic fin which it enters. A more complete description will be published elsewhere.

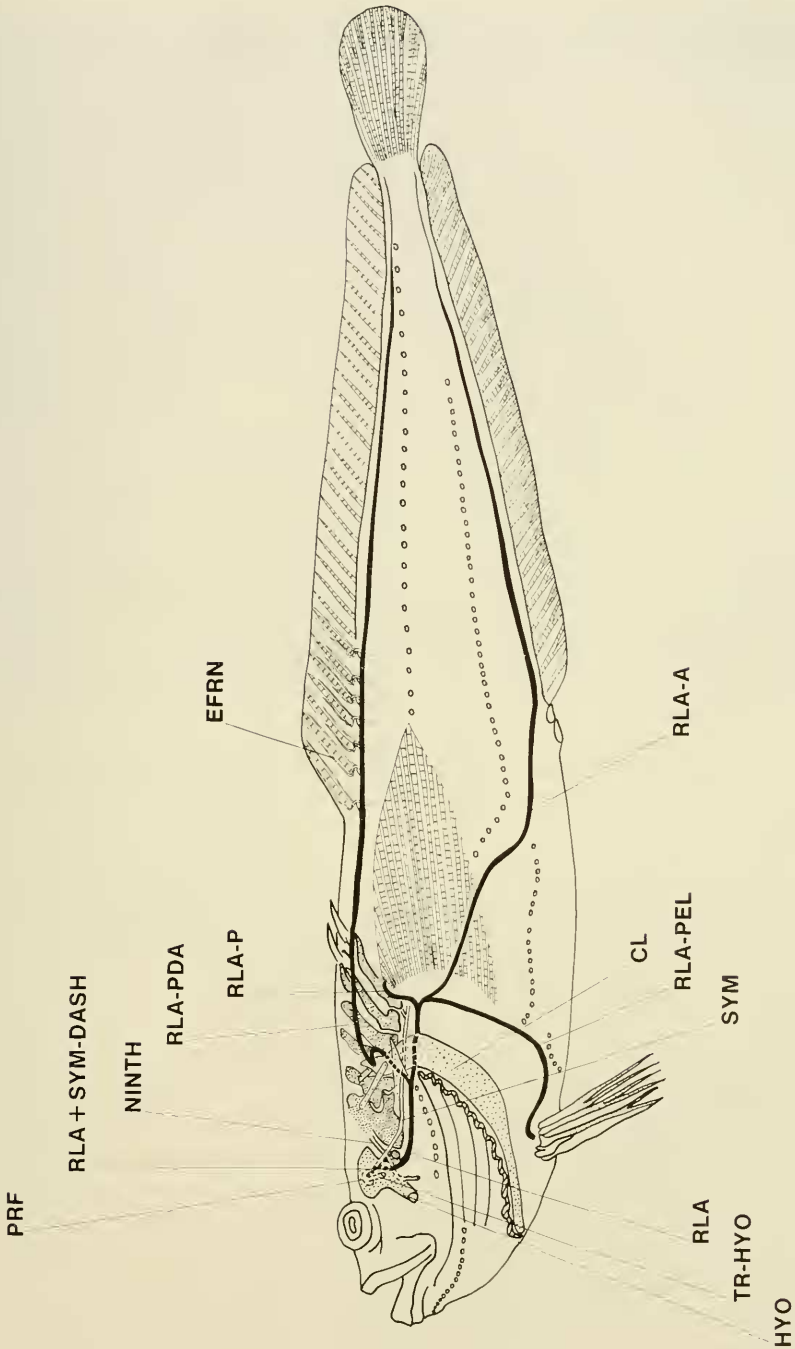


FIGURE 8. Pattern of ramus lateralis accessorius in *Poricthys margaritatus* (Batrachoididae). Prootic foramen shown as dashed circle medial to hyomandibular, the prootic trunk shown as dashed black line medial to hyomandibular.

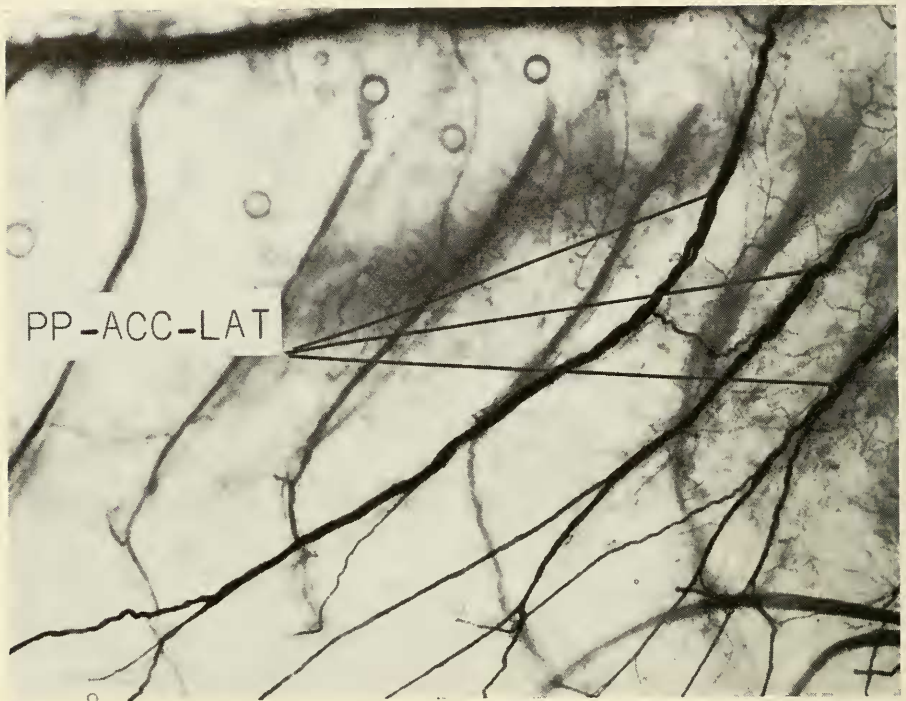


FIGURE 9. *Dicrolene intronigra* (Brotulidae) showing pectoral accessory lateral-line nerve (PP-ACC-LAT) and several succeeding ventral segmental accessory lateral-line branches. Nerve endings for scattered free lateralis organs visible as relatively short horizontal lines extending towards left (posteriorly) on six secondary branches of the ventral lateral-line nerves. Sihler preparation.

PECTORAL-PELVIC ACCESSORY LATERAL-LINE NERVES IN  
PERCOPSIFORM, GADOID, OPHIDIROID, BATRACHOIDID AND GOBIOID FISHES

Accessory, ventrally directed, segmental lateral-line nerves are poorly known in other fishes. They were known previously apparently only for the hatchet-fish, *Argyropspecus* (Handrick, 1901). The account given here is brief; an extended treatment is to be published later. In *Percopsis* as in *Aphredoderus* (fig. 10, Pec-Pel ACC) a large branch is detached from the base of the ramus dorsalis of the main lateral-line nerve directly past the supracleithrum, the branch passing in the skin paralleling the cleithrum, curving anteriorly around the ventral end of the base of the pectoral fin, and sending out branches from where it begins to curve and on all the way around below the base of the fin onto the skin of the anterior surface of the muscular base of the pectoral fin. The branches radiate out towards the midventral line and the base of the pelvic fin. Two segments further posteriorly, there is another sizable but much smaller branch from

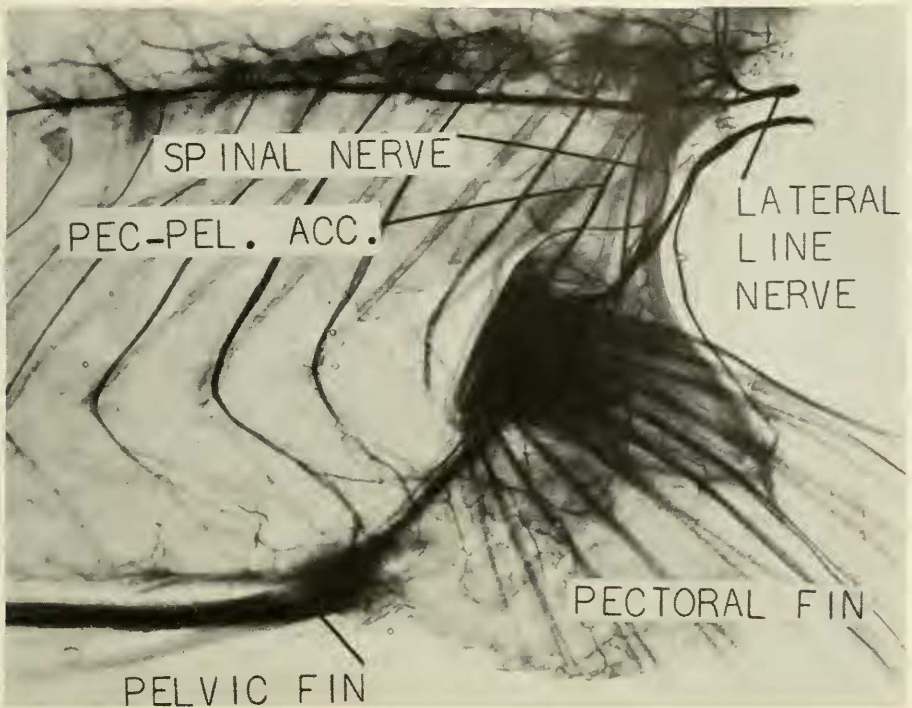


FIGURE 10. Pectoral-pelvic area of *Aphredoderus sayanus* showing pectoral-pelvic accessory ventral lateral-line nerve (PEC-PEL. ACC.). Another nerve appears connected to the main lateral-line nerve close to PEC-PEL. ACC. but it is a cut spinal nerve. Sihler preparation.

the ramus dorsalis of the lateral-line nerve. It passes ventrally, parallel to the large pectoral-pelvic accessory lateral-line nerve but this smaller one serves mostly only skin at the ventral end of its segment. In each succeeding segment there is a similar but much smaller branch running ventrally. These lateral-line branches innervate free lateral-line organs scattered in the skin which are especially abundant in the area below and in front of the pectoral base and back to the pelvic base (fig. 11). The organs are borne on the scales.

The same large accessory lateral-line nerve is present in *Aphredoderus*.

