

Study of the Monotypic  
Fish Family Pholidichthyidae  
(Perciformes)

VICTOR G. SPRINGER  
and  
WARREN C. FREIHOFER

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 216

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## ABSTRACT

Springer, Victor G., and Warren C. Freihofer. Study of the Monotypic Fish Family Pholidichthyidae (Perciformes). *Smithsonian Contributions to Zoology*, number 216, 43 pages, frontispiece, 23 figures, 1976.—Aspects of the osteology, cranial nerves 5, 7, 9 and 10, lateral-line canals, free lateralis organs and miscellaneous anatomical features of *Pholidichthys leucotaenia* (the only species in the Pholidichthyidae) are described and illustrated.

*Pholidichthys* is known only from the western Pacific Ocean, from the Philippines east to the Solomon Islands. It has an eel-like body form and undergoes striking ontogenetic changes in color pattern. Anatomically the species is most notable for having an autogenous, unpaired ossification of the interorbital septum (which is not a modified orbitosphenoid); no ascending process on the parasphenoid; a large complex metapterygoid; fused 5th ceratobranchials (at sizes at least as small as 16.9 mm); a sagittal sulcus with the ostium completely separated from the cauda by a raised area; an incomplete, disjunct ring of infraorbital bones and interrupted infraorbital sensory canal; no scales; no spines in the vertical fins; apparent displacement dorsally and freeing of the lateralis organs (innervated by the ramus buccalis facialis) of the infraorbital canal in the gap area and partial invasion of the gap by free lateralis organs innervated by the ramus buccalis accessorius facialis of the truncus hyomandibularis; presence of free lateralis organs along the horizontal septum anteriorly ventral to the dorsal collector lateral-line nerve; *Serranus* pattern (pattern 9) of the recurrent facial nerve; return of the dorsal collector lateral-line nerve to the horizontal septum at a point above, or near, the anus; only two dorsal collector rami joining the dorsal longitudinal lateral-line nerve; an extremely heavy innervation of the conjunctiva of the eye; a single nostril on each side.

Based on its pattern 9 recurrent facial nerve, *Pholidichthys* is a perciform fish and within that grade is highly specialized. With the possible exception of two specializations concerning the dorsal longitudinal lateral-line nerve (point of return to the horizontal septum; number of collector rami), which *Pholidichthys* shares only with the tropical blennioids, there is no unequivocal conclusion that can be drawn about its subordinal relationships. The osteological evidence does not indicate a close relationship with the tropical blennioids.

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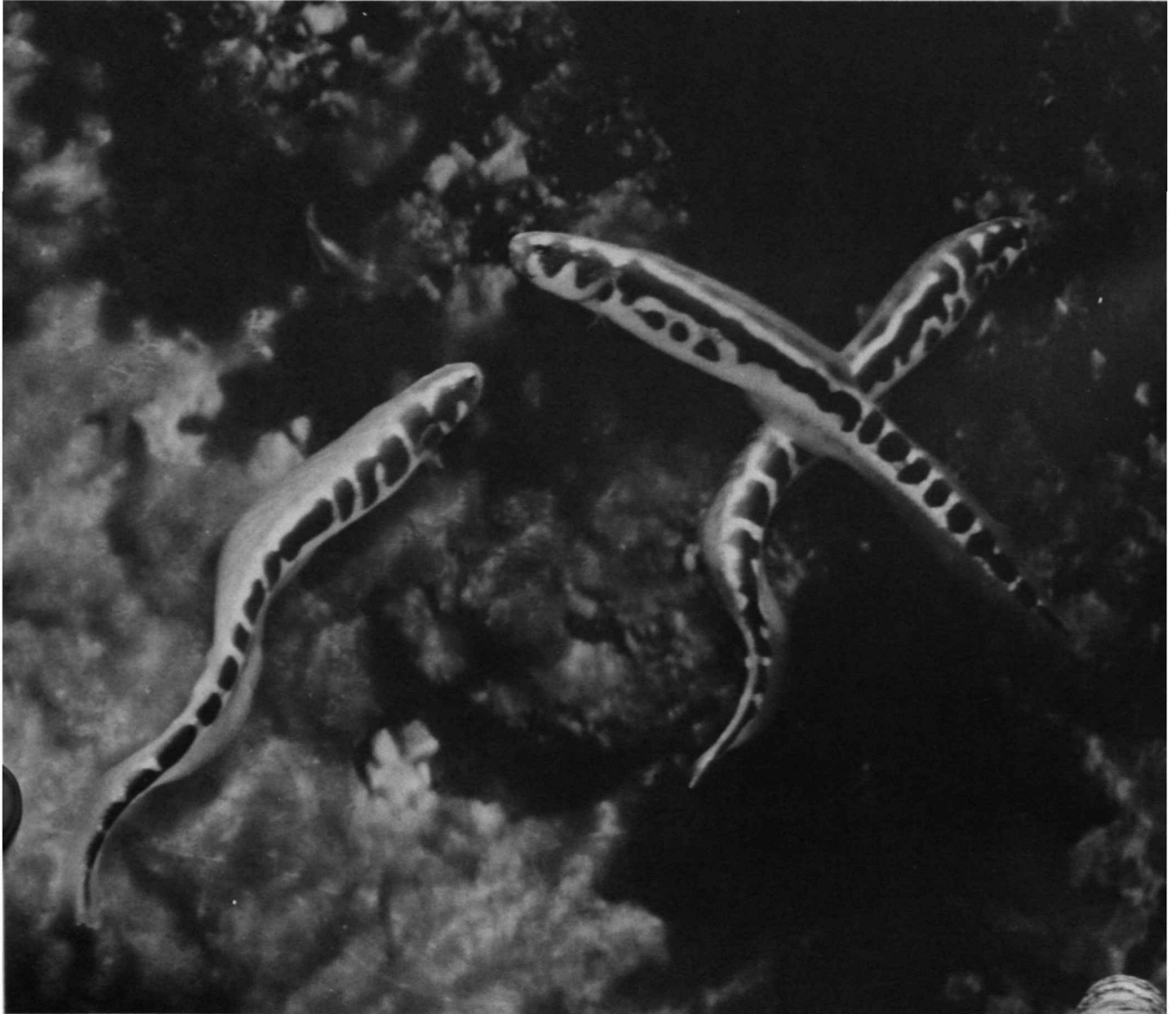
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*Pholidichthys leucotaenia*, photographed in aquarium.  
(Courtesy of T. F. H. Publications, Inc.)

# Study of the Monotypic Fish Family Pholidichthyidae (Perciformes)

*Victor G. Springer*  
and *Warren C. Freihofner*

## Introduction

The family Pholidichthyidae comprises a single species, *Pholidichthys leucotaenia* Bleeker.<sup>1</sup> Until recently (Kailola, 1973), this species was known in the scientific literature from only three juvenile specimens (Bleeker, 1856; Herre and Herald, 1951). The lack of specimens for detailed study probably contributed to the present confusion surrounding the familial placement and relationships of *Pholidichthys*. About 1968, specimens of *Pholidichthys* were first imported into the United States by the aquarium industry (Michaelis, 1972). Most, if not all, of these specimens were juveniles and seem to have been confused by the importers with cleaner wrasses (*Labroides dimidiatus*) and reef

catfishes (*Plotosus lineatus*) with which they apparently had been caught. The geographic origin of the aquarium specimens is not clear, but aquarium dealers report that they received the specimens from suppliers in the Philippines. The verified distribution of *Pholidichthys* (Figure 1: we have accepted Herre and Herald's, 1951, Philippine record, although we have not seen their specimens, which apparently are lost) does include the southwesternmost of the Philippine Islands, and we have been told by Philippine aquarium exporters that it occurs as far north as Calatagan, Batangas Province. In any event, a reasonably large number of *Pholidichthys* specimens found their way into the hands of ichthyologists by way of aquarium dealers. In some instances aquarium specimens were maintained alive, and a record of their growth and radical ontogenetic changes in color pattern were documented in the aquarium literature (Michaelis, 1972; Brittan, 1972).

During 1970, the Steinhart Aquarium obtained a large series of live young *Pholidichthys*, which were put on display. Freihofner observed these individuals as they grew and changed color pattern and decided that a description of these changes, which had not been reported in the scientific literature, and the nerve patterns of the species were desirable. In 1971, Craig Phillips, then with the National Aquarium, gave Springer a large aquarium specimen of *Pholidichthys* for identification. Initially, Springer believed that *Pholidichthys* might be related to the blennioids and he, thus,

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<sup>1</sup> Lockington (1882) described *Pholidichthys anguilliformis* from a single specimen from the Gulf of California. No additional specimens have been reported, and the location of the holotype (Academy of Natural Sciences of Philadelphia 10843) has been unknown for many years (Smith-Vaniz, in litt.). Lockington reported that there were only spines (more than 60) in the dorsal fin, and thus it seems unlikely that his generic allocation was correct. Jordan (1887), Jordan and Evermann (1896, 1898), Jordan, Evermann and Clark (1930), and Fowler (1944) all listed *P. anguilliformis* based on Lockington.

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*Victor G. Springer, Division of Fishes, National Museum of Natural History, Washington, D.C. 20560. Warren C. Freihofner, Department of Ichthyology, California Academy of Sciences, San Francisco, California 94118.*

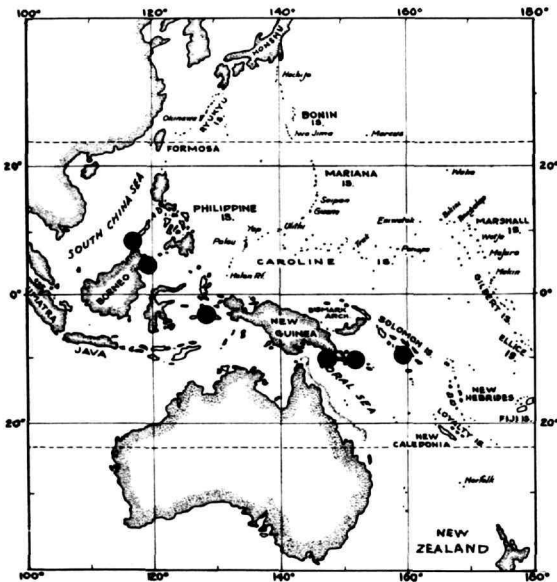


FIGURE 1.—Distribution of *Pholidichthys leucotaenia*.

became interested in investigating its relationships in more detail. On learning of our mutual interests in *Pholidichthys*, we decided to pool our efforts in the investigation of this interesting fish.

**METHODS.**—The three specimens (16.9, ca. 70, ca. 140 mm standard length) used for the osteological description of *Pholidichthys* were cleared and stained using Taylor's (1967) trypsin technique. The two largest specimens lacked the last few vertebrae. All of the osteological illustrations, except that of the caudal fin (Figure 11), are based on the 140 mm specimen. The caudal fin was illustrated from a radiograph of a larger specimen (CAS 32048). Base drawings of the bones in the other illustrations were made by Springer using a Wild M5 stereomicroscope with camera lucida attachment. The final drawings were inked, contoured, and labeled by J. R. Schroeder under Springer's supervision. Cartilage is indicated on these drawings by the use of small, open circles (for example, see rostral cartilage on Figure 5). Osteological features on the 140 mm specimen were checked for consistency with the two smaller specimens. Vertical-fin ray and vertebral counts were taken from radiographs and, as possible, from the cleared and stained specimens.

The five specimens (111–150 mm SL) used for the description of the nerves of *Pholidichthys*

were cleared and stained by the Sihler technique (Williams, 1943; Freihofer, 1966; Fraser and Freihofer, 1971). The nerve illustrations were drawn by Freihofer.

**ABBREVIATIONS.**—AMNH = American Museum of Natural History; ANSP = Academy of Natural Sciences of Philadelphia; BPBM = Bernice P. Bishop Museum; CAS = California Academy of Sciences; NMNH = National Museum of Natural History, Smithsonian Institution; USNM = former United States National Museum (specimens in NMNH); SL = standard length.

**MATERIAL OF *Pholidichthys*.**—The two largest cleared and stained specimens used for the bone descriptions (USNM 206237) were aquarium specimens of unknown origin. The smallest specimen (out of USNM 212162) was from Darvel Bay, Borneo. The five specimens used for the nerve descriptions were all aquarium specimens (CAS 32048).

Other aquarium specimens (preserved) examined included: USNM 212163 (1: 337 mm), USNM uncataloged (1: 205 mm), CAS 32048 (9: 58–275). Specimens examined from known localities include: BPBM 15667 (3: 18–19 mm SL), Florida Island, Solomon Islands; BPBM 15688 (7: 45–49), Guadalcanal, Solomon Islands; BPBM 15916 (4: 34–40), Port Moresby, New Guinea; USNM 212162 (6: 15–18), Darvel Bay, Borneo; BPBM 18050 (5: 87–94), Ambon, Indonesia.

Live specimens at the Steinhart Aquarium (CAS) were the basis for our observations on behavior.

**COMPARATIVE MATERIAL FOR STUDY OF BONES.**—Many diverse fishes were examined, including whole specimens, partial dissections, radiographs of specimens, disarticulated skeletons (USNM), and cleared and stained specimens. In addition, numerous published osteologies of fishes, which are not cited, were referred to. Only the cleared and stained specimens of perciforms are listed here.

**ACANTHOCLINIDAE:** *Acanthoclinus* sp., USNM 200546; *Belonepterygion fasciolatum*, USNM 211306. **ALABETIDAE:** *Alabes rufus*, USNM 201415. **AMMODYTIDAE:** *Ammodytes americanus*, USNM 189223. **BATHYMASTERIDAE:** *Ronquilus* sp., USNM 214099. **BATRACHOIDIDAE:** *Opsanus beta*, USNM 104906; *Porichthys porosissimus*, USNM uncataloged; *Thalassophryne maculosa*, USNM 200558. **BLENNIIDAE:** (see Springer, 1968). **BOVICHTHYIDAE:** *Bovichthys variegatus*, USNM 213829. **BROTULIDAE:** *Bidenichthys*

*capensis*, USNM uncataloged; *Dinematichthys* sp., USNM uncataloged. CALLIONYMIDAE: *Synchiropus ocellatus*, *S. splendidus*, both USNM uncataloged. CARACANTHIDAE: *Caracanthus unipinnis*, USNM 214028. CEPOLIDAE: *Cepola pauciradiata*, USNM 213502. CHAENOPSIDAE: (see Springer, 1968). CHAMPSODONTIDAE: *Champsodon capensis*, USNM uncataloged. CHEIMARRICHTHYIDAE: *Cheimarrichthys fosteri*, USNM 214024. CICHLIDAE: *Cichlasoma cyanoguttatum*, USNM 213531. CLINIDAE: (see Springer, 1968). CONGROGADIDAE: *Blennodesmus scapularis*, USNM 205026; *Congrogadus subducens*, USNM 173804; *Haliophis guttatus*, USNM 212290. COTTIDAE: *Cottus bairdi*, USNM 193153; *Myoxocephalus aeneas*, USNM uncataloged. CYCLOPTERIDAE: *Liparis koefoidi*, USNM 157704. DACTYLOSCOPIDAE: *Dactylagnus mundus*, USNM uncataloged; *Dactyloscopus tridigitatus* CAS SU22155. GADIDAE: *Rhinonemus cimbricus*, USNM uncataloged; *Urophycis tenuis*, USNM 200115. GOBIESOCIDAE: *Trachelochismus pinnulatus*, USNM uncataloged. GOBIIDAE: *Awaous tajassica*, USNM 213491. HEXAGRAMMIDAE: *Hexagrammos decagrammus* USNM 104656. KRAEMERIIDAE: *Kraemia bryani*, USNM 143153. LABRIDAE: *Labrichthys unilineatus*, USNM 208451; *Pseudolabrus japonicus*, USNM 208589; unidentified post larvae, USNM uncataloged. LEPTOSCOPIIDAE: *Leptoscopus macropygus*, USNM 213490. MELANONIDAE: *Melanonus* sp., USNM uncataloged. MACROURIDAE: *Bathygadus macrops*, USNM 202778; *Steindachneria* sp., USNM 186365. MASTACEMBELIDIDAE: *Mastacembelus armatus*, AMNH 10274. MORIDAE: *Lotella fernandeziana*, USNM uncataloged. MUGILOIDIDAE: *Parapercis cephalopunctata*, USNM 140786. NOTOGRAPTIDAE: *Notograptus guttatus*, USNM 173798. OPHIDIIDAE: *Ophidion holbrookii*, USNM 196039. OPISTHOGNATHIDAE: *Opisthognathus aurifrons*, ANSP 94307; *O. maxillosus*, ANSP 120715; *O. whitehursti*, ANSP 120714; *Stalix moenensis*, USNM 211963. PHOLIDAE: *Xerorpes fucorum*, CAS 27861. PLESIOPIDAE: *Plesiops caeruleopunctatus*, USNM 211304. POMACENTRIDAE: *Abudefduf saxatilis*, USNM 192029. PSEUDOCROMIDAE: *Pseudochromis flavivertex*, USNM 211305. SCIAENIDAE: *Aplodinotus grunniens*, USNM 172278; *Pogonias cromis*, USNM uncataloged. SCORPAENIDAE: *Setarches guentheri*, USNM 157704. SCYTALINIDAE: *Scytalina cerdale*, USNM 213832. STICHAEIDAE: *Chirolophis nugator*, CAS 30962; *Poroclinus rothrockii*, CAS 15099; *Lumpenella longirostris*, USNM 213535; *Lumpenus medius*, USNM 213534; *Ulvaria subbifurcata*, USNM 201949; *Xiphister mucosus*, USNM 213533. SYNBRANCHIDAE: *Synbranchus marmoratus*, USNM 213805. SYNANCIIDAE: *Synanceia verrucosa*, USNM 149901. TRACHINIDAE: *Trachinus draco*, USNM 201573. TRICHODONTIDAE: *Trichodon trichodon*, USNM 213532. TRICHONOTIDAE: *Crystallodytes enderburyensis*, USNM 202584. TRIPTERYGIIDAE: *Forsterygium varium*, USNM 204997 (see also Springer, 1968). URANOSCOPIIDAE: *Astroscopus y-graecum*, USNM 185669; *Kathetostoma albigutta*, USNM 185666; *Uranoscopus scaber*, USNM 198087. ZOARCIDAE: *Lycodes turneri*, USNM 165153.

COMPARATIVE MATERIAL FOR THE STUDY OF NERVES (unless noted otherwise, the material is

CAS uncataloged).—

APHREDODERIDAE: *Aphredoderus sayanus*. APOGONIDAE: *Apogon atradorsatus*. ARRIPIDAE: *Arripis georgianus*. ATHERINIDAE: *Atherinops affinis*. BATRACHODIDAE: *Porichthys notatus*. BLENNIIDAE: *Entomacrodus caudofasciatus*, *Salarias fasciatus*. CALLIONYMIDAE: *Synchiropus splendidus*. CHAETODONTIDAE: *Chelmon rostratus*. CIRRHITIDAE: *Cirrhites rivulatus*. CLINIDAE: *Gibbonsia metzi*, *Malacoctenus zonifer*, *Neoclinus blanchardi*. CORYPHAENIDAE: *Coryphaena hippurus*. COTTIDAE: *Scorpaenichthys marmoratus*. DACTYLOSCOPIDAE: *Gillellus rubellulus*, CAS 32306. GASTEROSTEIDAE: *Gasterosteus aculeatus*. GOBIESOCIDAE: *Gobiesox maeandricus*. GOBIIDAE: *Bathygobius lineatus*, *Gobiodon histrio*, *Gobionellus* sp. HOLOCENTRIDAE: *Holocentrus* sp. KUHLIIDAE: *Kuhlia rupestris*. KYPHOSIDAE: *Kyphosus analogus*. LABRIDAE: *Labroides dimidiatus*, *Lepidaplois mesothorax*, *Novaculichthys taeniorurus*. LOBOTIDAE: *Datnioides microlepis*. LUTJANIDAE: *Lutjanus vaigiensis*. MALACANTHIDAE: *Malacanthus nordtii*. MASTACEMBELIDAE: *Mastacembelus* sp. MERLUCIIDAE: *Merluccius productus*. MONODACTYLIDAE: *Monodactylus argenteus*. MORIDAE: *Physiculus talarae*. MUGILIDAE: *Xenomugil thoburni*, CAS 14407. MUGILOIDIDAE: *Parapercis cylindrica*. OGCOEPHALIDAE: *Zalieutes elater*. OPHIDIIDAE: *Brotula clarkae*, *Dicrolene intronigra*, *Lepophidium prorates*. PERCICHTHYIDAE: *Morone saxatilis*. PERCOPSIDAE: *Percopsis omiscomaycus*. POLYCENTRIDAE: *Polycentrus schomburgkii*. POLYNEMIDAE: *Polydactylus approximans*. POMACANTHIDAE: *Holacanthus tricolor*. POMADASYIIDAE: *Plectorhynchus chaetodontoides*. PHOLIDAE: *Apodichthys flavidus*, *Xerorpes fucorum*. PRISTOLEPIDAE: *Pristolepis fasciatus*, CAS 32307. RACHYCENTRIDAE: *Rachycentron canadum*. SALMONIDAE: *Oncorhynchus tshawytscha*. SCIAENIDAE: *Larimus pacificus*. SCORPAENIDAE: *Pterois antennata*, *Sebastes* sp. SIGANIDAE: *Siganus guttatus*. SPHYRAENIDAE: *Sphyraena barracuda*. TRYPAUCHENIDAE: *Ctenotrypauchen microcephalus*. ZOARCIDAE: *Lycodopsis pacifica*.