In the gadoid *Merluccius gayi* the segmental lateral-line nerves are present and in the same pattern as for *Percopsis* except that the anterior nerves are not enlarged.

In the brotulid *Dicrolene intronigra* (fig. 9, PP-ACC-LAT), in addition to the large first pectoral-pelvic accessory lateral-line nerve, there is a second large one in the following segment and then 3 more smaller ventral lateral-line nerves at about trunk segments 5, 8, and 14 and at least 4 more on the remainder of the trunk. The first and largest has a very similar course and distribution to

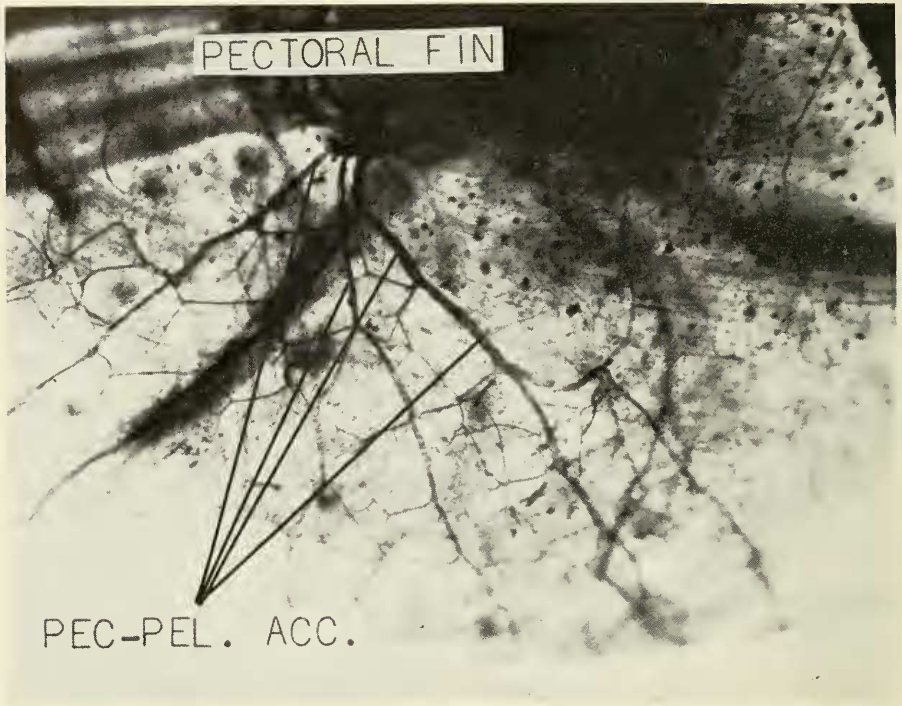


FIGURE 11. Detail of pectoral-pelvic accessory lateralis nerve breaking up into smaller branches below base of pectoral fin in *Aphredoderus sayanus*. Sihler preparation.

the first one in *Percopsis* except that it arises from the main trunk of the lateral-line nerve, not from the ramus dorsalis. It supplies large lateralis organs scattered in the skin ventral and anterior to the pectoral fin and up to the jugular pelvics. The second large branch passes ventroposteriorly and divides about halfway to the midventral line. The branches diverge supplying large lateralis organs in skin on the ventral body surface (fig. 9). The other branches start towards the anal fin and run horizontally at the ventral longitudinal septum supplying lateralis organs near this line.

Other brotulid genera examined showing similar pectoral-pelvic and ventral accessory lateralis nerves are *Bassozetus*, *Monomitopus*, *Monomerepus*, and *Porogadus*.

In the batracoidid *Porichthys margaritatus* a pectoral-pelvic accessory lateral-line nerve arises from the deep main trunk of the lateral-line nerve as this nerve approaches medial to the supracleithrum. Further ventrally the pectoral-pelvic accessory lateral-line nerve divides into a large branch which drops ventrally close to the posterior edge of the postcleithrum, curves anteriorly at the ventral end of the pectoral base, and supplies the ventral lateral line from a little pos-

terior of the pectoral fin all the way to the most anterior extent of the ventral lateral line. The other smaller branch from the main pectoral-pelvic accessory lateral-line nerve passes ventroposteriorly and shortly divides into a branch that drops down to supply a segment of the ventral lateral line posterior to the pectoral fin and a branch which continues posteroventrally, joining consecutively with 2 small and 1 large branch all separated from each other by some distance where they come off the main deep lateral-line nerve. These fused longitudinal branches supply the ventral lateral line to the end of the abdominal area where additional branches from the main lateral-line nerve continue supplying the post-abdominal part of the ventral lateral line, these branches passing laterally out the horizontal septum independently of spinal rami. They leave from the deep lateral-line nerve located at the side of the vertebral column.

The ventral lateralis organs and nerves of *Dicrolene* and *Porichthys* are a very noteworthy similarity between these fishes.

In the gobies *Bathygobius lineatus* and *Acanthogobius flavimanus*, there is an accessory pectoral lateral-line nerve. In *Bathygobius* it detaches from the main lateral line midway between the location of the second and third ribs and courses ventrally close to the anterior edge of the third rib. The accessory pectoral branch innervates a row of about a dozen free neuromasts which ends at the ventral edge of the pectoral fin but 2 segments posterior to it. No other ventral segmental accessory lateral line branches were observed.

For the Gonostomatidae (*Gonostoma elongatum*) and Chauliodontidae (*Chauliodus macoumi*) segmental ventral accessory lateral-line nerves extend to near the midventral line. The second such nerve is the largest and passes around the base of the pectoral fin. A single large accessory pectoral lateral-line nerve was reported for *Argyropelecus* (Sternoptychidae) by Handrick (1901). In the Osmeridae (*Hypomesus pretiosus*) a ventral segmental lateral-line nerve occurs in each body segment. The fourth and fifth are the largest and come close together as they pass anteriorly around the base of the pectoral fin. The rest form an interlocking network on the ventrolateral side where they innervate free neuromasts.

#### PATTERN OF RLA IN OSMERIDAE

In *Hypomesus pretiosus* there is the same type of nerve as in *Percopsis* that leaves the truncus hyomandibularis and courses over the wall of the otic bulla, that is crossed by the ninth cranial nerve, that forms ganglia along its trunk, and that courses alongside the ventrolateral side of the vertebral column as far as the caudal fin.

In osmerids, however, this nerve is the sympathetic trunk and ganglia. The presence of RLA in it cannot yet be demonstrated. From leaving the truncus hyomandibularis up to halfway across the otic bulla, the sympathetic consists of 3 separated parts. Proximally, two of these parts pass anteriorly inside the

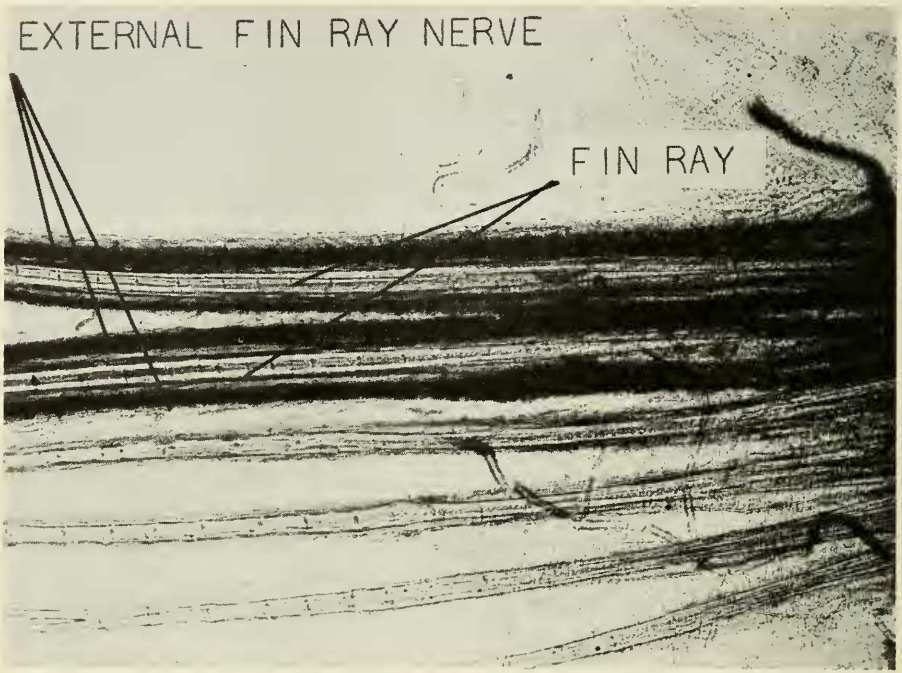


FIGURE 12. Pelvic fin of *Physiculus talarae* (Moridae) showing fin-ray nerves coursing external to fin rays. Sihler preparation.

cranium. They do not end in the geniculate ganglion. The third could not be followed. It is hypothesized that in some osmerid it may be found to contain RLA fibers. This prediction is based on the fact that osmerids and percopsids have both the ramus canalis lateralis system of cranial nerves as well as the pectoral accessory ventral lateralis nerves and the similar successive segmental ventral lateralis nerves for all body segments. Osmerids may be basically much like *Percopsis* and may have given rise to them.

#### THE RAMUS CANALIS LATERALIS SYSTEM

The ramus canalis lateralis nerves first named by Ray (1950) for the lantern fish, *Lampanyctus leucopsarus*, are here recognized as evidently a secondary system of lateralis innervation and perception that is found in numerous lower groups of fishes, the primary system being the neuromasts located in the cephalic lateral-line canals.

The ramus canalis lateralis system consists of several facialis and occasionally of one or more vagal lateral-line branches that usually course lengthwise anteriorly in the membranous roof of the cephalic lateral-line canals. Several of these canal branches radiate from a short trunk coming off the truncus hyo-



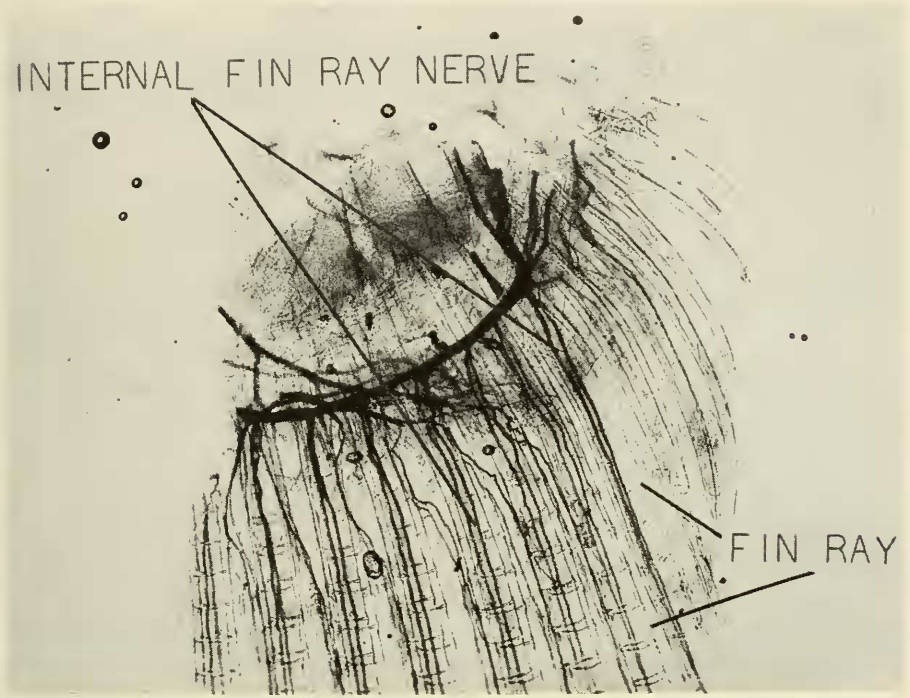


FIGURE 13. Caudal fin rays of *Aphredoderus sayanus* showing fin-ray nerves coursing internally down the centers of the hollow fin rays. Sihler preparation.

mandibularis close to the articulation between the opercle and hyomandibular bones. Although the system of branches looks complex (fig. 16), the presence of the system is simple to detect. If the skin is removed in the upper cheek region posterior to the eye, the most conspicuous branch will be seen. It comes up through cheek muscle close to the preopercle and runs forward beneath skin and into the cavity of the middle infraorbital bones and out along the overlying membrane of the anterior infraorbitals. This branch has been called the ramus buccalis accessorius. Branches of the canalis lateralis nerves innervate naked lateral-line organs (neuromasts) lying in the membrane roofing the canals and also innervate the same kind of organs lying in skin adjacent to the canals if such organs are present. The ramus canalis nerves do not supply the neuromasts (seismosensorial organs) lying in the floor of the head canals. The branches of the ramus canalis system appear to have great taxonomic importance. Patterns vary with different groups of fishes or are the same or similar for other groups. As far as presently known, these nerves are found only in certain fish groups of lower taxonomic placement; that is, not in the Perciformes or higher orders, or if they are, then the classification of such fishes should be questioned.

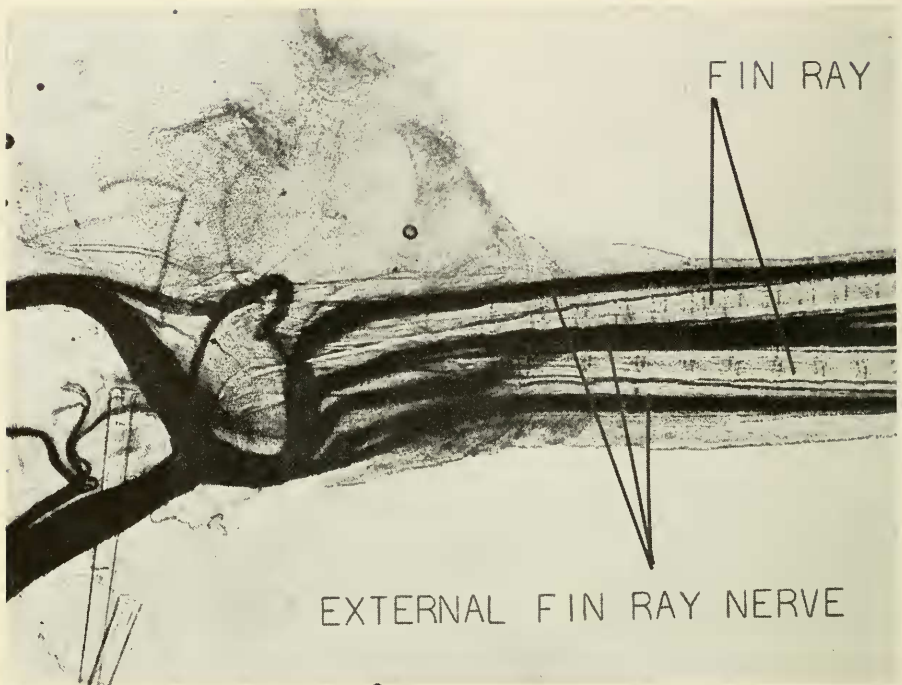


FIGURE 14. Pelvic fin of *Brotula clarkae* showing fin-ray nerves coursing external to fin rays. Sihler preparation.

The descriptions which follow are brief and preliminary. The ramus canalis lateralis nerves will be given extensive treatment in a later publication. *Percopsis omiscomaycus* is used as the basic reference form to which other forms are compared. Descriptions are reduced to cover 7 rami. The basic branches and their abbreviations are as follows:

- r.c. 1a = supraorbital branch.
- r.c. 1b = temporal branch of r.c. 1a.
- r.c. 2 = anterior infraorbital branch plus dorsoanterior dentary and rictus branches.
- r.c. 3 = posteroventral dentary branch plus rictus branches.
- r.c. 4a = preopercular branch.
- r.c. 4b = medial preopercular-mandibular ridge prolongation of r.c. 4a.
- r.c. 5 = supratemporal branch.
- r.c. 6 = posterior infraorbital branch.
- r.c. 7 = branch from r.c. 4 arching dorsoposteriorly from operculum to anterior end of dorsal fin.

Some patches of naked lateralis organs are supplied by nerve fibers that course indistinguishably with the supraorbital and infraorbital trunks. These fibers are not considered further in the present report although they probably are part of the same system of nerve fibers as are the ramus canalis lateralis nerves.

#### RAMUS CANALIS LATERALIS SYSTEM IN PERCOPSIDAE

The branches of the ramus canalis lateralis system for *Percopsis omiscomaycus* are shown in figure 15. Branches r.c. 1 through r.c. 5 are present and well-developed. No group other than the percopsiform fishes yet examined has branch r.c. 4b, the extension of r.c. 4a into the medial preopercular-mandibular ridge. The approximate distribution of the naked lateralis organs supplied by the ramus canalis lateralis system of the head is also depicted in figure 15. The branches are closely similar for the Aphredoderidae.

#### RAMUS CANALIS LATERALIS SYSTEM IN MYCTOPHIDAE

The ramus canalis lateralis nerves have been reported only in *Lampanyctus* (see Ray, 1950). A more complete description of them is given in figure 16 of the present work. The skin in lantern fishes is often damaged in capture. Complete descriptions of the nerves and the distribution of the organs they innervate therefore await specimens with nearly intact skin and organs.

Branch r.c. 1a is basically the same in both *Percopsis* and *Lampanyctus* except that the temporal branch, r.c. 1b, is absent in the latter. Branch r.c. 2 is essentially the same also if allowance is made for the very large mouth in *Lampanyctus*. Branch r.c. 3 is basically like that in *Percopsis*, but comes off the truncus hyomandibularis further down in *Lampanyctus*. Likewise for r.c. 4, except r.c. 4 is not prolonged into the medial preopercular-mandibular ridge, as is branch r.c. 4b. Branch r.c. 5 innervates the temporal and posttemporal canal membrane in *Lampanyctus*, a difference from what r.c. 5 innervates in *Percopsis*, where it supplies a patch of organs medial to the small supratemporal canal bone.

#### RAMUS CANALIS LATERALIS SYSTEM IN APOGONIDAE

Free or naked neuromasts, all over the head in *Apogon*, are randomly but densely distributed on the snout, becoming progressively arranged in definite rows posteriorly.

Branch r.c. 1 seems to be basically the same as in *Percopsis* with both similar "a" and "b" branches (fig. 17). Branches r.c. 2 and r.c. 3 arise together as a main unit from the truncus hyomandibularis, whereas in *Percopsis* these branches arise separately. This origin of r.c. 2 and 3 as a common trunk would seem to explain the fact that r.c. 2 has no visible branch to the lower jaw as in *Percopsis*. That is, since r.c. 2 and r.c. 3 have a common trunk going back to the truncus hyomandibularis, it would seem likely that the part of r.c. 2 that

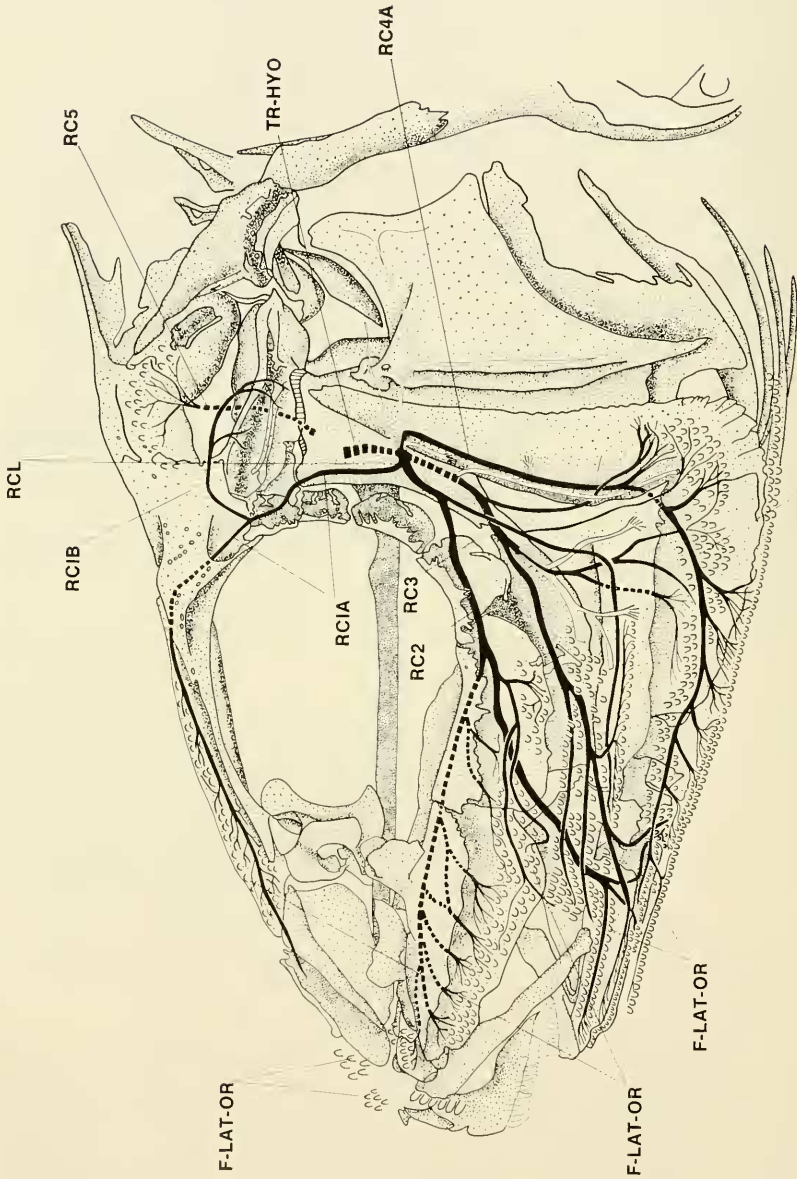


FIGURE 15. *Percopsis omiscomaycus* (Percopsidae) showing branches of ramus canalis lateralis system. Most of truncus hyomandibularis is omitted. See list for abbreviations.