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### Synonymy

There are no junior synonyms of *Pholidichthyidae*, *Pholidichthys* or *P. leucotaenia*. We have, therefore, lumped all references to these taxa in the synonymy that follows, which purports to be complete:

*Pholidichthys leucotaenia* Bleeker, 1856 [description of genus and species; Kajeli, Boeroe].—Troschel, 1857 [listed].—Bleeker, 1857 [listed]; 1859 [listed]; 1865 [listed].—Günther, 1861 [based on Bleeker].—Jordan, 1887 [based on Bleeker].—Jenkins and Evermann, 1889 [similar to *Pseudoblennius*].—Jordan and Evermann, 1896 [listed].—Jordan and Evermann, 1898 [genus based on Bleeker; *Pholidichthyinae*].—Boulenger, 1904 [listed, misspelled].—Weber, 1913 [based on Bleeker].—Jordan, 1919 [listed]; 1923 [included in *Chaenopsidae*].—Jordan, Evermann, and Clark, 1930 [listed].—De Beaufort, 1951 [holotype redescribed, figured, *Pholidichthyidae*].—Herre and Herald, 1951 [Candaraman Bay off Albay Island, Philippines; description].—Herre, 1953 [listed].—Gosline, 1955 [excluded from gobioids by inference].—Norman, 1966 [included in *Blenniidae incertae sedis*].—Greenwood et al., 1966 [synonym of *Microdesmidae*].—Schultz, 1966 [redescription of holotype; dentition figured; classification].—Lindberg, 1971 [included in *Microdesmidae*].—Michaelis, 1972 [color pattern, aquarium behavior, photograph of adult].—Brittan, 1972 [color pattern, aquarium behavior, photographs of juveniles and adult].—Burgess and Axelrod, 1972 [Philippine Islands, photograph of juveniles]; 1973 [photographs of juveniles and adults].—Kailola, 1973 [Yule Island, Samarai, and Port Moresby, Papua; description, photograph, illustrations].—Miller, 1973 [placed in *Microdesmidae*].—Frehofer and Lin, 1974 [placed in superfamily *Blennioidea*]. See also footnote 1.

### Descriptions of the Bones

**THE CRANIUM** (Figures 2 and 3).—Anteriorly, there is a large mass of ethmoid cartilage, which is bordered dorsoanteriorly by the median ethmoid, ventrally by the vomer, laterally by the lateral ethmoids, and posteriorly by the septal bone. The anteriormost portion of the ethmoid cartilage is not sheathed by bone, nor is a small, slender section that reaches the dorsal surface of the cranium between the anterior ends of the frontals. The cartilage is continuous posteriorly as the interorbital septum, which extends below the septal bone and above the parasphenoid, and envelops a low, long, thin dorsomedian crest on the parasphenoid. The ethmoxillary ligament originates dorsolaterally on the median ethmoid and inserts on the maxillary in the region of the maxillopalatine articulation.

The septal bone is an unpaired, median ossification of the interorbital septum. Anteriorly the bone bifurcates laterally into two thin flanges that embrace the posterior portion of the ethmoid cartilage. Dorsally the septal bone joins, and is slightly overlapped on each side by, the frontals. The septal bone extends ventroposteriorly as a ventrally open, trough-shaped arm whose posterior end is sheathed dorsally by the anterior end of the basisphenoid.

In the 16.9 mm SL juvenile with a skull length of 4 mm, the septal bone consists of a small, unpaired, thin, bladelikey island of bone in the cartilage of the interorbital septum, with the posterior margin of the bone bordered by the anterior margin of the membranous portion of the interorbital septum.

The lateral ethmoid bears two thin, internal processes, dorsal and ventral, that abut on the anterolateral surface of the septal bone. The lateral ethmoid is perforated anteromedially by a large canal (anterior myodome) into which the superior and inferior oblique muscles of the eye enter and attach, and through which the olfactory tract passes. Medially, the lateral ethmoid also joins the frontal, median ethmoid, ethmoid cartilage and vomer.

The most noteworthy feature of the frontal is an irregular, dorsally open trough on its dorsoanterior surface, along which the supraorbital sensory canal passes. Posteriorly, the frontal overlaps

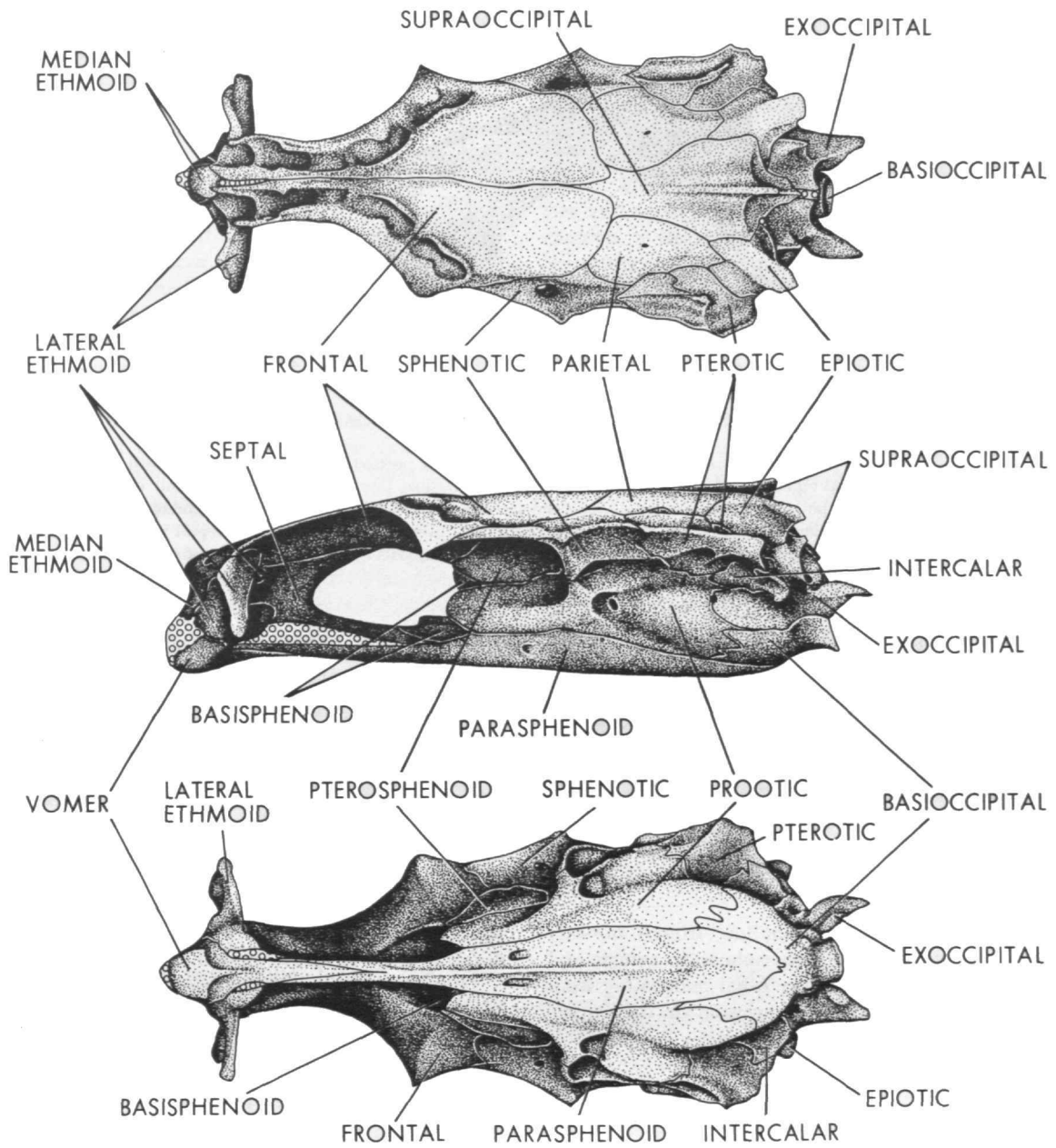


FIGURE 2.—*Pholidichthys leucotaenia*: dorsal, lateral, and ventral views of skull.

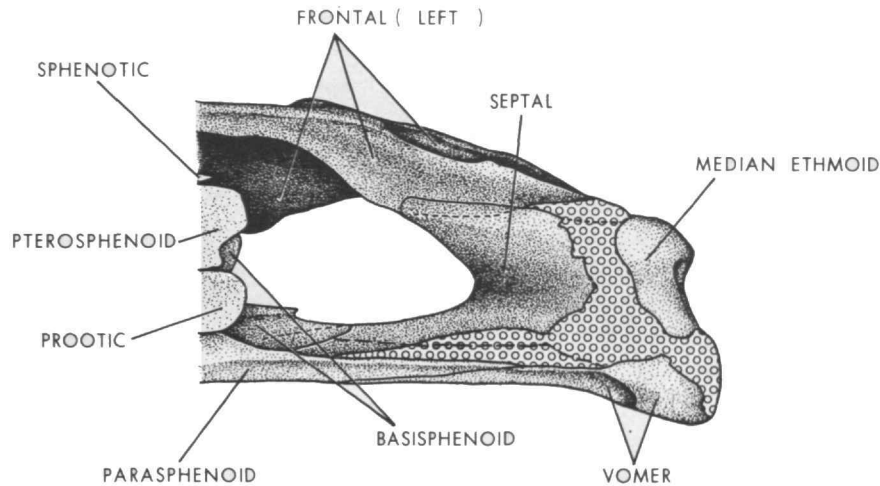


FIGURE 3.—*Pholidichthys leucotaenia*: lateral view of anterior portion of right side of skull with right lateral ethmoid and right frontal bones removed. Dashed line dorsally represents limit of left frontal bone overlapped by septal bone and cartilage; dashed line ventroanteriorly represents limit of median dorsal crest on parasphenoid overlapped by ventroposterior arm of septal bone and cartilage of interorbital septum; dashed line dorsoposteriorly represents limit of septal bone overlapped by basisphenoid.

flanges of the sphenotic, parietal, supraoccipital, and pterospheoid; medially it abuts against, but does not overlap, its fellow on the opposite side.

The sphenotic bears a shallow trough dorsally, along which the unroofed (by bone), autogenous dermosphenotic loosely attaches. A large fenestra completely penetrates the sphenotic at about the center of the trough. Ventrally the sphenotic contributes to the dorsal portion of the socket into which the anterior condyle of the hyomandibular inserts.

The pterotic bears a shallow trough dorsally that is continuous with the sphenotic trough and which underlies the sensory canal continuing from the sphenotic. A shallow depression on the ventrolateral surface of the pterotic serves as the point of attachment of the posterodorsal condyle of the hyomandibular.

The parietals are completely separated by the low-crested supraoccipital. Each parietal is perforated by a small centrally located foramen through which the recurrent facial nerve passes and extends to the dorsal fin.

The exoccipitals are separated ventrally by the basioccipital and dorsoanteriorly by the supra-

occipital. They form a narrow synchondral joint dorsoposteriorly. Just dorsoanteriorly to the exoccipital condyle is a foramen for passage of the occipital nerves (Figure 2, lateral view, not labeled). The vagal foramen is present in the exoccipital just posterior to the posterior end of the intercalar (Figure 2, ventral view, not labeled) and the glossopharyngeal foramen lies in the joint between the prootic and exoccipital (Figure 2, lateral view, not labeled).

The epiotic bears a rather large articulating surface dorsally, which joins the ventral surface of the dorsal arm of the posttemporal.

The intercalar overlies portions of the prootic, pterotic, and exoccipital. Posteriorly, the intercalar bears a thickened ridge, which serves as the point of attachment for the ligament that inserts on the ventral arm of the posttemporal.

The prootic is quite large and extends for two-thirds the postorbital length of the cranium. In the medial wall of the pars jugularis, the prootic bears two foramina, through which the V-VII complex of nerves passes. The larger (anterior) of the two foramina is occluded from lateral view by the lateral wall of the pars jugularis. The larger

foramen is not (yet) completely bordered by bone anteriorly in the 70 mm specimen. The prootic contributes the ventral portion of the socket with which the anterior condyle of the hyomandibular articulates; the dorsal portion is formed by the sphenotic. The prootic does not have a ventromedially projecting flange and, hence, does not contribute to the osseous roof of the posterior myodome. The prootic and pterosphenoid enter the orbital region of the skull without restriction as there is no ascending process on the parasphenoid; however, there is a low ascending parasphenoid process, which partially borders the prootic, in the 70 mm specimen.

The parasphenoid extends for most of the skull length. On its dorsal surface, from the region overlapped by the belophram of the basisphenoid to a point just posterior to the region of the broad anterior end of the vomer, the parasphenoid bears a low, thin median crest that is completely enveloped by the cartilage of the interorbital septum (Figure 3). At about its midlength, the parasphenoid bears a foramen (on each side) that leads to a canal that opens internally between the parasphenoid and basisphenoid (internal carotid foramen). Posteriorly, the parasphenoid overlaps the median anterior portion of the basioccipital.

Laterally and dorsally, for about three-fourths its length, the toothless vomer is overlapped by the parasphenoid. Dorsolaterally, on each side, the vomer bears a flange that joins the lateral ethmoid posteriorly and anteriorly cups the ventral portion of the ethmoid cartilage.

The basioccipital is relatively short. It bears the concave articulating surface that joins the centrum of the first vertebra. This surface is well separated from the exoccipital condyles. Just anterior to the basioccipital concave surface and ventrolaterally on each side, the basioccipital bears a low, knob-like process on which Baudelot's ligament originates. The ligament inserts on the dorsoanterior internal surface of the cleithrum.

The basisphenoid is a complex bone. It bears a broad, dorsolaterally extending wing (meningost) on each side of its median, anteriorly and ventrally extending portion (belophram), which overlaps the posterior end of the septal bone. The meningosts articulate dorsally with the pterosphenoids and posteroventrally with the parasphenoid. Ventrally, each meningost forms a narrow, medially

extending projection that meets its fellow at the midline of the skull just ventral and posterior to the belophram. In so doing, the meningosts create a small foramen between themselves and the belophram, and a narrow, roofing shelf over the parasphenoid. The only osseous contributions to the roof of the posterior myodome are derived from the meningosts (the wings and medial projections). The posterior extent of the myodome was not determined, but appears to lie within the cranium a short distance posterior to the medial projections of the meningosts, and well in advance of the anterior end of the basioccipital (there is no passageway for the eye muscles from the inside to the outside of the cranium via the ventral surface of the basioccipital, as occurs in some fishes).

The sagitta (Figure 4) has roughly parallel dorsal and ventral margins; its posterior end is evenly rounded except for minor irregularities; its rostrum is short and bluntly pointed. The antirostrum scarcely projects. The medial and lateral surfaces of the sagitta are convex, and the lateral surface has a small, rounded depression slightly in advance of its midlength, but is otherwise lacking in distinctive features. The sagitta is narrowly ellipsoidal in cross section. The sulcus is slightly sigmoidal with the ostium and cauda separated by a raised central portion. The ostium is a flat-bottomed channel, widest anteriorly, converging posteriorly, and the cauda is a round-bottomed trough, widest posteriorly, and terminating more than a sulcus width in advance of the posterior end of sagitta. The crista superior is moderately strong, and most prominent between the midpoints of the ostium and cauda. Measurements (in mm) of right sagittae from three individuals are:

	1*	2*	3
Fish length	not taken	not taken	ca. 140
Sagitta length	2.75	2.06	2.69
Sagitta height	1.31	1.01	1.30
Sagitta thickness	0.70	0.57	0.65
Ostium length	1.10	0.83	1.05
Cauda length	0.85	0.65	0.99
Sulcus length	2.35	1.70	2.47

\* Data furnished by John E. Fitch.

**SUPERFICIAL BONES, JAWS, AND SUSPENSORIUM** (Figure 5).—There are four infraorbital bones. These are thin and unroofed (by bone), and none is in bony contact with another. The lacrymal articulates loosely with a facet on the lateral ethmoid.

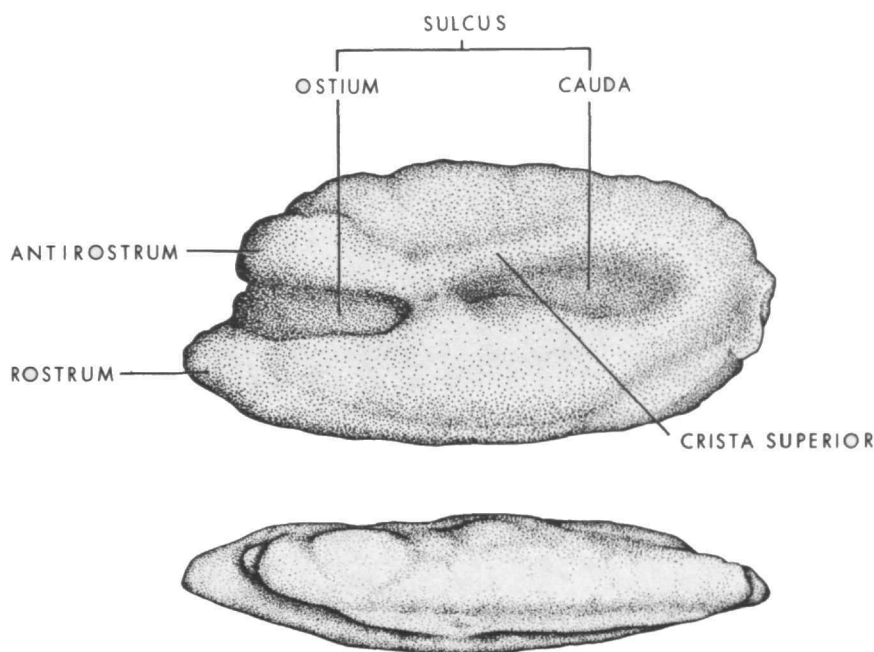


FIGURE 4.—*Pholidichthys leucotaenia*: medial and dorsal views of right sagitta.

The next two infraorbitals posteriorly are suspended in the skin and neither bears a subocular shelf. The infraorbital sensory canal passes along these three bones. The dorsalmost infraorbital is well separated from the others, lies in the skin, and is loosely connected dorsally to the frontal, dermosphenotic and sphenotic. The infraorbital sensory canal is interrupted between the third and the dorsalmost infraorbital. The canal passes along the dorsalmost infraorbital and is continuous with the supraorbital canal anteriorly and the canal of the autogenous dermosphenotic posteriorly. On the left side of the illustrated specimen, there is a minute osseous inclusion between the second and third infraorbitals. The inclusion is not present on the right side or on either side of the 70 mm specimen.

The nasal bone is a thin, trough-shaped bone with a nonstaining ventral portion. The sensory canal that passes along the nasal bone is continuous with the anterior end of the supraorbital canal.

There are two trough-shaped extrascapulars (on each side), which lie loosely in the skin, perpendicular to each other and dorsal to the pterotic

and epiotic. The medial extrascapular is widely separated from its fellow on the opposite side of the skull, and there is no supratemporal commissural sensory canal between the medial extrascapulars. The sensory canals of the medial and lateral extrascapulars are continuous via the sensory canal that passes along the pterotic.

The premaxillary bears a relatively high ascending process (hidden from view by the nasal bone in Figure 5). The large, unpaired rostral cartilage is attached to the posterior surface of the ascending process and the palatopremaxillary ligament inserts on the dorsal end of the process. The teeth are caniniform, slightly compressed, and with slightly recurved tips. In specimens 140 mm and larger there is an outer row of teeth, which decrease in size posteriorly, on the outer margin of the premaxillary, and an inner row of smaller teeth posterior to the outer largest teeth. In specimens up to about 100 mm, the teeth on the lateral margin of the premaxillary are arranged in three rows. The teeth in the anteriormost row are the largest of the three rows and this row overlaps the anterior end of the next row of teeth, which are slightly

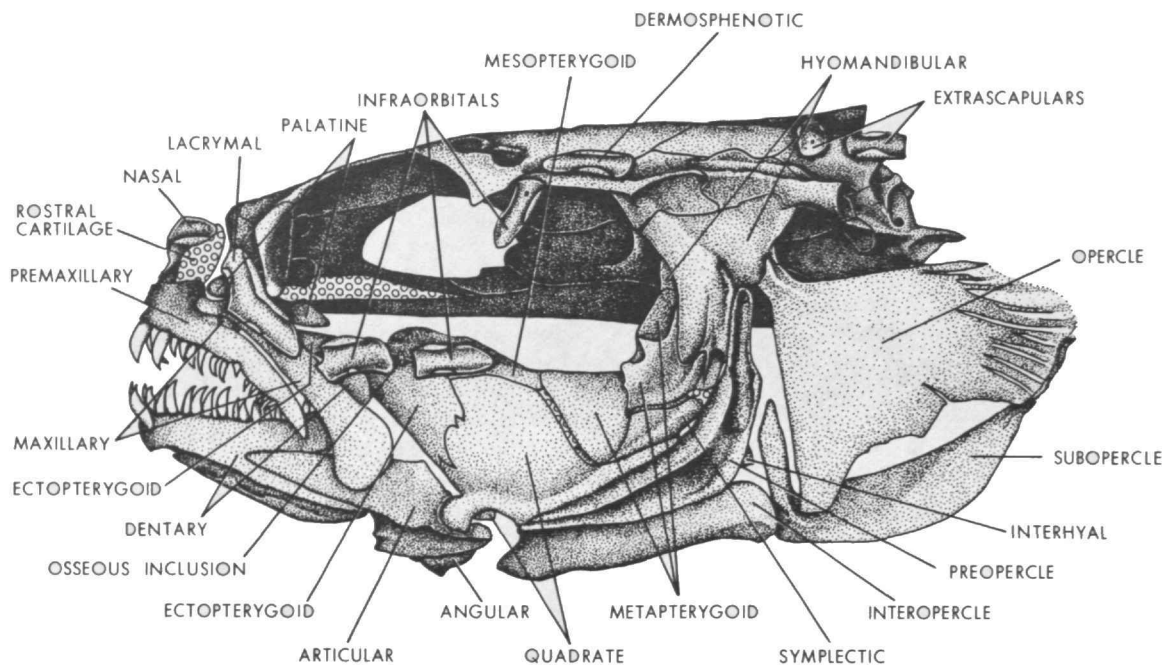


FIGURE 5.—*Pholidichthys leucotaenia*: lateral view of skull and superficial bones.

smaller. The second row of teeth overlaps the anterior end of the third row, which is formed by the smallest teeth. Anteriorly on the premaxillary are several teeth, the largest, and just behind these large teeth is an irregular row of very small teeth. The arrangement of the teeth in juveniles has been illustrated by Schultz (1966, fig. 133) and Kailola (1973, fig. 1).

The dentary forms an open, lengthwise trough ventrolaterally, along which the anterior portion of the mandibular sensory canal passes. The canal is continuous with that of the opposite dentary and the two canals open by a common pore at the symphysis. At its posterior end, the dentary forms a triangular pocket, open laterally, closed medially, into which the anterior end of the articular inserts. The dentary teeth are similar in shape to the premaxillary teeth. There is an outer row of teeth, which increase in size as one progresses anteriorly, except that the two anteromedialmost teeth (possibly atypical) are abruptly smaller. There is a second row of smaller teeth anteriorly behind the largest teeth, and a third, inner row consisting of only one or two small teeth. The disposition of the

dentary teeth in small specimens is similar to that described above for the premaxillary (disposition of dentary teeth in juveniles is illustrated by Schultz 1966, and Kailola, 1973).

The articular bears an open trough ventrolaterally along which the posterior portion of the mandibular sensory canal passes. There is a small, irregularly shaped sesamoid articular (coronomeckelian) on the posteroventral medial surface of the dentary (not illustrated).

The toothless palatine has a facet dorsally at the point where the anterolaterally extending arm, which overlaps the anterior end of the maxillary, joins the internal, posteriorly projecting portion of the palatine. This facet articulates loosely with a similar facet on the proximal, ventral portion of the lateral ethmoid. The palatopremaxillary ligament originates on the palatine close to the palatine facet and inserts on the dorsal end of the premaxillary ascending process. The palatine forms a loose, but strong, joint on its ventroposterior medial surface with the conjoined anterior ends of the ectopterygoid and mesopterygoid.

The mesopterygoid is sharply differentiated into

a ventral staining portion and a dorsal nonstaining portion. The nonstaining portion is very thin, broad, medially curved and has its lower boundary along a level that connects the dorsal margin of the ectopterygoid with the dorsal margin of the ventroanterior portion of the metapterygoid (the staining and nonstaining portions of the mesopterygoid are not differentiated in Figure 5). The staining portion of the mesopterygoid is elongate anteriorly where it is joined to the dorsomedial surface of the ectopterygoid for the entire anterior extent of the ectopterygoid. Ventrally, the staining portion is broadly overlapped by the quadrate, and posteriorly, it is slightly overlapped by the metapterygoid.

The ectopterygoid broadly overlaps and clasps the anterior portion of the quadrate. The ectopterygoid tapers anteriorly, and at its anterior end, with the mesopterygoid, forms a loose connection with the palatine.

The quadrate is a relatively large bone that forms broad, overlapping syndesmotomic joints with the ectopterygoid, mesopterygoid, symplectic, and preopercle, a condylar connection with the articular, and a synchondral joint with the metapterygoid.

The symplectic is an elongate bone that extends from just below the ventral end of the hyomandibular, with which it forms a synchondral joint, to a position on the medial surface of the quadrate that is just dorsal to the anterior end of the preopercle. At this position the quadrate forms a pocket into which the cartilaginous end of the symplectic inserts and ligamentously attaches. For most of its length, the symplectic bears a thin, broad flange that joins the medial surface of the metapterygoid and quadrate.

The hyomandibular bears three condyles, two dorsally and one posteriorly. These condyles articulate with sockets on the skull and with the opercle. The posterior surface of the ventral shank of the hyomandibular attaches to the anterodorsal surface of the preopercle. Just dorsal to the ventral end of the shank is the ventral, external opening of the canal for the truncus hyomandibularis nerve. The dorsal entrance to this canal is on the medial surface of the hyomandibular somewhat ventral to the anteriormost condyle. Just anterior to the canal's ventral opening is a shallow pocket into which a flange of the metapterygoid inserts. This metapterygoid flange forms the lateral and ante-

rior margins of a short passageway whose posterior margin is formed by the anterior surface of the ventral shank of the hyomandibular, and whose medial margin is formed by a medial flange of the metapterygoid. The structures, if any, passing through this passageway were not investigated. The cartilaginous ventral end of the hyomandibular forms a synchondral joint with the cartilaginous dorsal end of the interhyal. A small cartilaginously tipped process on the posteromedial margin of the metapterygoid articulates with this synchondral joint. Anteriorly on its medial surface, the hyomandibular forms a suturing joint with a dorsoposterior medial flange of the metapterygoid.

The metapterygoid is an unusually large and complex bone consisting primarily of a smaller, irregularly surfaced and margined lateral portion and a larger, flattened medial portion. The metapterygoid synchondrally joins only the dorsoposterior end of the quadrate. On its posteromedial surface the metapterygoid bears a small cartilaginously tipped process that articulates with the synchondral joint between the hyomandibular and symplectic. The syndesmotomic articulations of the metapterygoid are with the hyomandibular, symplectic and mesopterygoid.

The preopercle bears a shallow, trough-shaped channel, which is almost divided into two portions by a raised, flattened area at its middle. The sensory canal of the preopercle passes along this channel and is continuous with the canal coming from the articular, but ends dorsally a short distance dorsal to the preopercle. The preopercle is strongly joined to the quadrate and hyomandibular, but only weakly attached to the other opercular bones.

The opercle is a thin, broad, flat bone whose posterior and ventral margins change imperceptibly into the membrane that connects it with the dorso-lateral surface of the subopercle. Dorsoanteriorly, the opercle joins the posterior condyle of the hyomandibular.

The subopercle is roughly a reversed L-shaped bone with the short, strong shank of the L rising dorsally; the long shank is thin and horizontal. The subopercle forms a shallow depression at the junction of its two shanks into which the opercle fits and attaches. The posterior end of the subopercle becomes very thin and threadlike, and attaches for most of its length to the medial surface of the opercle, which is thin and membranous in this area.

The interopercle is a long, flat bone whose dorsal margin is overlapped by, and connected to, the preopercle. A ligament attaches on the dorsomedial surface just anterior to the posterior end of the interopercle and extends to a point just anterior to the dorsoposterior end of the epihyal. Another ligament extends from the anterior end of the interopercle to the angular. Less discrete ligamentous tissue connects the interopercle to the subopercle.

**PECTORAL AND PELVIC-FIN GIRDLES AND SUPPORTS** (Figure 6).—The posttemporal is thin and depressed anteriorly where it articulates with the epiotic. Posterolaterally, the posttemporal forms a laterally open trough, along which the posterior-most portion of the laterosensory canal of the head passes. Posteroventrally, the posttemporal forms a strong process that is attached by a ligament to the intercalar. On its posteromedial surface, the posttemporal joins the bladlike supracleithrum, which in turn attaches to the dorsolateral surface of the cleithrum.

The cleithrum is roughly arc shaped with a lateral ridge ventroanteriorly. Ventromedially, the cleithrum is broadly trough shaped. Baudelot's ligament attaches to the dorsoanteriormost surface of the cleithrum and the two cleithra are joined at their ventroanterior ends. The small, thin, poorly staining, platelike dorsal postcleithrum is loosely attached to the dorsoposterior medial surface of the cleithrum and strongly attached to the distal end of the first epipleural rib. There is no ventral postcleithrum. The scapula, which completely encloses the scapular foramen, and dorsoanterior end of the coracoid join by a large cartilaginous area, which extends into a shallow pocket on the medial surface of the cleithrum. The ventral end of the coracoid, which is tipped with cartilage, attaches ligamentously to the ventrolateral surface of the cleithrum. A short ligament connects the midanterior surface of the cleithrum with the posterolateral corner of the fused 5th ceratobraobranchials.

There are four pectoral-fin radials, each with both ends cartilaginous. The dorsalmost radial bears marked dorsal and ventral processes that attach by short ligaments to a process on the scapula and the second from dorsalmost radial, respectively. The second radial is connected to the third, and the third to the fourth, by similar, but less-defined ligaments. There are 15 segmented pectoral-

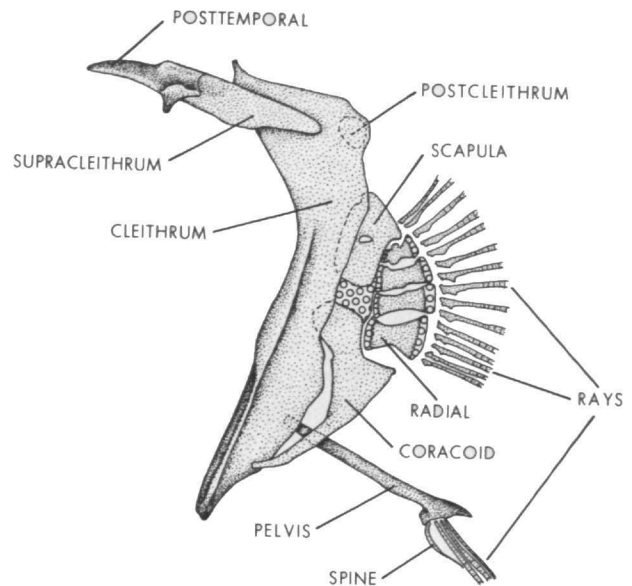


FIGURE 6.—*Pholidichthys leucotaenia*: lateral view of pectoral and pelvic-fin girdles and supports (fin rays truncated; dashed lines indicate extent of postcleithrum, scapula, coracoid, and pelvis overlapped by cleithrum).

fin rays (8 specimens; 15–16 according to Kailola, 1973), all but the dorsalmost one or two and ventralmost of which are branched in large specimens. Each ray embraces a small, cartilaginous distal radial (not shown). The two dorsalmost rays are loosely associated with the scapula.

The pelvis is a long, rod-shaped bone with a roughly cup-shaped distal end. The proximal end is tipped with cartilage and is closely joined, ligamentously, to the ventromedial surface of the cleithrum. The proximal ends of the two pelvises are widely separated from each other and are not connected, but they are joined posteriorly along two vertical processes (on each pelvis), one dorsal, one ventral, on the medial surface of the cup-shaped portion. The cup-shaped portion bears a tiny cartilaginous process (not shown) ventroanteriorly to which the pelvic-fin elements attach. The fin consists of a delicate spine with a deeply forked base and two or three delicate, segmented rays (in some specimens the fins are malformed on one or both sides or missing on one side). Cartilaginous radials, if present, were not apparent.

**GILL ARCHES AND HYOID APPARATUS** (Figures 7 and 8).—The only cartilage shown in Figure 7 is

that representing the 4th basibranchial. However, the following bones bear cartilaginous ends: basihyal, anteriorly only; 1st basibranchial, posteriorly only (the posterior end of the basihyal and anterior end of the 1st basibranchial appear to be connected by fibrocartilage); 2nd and 3rd basibranchials, both ends; hypobranchials 1-3, both ends; ceratobranchials 1-4, both ends; the apex and corners of the fused 5th ceratobranchials; epibranchials 1-4, both ends; the uncinat processes of the 1st, 3rd and 4th epibranchials (but not that of the 2nd); the 1st infrapharyngobranchial, both ends; the three corners of the toothless 2nd infrapharyngobranchial (which articulate ligamentously with the uncinat process of the 1st epibranchial, distal end of the 2nd epibranchial and anterodistal end of the 3rd infrapharyngobranchial, respectively); the toothed 3rd infrapharyngobranchial, proximally and anterodistally.

There is no interarcual cartilage between the

uncinate process of the 1st epibranchial and the 2nd infrapharyngobranchial.

The teeth of the fused 5th ceratobranchials and 3rd infrapharyngobranchials are similar. The smaller teeth are round in cross section; the larger are narrowly elliptical. The teeth are notched anteriorly just below their anteriorly recurved tips.

The 5th ceratobranchials are completely fused without indication of a median joint. The same condition exists even in the 16.9 mm early juvenile (greatest dimension of 5th ceratobranchials 1.2 mm). A short ligament connects each posterolateral corner of the fused 5th ceratobranchials to its respective cleithrum's anterior surface.

The tooth plate of the 4th infrapharyngobranchial is either fused to the 3rd infrapharyngobranchial or lost; it is not possible to tell which (the condition is the same in the 16.9 mm juvenile).

The anterior end of the 1st basibranchial lies ventral to the posterior end of the basihyal. The

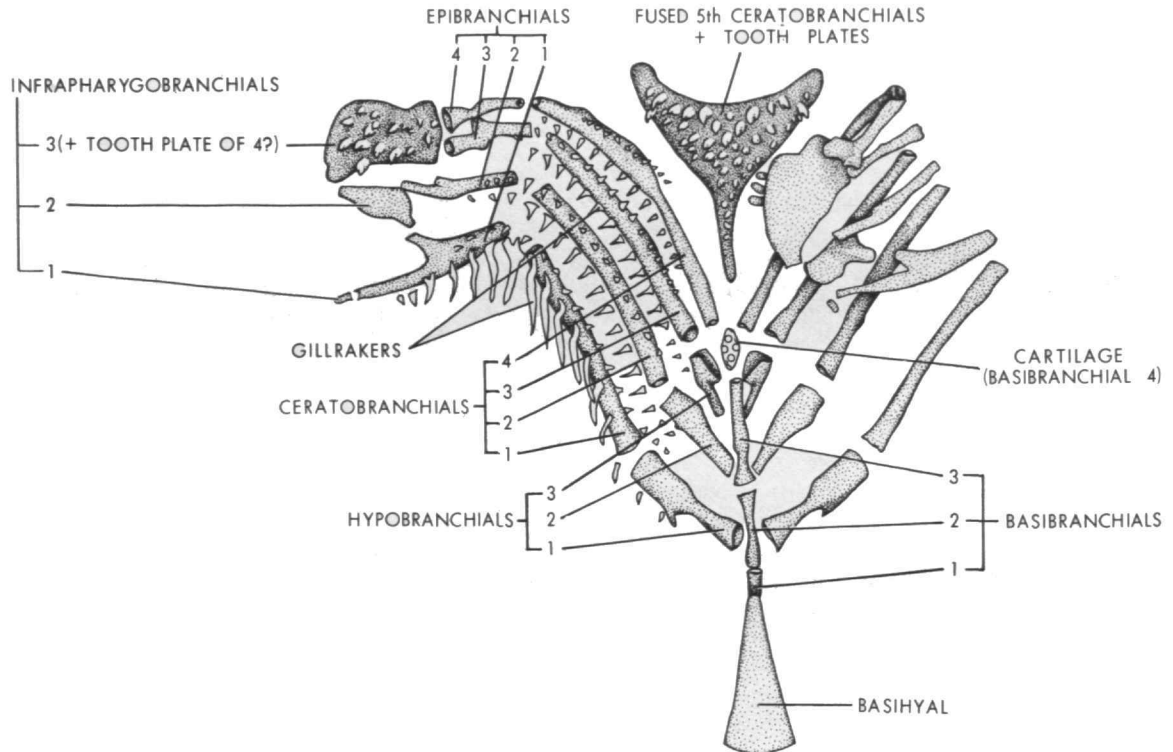


FIGURE 7.—*Pholidichthys leucotaenia*: gill arches (only cartilage shown is that of basibranchial 4; see text for description of other cartilage; gill rakers removed from left arches).

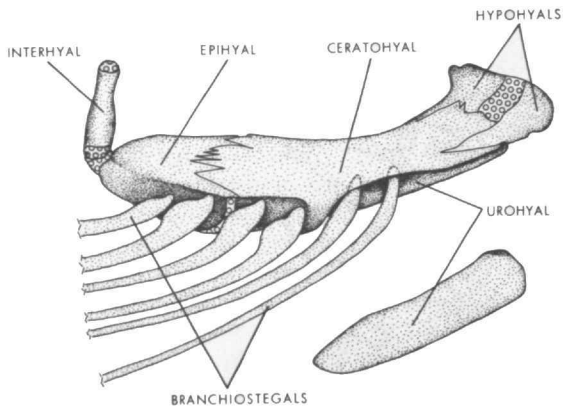


FIGURE 8.—*Pholidichthys leucotaenia*: right hyoid arch (branchiostegals truncated; urohyal shown in normal position and separately).

anteroventral surface of the 1st basibranchial is ligamentously connected to the anterodorsal surface of the urohyal.

The distal portion of the 2nd epibranchial overlies the dorsal surface of the 2nd infrapharyngobranchial. Ligamentous tissue tightly attaches the cartilaginous distal end of the 2nd epibranchial to the dorsoposterior surface and posterior, cartilaginous tip of the 2nd infrapharyngobranchial. An uncinat process arises at about the midposterior margin of the 2nd epibranchial and is connected by a ligament to a process at about the midanterior margin of the 3rd epibranchial. The uncinat process of the 3rd and 4th epibranchials are closely and tightly joined by ligaments.

The gill rakers are all simple and there are no tooth plates on the gill arches.

Dorsally the interhyal bears a plug of cartilage that joins the synchondral joint between the hyomandibular and symplectic. The ventral end of the interhyal is cartilaginous and is joined to the cartilage on the posteromedial surface of the epihyal. There is a ligament connecting the dorso-posterior end of the epihyal to the medial surface of the interopercle. The epihyal and ceratohyal are joined dorsally by a suturing joint. Ventral to this joint the bones are joined synchondrally. The dorsal and ventral hypohyals tightly clasp the ceratohyal and form a broad synchondral joint between themselves. There are six branchiostegals. The anterior two attach on the ventromedial sur-

face of the ceratohyal; the next two attach on a ventrolateral shelf on the ceratohyal that is continuous with a shelf on the epihyal, to which the posteriormost two branchiostegals attach.

The urohyal is a bladelike bone. A pair of short ligaments extend from the ventroanterior end of the urohyal, one ligament to each of the ventral hypohyals. Anterodorsally, the urohyal bears an articulating facet that impinges on the ventral surface of the 1st basibranchial. A long ligament extends from the posterior end of the urohyal to the joined ventroanterior ends of the cleithra.

**VERTEBRAL COLUMN, DORSAL, ANAL, AND CAUDAL FINS** (Figures 9–11).—The total number of vertebrae (including urostylar vertebra) varies from 71 to 79 (22 specimens). Precaudal vertebrae vary from 22 to 26 (24 specimens) and caudal vertebrae, from 48 to 56 (24 specimens). These counts include each anomalous vertebra (those with two or three neural and/or hemal spines, Figures 9 and 11) as one vertebra.

Anomalous vertebrae are common in *Pholidichthys*: at least 14 of the 27 specimens examined had them, and a specimen might have as many as three. The anomalous vertebrae occur in both the precaudal and caudal portions of the vertebral column, but are more common in the caudal portion. It is not known whether the anomalous vertebrae represent fusions between two or more vertebrae; the centra are not noticeably larger than those of adjacent normal vertebrae. Usually there is only one dorsal-fin pterygiophore associated with any given vertebra, but in each of three specimens the multiple neural spines of a vertebra were each associated with an equal number of pterygiophores. In another specimen, a vertebra with three neural spines was associated with only one pterygiophore. The single specimen with the most vertebrae (79) had no anomalous vertebrae. Of the five specimens with 78 vertebrae, four exhibited no anomalous vertebrae and one had three such vertebrae, all in the region below the dorsal fin. The single specimen with the least vertebrae (71) had no anomalous vertebrae.

The anteriormost precaudal vertebra bears articulating facets for the exoccipitals and basioccipital, and a posteriorly projecting flange on each side that connects with the adjacent (second) vertebral centrum. The second vertebra also possesses a similar, but much reduced, flange. The third

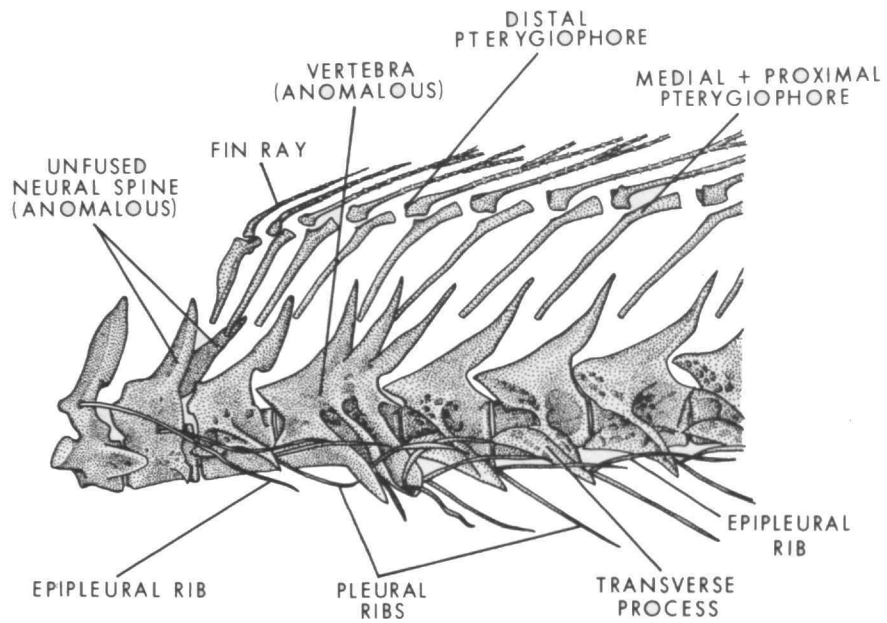


FIGURE 9.—*Pholidichthys leucotaenia*: anteriormost precaudal vertebrae and dorsal-fin elements, lateral view.