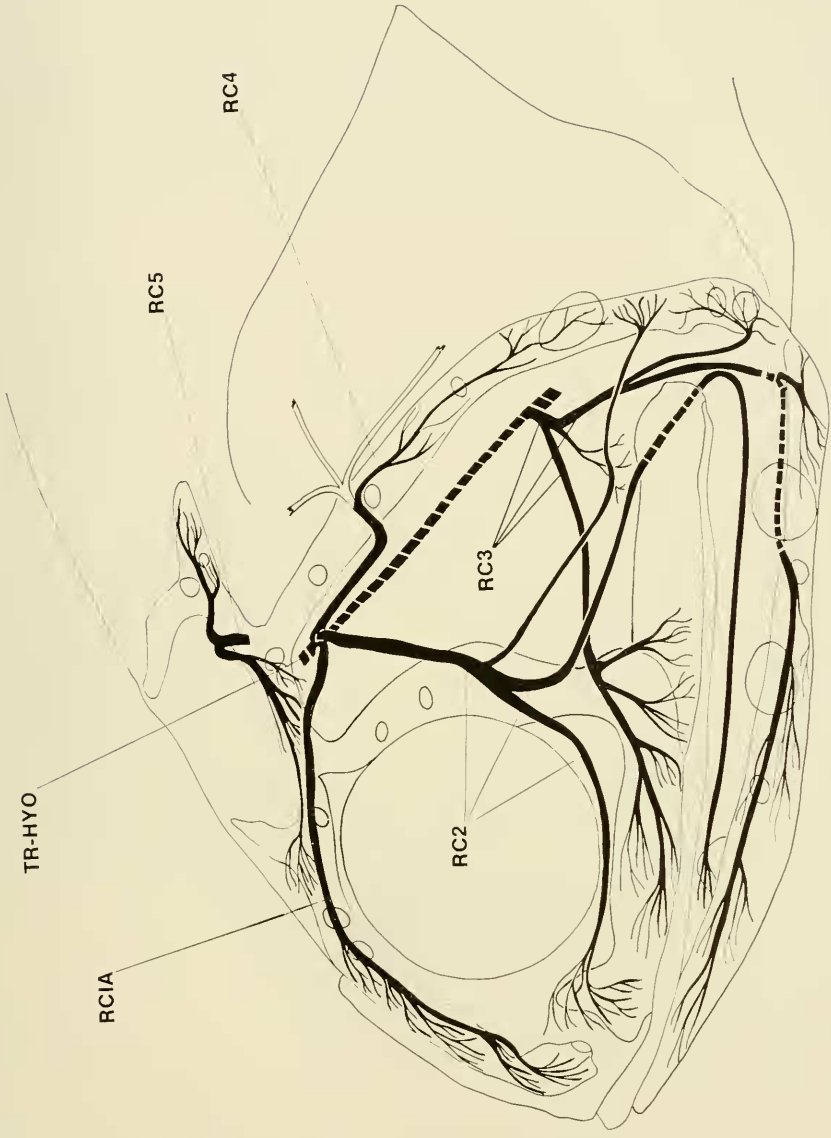


FIGURE 16. *Lamppanyctus leucopsarus* (Myctophidae) showing branches of ramus canalis lateralis system. Most of truncus hyomandibularis is omitted. See list for abbreviations.

goes to the lower jaw as a separate branch in *Percopsis* would remain bound in *Apogon* with r.c. 3 which also goes to the lower jaw. Branches which go to the part of the preopercular canal that lies in the angle of this bone detach in *Percopsis* from the truncus hyomandibularis, but they detach from r.c. 3 in *Apogon*. Branch r.c. 4 is as it is in *Lampanyctus*; that is, without the extension of r.c. 4b. Branch r.c. 5 is similar to that of *Percopsis*. Branch r.c. 6 is apparently not represented in *Lampanyctus* or *Percopsis*. The branches in *Apogon* are in some ways more like those in *Lampanyctus* and in others more like those in *Percopsis*. *Synagrops bella* has a large branch r.c. 3 and branch r.c. 5 but apparently no r.c. 1 or r.c. 2 or r.c. 4. *Epigonus robustus* has a smaller r.c. 3 than has *Synagrops* but apparently none of the other independent rami.

#### RAMUS CANALIS LATERALIS SYSTEM IN NEOSCOPELIDAE

On *Scopelengys tristis* (fig. 19) free neuromasts are variously arranged in short and long rows on all parts of the head. The pattern of the branches of the ramus canalis lateralis system in *Scopelengys* is closest to that of *Lampanyctus* but with differences. Closely similar are branches r.c. 1a and r.c. 2 in *Percopsis*, *Lampanyctus* and *Scopelengys*. Branch r.c. 3 has a distinctive branch, r.c. 3a, that goes to the membrane of the infraorbital canal lying above the posterior end of the maxillary ramus. The same branch is present in *Lampanyctus*. Branch r.c. 3b detaches from the truncus hyomandibularis further distally. *Scopelengys*, *Lampanyctus*, and *Apogon* all agree in having all of branch r.c. 3 come off the truncus hyomandibularis as one branch, whereas in *Percopsis* several smaller branches supplying the angle of the preopercular canal detach from different points of the truncus hyomandibularis. In *Scopelengys* branch r.c. 1b detaches independently from r.c. 1a, and branch r.c. 3c, not found in the others, detaches from the common trunk of the ramus opercularis superficialis facialis. No branches associated with the ramus supratemporalis vagi were observed. *Neoscopelus* differs interestingly from *Scopelengys* in having r.c. 7 which extends in an arch from near the opercular articulation dorsoposteriorly back to the anterior end of the dorsal fin, decreasing in size and ending there.

#### RAMUS CANALIS LATERALIS SYSTEM IN MELAMPHAIDAE

Only one specimen of *Melamphaes* species prepared by the Sihler technique was available. Free neuromasts are extremely abundant on the head, especially in the membranous roofs of the cephalic canals as in *Lampanyctus*.

The ramus canalis lateralis nerves are thin. Branches r.c. 1a, r.c. 1b, and r.c. 2 are present. No independent r.c. 3 was observed. Branch r.c. 3 runs with the ramus mandibularis facialis to the lower jaw as part of the latter. Branch r.c. 4 extends at least halfway down the preopercular canal. No branch r.c. 5 was observed.

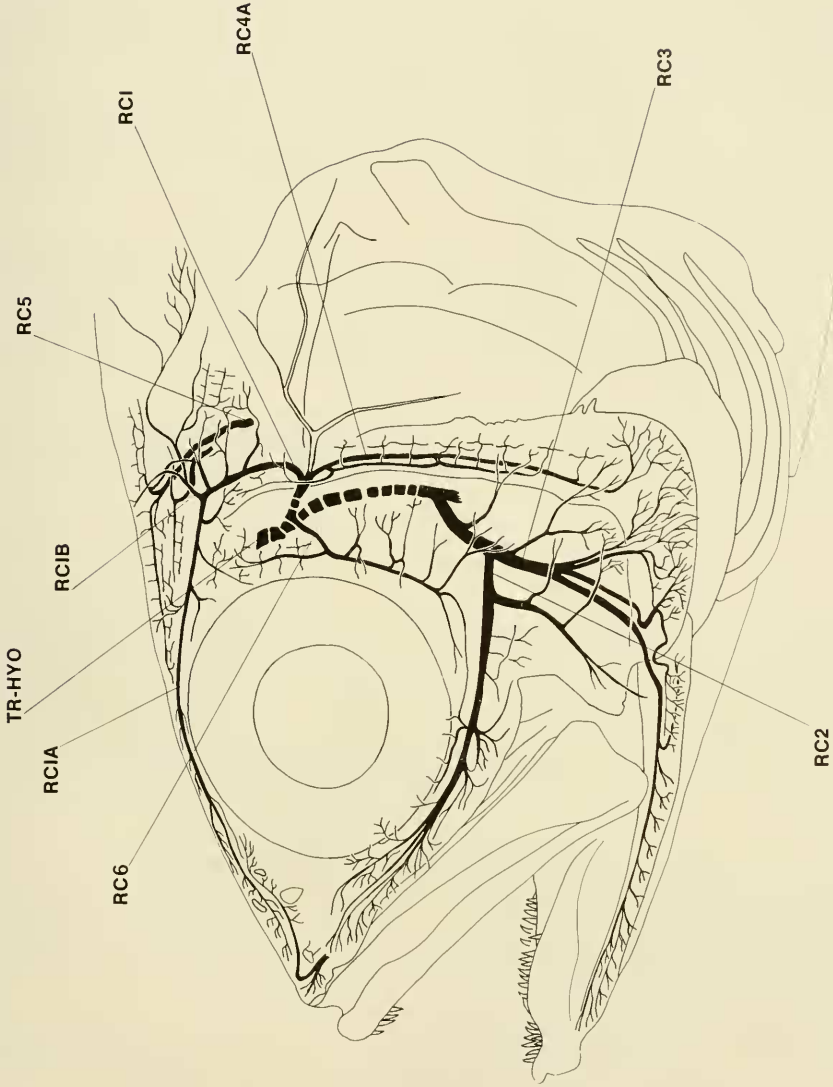


FIGURE 17. *Apogon astradorisatus* (Apogonidae) showing branches of ramus canalis lateralis system. See list for abbreviations.