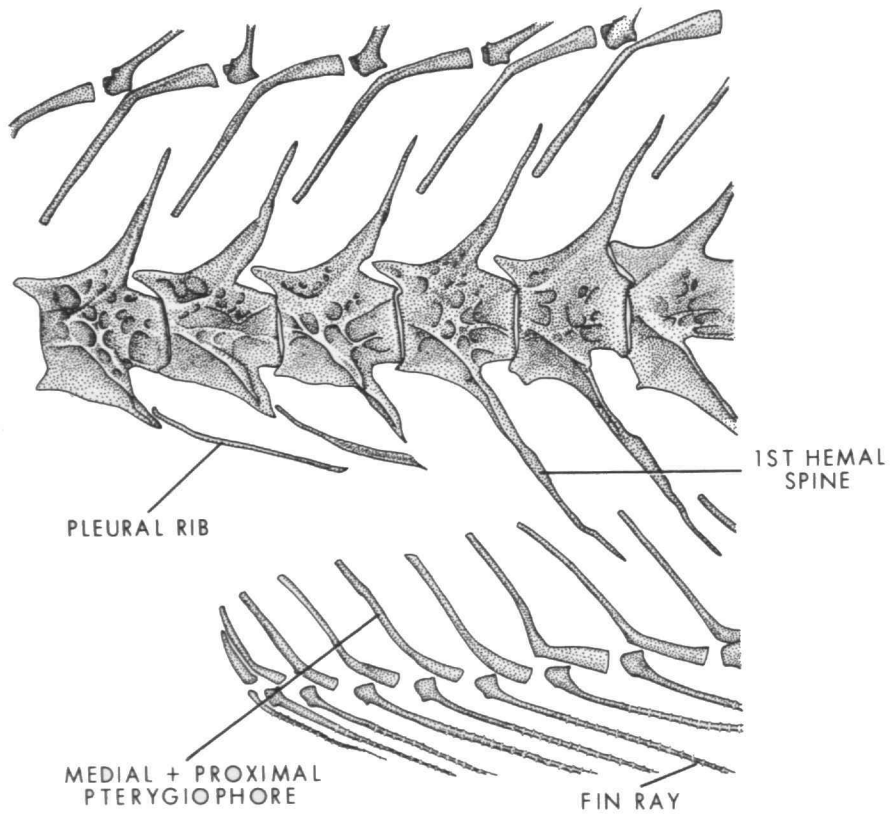


FIGURE 10.—*Pholidichthys leucotaenia*: posteriormost precaudal and anteriormost caudal vertebrae and anal-fin elements, lateral view.

through last precaudal vertebrae bear broad, roughly triangular transverse processes that, except for the third vertebra, overlap the next vertebral centrum anteriorly. The transverse processes support the pleural ribs, which commence on the third vertebra and terminate on the 22nd (next to last) in the single specimen in which rib counts were made. The epipleural ribs begin on the first and terminate on the 19th vertebra in the same specimen. In this specimen the fourth precaudal vertebra had three neural spines and three transverse processes on each side. Each of the transverse processes supported a pleural rib and its associated epipleural rib (Figure 9). None of the precaudal vertebrae has parapophysial stays. The caudal vertebrae all bear hemal arches, none of which are autogenous.

The urostylar (caudal fin) vertebra consists of a single element (Figure 11). The hypurals and parhypural are fused into fans that are in turn fused with the urostylar centrum. There are no epurals or other autogenous elements associated with this vertebra except for the 10 segmented, branched fin rays, 5 each on the dorsal and ventral hypural fans (21 specimens; 8–10 rays according to Kailola, 1973). There is no hypurapophysis. In the illustrated caudal fin, the hemal spine of the penultimate vertebra is forked; it is normally simple.

The dorsal fin originates dorsal to the level of the posterior margin of the head, and the anal fin originates a little anterior to the midpoint of the body. Both fins are joined membraneously to the caudal fin.

The dorsal and anal fins contain only segmented rays; all except the anteriormost one or two are branched and embrace paired distal radials. Each ray, except the anteriormost two in each fin, is associated with its own fused proximal + medial radials. The anteriormost two rays are associated with a single fused proximal + medial radial. The pterygiophores (= distal + medial + proximal radials) bear a one-to-one relationship with the vertebrae, except anteriorly, and except occasionally where a vertebra bears multiple neural or hemal spines. The number of dorsal-fin rays varies from 72 to 79 (20 specimens; 66–77 according to Kailola, 1973), and there are usually fewer rays than vertebrae, ranging from three less to three more rays than vertebrae. The number of anal-fin rays varies from 57 to 62 (17 specimens; 49–62 ac-

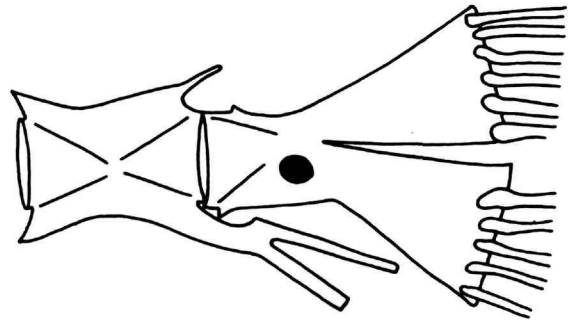


FIGURE 11.—*Pholidichthys leucotaenia*: posteriormost two caudal vertebrae and caudal-fin rays (from radiograph of USNM 212163; rays truncated; forked hemal spine unusual).

ording to Kailola, 1973), and there are 5 to 10 more rays than caudal vertebrae.

#### Seisimosensory Canals and Free Lateralis Organs

The bony canal elements and bony depressions on the cranium associated with different parts of the membranous cephalic canals are shown in Figures 2 and 5. The cephalic membranous canals are shown in Figure 12. The distributions of the free lateralis organs of the head and trunk are shown in Figures 12 and 13. The openings (pores) to the cephalic canals are shown in Figure 14. Although the pores are typically simple, small accessory pores may occur at almost any pore position.

Most of the external openings of the head canals are large, circular, deep depressions, each with an almost sphincterlike inner opening at its base. Some of the pores appear as horizontal slits; others, especially those of the preopercular canal, are noticeably small (Figure 14). The pores shown in Figure 12 are drawn from a Sihler nerve preparation in which the tissues have been relaxed through maceration and the pores have all become rather large and round.

A gap occurs in the infraorbital canal (Figure 12). This gap is considered below in connection with the vertical line of free lateralis organs and its innervation. There is also a gap between the mandibulo-preopercular and supratemporal canals. The canal system of the two sides of the head are connected dorsally only by an interorbital commissure. There apparently once was a supratemporal commissure in pholidichthyid ancestry as is indi-

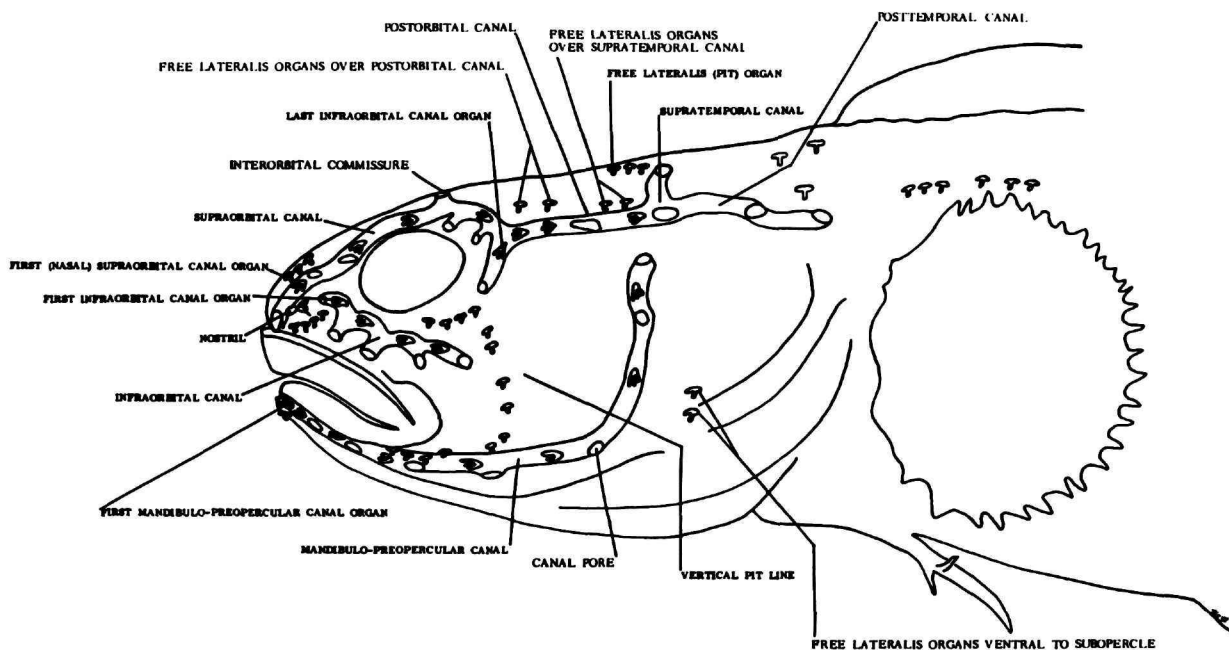


FIGURE 12.—*Pholidichthys leucotaenia*: lateral view of head showing cephalic lateralis canals, canal pores, canal organs, and free lateralis (pit) organs.

cated by the three free lateralis organs of each side of the head extending anteromedially toward the middorsal line. The anterior end of the mandibulo-preopercular canal is connected membranously across the symphysis of the lower jaw, a pore (Figure 14) occurring at the symphysis. There is no cross-connection between the nasal canal of each side. There is only one canal organ in the nasal canal, a location where the number of canal organs can be significant in systematic studies.

The free lateralis organs of the head and trunk are embedded in a thick epidermis consisting mainly of mucous cells of various sizes, many of large size. The tip of the lateralis organ is open to the outside. The organ can be termed a "pit" organ, but we prefer the general term "free lateralis organ."

Some of the clusters of free lateralis organs of the head correspond to similar clusters or lines in other fishes. The row of 4 or 5 organs below the base of the single nostril (Figure 12) corresponds to a similar cluster in the percoid *Polycentrus* (Freihofer, in press). The row of three organs above the posterior end of the nasal canal corre-

sponds to a similar cluster in *Polycentrus*. The vertical line of organs on the cheek corresponds to such a line on *Amia*, *Polycentrus*, and many teleosts. The unusual feature of this line in *Pholidichthys* is that the organs have partially invaded the area where the infraorbital canal organs would be expected to occur. This statement is based on the fact that these organs are innervated from the ramus buccalis accessorius facialis of the truncus hyomandibularis (Figures 13 and 20), not from the ramus buccalis facialis of the infraorbital trunk. The row of four free organs lying more dorsally in the gap of the infraorbital canal is supplied from the ramus buccalis of the infraorbital trunk (Figure 16). These four free organs apparently represent one or more canal organs of the missing segment of the infraorbital canal.

The single free organ near the anterior end of the chin corresponds to a large patch of such organs on *Polycentrus* and some other percoids. The row of four or five free lateralis organs over the articular part of the mandibular canal (Figures 12 and 17) corresponds to a larger row in *Polycentrus* innervated also by the r. buccalis accessorius facia-

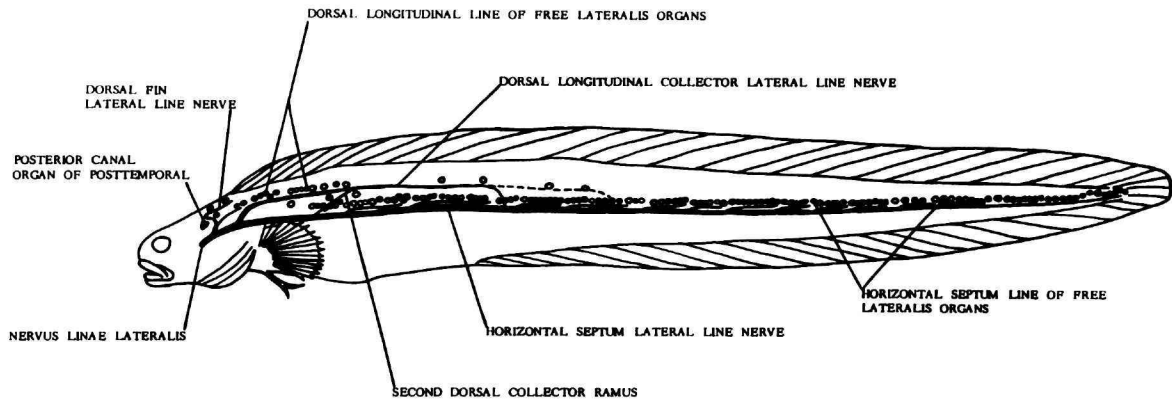


FIGURE 13.—*Pholidichthys leucotaenia*: complete lateral view showing trunk lateral-line nerves and lines of free lateralis organs. The dotted line is a continuation of the dorsal collector lateral-line nerve more posteriorly on one side of some specimens.

lis. The two free organs in the region external to the anteroventral area of the subopercle (Figure 12) correspond to a similar patch on *Polycentrus*. The two clusters of two organs each, one above the postorbital canal and the other above the anterior horizontal segment of the supratemporal canal (Figure 12), may correspond to the anterior and middle pit lines of *Amia* (Allis, 1889).

The trunk lateral line consists of three longitudinal rows of free lateralis organs embedded in a thick skin containing great numbers of mucous cells, the lateralis organs opening to the exterior at the surface of the skin (Figure 13). The first row, constituting the dorsal-fin lateral line, is short, consisting of only three organs (Figures 12 and 13). This line curves dorsally from the supracleithral area up to the front of the dorsal fin. The second row, constituting the main or dorsal longitudinal lateral line, curves dorsally from the cleithral area up to about halfway between the horizontal septum to a point above the anus, or above the fourth or fifth anal-fin ray on some specimens, and then returns to the horizontal septum. The third line of organs, constituting the horizontal septum lateral line, lies along the horizontal septum. It begins at a point dorsal to the posterior end of the pectoral fin and extends along the septum to the base of the caudal fin. In addition to the three trunk lateral lines there are three free lateralis organs, forming a short longitudinal row lying halfway between the horizontal septum and the dorsal longitudinal lateral line.

There are 138 free lateralis organs along the horizontal septum lateral line on the right side of one specimen examined and 133 on the left side. The organs usually occur in a series of from four to six organs separated by a short space. There were 19 organs on each side along the dorsal longitudinal lateral line.

#### Descriptions of the Nerves

The cranial nerves described are the trigeminal (fifth), facial (seventh) and parts of the glossopharyngeal (ninth) and vagal (tenth). These nerves have more numerous and complex branches and offer more promise as a source of systematic characters than do the other cranial nerves.

The illustrations (Figures 12–13 and 15–21) are moderately detailed and diagrammatic. The nerves are shown with the main kinds of functional nerve fibers their branches contain. In the absence of serial section preparations, these determinations were made on the basis of present knowledge of the distributions of the functional nerve fiber bundles in fishes for which such information is best known (see Herrick, 1899, for *Menidia*, 1900, for *Gadus*, and 1901, for *Ameiurus*).

Analysis and representation of nerves according to their functional components leads to a ready understanding of the distribution of the nerves. For the nerves described, there are four kinds of functional components present: (1) the general cutaneous component, represented by nerve fibers

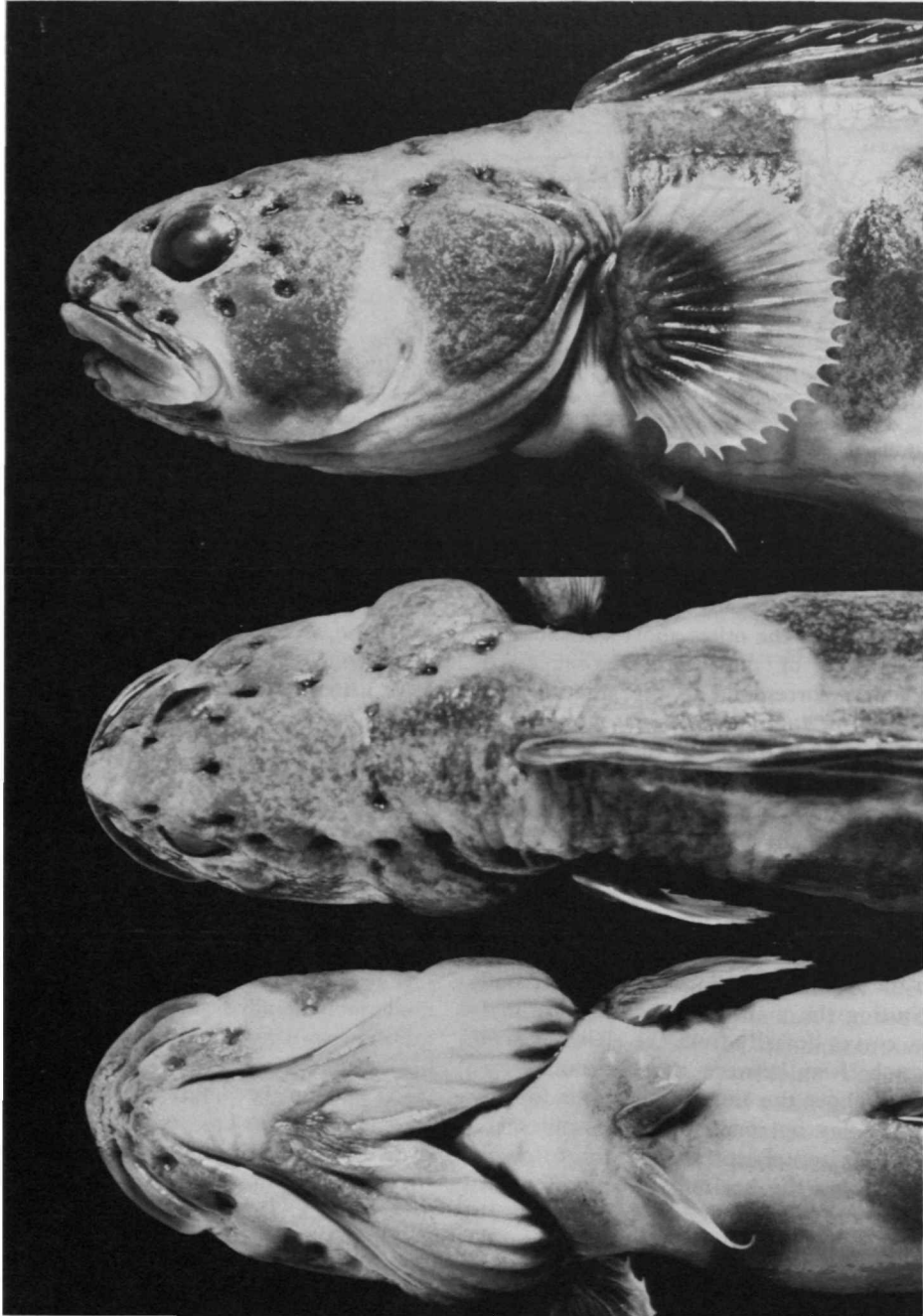


FIGURE 14.—*Pholidichthys leucotaenia*: lateral, dorsal, and ventral views of head of adult specimen in Figure 23 illustrating cephalic sensory canal openings. Note insertion of pelvic-fin relative to insertion of pectoral-fin. (Photograph by M. Giles.)

emanating from the Gasserian ganglion of the trigeminal nerve and going to the skin, where the fibers have undifferentiated, free endings (that is, not terminating in multicellular end organs); (2) the communis or taste component, represented by nerve fibers emanating from the geniculate ganglion of the facial nerve, from the petrosal ganglion of the glossopharyngeal nerve and the ganglia of the vagal branchial rami. The communis nerve fibers end in either taste buds of the pharynx, buccal cavity, and lips or in the external skin, or by simple terminations in the mucosa of the mouth and pharynx; (3) the visceral motor or, simply, motor component, represented by nerve fibers to muscles of the gill arches or of former (phylogenetically) gill arches; and (4) the lateralis component, represented by nerve fibers coming from the lateralis ganglia of the facial and vagal nerves and going to canal lateralis organs or free lateralis organs in the skin. A nerve branch may contain more than one functional component. The symbols for each component depicted in the illustrations and for the free and canal lateralis organs are given in Figure 15.

The nerve terminology follows mainly that of Herrick (1899). The words "branch" and "nerve" are used broadly to refer to any separately coursing group or unit of nerve fibers. The term "truncus" denotes the most proximal, unbranched part of a nerve after its cranial exit; the term "ramus" usually denotes a first division branch of a truncus, but the branches of some major rami are also termed rami; a "ramulus" is a first division branch of a ramus.

#### TRUNCUS SUPRAORBITALIS

The truncus supraorbitalis and the truncus infraorbitalis emerge together from the prootic's trigeminal foramen, which is far posterior to the orbital socket. The two trunks diverge as they pass anteriorly from the facial foramen.

The truncus supraorbitalis is composed of two rami: the ramus ophthalmicus superficialis trigeminus, which consists of general cutaneous fibers, and the ramus ophthalmicus superficialis facialis, which consists of lateralis fibers. There are no motor fibers and probably no communis fibers in the truncus supraorbitalis. The two rami course together closely and are indistinguishable macroscopically.

Associated with the proximal intracranial part of the truncus supraorbitalis are the two main branches of the recurrent facial nerve: the orbito-pectoral and the parieto-dorsal branches (Figure 15). The ramus oticus is also associated with the truncus and with the orbito-pectoral branch of the recurrent facial nerve. All of these associated nerves are described following the description of the two rami of the supraorbital trunk.

#### *Ramus ophthalmicus superficialis trigeminus*

There are several intracranial, apparently general cutaneous branches, most rather small, that course partway toward the cranial roof with the parieto-dorsal branch of the recurrent facial nerve. These small branches leave the parieto-dorsal branch, pass anterodorsally up to the frontal roof of the cranial cavity, where they exit, and pass to overlying skin, turning posteriorly in the skin. The number and exact locations of where they leave the supraorbital trunk varies on different sides of the study specimens. A few of these cutaneous branches leave the ramus ophth. supf. trigeminus separately and pass anterodorsally to the area of the postero-lateral corner of the frontal bone above the posterior end of the eye, where they pass through the bone to overlying skin, coursing posteriorly in the skin. One cutaneous branch detaches from the lateralis branch to the sphenotic canal organ, and one detaches from the lateralis branch to the posterior-most frontal canal organ. Both of these cutaneous branches pass posteriorly in the skin over the top of the head. Some of the intracranial cutaneous branches for the skin over the top of the cranium are shown in Figure 15. The intracranial vagal ramus joins the parieto-dorsal branch of the recurrent facial nerve close to the parietal bone and could not be followed separately in any of the specimens.

There is one fair-sized general cutaneous branch that leaves the truncus supraorbitalis posterior to the eye near the branch for the fourth supraorbital canal organ. This cutaneous branch passes anteriorly medial to the frontal canal and innervates the skin over the frontal canal for half the distance to the anterior margin of the eye. Another cutaneous branch detaches near the third supraorbital canal organ and innervates the skin of the interorbital region anterior to the previous cutaneous branch.

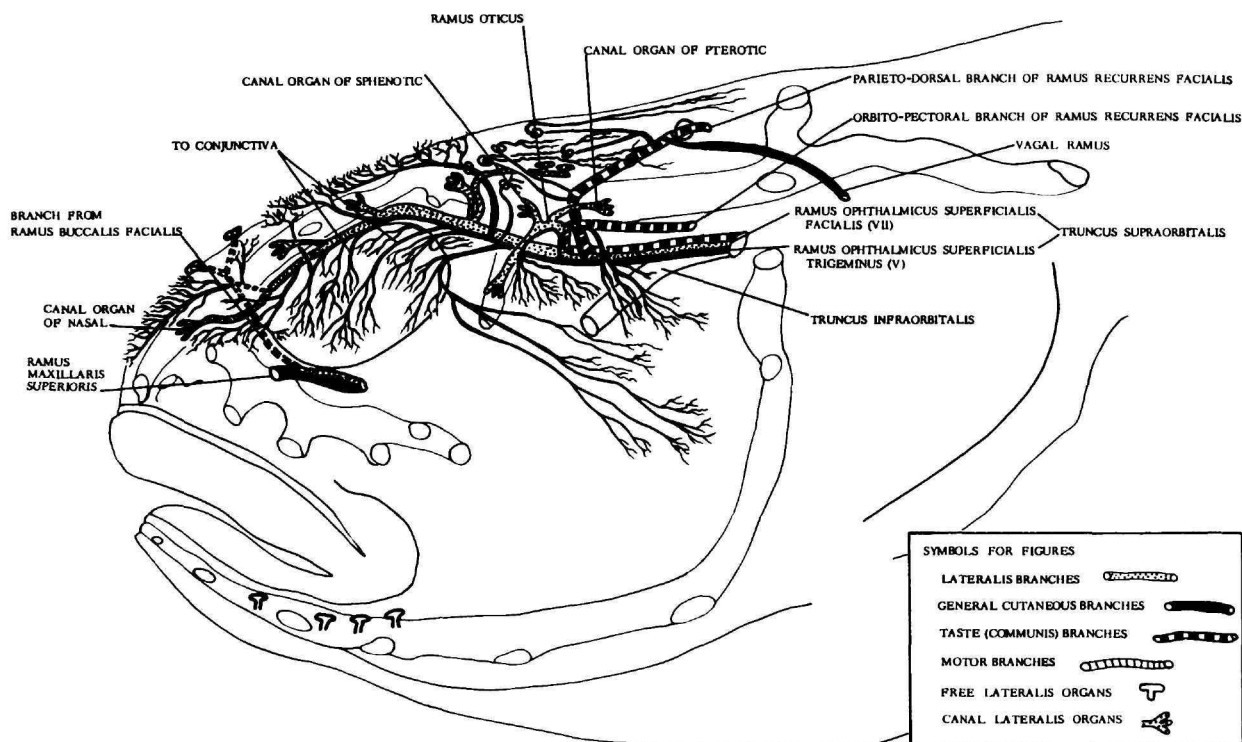


FIGURE 15.—*Pholidichthys leucotaenia*: lateral view of head showing distribution of branches of truncus supraorbitalis. Symbols for all figures given at lower right-hand corner.

The last noticeable cutaneous branch to the skin of the supraorbital region detaches near the front of the orbit and passes to the skin of the snout medial to the frontal and nasal canals.

There are general cutaneous branches that leave the ramus ophth. supf. trigeminus and pass ventrally to skin of the upper posterior part of the cheek, to the conjunctiva (and undoubtedly into the cornea), and to the snout ventral to the nasal canal. The first of these branches detaches far posterior to the eye, and passes anteriorly up to the orbital cavity, then over the posterolateral wall of the cavity where it detaches branches to the adjacent conjunctiva. The remainder then passes posteriorly under the skin over the upper cheek almost to the preopercular canal. Several more ramuli leave the ramus ophth. supf. trigeminus along its orbital course and pass down over the conjunctiva, innervating it. One of the anterior of these branches detaches a branch that passes dorsally to

supply the skin above the eye. The anteriormost of these ventrally directed branches of the ramus ophth. supf. trigeminus passes mainly to the skin above the anterior end of the infraorbital canal (lacrimal) and below the nasal canal. The innervation of the conjunctiva of *Pholidichthys* is the heaviest by far that we have seen on any fish. (It is from one of the posterior of these conjunctival branches that the orbital cirrus is innervated on the blennioid *Salaria*s). Most posteriorly on the tr. supraorbitalis are general cutaneous branches associated with the ramus oticus. These branches are part of the ramus ophth. supf. trigeminus, and they are described with the ramus oticus.

#### *Ramus ophthalmicus superficialis facialis*

This ramus courses in intimate contact with the ramus ophth. supf. trigeminus and is easy to describe because there are usually far fewer later-

alis branches than there are cutaneous branches. The ramus ends anteriorly by innervating the single canal organ of the nasal bone (Figure 15). It also innervates the three canal organs of the frontal bone, and close to the base of the ramulus for the posteriormost of these organs is a ramulus that passes up through the frontal bone and then posteriorly, ending by innervating the two free lateralis organs on the side of the head dorsal to the sphenotic and pterotic canal organs.

The supraorbital trunk of *Pholidichthys* terminates anteriorly, where it does in most fishes, at about the anterior end of the nasal canal and rather high on the side of the snout. Also, as in most other fishes, the rest of the snout, including its tip and the upper jaw, are the domain of the infraorbital trunk, as are the free lateralis organs lying medial to the posterior end of the nasal canal.

#### TRUNCUS INFRAORBITALIS

The truncus infraorbitalis of fishes has three main rami: ramus maxillaris trigeminus, ramus buccalis facialis, ramus mandibularis trigeminus. The ramus max. trigeminus typically carries general cutaneous fibers (branches shown in black in Figure 16). The ramus buccalis facialis carries lateralis fibers (branches stippled in Figure 16). The ramus mand. trigeminus carries general cutaneous and visceral motor fibers (branches appropriately coded in Figures 17 and 18).

#### *Ramus opercularis trigeminus*

This is the first ramus to detach from the truncus infraorbitalis (Figure 16). It has two ramuli that pass ventrally into the levator arcus palatini muscle for a considerable distance and innervate it. At about the point of division of the ramus into these two ramuli, a third ramulus is detached, which passes posteriorly lateral to the sphenotic and hyomandibular bones and innervates the dilator operculi muscle.

#### *Ramus maxillaris trigeminus*

We were unable to determine if communis fibers are present in the ramus max. trigeminus, but there is no reason to expect any as there are no

barbellike developments on the upper jaw. In drawing the branches of the ramus max. trigeminus, the cutaneous fibers are shown as two separate divisions at the base of the tr. infraorbitalis. These join at some point (not illustrated) more proximal in the truncus. The ramus max. trigeminus has three ramuli.

The first ramulus of the ramus max. trigeminus detaches far posteriorly on the truncus and passes anteriorly alongside the cranium up to the orbital cavity, where it curves laterally over the orbital rim and then courses ventroposteriorly beneath the skin, which it innervates at the posterior part of the cheek region (Figure 16). Before curving over the orbital rim it detaches some small branches to the conjunctiva at the posterior end of the eye.

The second ramulus to detach, shown leaving the ventral surface of the tr. infraorbitalis, passes anterolaterally over the orbital rim and medial to the posterior end of the infraorbital canal lying before the gap in this canal. Before reaching the infraorbital canal, the ramulus divides into a ventroposterior branch, which innervates the skin of the cheek anterior to the ventral ramulus of the ramus mand. trigeminus, and an anteroventral ramulus, which innervates the skin of the cheek below the infraorbital canal but some distance above the angle of the mouth.

The third ramulus of the ramus max. trigeminus courses as part of the lateralis branch of the ramus buccalis to the second infraorbital canal organ. It leaves this buccalis ramulus and innervates the skin below and between the second and third infraorbital canal pores. A second cutaneous branch detaches from this same buccalis ramus that innervates the second infraorbital canal organ. This second cutaneous branch innervates a small part of the conjunctiva in the anteroventral quadrant of the eye, which it reaches by first coursing for a short distance in the ramulus that innervates the four free lateralis organs along the base of the nostril.

The ramus maxillaris next divides into its two major parts: the ramulus maxillaris superioris trigeminus and the ramulus maxillaris inferioris trigeminus.

RAMULUS MAXILLARIS INFERIORIS TRIGEMINUS.— This ramulus passes anteroventrally toward the upper jaw and divides into a large anterior and a smaller posterior branch (Figure 16). The latter

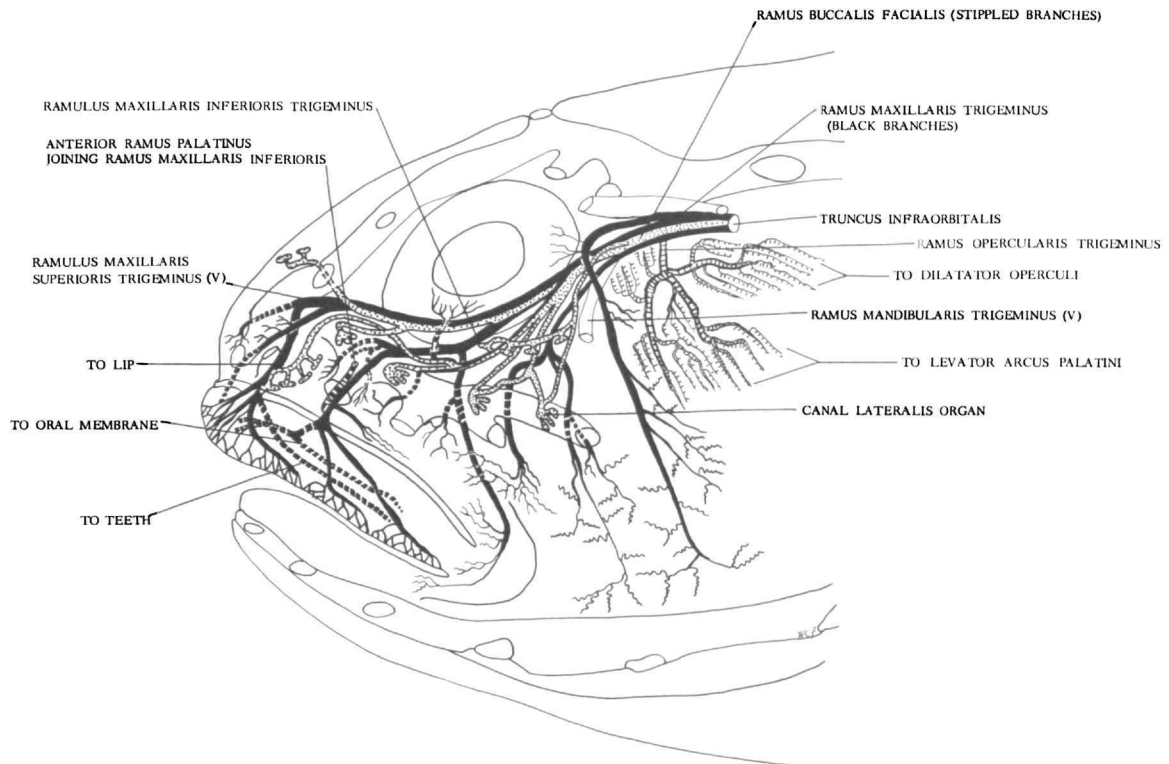


FIGURE 16.—*Pholidichthys leucotaenia*: lateral view of head showing distribution of branches of truncus infraorbitalis except for the ramus mandibularis trigeminus (see Figure 17). See Figure 15 for symbols designating nerve components, free lateralis organs, and canal organs.

passes ventrally toward the maxillary bone and then distally along the dorsal edge of the maxillary, crossing the maxillary near its end and passing into the tissue at the junction of the posterior ends of the upper and lower lips. En route it gives off a branch to the skin between the third and fourth infraorbital canal pores.

The anterior, larger branch of the ramulus passes ventrally medial to the second intraorbital canal pore, and detaches two branches to the skin, one anterior and one posterior to the second pore. The main part of the ramulus continues across the medial surface of the maxillary bone. In the intervening jaw membrane it breaks up into several branches for the upper lip, teeth, and alveolar tissue. One large branch continues onto the lateral surface of the premaxillary and breaks up into branches innervating the posterior half of the upper lip. The other large branch continues onto

the medial side of the premaxillary, where it divides into two branches: one coursing along the alveolar region toward the symphysis and, apparently, innervating the teeth, and one coursing distally and innervating the oral membrane and mucosa of the premaxillary. Just before the ramulus max. inferioris crosses the maxillary bone, it detaches a branch that passes anteriorly in the jaw membrane along the dorsal edge of the maxillary bone and out toward the bone's posterior end. Before passing the maxillary bone, the ramulus max. inferioris receives the remainder of the anterior ramus palatinus facialis (see under this heading), which carries communis fibers to the upper jaw.

**RAMULUS MAXILLARIS SUPERIORIS TRIGEMINUS.**—This large ramulus leaves the ramulus max. inferioris and continues anteriorly in a medial position over the palatine bone (Figure 16). It passes under the lateral ethmoid and over the maxillary

process of the palatine bone, lying en route medial to the nasal organ. It passes onto the external surface of the premaxillary and over the premaxillary-maxillary articulation, not far from the symphysis. It then divides into several branches. One penetrates the bone and, beneath the teeth, divides, sending one branch toward the symphysis and another branch, which innervates teeth, distally under the rear edge of the premaxillary alveolar region. The rest of the ramulus breaks up into branches supplying the lip tissue and skin of the external surface of the premaxillary lying anterior or medial to that supplied by the ramulus max. inferioris. On its way down the snout, the ramulus max. superioris detaches two small cutaneous branches. One branch supplies the skin medial to the anterior end of the nasal bone and the other supplies the skin lateral to the nasal bone, after which the ramulus continues ventrally and passes into the premaxillary bone near the symphysis. Before the ramulus turns downward toward the premaxillary, a branch of the ramus buccalis facialis coursing with it leaves and passes medial to the nasal canal and ends by innervating the two free lateralis organs above and a little ahead of the posterior end of the nasal canal.

#### *Ramus buccalis facialis*

This ramus innervates all four of the infraorbital canal lateralis organs lying anterior to the gap separating the two parts of the canal (Figure 16). It also supplies the free lateralis organs associated with the infraorbital and nasal canals, but not those free organs that lie at the edge of the gap. The organs at the edge of the gap are part of the vertical line of free lateralis organs, as evidenced by their innervation from the ramus buccalis accessorius facialis. The ramus buccalis facialis splits into three ramuli.

The first ramulus passes ventrally and supplies part of the innervation to the fourth infraorbital canal organ. On its way to the fourth organ it detaches a branch that supplies the four free organs located opposite the gap in the canal.

The second ramulus, which is moderately large, splits into three branches. The posterior branch (Figure 16) innervates the fourth canal organ (which is also innervated by the first ramulus!) and supplies half the innervation of the third

canal organ. The middle branch supplies the rest of the innervation of the third canal organ. The anterior branch, which also carries some general cutaneous fibers, courses anteriorly and divides into three more branches. One of these branches supplies the second canal organ. Another branch (general cutaneous) supplies skin between the second and third canal pores, and the third branch, which passes anteriorly some distance, innervates the four free organs along the base of the nostril. In the macerated Sihler specimen, the free organs are not visible, but the type of nerve ending, plus the fact that this is the only lateralis branch supplying this area, makes the identification of the source for innervation reasonably certain. The branch that supplies the free lateralis organs of the nostril also detaches a branch to the adjacent skin and conjunctiva of the anteroventral quadrant of the eye.

The third and most anteriorly coursing ramulus of the ramus buccalis facialis detaches from its association with the ramulus max. superioris at the anterior end of the orbit and divides into two branches. One branch supplies the first organ of the infraorbital canal and the other passes dorsally, medial to the posterior end of the nasal canal, and innervates the two free organs in this area.

#### *Ramus mandibularis trigeminus*

The functional components of this large ramus, as far as can be determined, are only motor and general cutaneous (Figure 17). Communis fibers are probably lacking.

Herrick (1899) suggested that the ramus opercularis trigeminus be treated as a branch of the ramus mand. trigeminus instead of its usual treatment as an independent ramus of the truncus infraorbitalis. We prefer the usual treatment and describe it under the tr. infraorbitalis.

The first ramulus (here unnamed) of the ramus mand. trigeminus directly divides into three large branches, which innervate the adductor mandibulae muscle. The remainder of the ramus mand. trigeminus continues ventrally toward the angle of the jaw, above which it detaches its second branch, the ramulus mandibularis cutaneus trigeminus, a moderate-sized general-cutaneous nerve.

RAMULUS MANDIBULARIS CUTANEUS TRIGEMINUS.—En route to the angle of the jaw this ramulus de-

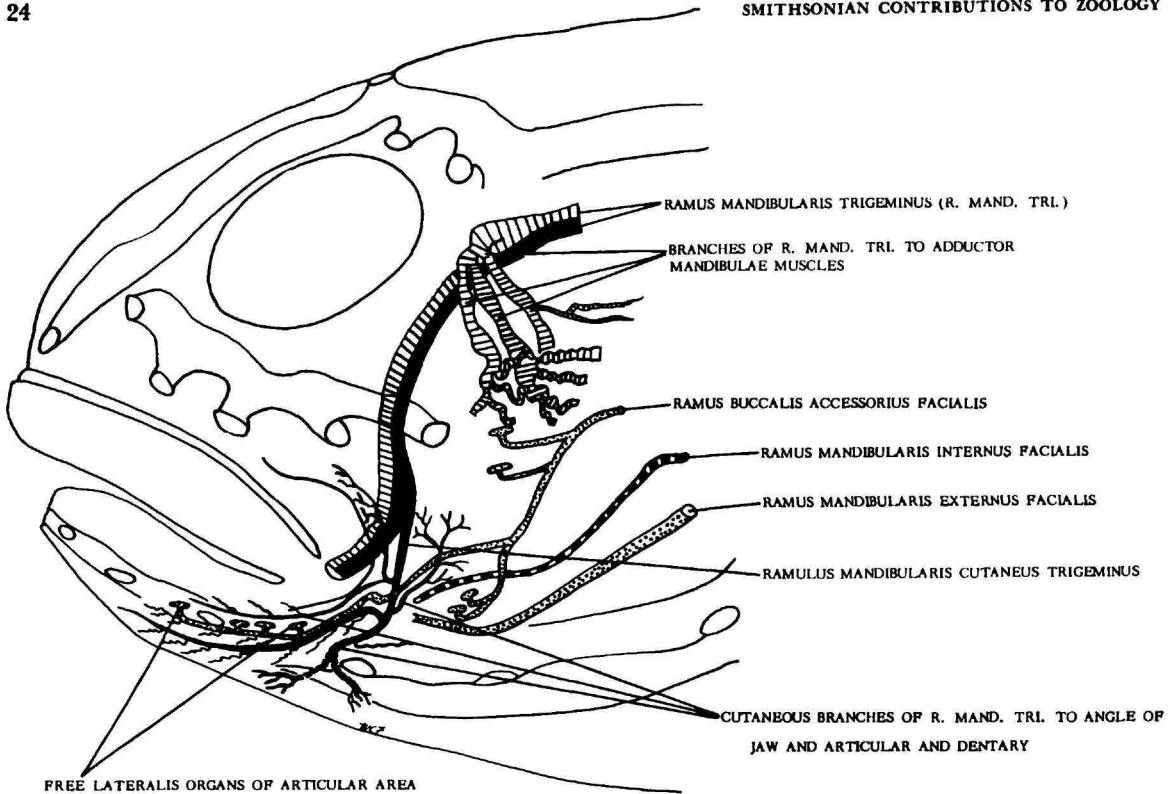


FIGURE 17.—*Pholidichthys leucotaenia*: lateral view of head showing proximal half of ramus mandibularis trigeminus. See Figure 15 for meaning of symbols.

taches a small nerve (Figure 18) that passes ventrally toward the articulating head of the quadrate, breaking up in tissue that appears to be in an area near the base of the maxillary tendon. The rest of the ramulus cutaneus continued toward the angle of the jaw (Figure 17), where it divides into four smaller branches. The first of these is an anterior branch that divides very shortly into two twigs. The first twig follows a dorsal curve in the skin behind the end of the maxillary bone. The second twig passes anteroventrally onto the posterior end of the lower jaw and innervates the skin dorsal to the mandibular canal. The second branch detaching from the ramulus cutaneus passes dorso-posteriorly, innervating the skin of the anteroventral area of the cheek anterodorsal to the quadrate articulating head. The third branch, the largest, detaches at the posterior end of the articular, comes into contact with the dentary branch of the ramus buccalis accessorius facialis, apparently gives off some branches to it, and continues ante-

riorly along the ventrolateral side of the articular and onto the dentary, where it innervates the skin. The fourth branch and remaining part of the ramulus cutaneus passes ventrally medial to the articular canal and innervates skin over the ventro-posterior part of the articular.