## RAMUS CANALIS LATERALIS SYSTEM IN MERLUCCIIDAE

In *Merluccius gayi* branch r.c. 1 does not come off the truncus hyomandibularis as a separate branch at the same point that the ramus opercularis superficialis facialis does in *Percopsis*. Instead it detaches from the truncus supraorbitalis together with the branch that supplies the third neuromast from the posterior end of the supraorbital canal. From there on it runs separately in the membranous roof of the canal to its anterior end.

Branch r.c. 2 detaches from the truncus hyomandibularis high up on the cheek. It has two divisions: one to the membranous roof of the infraorbital canal all the way to its anterior end and one to the membranous roof of the mandibular canal up to its anterior end.

Branch r.c. 3 runs in common with, then separates from, r.c. 2, and goes to the lower jaw, giving off en route a branch to the angle of the preopercular canal roof and to a long horizontal row of organs located midway up the cheek. The rest of r.c. 3 innervates the posterior end of the mandibular-articular part of the canal membrane and extends along the membranous roof of the canal to its anterior end.

Branch r.c. 4 detaches from the ramus opercularis superficialis facialis and runs ventrally down the membranous roof of the preopercular canal to the angle of this canal.

## RAMUS CANALIS LATERALIS SYSTEM IN BROTLIDAE

In *Dicrolene intronigra* one large branch of the ramus canalis lateralis system is present. The first branch detached from it is small and passes to the infraorbital canal below the eye and ends there. The remainder passes to the lower jaw, giving off branches en route supplying large free neuromasts lying near the angle and horizontal arm of the preopercle, the rest supplying free neuromasts on the membranous roof of the mandibular canal extending almost to its anterior end.

## RAMUS CANALIS LATERALIS SYSTEM IN OSMERIDAE

The distribution of free neuromasts for *Hypomesus pretiosus* (fig. 18) is generally over all of the head even on the maxillary and supramaxillary and on exposed branchiostegal rays as well as on the membranes of all the fins and on the leading edges of the pectoral, pelvic, dorsal, and anal fins.

Branch r.c. 1a and r.c. 1b are both large and long. Branch r.c. 1b arches posteriorly all the way to the segment of the lateral-line canal attached to the supra-cleithrum. Branch r.c. 1a extends to the nasal canal.

Branch r.c. 2 runs along the infraorbital canal to its anterior end and detaches a branch which drops vertically down across the cheek to the canal of the horizontal arm of the preopercle. There is no independent branch of r.c. 3



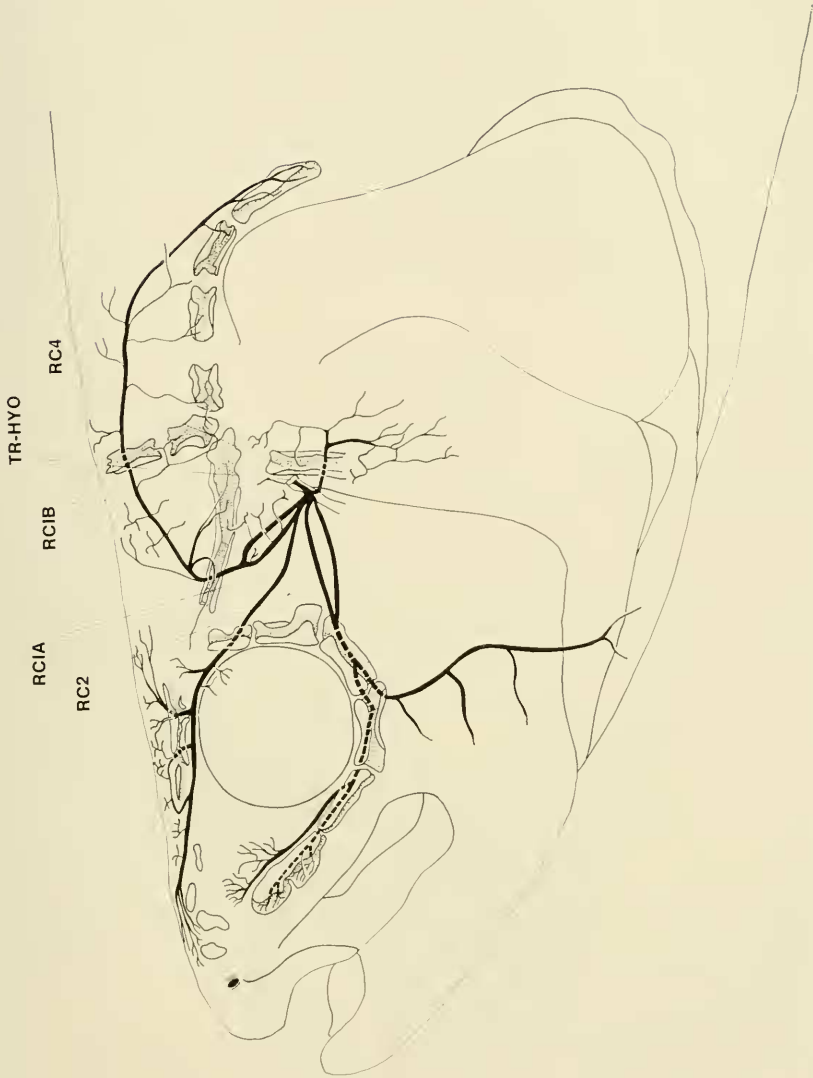


FIGURE 18. *Hypomesus pretiosus* (Osmeridae) showing pattern of ramus canalis lateralis nerve. Sihler preparation. See list for abbreviations.

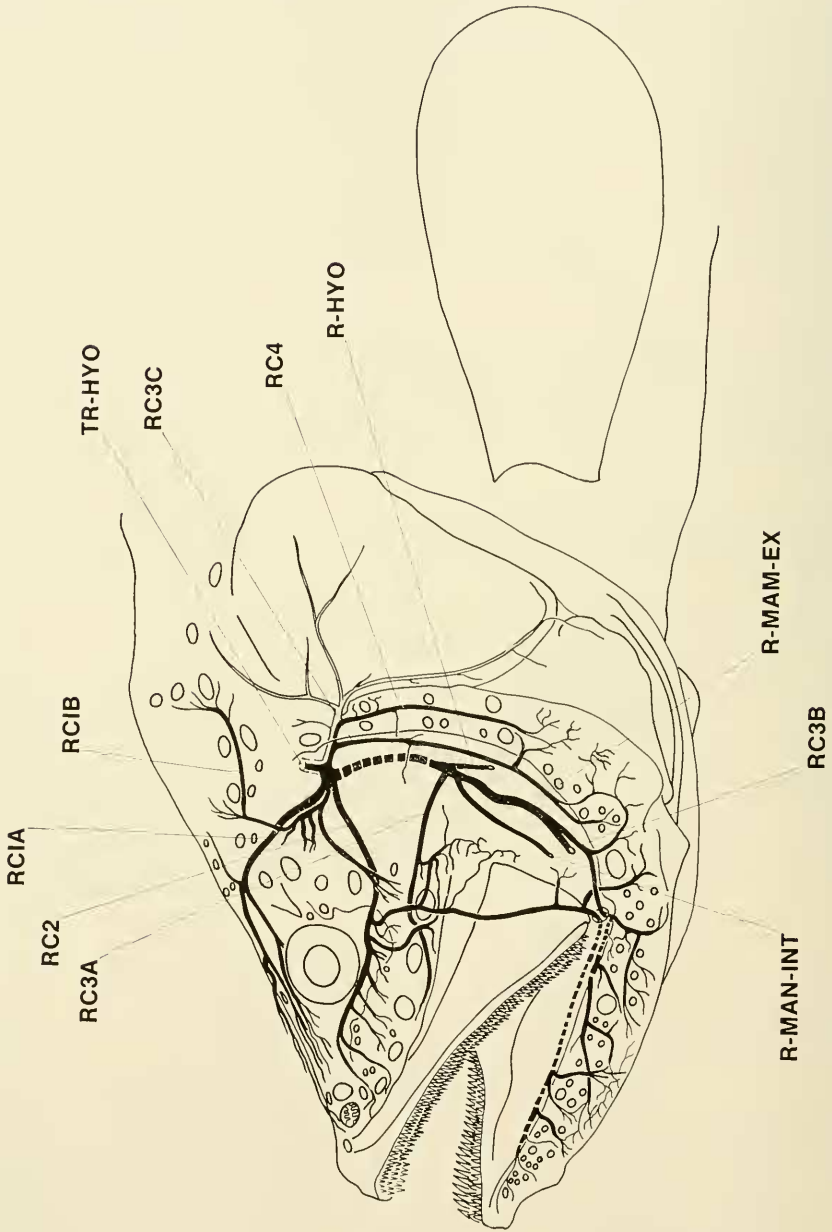


FIGURE 19. *Sceloporus tristis* (Neoscolopelidae) showing pattern of ramus canalis lateralis system. See list for abbreviations.

to the lower jaw. Branches innervating free neuromasts of the preopercular-mandibular canal detach from the ramus mandibularis facialis to the lower jaw.

Practically the same pattern is present in *Spirinchus thaleichthys* and *Thaleichthys pacificus* as seen from dissections on alcoholic specimens; the same holds for *Bathylagus alascanus*.

#### RAMUS CANALIS LATERALIS SYSTEM IN GOBIIDAE

In *Bathygobius lineatus* as in all gobioids there are various rows of free neuromasts associated with most of the cephalic head canals. These are innervated by several branches of what evidently is the ramus canalis lateralis system. Branch r.c. 1 is short, extending only from where the superficial opercular facial ramus passes onto the operculum and on up the dorsal end of the preopercle, ending at the posterior end of the temporal canal. The shortness of r.c. 1 reflects the fact that there are no free neuromasts for the supraorbital canal except at its anterior end.