The ramus mand. trigeminus next passes onto the medial side of the lower jaw (Figure 18), crossing some distance dorsoanterior to the quadrate-articular articulation and divides into two large ramuli: the ramulus mandibularis externus trigeminus, which innervates the lip, the skin ventral to the lip, and the teeth of the lower jaw; and the ramulus mandibularis internus trigeminus, which innervates the intermandibularis and protractor hyoidei muscles and the skin of the floor of the mouth.

**RAMULUS MANDIBULARIS INTERNUS TRIGEMINUS.**—This ramulus passes laterally down the side and medially under Meckel's cartilage, and then slants anteromedially toward the belly of the intermandi-

bularis muscle. As it leaves the area of Meckel's cartilage, a lateralis branch from the ramus mandibularis externus facialis joins it. This lateralis branch detaches well anteriorly and innervates by three different branches the anterior dentary free lateralis organ (Figure 18), the first dentary canal organ, and the free lateralis organ of the chin near the symphysis. The ramulus internus, after leaving the side of the dentary and detaching the preceding lateralis branches, passes in the membrane of the jaw floor. There it detaches a general cutaneous branch, which passes anteriorly to near the symphysis of the lower jaw together with the lateralis branch to the free lateralis organ of the chin. The cutaneous branch continues anteriorly beyond the detachment of the lateralis branch and innervates the skin ventroposterior to the lip. (This portion of the skin is located more or less on the curvature of the dentary below the lip.) The rest of the ramulus internus supplies several branches to the muscles and skin of the floor of the lower jaw. The first of these branches innervates the anterolateral slip of the protractor hyoidei muscle. The next, more medial, larger branch innervates the intermandibularis muscle and overlying skin, being joined at the center of the muscle by a corresponding branch from the opposite side. The most medial, largest branch curves anteromedially and enters the anterior end of the dividing protractor hyoidei muscle (Figure 18). It then sends a branch to the anteromedial slip of the muscle and is met by a corresponding branch from the opposite side of the specimen. The two corresponding nerves, however, exchange branches in a cross innervation of the two halves of the protractor hyoidei muscle. The nerve then passes back in the muscle to the muscle's attachment to the ceratohyal and innervates en route both the muscle and overlying skin. The nerve is not met posteriorly by an anteriorly coursing branch of the ramus hyoideus as occurs commonly in fishes. In *Pholidichthys* the ramus hyoideus branch to the protractor hyoidei muscle only innervates skin over the muscle. In most fishes it is reported to share with the trigeminal ramulus in the innervation of the posterior part of this muscle.

#### RAMULUS MANDIBULARIS EXTERNUS TRIGEMINUS.—

This ramulus departs from the medial trigeminal mandibular ramulus and passes down the medial side of the articular to the top of Meckel's cartilage.

Before reaching Meckel's cartilage it detaches a small branch that innervates a rather small mentalis ( $A_w$ ) division of the adductor mandibulae muscle (Figure 18). The ramulus then continues anteriorly toward the tip of the lower jaw, detaching shortly before reaching it a branch that curves posterolaterally in the bone of the dentary and innervates teeth. The remainder and much larger part of the external ramulus continues anteriorly through the dentary near the symphysis and, coursing in the lip tissue, gives off numerous branches to papillae and skin. As there is no apparent connection of the ramulus mand. exter. trigeminus with the ramus mand. internus facialis, which carries the communis component, it is not evident that there are any taste fibers in the ramus mand. exter. trigeminus. If there are, and the nerve is of considerable size (although this may be the result of a large general cutaneous component), the taste fibers would have had to enter the infraorbital trunk intracranially and then been carried by the ramus mand. trigeminus.

#### RAMUS OTICUS

The ramus oticus (Figure 15), which has a lateralis and a general cutaneous component, passes together with the orbito-pectoral branch of the recurrent facial nerve into the orbital cavity through the trigeminal foramen. Both of these nerves are on the dorsal surface of the truncus supraorbitalis. These two rami directly leave the truncus and together pass dorsolaterally into a bony passageway through the sphenotic, emerging on the dorsal surface of this bone beneath the dermosphenotic, where the ramus oticus divides into three ramuli: one going to the dorsalmost (last) infraorbital canal organ, one to the dermosphenotic canal organ, and the third to the pterotic canal organ. The ramuli to the dermosphenotic and pterotic canals each detach a general cutaneous branch, the former innervating skin over the area of the levator operculi muscle and the latter innervating skin over the dilator operculi muscle.

#### RAMUS RECURRENS FACIALIS (RAMUS LATERALIS ACCESSORIUS)

The orbito-pectoral branch (RLA-OP, Figure 15) of the ramus recurrens facialis leaves the ramus

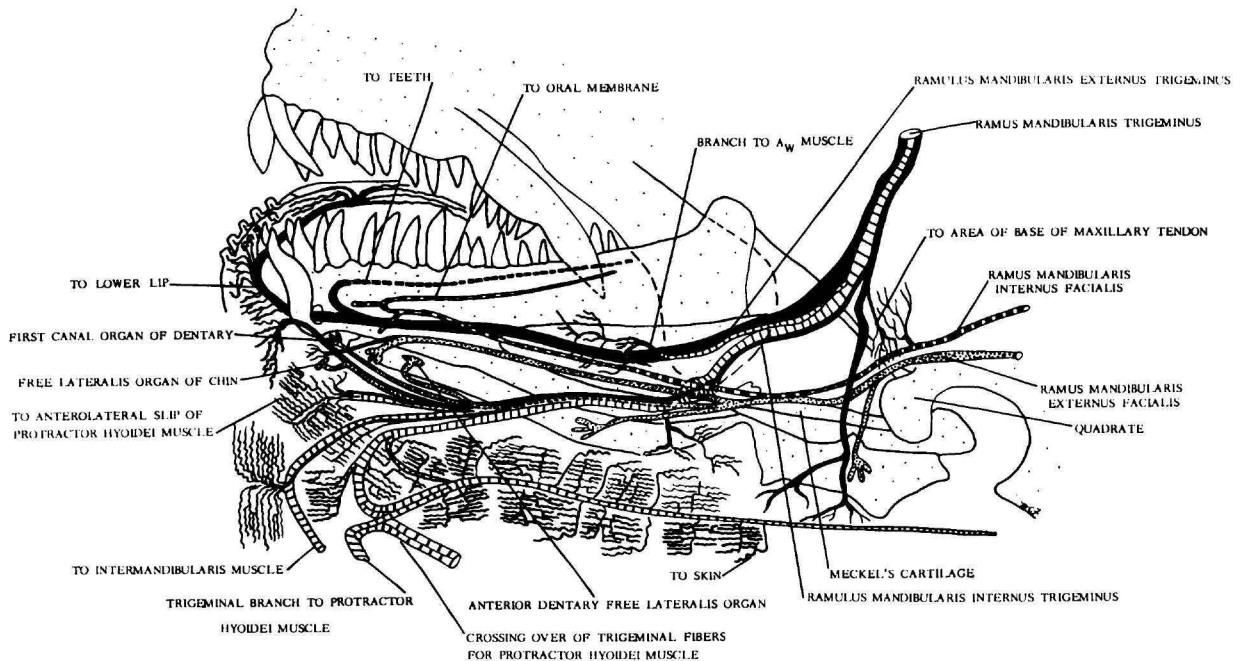


FIGURE 18.—*Pholidichthys leucotaenia*: lateral view of lower jaw showing branches of ramus mandibularis trigeminus and ramus mandibularis facialis to lower jaw. See Figure 15 for meaning of symbols.

oticus and continues posteriorly under the dermosphenotic canal, then under the anterior end of the bony pterotic canal. It crosses diagonally in a bony passageway underneath the pterotic canal, reaching the medial side of the pterotic canal, where it passes posteriorly beyond the pterotic through muscle. It continues rather deeply below muscle medial to the supratemporal (extrascapular) canal and onto the medial side of the epiotic arm of the posttemporal bone. It then continues ventrally down the medial side of the posttemporal, supraclithrum and cleithrum, passing lateral to the nervus linæ lateralis (the lateral line nerve of the trunk, Figure 13) and, finally, not far above the base of the pectoral fin, RLA-OP gives off two branches. The first branch, which is thin, passes posteriorly and a little ventrally toward the bases of the dorsalmost pectoral-fin rays, which it apparently enters. The second branch splits off a little further along and detaches another branch that joins a branch of the pectoral plexus (not illustrated) passing out the medial side of the muscular

base of the fin toward the bases of the ventral and medial pectoral-fin rays, which it apparently innervates. Most of RLA-OP passes medially and joins a nerve made up of a joint branch from the fourth and fifth ventral spinal rami (assuming that the occipital nerves are made up of three ventral spinal rami). This combined branch, which most of RLA-OP enters, passes posteroventrally out the muscular base of the pectoral fin and supplies fin-ray innervation to the middle and ventral pectoral-fin rays. By backtracking in branches of the pectoral plexus, fibers of RLA-OP could reach the pelvic fin, but no distinct RLA-OP branch to the pelvic fin was observed. There is no branch of RLA-OP to the anal fin. The details varied on another specimen, but the main branches of RLA-OP to the pectoral fins are apparently essentially the same.

The parieto-dorsal branch (RLA-PD, Figure 15) is formed from two separate branches that course with the truncus supraorbitalis up to, or almost to, the trigeminal foramen. The two nerves either enter the foramen and then directly reenter

the cranial space through the prootic bone or they do not enter the foramen but leave the truncus supraorbitalis as two branches, which shortly unite and pass up through the cranial cavity dorsoposteriorly to the cranial exit for RLA-PD in the parietal bone. Near the parietal exit, RLA-PD meets a small intracranial vagal ramus. The vagal ramus, after joining RLA-PD, could not be followed separately. The vagal ramus may detach from RLA-PD on the top of the head and innervate the skin, as it has been observed to do in some other perciforms (Freihofer, in press). Outside the parietal, RLA-PD courses up through muscle to the overlying skin and then back close to the mid-dorsal line, where it passes alongside the dorsal-fin pterygiophores for apparently the length of the fin.

#### TRUNCUS HYOMANDIBULARIS

The truncus hyomandibularis has two intracranial branches that join as they pass anteriorly into the prootic (Figures 19 and 20). These two branches constitute the anterior ramus palatinus facialis, which is described separately. As the truncus hyomandibularis leaves the facial foramen it is joined by the ramus communicans from the Gasserian ganglion (not illustrated) of the trigeminal nerve. The ramus communicans is the source of general cutaneous fibers for the truncus hyomandibularis. The first external cranial branch of the truncus is the posterior ramus palatinus facialis.

##### *Posterior ramus palatinus facialis*

This short ramus (Figure 19) detaches from the truncus hyomandibularis shortly after the truncus leaves the facial foramen and directly meets a very large palatine ramus from the glossopharyngeal nerve a little anterolaterally to the truncus. The two nerves form Jacobson's anastomosis close to the dorsal end of the large and well-developed pseudobranch (Figure 19). We are tentatively calling the resulting compound nerve the pseudobranch nerve. The glossopharyngeal palatine ramus supplies innervation to the pseudobranch (Laurent and Dunel, 1966). The compound nerve supplies communis innervation to the mucosa of the rear palatal area, hyoid arch and rear floor of the mouth. Shortly after formation of Jacobson's anastomosis, a branch

is detached posteriorly that courses to the mucosa dorsal and medial to the pseudobranch. Another branch passes ventroposteriorly near the vertical base of the pseudobranch. This branch continues around the ventral end of the interhyal on one side of the specimen; on the other side it ended close to the ventral end of the pseudobranch. The main part of the pseudobranch nerve passes ventrally near the anterior base of the pseudobranch, giving off en route several branches that pass well anteriorly in the palatal mucosa and include a large branch that passes near the lateral edge of the palate. The remainder of the nerve passes onto the hyoid arch, detaches branches to the medial side of the arch that extend down to the heads of the branchiostegals and anterolaterally into the mucosa of the floor of the mouth between the hyoid arch and the dentary. The pseudobranch nerve ends about three-fourths of the way along the arch.

The next branch that detaches from the truncus hyomandibularis, shortly after the posterior palatine ramus, is the ramus opercularis profundus facialis.

##### *Ramus opercularis profundus facialis*

This ramus consists of two large branches: one anterior and one posterior (Figure 19). The anterior branch innervates the adductor arcus palatini muscle, which is much the thickest posteriorly. The posterior branch courses a considerable distance posteriorly, where it innervates the levator operculi and adductor operculi muscles.

##### *Ramus opercularis superficialis facialis*

The next branch of the truncus hyomandibularis is the ramus opercularis superficialis (Figure 20), which contains lateralis and general cutaneous components and detaches at a level just below the dorsal end of the preopercular canal. This ramus passes posteriorly under the preopercular canal, detaching a lateralis branch to the last (eighth) mandibulo-preopercular canal organ. The rest of the ramus continues ventroposteriorly under the skin over the anterior end of the opercle, where it supplies the skin of this area and two (Figure 12) or three (Figure 20) free lateralis organs located about over the anterior end of the subopercle. The posterior part of the skin over the opercle is sup-

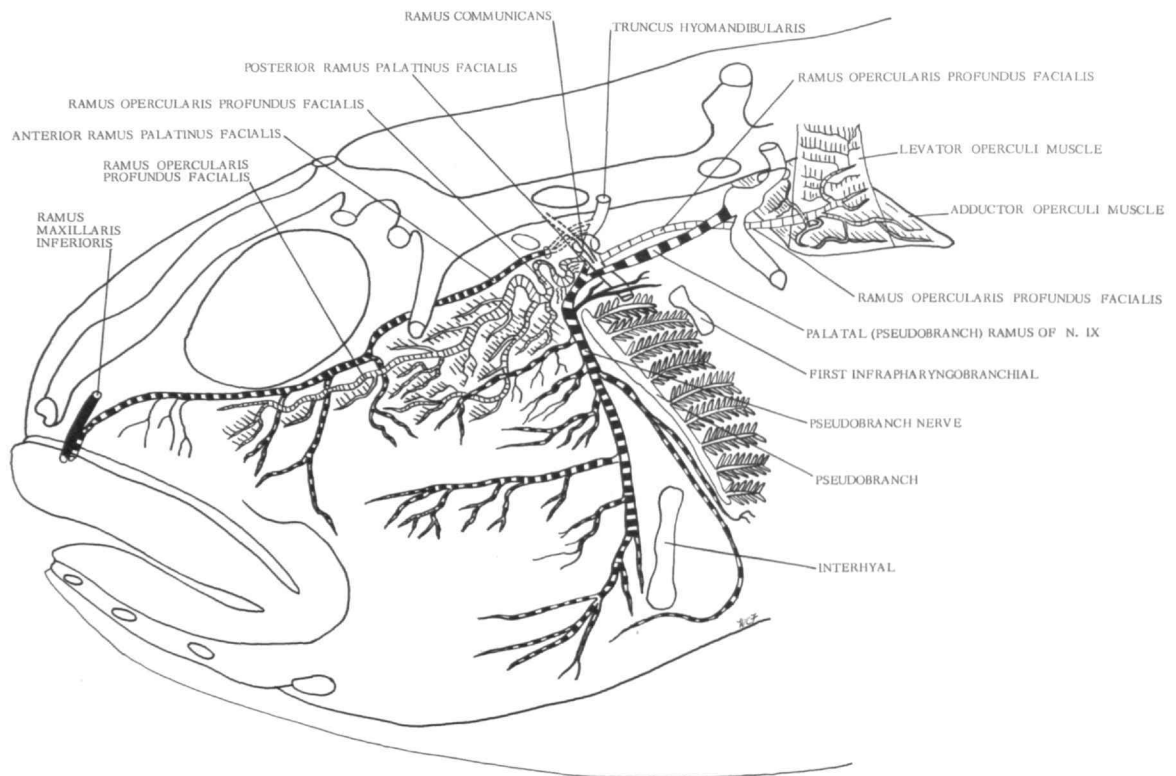


FIGURE 19.—*Pholidichthys leucotaenia*: lateral view of head showing distribution of anterior and posterior ramus palatinus facialis and the palatal ramus of the glossopharyngeal nerve. See Figure 15 for meaning of symbols.

plied by the ramus opercularis vagi, which is not discussed.

The next branch of the truncus hyomandibularis goes to the seventh mandibulo-preopercular canal organ. It is just ventral to this organ, but still some distance above the upper end of the interhyal, that the truncus divides into the anteriorly coursing ramus mandibularis facialis and the ramus hyoideus, which passes ventrally onto the hyoid arch (Figure 20).

#### *Ramus hyoideus*

The ramus hyoideus carries visceral motor and general cutaneous components. After detaching from the truncus hyomandibularis it passes ventrally posterior to the interhyal. At the ventral end

of the interhyal it turns anteriorly, coursing close to the bases of the branchiostegal rays, and gives off branches carrying motor fibers for the well-developed hyoidei adductores and abductores muscles of the branchiostegal rays (Figure 21). Its first branch (Figure 20), however, detaches shortly after it leaves the truncus, and is a general cutaneous nerve coursing ventrally between the opercle and preopercle, supplying skin in this area as far ventrally as the angle of the preopercle. Much further anteriorly, a branch detaches between the second and third branchiostegals, passes anteriorly along the ventral edge of the protractor hyoidei muscle, innervating skin, but not the muscle, and ends below the hypohyals. Most of the hyoidei adductores and abductores muscles are not indicated in Figure 21.

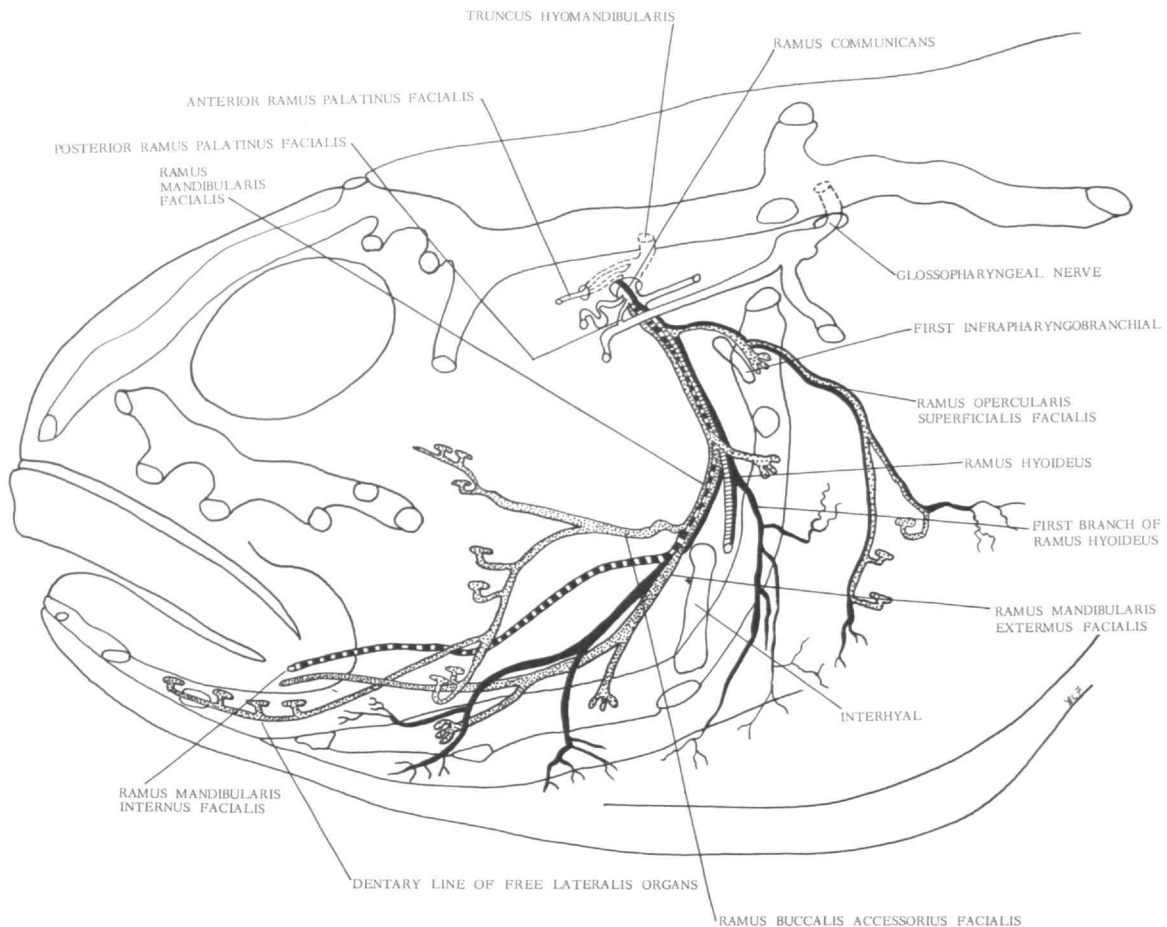


FIGURE 20.—*Pholidichthys leucotaenia*: lateral view of head showing proximal half of distribution of truncus hyomandibularis. See Figure 15 for meaning of symbols.

#### *Ramus mandibularis facialis*

Beyond the detachment of the ramus hyoideus the truncus hyomandibularis, now called the ramus mandibularis facialis, curves ventroanteriorly and passes in a bony canal in the preopercle close to the preopercular lateralis canal. The ramus detaches the ramus buccalis accessorius facialis, a lateral branch.