Branch r.c. 2 is the main independent branch of the ramus canalis system that is present. At the point where the superficial opercular facial ramus detaches from the truncus hyomandibularis, the first branch of r.c. 2 also detaches and innervates a long line of naked neuromasts extending from just posterior of the eye to a little below the middle of the eye. A row lies some distance dorsal to this row and another somewhat below this dorsal row that together form a somewhat continuous row innervated by several branches from the truncus infraorbitalis. The main part of r.c. 2 continues forward beneath the skin innervating the ventralmost row of free neuromasts lying below the eye and in the area of the infraorbital canal. The row ends some distance anterior and dorsal to the rictus of the jaw. The main branch of r.c. 2 next detaches 2 branches that supply a row of free neuromasts that lie along the lateral (or dorsal) edge of the preopercular-mandibular canal, beginning with the angle of the preopercle and continuing forward as far as the angular bone. A row of free neuromasts lying along the medial edge of the same length of canal is supplied by branches from the ramus mandibularis facialis. Shortly before the rictus of the mouth, branch r.c. 2 divides. The smaller part innervates the remainder of the row of free neuromasts already mentioned that ends shortly beyond and above the rictus. The larger part of r.c. 2 passes ventrally around the rictus of the mouth and onto the lower jaw where it extends anteriorly to near the symphysis innervating a long row of free neuromasts lying on the lateral or dorsal edge of the mandibular canal. The row of larger organs extending along the medial edge of the mandibular canal is supplied by branches from the ramus mandibularis facialis.

Branch r.c. 4, or what appears comparable to it, has two main parts. One continues posteriorly about on the level of the horizontal rib of thickened reinforcement bone of the opercle and supplies a row of 24 organs on the posterior third of the opercle. The larger part of branch r.c. 4 passes down the posterior edge

of the preopercular canal or close to it, out onto the ventral end of the preopercle and supplies a long vertical row of free neuromasts.

Branch r.c. 5 of the ramus supratemporalis vagi innervates free organs along the posttemporal and supratemporal canals and another branch passes forward supplying the temporal canal.

#### RAMUS CANALIS LATERALIS SYSTEM IN CYPRINIDAE

Manigk (1934, fig. 1) reports for *Phoxinus laevis* a nerve which he calls the ramus buccalis accessorius that apparently belongs to the ramus canalis lateralis system but which has important differences from the patterns seen in the Percopsidae, Myctophidae, Osmeridae, Apogonidae, and Gobiidae. The pattern in the Cyprinidae differs in that (1) the rami do not course in the membranous roof of the cephalic lateral-line canals; (2) there is only one distinct branch, r.c. 2; and that (3) branch r.c. 2 does not have a ramus going to the lower jaw as occurs in all other families except the most generalized, the Osmeridae.

#### RAMUS CANALIS LATERALIS SYSTEM IN OTHER FAMILIES

Other families among those examined having the ramus canalis lateralis system are, in the Salmoniformes, the Esocidae, Umbridae, Gonostomatidae, Sternoptychidae, Chauiodontidae, Alepocephalidae, and Chlorophthalmidae; in the Beryciformes, the Trachichthyidae, Berycidae, Polymyxiiidae, and Holocentridae. The Umbridae have r.c. 1, r.c. 2, r.c. 4, and r.c. 5. The pattern in *Gonostoma elongatum* is most like that in the Neoscopelidae and Myctophidae.

The beryciform families apparently have the ramus canalis lateralis pattern of *Melamphaes* or it is reduced.

Found not to have the system of nerves were the Amiidae; Elopidae; Clupeidae (*Clupea pallasii*); Salmonidae (*Salmo*, *Oncorhynchus*, *Coregonus*); Galaxiidae (*Galaxias*); Synodontidae; Atherinidae (*Menidia*); Plecoglossidae; Argentinidae.

#### EXTERNAL-INTERNAL FIN-RAY INNERVATION

So far as is known, most of the paracanthopterygian fishes have the fin-ray nerves coursing external to the fin rays, not internal in the space between the two halves of each fin ray as is true for percoid fishes and apparently for most other teleosts.

In the survey made thus far, the external position of the fin-ray nerves has been found for the codfishes, brotulids, ophidiids, zoarcids, gobiesocids, batrachoids, and ogcocephalids that have been examined. When external, the nerves course in contact with the surface of the fin ray or almost in contact. The fin-ray nerves are internal for the percopsiform fishes.

In *Gadopsis marmoratus*, a fresh-water percoid fish of Australia, in which the pelvic fins are long, narrow, and of 2 rays, similar to pelvic rays in bro-

tulids, the huge combined spinal and RLA nerves to them course down the centers of the rays with some fibers, apparently out of physical limitation of space, coursing outside the fin rays beside the longitudinal split that exists down the two halves of each ray. The nerves of ophidiid and brotulid pelvic rays are huge also, but the nerves course entirely external to the pelvic rays. The fin ray innervation in *Gadopsis* is not ophidioid.

The fin-ray nerves are external also in the Liparidae and Cottidae (*Scorpaenichthys*). They are external also in the stichaeids (*Epigeichthys*). Thus the condition of the fin-ray nerves being external to fin rays is not unique to the Paracanthopterygii, but it is apparently a specialization within the fishes of this group. A survey for this interesting condition is being conducted with the preparation of specimens of many families by the Sihler technique in addition to some serially sectioned.

#### DISCUSSION

New facts presented in preceding sections have bearings on the taxonomic position and phylogenetic considerations of numerous kinds of fishes. Only some of the problems can be discussed here.

The new facts concern 4 nerve patterns: (1) the ramus lateralis accessorius (RLA); (2) the pectoral accessory ventral lateralis branch and succeeding segmental branches; (3) the ramus canalis lateralis system of nerves; (4) the external or internal innervation of fin rays.

#### ORIGIN OF BATRACHOIDID FISHES

The presence of greatly similar patterns in the first two of these nerve complexes in batrachoidid and percopsid fishes indicates that the batrachoidid fishes have most probably been derived from percopsid ancestors.

The patterns of RLA in *Percopsis* and *Porichthys* are similar in three important ways in that in each genus (1) RLA leaves the cranium together with the truncus hyomandibularis; (2) RLA leaves the truncus hyomandibularis bound up with the sympathetic trunk; (3) RLA courses over the wall of the otic bulla. *Porichthys* differs from *Percopsis* in that RLA departs from the sympathetic trunk shortly after the two leave the truncus hyomandibularis bound together. RLA courses across the otic bulla slightly diverging from the sympathetic. *Porichthys* differs also in its course beyond the cleithrum. In *Porichthys* RLA breaks up into the dorsal, anal, and pectoral-pelvic branches near the cleithrum, these branches going independently to their fins, whereas in *Percopsis* RLA continues along the vertebral column to the caudal fin bound to the sympathetic trunk. The pattern of RLA in *Porichthys* appears to be an intermediate stage or an offshoot development between the *Percopsis* pattern and a gadoid or ophidioid pattern.

*Porichthys* has a pectoral-pelvic accessory ventral lateralis nerve as has

*Percopsis* and also has several of the succeeding segmental ventral lateralis branches enlarged which supply sections of the ventral lateral lines. *Percopsis* lacks ventral lateral lines, having instead only scattered, free, lateralis organs mostly in the pectoral-pelvic area. *Porichthys* does not have independent branches of the ramus canalis lateralis system. It has the external rather than internal fin-ray innervation which *Percopsis* has, but, so far as is known, all paracanthopterygian fishes have the external fin-ray innervation pattern except percopsiforms.

The pattern of RLA is the most distinctive feature of similarity between batrachoidid and percopsiform fishes. It more than any other character points to a percopsiform origin for batrachoidids. Possession of accessory pectoral-pelvic and ventral segmental lateralis branches is almost as significant and also helps tie batrachoidids in turn to other lower taxonomically placed fishes having this same nerve development.

#### ORIGIN AND RELATIONSHIPS OF GADOID AND OPHIDIROID FISHES

There are several patterns of RLA in ophidioids indicating evolutionary divergence within the group. The pattern in the brotulid *Ogilbia* (fig. 2) is most similar to that in a gadoid such as *Physiculus* (fig. 4) being alike in all important points, especially in having two or more anal fin branches detaching from the dorsal fin branch posterior to the origin of the dorsal fin. The pattern of *Lepophidium* and of numerous other ophidioids is like that of *Ogilbia* and *Physiculus* except that the branch for the dorsal fin and that for the anal fin exit from the cranium through separate foramina some distance apart in the parietal bone. The pattern in *Brotula* is distinctive for an ophidioid or gadoid in that the pectoral-pelvic branch leaves the cranium together with the truncus hyomandibularis and then courses posteriorly, passing medial to the supracleithrum. Such a cranial exit is an important similarity to the pattern in *Percopsis* and *Porichthys*.

The presence in the brotulids *Dicrolene*, *Monomitopus*, *Monomerepus*, and *Porogadus*, of the accessory pectoral-pelvic ventral segmental lateralis nerve and several succeeding similar branches greatly similar to such nerves in *Percopsis* and *Porichthys*, is evidence also for a taxonomic and phylogenetic connection between these fishes. So is the presence in both the gadoid *Merluccius* and the brotulid *Dicrolene* of significant branches of the ramus canalis lateralis nerves, although these nerves are somewhat different in parts of their patterns from that in percopsiform fishes. The pattern of the fin-ray nerves coursing external to the fin rays in gadoids and ophidioids (as well as in all paracanthopterygian fishes except percopsiforms) is a further interesting and significant similarity when it is contrasted with the internal fin-ray innervation of percoid fishes (20 families examined) and numerous other large groups of fishes such as atherinids,

cyprinodonts, salmonids and beryciforms. Other important similarities between gadoid and ophidioid fishes are (1) the large opisthotic, occupying part of the otic bulla wall, separating the prootic and exoccipital bones, and having the ninth cranial nerve exiting through it (McAllister, 1968); (2) presence of levator maxillae superioris muscle (Greenwood *et al.*, 1966); (3) a "percopsiform projection" often present on middle branchiostegal rays (McAllister, 1968).

#### RELATIONSHIPS OF ZOARCID FISHES

The Zoarcidae is still best placed together with the gadoids and ophidioids (Rosen, 1962; Freihofer, 1963; Greenwood *et al.*, 1966). The zoarcids have a pattern of RLA that is most like that of these fishes, especially like that of the ophidioids. Some zoarcids appear to have a remainder of the levator maxillae superioris muscle (Greenwood *et al.*, 1966). *Lycodapus* has what must be a good example of this muscle. Zoarcids have an external fin-ray innervation pattern.

Examination for RLA in *Lycodapus* has not yet been possible. Gosline (1968) has questioned the zoarcid affinities of *Lycodapus* and also tried to show that ophidioids and gadoids are not basically similar but that ophidioids are percoid derivatives. On the basis of patterns of RLA, the zoarcids most probably do not have a percoid ancestry as Gosline maintains, nor do they on the basis of ventral segmental lateral-line nerves present in zoarcids but not in percoids as far as is known.

#### RELATIONSHIPS AND CLASSIFICATION OF GOBIOID FISHES

Gobioid fishes show external similarities to percopsid and amblyopsid fishes. Gobioids and percopsids have weak spinous dorsal fins, rows of free lateralis organs on the head, and similar body form. McAllister (1968) lists many partial similarities between gobioids and percopsiforms and almost placed them in a relationship to the percopsiforms in his classification of teleostome fishes but could not quite do it. The problem has been that many of the similarities of gobioids to percopsiforms are halfway similarities, none being great enough to be convincing. Two important similarities of the nerves of gobioids and percopsiforms are now known. These are the presence of part of the ramus canalis lateralis system and of an accessory pectoral ventral lateralis branch. The only other spiny-rayed fishes so far known to have both of these nerve features are the Percopsiformes. This fact, plus all the other varying degrees of similarity listed by McAllister, suggests that the affinity of the gobies with the Percopsiformes is as he suspected. Examination of the opisthotic of *Eleotris fuscus* shows that it is large, separates the prootic and exoccipital, and has the ninth nerve coming out near its center. These opisthotic features in *Eleotris* are also those of gadoid and ophidioid fishes. The intermediateness of the condition of the opisthotic in *Eleotris* is suggested by the fact that the foramen for the ninth nerve on one side

of *Eleotris fuscus* was connected by a long thin opening to the edge of this bone; on the other side the indentation did not reach the ninth nerve foramen.

*Bathygobius lineatus* shows a great reduction in lateralis organs located in the cephalic canals, only a few being present in the region of the upper preopercular and temporal canals. This may be a feature of all gobioids. The canals themselves are mostly open troughs. These features of the head canals of gobioids should have interesting ecological, behavioral, and physiological significance. Their usually small size, many lines of free lateralis organs on the head with associated near loss of canal organs, and relatively sedentary habits give credence to a depiction of gobies as microhabitat fishes.

With new nerve evidence and the many features of similarity of gobies to percopsiform fishes as given by McAllister, it seems justified to make the gobioids an order, the Gobiiformes, placed in the superorder Paracanthopterygii with closest relationships to the Percopsiformes and with other characters as given by Regan (1911) for his suborder Gobiioidea.

#### RELATIONSHIPS AND CLASSIFICATION OF APOGONIDAE

Nerves identified as the ramus canalis lateralis system in *Apogon* (fig. 17) are strikingly similar to those of percopsiforms (fig. 15), myctophoids (figs. 16 and 19), stomiatoids, and osmerids (fig. 18). The ramus canalis lateralis system is recognized in an apparently reduced form in gadoids, ophidioids, beryciforms, and gobioids. If this system of nerves in *Apogon* is homologous with that in the other groups listed, it would be an important preperciform feature found even in salmoniforms but unknown in any perciform group except the gobioid fishes. That it is homologous in all these groups needs to be rigorously shown but judging from the similarity of the patterns illustrated in this paper I think that it is broadly homologous in these groups. It is one of the most complex and distinct system of nerves on the head. Its absence as far as known in the perciforms is explained as loss through reduction in preperciform ancestors. The system is apparently considerably reduced in beryciforms or absent in some. The great development and similarity of the canalis lateralis system in apogonids to that in *Percopsis*, *Scopelengys*, and melamphaeids is strong evidence for questioning the perciform character of apogonids.

There is also evidence of an apogonid-salmopercooid relationship from the otoliths. Frost's systematic statements, based as they were only on characters of the otoliths and made from study of otoliths of only certain species, have often been confusing. An example is in the salmopercooid fishes. Frost (1925) says that their otoliths "closely resemble (in some respects) those of *Ophichthys gomesii* (Apodes). —On the other hand there is a strong resemblance to those of the percooid genus *Apogon* which differs from the remainder of the percooids in the sulcus." We still do not have any other characters pointing to a systematic relationship between apodal and salmopercooid fishes but we do have an



important similarity in nerves identified in both salmopercooid and apogonid fishes as belonging to the ramus canalis lateralis system. Frost (1927) also states that "the sagitta of *Apogon melanotaenia* resembles that of *Acerina* (Percidae) in the sulcus" and that the otolith of *Cepola rubescens* (Cepolidae) resembles closely that of *Apogon*. The systematic significance of these similarities remains doubtful. Without doubt, however, there is a great need for atlases of fish otoliths published family by family until all families are covered.

A reasonable alternative hypothesis suggested here to that of Regan (1913) and of Greenwood (1966) for the origin of the Perciformes is that the percopsiforms gave rise to lines leading to both the Paracanthopterygii and the Acanthopterygii. In this hypothesis apogonids could lie on one of the lines tending towards the percooid expression. It is suggested that the Apogonidae be tried in a preperciform position in an experimental classification as a suborder of beryciform fishes allied to percopsiform fishes as all beryciforms may be so allied.

#### ORIGIN OF PERCOPSIFORM FISHES

Several important facts point to an origin of the percopsiform fishes from the salmoniforms, in particular, from the Osmeridae. The hypothesis in Greenwood *et al.* (1966)<sup>1</sup> leaves room for other possibilities.

The fact most weakening to the Greenwood hypothesis is that the nerve evidence in the descriptive section of the present paper indicates a percopsiform origin for the batrachoidids, gadoids, and ophidioids. In the Greenwood hypothesis, these fishes, including the percopsiforms, are each independently derived from a neoscopelid-like ancestor (e.g., *Sardinioides*), which in turn is derived from myctophoids.

In the percopsiform hypothesis, the myctophid and neoscopelid-like fishes evolved from a common ancestry with percopsiform fishes. Weitzman (1968) has shown osteologically that the origin of stomiatoid fishes evidently is in the Osmeridae. With present knowledge of the nerves, an osmerid ancestry is also hypothesized for the percopsiform fishes. The osmerids have a more generalized pattern of the ramus canalis lateralis system and also of the pectoral accessory ventral lateralis nerves and succeeding ventral segmental lateralis branches. Neither of these systems of nerves is present in the Salmonidae or Plecoglossidae as far as known. The Osmeridae are completely generalized in their freshwater-saltwater tolerance, a fact that a basal ancestral group for such a radiation should be expected to have. An observation of osmerid otoliths by Frost (1925) is of greater interest now. Frost said "In *osmerus eperlanus* . . . there is a distinct advance in this form (of the otolith) towards those observable in later groups, notably the berycoids."

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<sup>1</sup> The important paper of Rosen and Patterson, *The structure and relationships of the paracanthopterygian fishes*, Bulletin of the American Museum of Natural History, vol. 141, art. 3, pp. 357-474, came too late (July, 1969) to be used.

The ramifications of the percopsiform hypothesis are shown in figure 20.

No RLA is yet known for the osmerids nor for the suborder Myctophoidei nor is the pectoral accessory lateralis or succeeding segmental branches present in the myctophoids, *Lampancytus* and *Scopelengys*. The ramus canalis lateralis system apparently is not present in *Aulopus*, *Harpodon*, and *Synodus*.

In the words of its original describer, Louis Agassiz, no better candidate exists among known teleosts for being "a true intermediate type between Percoids and Salmonidae than my *Percopsis*" . . . as it "shows peculiarities which occur simultaneously in the fossil fishes of the chalk epoch, which however soon diverge into distinct families in the tertiary period, never to be combined again" (Agassiz, 1850).

*Aphredoderus* also is important in this picture but must be taken up in a later paper.

#### SUMMARY OF SYSTEMATIC RESULTS

Various combinations of four general features of the nerves plus some specific nerve characters were used to arrive at the systematic interpretations discussed above and summarized below. The nerve complexes are (1) the ramus lateralis accessorius (RLA or recurrent facial nerve), (2) the ramus canalis lateralis facialis system, (3) the ventral segmental lateral-line nerves of the trunk, and (4) the external or internal pattern of fin-ray innervation. The systematic results are as follows:

(a) Ophidioid relationships lie with gadoid fishes as advocated by Rosen and his coworkers (1962, 1966, 1969) and Freihofer (1963), not with blenniid-like perciforms. More complete descriptions in the present paper of RLA in these fishes show patterns of RLA to be more important systematically and more alike in these groups than was first thought. Possession of the ramus canalis lateralis facialis system and of ventral segmental lateral-line nerves in gadoids and ophidioids add strong support to the gadoid placement of the ophidioids. Both groups have the external pattern of fin-ray innervation.

(b) Specific relationship of ophidioids with percopsids is shown by cranial exit of RLA through the facial foramen beside the truncus hyomandibularis in *Brotula* and *Percopsis*. Similar cranial exit is known for *Anguilla*, the cobitid *Nemacheilus*, and the goatfish *Parupeneus*, but it is considered convergent in these groups. Doubt about the percoid affinities of the peculiar goatfishes is raised. Presence also of both the ramus canalis lateralis facialis system and of ventral segmental lateral-line nerves in the brotulid *Dicrolene*, and of the latter system and probably the former system also in the brotulids *Monomitopus*, *Monomerepus*, and *Porogadus*, are important nerve features found also in stomiatoid, myctophoid (only the ramus canalis lateralis system), and osmerid fishes but of neither system in salmonid fishes as far as known.



FIGURE 20. Scheme of possible relationships of percopsiform fishes. Two alternative hypotheses of relationship to perciforms are shown, one direct and one by way of the beryciforms.

(c) Gadoids have an affinity with percopsids as shown by the presence in *Merluccius* of both the ramus canalis lateralis facialis system and of ventral, segmental lateral-line nerves on the trunk, the latter more generalized in *Merluccius* than in *Percopsis*.

(d) Batrachoidids have an affinity with percopsids. *Porichthys*, *Percopsis*, and Amblyopsids are the only fishes known to have RLA leave the cranial cavity through facial foramen and bound with the trunk of the sympathetic nervous system. *Porichthys* possesses ventral segmental lateral-line nerves but in a more specialized condition than in *Percopsis*.