#### *Ramus buccalis accessorius facialis*

This ramus (Figure 17) innervates the 6 or 7 free lateralis organs, which form a rather well-

developed vertical line on the cheek. It also innervates four free lateralis organs over the posterior end of the mandibular canal on the lower jaw. The dorsal organs of the vertical cheek line appear to have invaded part of the area of the infraorbital canal. They are, at least, in the area of the gap in this canal, which is complete in most fishes. The ramus contacts a general cutaneous branch of the ramus mand. trigeminus at the posterior end of the lower jaw (Figure 17) and apparently receives some general cutaneous fibers from it. The ramus buccalis accessorius should not carry general cutaneous fibers in its branch supplying the vertical free lateralis organ line, as this branch is in the

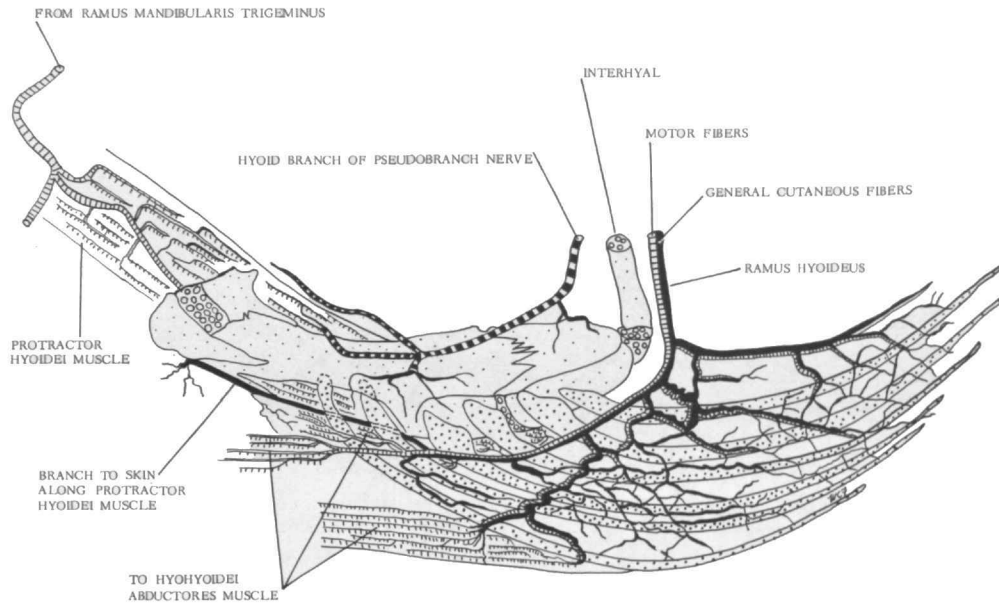


FIGURE 21.—*Pholidichthys leucotaenia*: lateral view of hyoid arch showing distribution of ramus hyoideus. See Figure 15 for meaning of symbols.

area of general cutaneous nerves of the intraorbital trunk.

Shortly after detachment of the ramus buccalis accessorius the ramus mand. facialis divides around the symplectic bone (as it does in most teleosts) into the ramus mandibularis internus facialis and the ramus mandibularis externus facialis (Figure 20).

#### *Ramus mandibularis internus facialis*

This ramus carries communis fibers for taste buds of the floor of the mouth and lower lip. It passes anteriorly dorsal to the symplectic and approaches the ramus mand. externus as both rami pass anteriorly dorsal to the quadrate articulating head and onto the medial side of the lower jaw (Figures 18 and 20). The ramus mand. internus facialis contacts the ramus mand. externus facialis slightly on the medial side of the articular bone and continues anteriorly to near the symphysis of the lower jaw. Near the symphysis the ramus internus curves laterally in the oral membrane, innervating taste buds on it and, apparently, taste buds around the teeth and probably out on the lower lip, although

no branches could be seen reaching the lip. As the ramus passes the articulating head of the quadrate it detaches a branch dorsally to the mucosa of this part of the mouth.

#### *Ramus mandibularis externus facialis*

This ramus separates from the ramus mand. internus above the symplectic and courses anteriorly ventral to this bone. It carries mainly a lateral component and some general cutaneous fibers. The cutaneous fibers detach as two cutaneous branches along the horizontal arm of the preopercle, innervating skin (Figure 20). No cutaneous fibers are apparently left in the ramus at the point of its crossing onto the lower jaw. The ramus innervates the sixth mandibulo-preopercular canal organ and farther on the fifth organ (Figure 20). The ramus passes anteroventrally above the articulating head of the quadrate and onto the lower jaw (Figure 18). Just beyond the quadrate it sends a branch to innervate the last (fourth) mandibular canal organ, which lies in the articular bone. Further anteriorly, coursing underneath Meckel's cartilage, the ramus detaches a branch to the third

mandibular canal organ (in the dentary). A little anterior to the origin of the fourth canal organ branch is a lateralis branch, which courses with the ramulus mandibularis medialis trigeminus that innervates the protractor hyoidei and intermandibularis muscles. The lateralis branch extends anteriorly as three lateralis ramuli. The posteriormost ramulus innervates the anterior free lateralis organ of the dentary (Figure 18); the middle ramulus innervates the first canal organ of the dentary; and the anteriormost ramulus innervates the free lateralis organ near the anterior end of the chin (general cutaneous fibers from the ramus mandibularis trigeminus continue anteriorly beyond the third ramulus to supply the skin of the anterior end of the chin). The remainder of the ramus mandibularis externus facialis continues anteriorly under Meckel's cartilage as far as the second dentary canal organ, which it supplies.

#### ANTERIOR RAMUS PALATINUS FACIALIS

This ramus (Figure 19) carries communis fibers. It originates intracranially as two branches from the truncus hyomandibularis, which join in the bone of the prootic and form a ramus that passes through the anterior wall of the prootic and into the orbital cavity. The ramus continues forward on the dorsolateral side of the parasphenoid across the floor of the orbital cavity. It detaches en route three large branches that pass ventrally through the adductor arcus palatini muscle to the mucosa of the palate. Beneath the vomer the ramus sends a number of thin branches to the mucosa. It continues anterolaterally under the vomer, joining the ramus maxillaris inferioris trigeminus as this nerve crosses the ventral surface of the maxillary.

#### TRUNK LATERAL-LINE NERVES

The nervus lineae lateralis (Figure 13), which innervates the lateralis organs of the trunk, emerges from the cranium on the posterodorsal side of the vagus (tenth) nerve (not illustrated). The nervus lineae lateralis directly leaves the vagus, passes posteriorly and laterally toward the pectoral girdle, and detaches the ramus supratemporalis vagi, which we do not describe further. Shortly before the cleithrum, the nervus lineae lateralis detaches the dorsal-fin branch, which innervates three free

lateralis organs (Figure 13). Medial to the cleithrum, the nervus lineae lateralis detaches the first dorsal longitudinal collector lateral-line nerve. The remainder of the n. lineae lateralis continues posteriorly as the horizontal septum lateral-line nerve along the horizontal septum to the end of the trunk, innervating en route the overlying free lateralis organs. Above the end of the pectoral fin the second dorsal collector lateral-line nerve detaches from the horizontal septum nerve and joins the first dorsal collector nerve. The second collector nerve is noticeably smaller than the first. The dorsal collector lateral-line nerve ends above the anus on one side and somewhat posterior to the anus on the other side of two specimens examined.

The trunk lateral-line nerve pattern of *Pholidichthys* has the main characteristic of the acanthopterygian pattern: the dorsal longitudinal "collector" lateral-line nerve (Figure 13). In generalized percoids, such as *Perca flavescens* (Freihofer, 1972, fig. 7), this collector nerve typically leaves the main trunk lateral-line nerve (the horizontal septum lateral-line nerve) medial to the supracleithrum, curves dorsoposteriorly to a point about halfway between the horizontal septum and the dorsal contour of the trunk, and continues in a gradually descending course toward the horizontal septum, to which it returns at the beginning of the caudal peduncle. En route, the dorsal longitudinal collector lateral-line nerve is usually joined by four or five dorsal segmental rami that detach from the horizontal septum. The beryciform *Holocentrus* also has a dorsal longitudinal collector lateral-line nerve.

The pattern in *Pholidichthys* differs from the generalized acanthopterygian pattern in that the dorsal longitudinal collector nerve collects only two dorsal rami. The line of free lateralis organs in *Pholidichthys* appears to be breaking up and the organs moving toward the horizontal septum. This movement is suggested by the presence of at least three free organs lying midway between the dorsal longitudinal collector nerve and the horizontal septum nerve (Figure 13). It is also evidenced by the presence of a line of free organs along the horizontal septum beginning below the tip of the pectoral fin and extending to the point of return of the dorsal collector nerve to the horizontal septum above the anus or somewhat posterior to it. In the more generalized percoids, there are no lateralis organs, either free or in tubed scales, along the horizontal

septum on its course below the dorsal longitudinal collector nerve.

In addition to the two trunk lateral-line nerves just discussed, *Pholidichthys* has a third, the dorsal-fin lateral-line nerve. It is in the form typical for many teleosts (Figure 13).

There are other perciforms with a trunk lateral-line development similar to that in *Pholidichthys*. Although they are not particularly elongate fishes, they show a tendency toward elongation. The comparisons are discussed in another section.

#### INNERVATION OF THE FIN RAYS

All the fin rays of *Pholidichthys* are innervated by the fin-ray nerves coursing external to the fin rays, not down the hollow center of the rays as the fin-ray nerves do in many fishes.

#### *Pectoral and Pelvic-fin Innervation*

The complex of occipital and spinal nerves making up the pectoral plexus was not studied in detail. The innervation was examined in the hope of gaining some indication of whether or not the pelvic fins of *Pholidichthys* show any signs of being or having been more forward than are percoid pelvic fins. A nerve marker was sought that might enable a comparison of the pelvic-fin position in *Pholidichthys* with the position of this fin in percoids and blennioids. A marker chosen for comparison was the particular ventral spinal ramus that enters the medial base of the last pelvic-fin ray and supplies fin-ray innervation to the medial pelvic-fin rays.

The spinal nerves were numbered by assuming that the occipital nerves consist of three spinal nerves. Herrick (1899) states that there are at least three spinal nerves represented in the occipital nerves. Whatever the number actually is, according to Ray (1950) it is apparently rather constant for most bony fishes. The occipital nerves are the first postvagial segmental nerves that leave the cranium through the exoccipital bone.

In *Pholidichthys* it is the seventh ventral spinal ramus that enters the base of the last pelvic-fin ray.

#### Miscellaneous Anatomical Notes

The following brief description of the swim bladder of *Pholidichthys* was provided us by N. B.

Marshall: bladder divided into anterior and posterior chambers by a fragile diaphragm; retia in anterior chamber; retia have common origin; gas gland with six or seven lobes.

The gill openings are wide but restricted ventrally (gill membranes attached lateral to isthmus) and there is a large opening (slit) posterior to the fourth gill arch. The pseudobranchiae have well-developed gill filaments that extend into the gill cavity.

The adductor mandibulae muscles of the cheek are massive. There is no indication of an  $A_1\beta$  division. A large part of the  $A_2A_3$  divisions insert on the coronoid process of the dentary.

#### Color Pattern Changes

The smallest specimens of *Pholidichthys* (15–49 mm SL) are characterized by having two longitudinal dark stripes, separated by a luminous white stripe, on the body (Figure 22). The dorsal dark stripe is narrower and extends along the dorsal body contour. At this stage the anal fin is unmarked and the dorsal fin is either unmarked or faintly dusky; the belly is white. Between 49 and 108 mm SL the dark stripes break up into rows of dark spots, and some faint dark spots appear in the dorsal fin, which has a narrow, pale distal margin (Figure 23; Kailola, 1973, pl. 4, shows a striped phase, wild caught specimen 123 mm total length). At larger sizes the color pattern is quite variable, but, in general, the dark spots on the body increase in size (especially those in the ventral row), grow together to form irregular vertical spots and bars, and may send out dorsal and lateral extensions (Frontispiece and Figure 23). There is a row of dark spots along the dorsal fin, which extend onto the body dorsally, and a lateral row of large spots, which tend to fuse with one another posteriorly and with the posterior dorsal-fin spots. The anal fin also exhibits irregular dark spots, and there is a continuous, narrow, pale distal margin around the vertical fins. Burgess and Axelrod (1973, fig. 265) show a large specimen with a pattern of broad black bands separated by narrow pale bands posteriorly on the body, and white spots on the dorsum and belly anteriorly.

In living adults the dark areas are dark brownish and the pale areas are whitish, yellowish, or pale chartreuse.



FIGURE 22.—*Pholidichthys leucotaenia*: swarm of juveniles, Honiara, Guadalcanal, Solomon Islands. (Courtesy of T.F.H. Publications, Inc.)

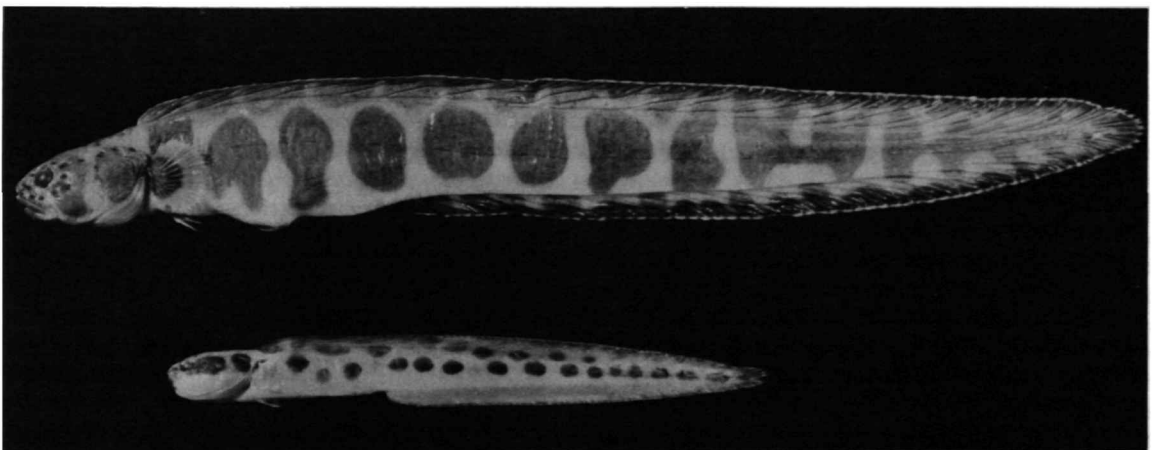


FIGURE 23.—*Pholidichthys leucotaenia*: lateral views of adult, 205 mm SL, exhibiting banded color pattern, and preadult, 108 mm SL, exhibiting spotted color pattern. Aquarium raised specimens. (Photograph by M. Giles.)

### Notes on Behavior

Striped phase juvenile *Pholidichthys* have been captured inadvertently by collectors seeking plotoid catfishes, which the juveniles resemble in color pattern and in forming large aggregations. Swimming behavior apparently changes with growth. Striped phase and preterminal color pattern juveniles have been observed in the wild swimming in the open water, usually close to the substrate and in large schools. The adults apparently remain hidden and no sightings of adults in the wild have been reported.

In aquaria, *Pholidichthys* has been observed to move mouthfuls of sand and gravel from their hiding places and discharge them some distance away, a habit that has earned *Pholidichthys* the name "engineerfish" among Philippine aquarists. Adults exposed to a current of water over sandy bottom exhibited "nervous" short backward and forward movements. The main means of propulsion was a lateral undulation moving along the entire body. Backward movement was usually initiated by reversing the direction of movement of the pectoral fins. In backward swimming the tail end becomes the fulcrum and the undulations of the body proceed anteriorly; the head moves through the widest lateral swing. Specimens we attempted to catch in aquaria sometimes did not turn around and flee but moved backward, avoiding obstacles. The row of free lateralis organs on the side of the body in *Pholidichthys* probably aids in sensing obstacles during backward swimming.

The dorsal and anal fins have a specialized role in swimming. These fins are relatively tall and very flexible and can be turned to a 90° angle to the body, both fins sometimes tilted to the same side.

### Relationships of *Pholidichthys*

Based on its general morphology, and especially the pattern of the recurrent facial nerve (RLA) and the anterior position of its pelvic fins, we place *Pholidichthys* among the Acanthopterygii, in which we include the Paracanthopterygii of recent authors (Greenwood et al., 1966; Rosen and Patterson, 1969). Within the Acanthopterygii we recognize two groups (grades): the Beryciformes and Perciformes.<sup>2</sup>

<sup>2</sup> For the purposes of our study we do not distinguish the

In a study of the patterns of the recurrent facial nerve, Freihofer (1963) found the *Serranus*-type pattern (pattern 9) only among the perciform fishes. *Pholidichthys* has the *Serranus*-type pattern. Patterson (1964) characterized the Perciformes (as opposed to the Beryciformes) on the basis of their having lost the orbitosphenoid and reduced the number of segmented pelvic-fin rays to 5 and the number of principal caudal-fin rays to 17. *Pholidichthys* has no orbitosphenoid, has further reduced the number of pelvic and caudal-fin rays, and has developed what appears to be a de novo ossification, the septal bone, in the interorbital septum. On these grounds we consider *Pholidichthys* to be a specialized perciform. Further comment on the possibility that the septal bone is a modified beryciform orbitosphenoid is in order.

Whatever its other articulations, the orbitosphenoid of beryciforms, and other more primitive fishes, articulates with the pterosphenoïds (and frontals). The septal bone of *Pholidichthys* does not articulate with the pterosphenoïds.

The orbitosphenoid, like the septal bone, is an autogenous ossification formed in the interorbital septum. The orbitosphenoid may originate as a bilateral pair of ossifications that ankylose medially (Goodrich, 1930, for *Salmo*; De Beer, 1937, for *Ameiurus* = *Ictalurus*; Daget, 1964, for *Coregonus*) or from what appears to be a single center of ossification in an unidentified engraulid we examined (there is no information on the ontogeny of the orbitosphenoid of beryciforms, although in a 12 mm specimen of *Adioryx* we examined, the orbitosphenoid was an unpaired median ossification; smaller specimens should be examined for this bone). The rhinosphenoid of characins, which is probably a separate ossification of the orbitosphenoid (Daget, 1964), also originates as a bilateral pair of ossifications that ankylose medially (Weitzman, 1962). The septal bone originates as a single, median ossification, which originates at

Paracanthopterygii as separate from the Acanthopterygii. This consideration does not reflect our individual beliefs concerning the validity of the Paracanthopterygii as a phylogenetic group. Freihofer accepts the group (at a perciform grade), but Springer does not. Our treatment of the Paracanthopterygii within the Acanthopterygii does not affect our conclusions concerning the relationships of *Pholidichthys*, but avoids lengthy discussions that are tangential to our primary concerns. In the ordinal classification we use, the Paracanthopterygii would fall into the perciform grade.

the junction of the posterior membranous and anterior cartilaginous portions of the interorbital septum and spreads anteriorly, ultimately cupping the posterior portion of the ethmoid cartilage (Figure 3).

The orbitosphenoid of the beryciforms, except *Paratrachichthys*, *Cleidopus*, and *Anoplogaster*, articulates only (exclusive of cartilage) with the frontals and pterosphenoids (S. Zehren, pers. comm.). In *Paratrachichthys* it articulates also with the basisphenoid, and in *Cleidopus*, also with the lateral and median ethmoids. In *Anoplogaster*, the orbitosphenoid articulates with the frontals, pterosphenoids, basisphenoid, parasphenoid, and lateral ethmoids, and the orbitosphenoid, basisphenoid, and pterosphenoids form a double bony orbital septum with the anterior part of the brain lying between (Woods and Sonoda, 1973). Except that it does not articulate with the pterosphenoids, the septal bone of *Pholidichthys* articulates with the same bones as the orbitosphenoid of *Anoplogaster*, but it does not form a double septum, except for a short distance anteriorly, and the brain is entirely restricted to the cranium posterior to the septal bone. The articulations of the orbitosphenoid in *Anoplogaster* appear to represent a specialized condition for beryciforms.

While the possibility that the septal bone is a specialized orbitosphenoid that has lost its connections with the pterosphenoids cannot be excluded, we believe it unlikely. Patterson (1975), who was unaware of *Pholidichthys*, reported that the only possible example of fragmentation or increase in the bones of the occipital, otic, and orbitotemporal regions of teleosts is the rhinosphenoid of characins.

Among the perciforms the gadoid fishes have been described as having an ossified interorbital septum (Svetovidov, 1948). This ossification is not autogenous, however, but represents paired, thin, dorsal crests on the parasphenoid. The median ethmoid of callionymids is highly modified and has a ventral flange that forms a bony interorbital septum (Starks, 1923, fig. 5). We have no basis for relating either of these interorbital ossifications to the septal bone of *Pholidichthys*.

The family relationships of *Pholidichthys* have received little critical attention in the literature, probably because few specimens, until recently, were available for study. Assignments of *Pholidi-*

*chthys* to a family often reflected indecision and were based only on external characters (often erroneously recorded) or assumed states of internal characters. In the following discussion we briefly summarize all the references that relate to the systematic position of *Pholidichthys*.

Bleeker (1856) first described *Pholidichthys leucotaenia* (both the genus and the species) based on a 97 mm juvenile. He placed the genus in his family Blennioidei and stated that *Pholidichthys* was between *Pholis* and *Petroscirtes* in its relationships, but also exhibited similarities to *Zoarces*, *Iluocoetes*, and *Phycocoetes*. Bleeker (1859) placed *Pholidichthys* in his subfamily Blenniiformes, in which he also included *Gunnellichthys* (presently classified in the Microdesmidae). Günther (1861) based on Bleeker (1856), included *Pholidichthys* in the Blenniidae. Jordan and Evermann (1896) included it in the Chaenopsidae, but Jordan and Evermann (1898) included it under the Blenniidae in their subfamily Pholidichthyinae (first appearance of a family-group name based on *Pholidichthys*), which also included *Pseudoblennius* (= *Emblemaria*, a chaenopsid) as the only other genus. Interestingly, Jordan and Evermann (1898) recognized the Chaenopsinae as distinct from the Pholidichthyinae.