(e) Amblyopsids have a closer affinity with percopsids than with *Aphredoderus*. Pattern of RLA in *Percopsis* is found also in *Chologaster* and *Porichthys*. It is judged more primitive than the pattern in *Aphredoderus*, a pattern much different from that in *Percopsis* and more like that found in gadoids, ophidioids (except for the percopsid-like cranial exit in *Brotula*), and higher fishes.

(f) A percopsid-like ancestry is hypothesized for batrachoidid, gadoid, and ophidioid fishes based on evidence from the nerves.

(g) RLA in *Percopsis*, *Porichthys*, and *Physiculus* are described for the first time.

(h) Pattern of RLA in Macruridae is more like that in Moridae than in Gadidae.

(i) Pattern of RLA in *Ogilbia* and *Dinematichthys* resembles that in Moridae and Gadidae more than does RLA pattern in other brotulid and ophidiid fishes. *Ogilbia* and *Dinematichthys* and related genera merit familial rank.

(j) A well developed ramus canalis lateralis facialis system is present in osmerids, stomiatoids, myctophoids, percopsiforms, gadoids, ophidioids, and batrachoidids; reduced patterns are present in berycomorphs; the system is absent in advanced paracanthopterygians and in perciforms, except in gobioids and apogonids.

(k) Ventral segmental lateral-line nerves are present in osmerids, stomiatoids, percopsiforms, gadoids, batrachoidids, ophidiids, zoarcids, and gobioids.

(l) Presence of ventral segmental lateral-line nerves in zoarcids is strong evidence for continued placement of zoarcids close to gadoids and ophidioids. Zoarcids also have the external pattern of fin-ray innervation.

(m) External pattern of fin-ray innervation is found only in certain groups: all paracanthopterygian fishes, except percopsiforms and gobiiforms (placed in Paracanthopterygii in present paper); scorpaenids, cottids, liparids, stichaeoids. The survey is incomplete. Apparently most fishes have internal pattern of fin-ray innervation. Presence of the external pattern in nonparacanthopterygian fishes is considered convergent.

(n) Osmerids have the ramus canalis lateralis facialis system and ventral segmental lateral-line system in the most generalized state but have no RLA. Stomiatoids have the first two systems and lack RLA as far as known. Salmonids, aulopids, and synodontids lack all three systems so far as known. It is hypothesized that percopsids have an osmerid ancestry.

(o) Apogonids may be quasi-percid. They possess a well developed non-

perciform ramus canalis lateralis facialis system. It is proposed that they be placed with the beryciforms as a percopsid offshoot.

(p) Nerves identified as belonging to the ramus canalis lateralis system have been found in gobioid fishes. One anterior nerve identified as belonging to the ventral segmental lateral-line system known elsewhere only from preacanthopterygian fishes has also been identified in gobioids. These two systems are known to occur together in spiny-rayed fishes only in percopsiforms. These important similarities of the nerves, together with those summarized by McAllister (1968), add strongly to his suggestion that these fishes should stand in systematic relationship to the percopsiform fishes. It is proposed they be given ordinal status, the Gobiiformes, with characters as given in McAllister (1968), Regan (1911), and with the nerve and sensory canal features given in the present paper.

#### ADDENDUM

The excellent paper by Rosen and Patterson (1969) on the structure and relationships of paracanthopterygian fishes was received too late to be of use in the present study. The systematic results in both papers are mostly in agreement. Four differences are noted. One is the addition of gobioid fishes to the Paracanthopterygii. Rosen and Patterson state that they could not find any other group that should be included. Gobioids lack the caudal fin structure of percopsiforms but some (*Dormitator* and *Gunnellichthys*) have what may be a levator maxillae superioris muscle (W. Eschmeyer, unpublished information). So do the Sciaenidae, but here it is evidently convergent. The Gobiesocidae have neither of these features but are included by Rosen and Patterson on other evidence. The gobies qualify by the nerves and numerous other similarities to percopsids which together add weight to an argument for percopsid relationships. Another difference concerns the placement of the Amblyopsidae. Rosen and Patterson put them in the same suborder with the Aphredoderidae. The occurrence of the same unique pattern of RLA in both the Amblyopsidae and Percopsidae, and of a very different pattern in *Aphredoderus* resembling those of other paracanthopterygians and of acanthopterygians, would seem to outweigh the similarities Rosen and Patterson used for their placement of amblyopsids. The question needs further study. Maybe no suborders are needed here. Another difference concerns the origin of the Paracanthopterygii, needless to say a difficult question on which to have good information. In the present paper an osmerid ancestry is hypothesized for the percopsiforms. Rosen and Patterson thought (as of going to press in 1969) that important parallel developments of myctophoids to paracanthopterygians and acanthopterygians do not indicate that paracanthopterygians originated from myctophoid fishes. They give these three groups superordinal rank representing three "parallel radiations into a neoteleostean grade" (Rosen and Patterson, 1969). They state further that "poly-

mixioids can tentatively be viewed as the closest relatives of the paracanthopterygians." Figure 20 of the present paper agrees in general with their superordinal relationships but it shows a percopsiform ancestry for the acanthopterygii and an osmerid ancestry for the percopsid fishes. Nerve evidence and an intuitive finger point in an osmerid direction. In the search for percopsiform ancestors the guidelines of levator maxillae superioris muscle and percopsiform caudal fin structure break down. New guidelines have to be looked for and followed. These at present are nerves. An exciting problem emerges as to what living fishes may be closest to the ancestors of the percopsids.

A final point of difference to be mentioned is that Rosen and Patterson suggest that primitive percopsiforms had sensory head canals enclosed in bone and spinous suborbitals and preopercle and that these features were reduced and lost in paracanthopterygian but not acanthopterygian derivatives. Their evidence for these assumptions is slim. An osmerid ancestry makes it unnecessary to build closed canals. None of the percopsiform fishes living or fossil, have enclosed canals except for a very small part at the posterior end of the supra-orbital canal in *Percopsis*. Osmerids have open canals in all bones; smooth suborbitals, lacrymal, and preopercle; an antorbital; an adipose fin; the ramus canalis lateralis system less specialized; and ventral segmental lateralis nerves less specialized than in *Percopsis*. Closed and spinous canals would have come afterward in percopsiform lines leading to beryciform fishes.

Evidence in support of the Paracanthopterygii is now substantial and comes from bones, muscle, nerves, and fossils. It provides new understanding of fish evolution. We should thank Dr. Rosen and his coworkers for their achievements.

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## LIST OF ABBREVIATIONS

- BBP.—branch from brachial plexus.  
BDL-L.—Baudelot's ligament.  
BLLOV.—branch to lateral-line nerve and opercular nerve of vagus.  
B-OCC-SP-CO.—branches to occipito-spinal complex.  
BVSr.—branch to ventral spinal ramus.  
CL.—cleithrum.  
CM.—cartilaginous membrane.  
DRSN.—dorsal ramus of spinal nerve.  
EFRN.—external fin-ray nerve.  
F-LAT-OR.—free, naked lateralis organ.  
FDR-OCC-SP.—first dorsal ramus of occipito-spinal complex.

- FR.—fin ray.  
 GG.—geniculate ganglion.  
 HYO.—hyomandibular.  
 IDR-OCC-SP-CO.—first dorsal ramus of occipito-spinal complex.  
 LLN.—lateral-line nerve.  
 NINTH.—glossopharyngeal nerve.  
 OBRN.—opercular branch from vagus nerve.  
 OCC-SP-N&G—occipito-spinal nerves and ganglia.  
 OP.—opisthotic.  
 PAR.—parietal.  
 PEC-PEL. ACC.—ventral pectoral-pelvic accessory lateral-line nerve.  
 PHBRV.—pharyngo-branchial nerves of vagus.  
 PP-ACC-LAT.—ventral, segmental accessory lateral-line nerves.  
 PRF.—prootic facial foramen shown as dashed black line medial to hyomandibular.  
 PRO.—prootic.  
 PTR.—pteroic bone.  
 PTR-SP.—pteroic spine.  
 PTT.—posttemporal.  
 RCIA.—supraorbital branch of ramus canalis lateralis system.  
 RCIB.—temporal branch of ramus canalis lateralis system.  
 RC2.—anterior infraorbital branch plus dorsoanterior dentary and rictus branches of ramus canalis lateralis system.  
 RC3, RC3A, RC3B.—posteroventral dentary branches plus rictus branches of ramus canalis lateralis system.  
 RC3C.—branch of ramus canalis lateralis system detaching from ramus opercularis superficialis facialis and extending to anteroventral area of preopercular canal membrane.  
 RC4, RC4A.—preopercular branch of ramus canalis lateralis system.  
 RC4B.—medial preopercular-mandibular ridge prolongation of RC4A.  
 RC5.—supratemporal branch of ramus canalis lateralis system.  
 RCL.—ramus canalis lateralis nerve.  
 R-HYO.—ramus hyoideus.  
 RLA.—ramus lateralis accessorius or recurrent facial nerve.  
 RLA-A.—branch of RLA to anal fin.  
 RLA-D.—branch of RLA supplying dorsal fin.  
 RLA-DFR.—branch of RLA to dorsal fin ray.  
 RLA-OCC-SP-CO.—branches of RLA to occipito-spinal complex.  
 RLA-P.—branch of RLA to pectoral fin.  
 RLA-PDA.—a main branch of RLA extending from parietal to dorsal fin.  
 RLA-PEL.—branch of RLA to pelvic fin.  
 RLA-PP.—a main division of RLA extending from parietal bone to pectoral and pelvic fins.  
 RLA + SYM.—common trunk of RLA + sympathetic.  
 RLA + SYM-DASH.—ramus lateralis accessorius plus sympathetic common trunk shown as dashed black line medial to hyomandibular.  
 RLA-THYO—a main division of RLA extending from prootic foramen to pectoral and pelvic fins.  
 R-MAN-EX.—ramus mandibularis externus.  
 R-MAN-IN.—ramus mandibularis internus.  
 SPH.—splenic.



SPN.—spinal nerve.

SUPCL.—supracleithrum.

SYM.—sympathetic trunk.

SYM-G.—sympathetic ganglion.

TR-COM-SYM.—transverse commissure of sympathetic.

TR-HYO.—truncus hyomandibularis.

VR-OCC-SP-CO.—ventral ramus of occipito-spinal complex

VSN.—branch of ventral spinal nerve.

VSR.—ventral spinal ramus.