Boulenger (1904) and Weber (1913) included *Pholidichthys* in the Blenniidae, but Jordan (1923) and Jordan, Evermann and Clark (1930) assigned *Pholidichthys* to the Chaenopsidae, which Jordan (1923) considered to be a provisional group of forms perhaps unrelated among themselves, and in which he also included, among other genera, *Gunnellichthys*. Herre and Herald (1951) also included *Pholidichthys* in the Chaenopsidae, but Herre (1953) included it in the Blenniidae. De Beaufort (1951) placed *Pholidichthys* in the Pholidichthyidae (first appearance as a family) under the order Blennioidea, and included *Gunnellichthys* as the only other genus in the family. Gosline (1955) removed *Gunnellichthys* from the Chaenopsidae and Pholidichthyidae and placed it properly in the Microdesmidae, which he demonstrated to be allied to the gobioid fishes, but mentioned nothing about the relationships of the Pholidichthyidae (by inference he eliminated it from the gobioid fishes). Norman (1966, posthumous) included *Pholidichthys* and *Gunnellichthys* in the Blenniidae as incertae sedis. Gosline (1968)

noticeably ignored the Pholidichthyidae in his treatment of the suborders of perciform fishes, even though its characteristics as reported by earlier authors should have caused him to consider it among the families he included in his suborder Blennioidei. Greenwood et al. (1966) and Lindberg (1971) either overlooked or disagreed with Gosline (1955) and included the Pholidichthyidae as a synonym of the Microdesmidae. Schultz (1966) examined the holotype of *P. leucotaenia* and tentatively allocated it to his gobioid suborder Gobiina without mention of its family placement.

Brittan (1972) briefly noted the previous confusion surrounding the relationships of *Pholidichthys*. Miller (1973) stated that there was no osteological evidence to support the removal of *Pholidichthys* from the Microdesmidae and he, therefore, included the Pholidichthyidae as a synonym of that family.

Finally, Freihofner and Lin (1974) included the Pholidichthyidae as one of the six families in their superfamily Blennioidea; the Notograptidae was another of the six.

*Pholidichthys*, thus, has been assigned only to the blennioid or gobioid fishes, or to its own family, Pholidichthyidae, with no mention of its ordinal-group relationships. Gosline's (1955) characterization of the gobioids (particularly the lack of parietals) adequately serves to exclude *Pholidichthys* from the gobioids.

The assignments of *Pholidichthys* to the blennioids were based primarily on observations that the pelvic fins are inserted slightly in advance of the pectoral fins. We find that the position of the pelvic fins varies from slightly in advance of the pectoral fins (striped juveniles) to directly under the pectoral fins (banded subadults or adults). This is more variation than we have encountered in other fishes usually placed among the blennioids, which always have the pelvic fins noticeably in advance of the pectoral fins. This variation might be considered sufficient to exclude *Pholidichthys* from the blennioids, but more discussion of this matter is required.

The innervation of the posteriormost pelvic-fin ray in *Pholidichthys* is by the 7th ventral spinal ramus, just as it is in blennioids and many other perciforms with jugular pelvic fins. Those perciforms with the most anterior pelvic fins (for instance brotulids) may have the posteriormost

pelvic-fin ray innervated by the 6th ventral spinal ramus, and those with nonjugular pelvic fins by the 8th, or a more posterior, ventral spinal ramus. If, therefore, the position of the pelvic fins is considered as a segmental, rather than a positional character, *Pholidichthys* cannot be excluded from relationship with the blennioids.

Gosline (1968) most recently treated the classification of the blennioids and defined them on the basis of the following three specializations: (1) pelvic fins, when present, inserted ahead of the pectoral fins; (2) dorsal and posterior soft anal-fin rays exactly equal in number to the vertebrae between them; (3) caudal fin usually rounded. Gosline, however, excluded several fish families that exhibited these three specializations because they also exhibited other specializations that made their inclusion among the blennioids unsatisfactory to him. Gosline's actions resulted in his blennioid fishes being a residual group with unclear relationships. Hennig (1966) has shown that in determining phylogenetic relationships, characters treated as specialized (apomorphic) at one level of classification must be treated as unspecialized (plesiomorphic) at the next higher level. Therefore, when a broader spectrum of specialized characters is examined, it is possible that some of the residual families that constitute Gosline's Blennioidei may be found to be more closely related to some of the excluded families (or even to some of the families Gosline did not consider) than they are to other residual families.

There are other problems with Gosline's definition of the Blennioidei. In particular, his character concerning the relationship of the dorsal and anal-fin elements to vertebrae is difficult to apply. For instance, a number of blenniids and clinids would be excluded from the blennioids because the last dorsal and/or anal-fin pterygiophore supports two rays that are related to only one vertebra (while procedurally in ichthyology these two rays in either fin are often counted as one ray, each of the two rays is a bilaterally paired structure and anatomically each must be considered as a separate ray). Gosline's fin-ray-to-vertebra character is a simplification that obscures complex situations that might have phylogenetic import. In *Pholidichthys*, for example, the dorsal fin originates above the second or third vertebra and the fin rays bear a one-to-one relationship with the vertebrae,

except that the anteriormost two or three rays are crowded and may associate with only one or two vertebrae. Yet, the number of rays at the anterior end of the fin equals the number of vertebrae in the same area (see Figure 9, but ignore the anomalous fourth vertebra with three neural spines and three associated fin rays). Does this condition in *Pholidichthys* actually violate Gosline's character for the blennioids, or does it only appear to do so?

In some tripterygiids, the anteriormost dorsal-fin spines are inserted in advance of the first vertebra, and these spines exceed in number the vertebrae anterior to the vertebra that begins the series relating one-to-one with the remaining dorsal-fin elements. Does this condition only superficially conform to Gosline's character? In many fishes, for example some labrids and acanthoclinids, which Gosline excluded from the blennioids, the dorsal fin begins immediately behind the head and the ratio of dorsal-fin elements to vertebrae is one-to-one except that well anteriorly there is always one vertebra associated with two elements. If the anterior portion of the dorsal fin of such a form became reduced during the course of evolution, the form might be allied to the blennioids (following Gosline) because the only dorsal-fin elements remaining would bear a one-to-one relationship with the vertebrae.

Without further belaboring the critique of Gosline's characters, suffice it to say that we believe his case for the homogeneity, or approximate completeness, of his Blennioidei is inadequately defended. Based on Gosline's definition, *Pholidichthys* might be a blennioid, but based on other specializations we believe that it shows equal evidence of relationships with certain fishes that have never been considered blennioid relatives.

*Pholidichthys* exhibits a number of specializations that remove it from the basal perciform level of organization. Most of these are of little help in establishing its suprafamilial relationships as the specializations are either unique (autapomorphic) or shared by various, apparently unrelated groups of perciforms. The most prominent autapomorphic characters are: (1) The presence of a septal bone. (2) The lack of an ascending process on the parasphenoid in adults (at least 140 mm) and resulting entry, unimpeded, of the exceptionally long prootic and large pterosphenoid into the orbital region. The gobiesocids and alabetids also lack an

ascending process on the parasphenoid. These fishes have the cranium greatly depressed, however, and what might be the parasphenoid's ascending processes are lateral projections. Both of these families also lack pterosphenoids. In some gadoids, the parasphenoid appears to lack an ascending process (Svetovidov, 1948). In these gadoids the pterosphenoid is almost entirely anterior, and dorsal, to the prootic, and the position of these two bones relative to each other is entirely unlike their position in *Pholidichthys*. In the highly specialized Mastacembelidae and Chaudhuriidae the parasphenoid also lacks an ascending process, but either the prootic is entirely blocked by the pterosphenoid-pleurosphenoid bones from entering the postorbital margin or the pterosphenoid-pleurosphenoid bones are absent (D. E. Rosen, pers. comm.). (3) the large, complex metapterygoid. (4) Apparent displacement dorsally and freeing of the lateralis organs (innervated by the ramus buccalis facialis) of the infraorbital canal in the gap area and partial invasion of the gap by free lateralis organs innervated by the ramus buccalis accessorius facialis of the truncus hyomandibularis. (5) Presence of free lateralis organs along the horizontal septum anteriorly ventral to the dorsal longitudinal collector lateral-line nerve.

Other specializations that we believe offer no evidence of relationships are the following apparently convergent or autapomorphic characters: (1) Single nostril (also present in such diverse groups as cichlids, congiiopodids, and zoarceoids). (2) Eel-like form (also in congrogadids, alabetids, blennioids, and microdesmids). (3-5) Gosline's (1968) blennioid specializations (see discussion on page 36). (6) Reduction of postcleithra. We have not seen an exact duplication of the pholidichthyid postcleithrum, but various perciforms have reduced the postcleithra; see Smith-Vaniz and Springer (1971, fig. 15) for certain blenniids; trichonotids, leptoscopids, and alabetids, among others, have no postcleithra. (7) Reduction of caudal-fin structure. We have not seen an exact duplication of the pholidichthyid caudal-fin structure, but various combinations of fusions and losses in the structure of this fin occur within and among a large number of families of fishes. The fusion of the ventral hypural plate to the urostyle centrum and loss of a few fin rays in the eel-like *Notograptus* (Notograptidae) would result

in a caudal-fin structure similar in appearance to that of *Pholidichthys*, as would the loss of an epural and a few procurrent fin rays in the blennioid *Xiphasia*, which is also eel-like. Caudal-fin reduction is apparently often correlated with an eel-like body form. (8) Reduction of cephalic seismosensory canals and associated loss of some circumorbital bones. We have not seen an exact duplication of the pholidichthyid cephalic seismosensory canal system, but an incomplete circumorbital canal with loss of some circumorbital bones also occurs in the clinid *Exerpes*, the ammodytids, some stichaeoids, the callionymids and the gobiesocids. Lack of a connection between the preopercular and more dorsal head canals occurs in *Exerpes* (Clinidae), the ophidioid *Brotulataenia* (Cohen, 1974) and stichaeoids (Makushok, 1961). Lack of a supratemporal commissure occurs in many fishes, for example, pseudochromids. (9–21) Lack of: scales, predorsal bones (Smith and Bailey, 1961), a subocular shelf (Smith and Bailey, 1962), vomerine and palatine teeth, dorsal and anal-fin spines, and a lateral-line canal on the body; fusion of: associated proximal and medial dorsal and anal-fin radials, and all hemal arches with their respective centra; possession of: a nonprotractile premaxillary and restricted gill opening. All these are characters found variously in a wide variety of perciform fishes. (22) Lack of a medially projecting flange on the prootic and consequent lack of an osseous contribution by the prootics to the roof of the posterior myodome (also, at least, found in some blennioids (Springer, 1968), gobiesocids, and dactyloscopids). (23) Wide separation, from each other, of the anterior ends of the (rodlike) pelvises (also found in cryptacanthodids and *Notographtus*). (24) Innervation of the posteriormost pelvic-fin ray by the seventh ventral spinal ramus (also in Blenniidae, Coryphaenidae, Mugiloididae, Rachycentridae).

We have found three specializations exhibited by *Pholidichthys* that we believe must be considered in a review of its subordinal relationships. These are the completely fused 5th ceratobranchials (and other gill-arch specializations), the interrupted sulcus of the sagitta, and the trunk lateral-line nerve pattern. A discussion of these characters follows.

GILL-ARCH SPECIALIZATIONS.—Fusion of the 5th ceratobranchials has been reported previously

among the perciforms only in the families Pomacentridae, Embiotocidae, Labridae, Odacidae, and Scaridae.<sup>3</sup> Nelson (1967 and pers. comm) investigated the gill arches of these families in an attempt to determine whether they were closely related. He concluded that aside from the fused ceratobranchials there was little in gill-arch structure to indicate that these families were, or were not, closely related. He did note that among these families there was a tendency for the 1st basibranchial to be displaced downward and for the 2nd infrapharyngobranchial to lose its typical connection with the 1st epibranchial.

The gill-arch structure of *Pholidichthys* exhibits a number of similarities, aside from its fused 5th ceratobranchials, with the structure of the families Nelson treated. Nelson (1967) did not discuss the Odacidae, although he included it among the labroids (1969). He has since commented (pers. comm.) that its gill arches were not appreciably different from those of the labrids and scarids. Most of the anterior end of the 1st basibranchial of *Pholidichthys* is ventral to the basihyal, just as it is in the pomacentrids, but the 1st basibranchial lacks the posterior process of that bone as found in the pomacentrids. In contrast, the 1st basibranchial is entirely ventral to the basihyal and 2nd basibranchial in the embiotocids, but is only expanded ventrally (both anteriorly and posteriorly) in the labroids.

<sup>3</sup>Norman (1966) reported fused lower pharyngeals in the sciaenid genera *Pogonias* and *Aplodinotus*. Juveniles of these two genera have distinctly separate 5th ceratobranchials. Gosline (1955) reported completely fused 5th ceratobranchials in the gobioid *Kraemeria samoensis*. We did not have that species available, but in an adult *K. bryani* we examined, the 5th ceratobranchials were completely separate. Matsubara and Iwai (1959) described and illustrated the osteology of *Kraemeria sexradiata*. They also reported that the 5th ceratobranchials were separate in their species. Gosline also reported that the tooth plates of the 5th ceratobranchials were fused in the gobioid *Awaous stamineus* but that a suture was evident between the bones on their ventral surface. A juvenile *A. tajasica* we examined had the 5th ceratobranchials completely separate. Cichlids are often reported to have fused 5th ceratobranchials. In a juvenile *Cichlasoma cyanoguttatum* we examined, the 5th ceratobranchials (and their associated tooth plates) were closely joined, but a suture was evident between them both dorsally and ventrally, and the two bones were easily separated. In contradistinction, the 5th ceratobranchials are completely fused, without a joint between, in the earliest stages of the Pomacentridae, Embiotocidae, labroid fishes, and *Pholidichthys*.

In *Pholidichthys* there is no interarcual cartilage between the uncinatous process of the 1st epibranchial and the 2nd infrapharyngobranchial, and the uncinatous process is ligamentously attached to the 2nd infrapharyngobranchial. The uncinatous process and interarcual cartilage are both present and attach to the 2nd infrapharyngobranchial in the pomacentrids. Neither the uncinatous process nor cartilage are present in the embiotocids, and the 1st epibranchial is not connected to the 2nd infrapharyngobranchial; the condition is essentially the same in the labroids except that there is an uncinatous process on the 1st epibranchial which attaches ligamentously to the 2nd epibranchial.

The 2nd infrapharyngobranchial bears no teeth in *Pholidichthys* and the labroids, but is toothed in the pomacentrids and embiotocids.

The tooth plate of the 4th infrapharyngobranchial is either fused to the 3rd infrapharyngobranchial or lost (not possible to tell which) in *Pholidichthys* and the labroids, but is autogenous in the pomacentrids and embiotocids.

Thus, the gill-arch structure of *Pholidichthys* is somewhat intermediate between that of the Pomacentridae and Embiotocidae, on the one hand, and the labroids, on the other, but perhaps more similar to that of the labroids.

All of those gill-arch specializations, except the fused 5th ceratobranchials, shown by these families occur in various other families. For example, the ventral displacement of the 1st basibranchial occurs in many diverse families, including, among others, the Sciaenidae, Cepolidae, Opistognathidae, and Blenniidae; a toothless 2nd infrapharyngobranchial is present in *Synanceia* and some Apogonidae (Fraser, 1972) and Opistognathidae; the interarcual cartilage is absent in a large variety of fishes including (but not limited to) the Blenniidae, Batrachoididae, Callinonymidae, Cottidae, Trichonotidae, Trichodontidae, Uranoscopidae, in which the uncinatous process of the 1st epibranchial is variously present or absent, but when present attaches ligamentously to the 2nd infrapharyngobranchial. Similarly, the 4th infrapharyngobranchial tooth plate is either missing or fused with the 3rd infrapharyngobranchial (not possible to tell which) in many families (*e. g.*, Batrachoididae, Blenniidae, Callinonymidae, Cottidae, Gobiocidae). The presence or state of the 1st infrapharyngobranchial in perciforms is widely variable;

for instance, it is present (as cartilage) in the clinids but absent in the related blenniids.

We conclude that the gill-arch structure of *Pholidichthys* offers no unequivocal information concerning its relationships.

Among the families with fused 5th ceratobranchials, only *Pholidichthys* and the labroids bear an essentially one-to-one relationship between the dorsal and anal-fin elements. We have already discussed the problems of using this specialization as a basis for relating groups of fishes. We know of no other specializations, except the single nostril of pomacentrids (also present in zoarceoids, congiopodids, and notothenioids), shared by *Pholidichthys* and the other fishes with fused 5th ceratobranchials.

THE SAGITTA.—Mr. J. E. Fitch provided us with his assessment of the relationships of *Pholidichthys* based on his examination of the sagitta. He informed us that the overall configuration and arrangement of the sagittal sulcus is the most important otolith character for determining teleost relationships; however, he noted that similarities in the sulcus of two forms does not necessarily indicate relationship, nor do dissimilarities necessarily indicate nonrelationship. To his knowledge, the only fish with a sulcus similar to that of *Pholidichthys* is *Cepola* (Cepolidae).

Fitch informed us that the *Cepola* sagitta differs from that of *Pholidichthys* in that the *Cepola* ostium opens more dorsad on the anterior margin, the crista superior is less pronounced, and the sulcus is more curved (sigmoid).

We have examined a cleared and stained specimen of *Cepola* and a whole specimen and radiograph of *Acanthocephala* (the only two genera in the Cepolidae) in a search for other shared specializations that might indicate a close relationship between the cepolids and *Pholidichthys*. In general, cepolids are much less specialized than *Pholidichthys*.<sup>4</sup> They are elongate, like *Pholidichthys*,

<sup>4</sup>Okada and Suzuki (1956) synonymized the Owstoniidae with the Cepolidae based on osteological characters. We are inclined to agree that the owstoniids are more closely related to the cepolids than they are to the opistognathids, near which they have often been classified. We do not have skeletal material of the owstoniids available, but based on Okada and Suzuki's study and our examination of radiographs and whole specimens of *Owstonia weberi* and *Sphenanthias sibogae*, we find that the owstoniids are even less specialized than the cepolids, and offer less evidence of relationships with

and have reduced the number of dorsal-fin spines to 2 and anal-fin spines to 1, which shows a trend toward only segmented rays in these fins, the condition found in *Pholidichthys*. Except anteriorly, the dorsal and anal-fin elements bear a one-to-one relationship with the vertebrae in *Cepola* (like *Pholidichthys*), but in *Acanthocephala* the dorsal-fin elements bear a 1.44 to 1, and the anal-fin elements (posteriorly) a 1.25 to 1, relationship with the vertebrae, an apparently less specialized condition. The cepolids (and owstoniids) have a single postcleithrum, but this element appears to occupy the extent of both the dorsal and ventral postcleithra of those fishes that have two postcleithra. Although *Pholidichthys* also has a single postcleithrum, it is represented only by a small, thin plate of bone dorsally. It is not possible to tell whether this plate represents a reduction of the single cepolid postcleithrum or the remains of a dorsal postcleithrum and associated loss of a separate ventral postcleithrum. As noted above, the first basibranchial of *Cepola* is ventral in position, even more so than in *Pholidichthys*, but this specialization does not indicate relationships unequivocally. We found no other shared specializations between the cepolids and *Pholidichthys*, nor did we find any others between the cepolids and the families of fishes with fused 5th ceratobranchials. Thus, we have no evidence that *Pholidichthys* is any more closely related to cepolids than to any of the families with fused 5th ceratobranchials.

*Pholidichthys* than do the cepolids. In addition, owstoniids have a pattern 8 recurrent facial nerve (Freihof, unpublished), whereas opistognathids, like *Pholidichthys*, have a pattern 9 nerve (Freihof, 1963). Cepolids do not have a recurrent facial nerve (Freihof, unpublished), but if cepolids and owstoniids are derived from an ancestor that had a pattern 8 nerve, it seems unlikely that these two families are closely related to either opistognathids or *Pholidichthys*. Owstoniid *sagittae* have not been described, nor have we or Fitch seen any.

**TRUNK LATERAL-LINE NERVE PATTERN.**—In *Pholidichthys* the trunk lateral-line nerve pattern has the main feature of an acanthopterygian pattern: the dorsal collector lateral-line nerve. This nerve exhibits two specializations in *Pholidichthys*: it has only two dorsal rami (versus five rami in a perciform such as *Perca*) and the nerve returns to the horizontal septum above the anus, or not far posterior to it (versus returning to the septum far posteriorly, on the caudal peduncle, as occurs in *Perca*).

While the information on trunk lateral-line nerve patterns in fishes is limited, we find that the pattern of *Pholidichthys* is duplicated only in the Clinidae, Blenniidae, and Dactyloscopidae (Springer, unpublished, considers these three families, together with the Tripterygiidae and Chaenopsidae, which have not been examined for the pattern, to form a closely related group, the tropical blennioids). On the basis of shared osteological specializations, however, these three families are not closely related to *Pholidichthys*, and although it is possible that *Pholidichthys* could be a member of the group including the primitive sister group of the tropical blennioids, considerably more information on other perciform fishes will be necessary to establish such a relationship. If the distinctiveness of the nerve pattern holds, it would furnish evidence for a common derivation of *Pholidichthys* and the families of tropical blennioids.

### Summary

Based on its having a *Serranus*-type pattern of the recurrent facial nerve, *Pholidichthys* is a perciform fish. Its subordinal relationships are unclear, but based on limited evidence from the trunk lateral-line nerve pattern, it shows possible relationship with the tropical blennioid fishes (suborder Blennioidei).

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