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INTRODUCTION

THE SUPRAORDINAL TERM Paracanthopterygii was introduced by Greenwood, Rosen, Weitzman, and Myers (1966, p. 387) to indicate that the percopsiform, gadiform, ophidioid, zoarcoid, batrachoidid, lophiiform, and gobiesocid fishes form a related group containing members that are in many ways more primitive than the acanthopterygians and "represent a spiny-finned radiation more or less comparable morphologically with that of the Acanthopterygii." Thus constituted, the superorder Paracanthopterygii contains between 200 and 250 living genera placed in 30 families and five orders. Only the five living genera of percopsiforms, the gadoid *Lota*, a few brotulids and batrachoidids, and the fluviatile gobiesocids are fresh-water fishes; the remainder are primarily marine. With the exception of the littoral and fluviatile gobiesocids, the paracanthopterygians generally occupy dysphotic environments. They range in size from a few centimeters (amblyopsids) to a meter or more.

The work reported here was begun as a combined neontological and paleontological investigation to test the limits and validity of the paracanthopterygian group. It may be said immediately that, although we have found a good deal of evidence supporting the validity of the Paracanthopterygii, we have found nothing to suggest that any member of the group as limited by Greenwood, Rosen, Weitzman, and Myers is incorrectly placed, or any firm indication that other fishes should be included. Questions of the origin and relationships of the basal paracanthopterygians have led us into subsidiary investigations and a discussion of the fishes previously grouped in the Myctophoidei, Beryciformes, and cognate groups, and for them we have attempted a classification consistent with new insights into their phylogenetic relationships.

Of the two most important specializations indicating that the paracanthopterygians form a related group, one is found in the upper jaw, the other in the caudal skeleton. In the upper jaw the maxilla is controlled by a muscle, the levator maxillae superioris, which originates on the palatoquadrate, passes medial to the bulk of the adductor mandibulae, and inserts on the maxilla. In the caudal skeleton the upper hypurals fuse with the free second ural centrum, the second pre-ural centrum has a complete neural spine, and there are never more than two epurals. The first of these specializations is found in all groups of paracanthopterygians except the gobiesocids; the second, in all except the lophiiforms and gobiesocids, which lack a free second ural centrum. This distinctive combination of jaw and tail specializations is unknown, and probably does not occur, in any acanthopterygian. Subsidiary characters uniting the paracanthopterygians include the form of the skull roof, with the postorbital part usually broad and flat, the open posttemporal fossa rather than the supratemporal fossa being the primary site of trunk muscle insertion, and the supraorbital sensory canal running in an open trough (except in gobiesocids); the form of the occipital condyle, which invariably has prominent, well-separated exoccipital components; the premaxilla, in which the postmaxillary process is usually notched posteriorly (the "gadoid notch") and the alveolar process is often flexible distally; the general absence of supramaxillae, a single supramaxilla being present only in one percopsiform and in ophidioids; the operculum, in which the opercular is reduced and angulate and the subopercular is large; the frequent occurrence of more than four pectoral radials (gadiforms, batrachoidiforms, lophiiforms, and possibly gobiesociforms); and the general absence or suppression of fin spines. Other paracanthopterygian characters are of more limited distribution but serve to demonstrate relationship between subgroups such as the percopsiforms and gadiforms, lophiiforms and gobiesocids, and others.

The origin and early evolution of the acanthopterygians have been recently discussed by Patterson (1964, 1967a, 1968b). In brief, the acanthopterygians can be traced back into the Cretaceous Beryciformes, the Berycoidei standing near the ancestry of the Perciformes and at least some of the preperciform groups. It is central to our conception of the paracanthopterygians that the

Percopsiformes stand in the same relation to the paracanthopterygians as the Beryciformes do to the acanthopterygians. In seeming confirmation of this, we have found that a Cretaceous marine fossil, previously placed among the polymixioid Beryciformes, is a percopsiform; and just as the only known Cretaceous acanthopterygians are Beryciformes, the only known Cretaceous paracanthopterygian is a percopsiform. Because of their long and moderately complete fossil record we have been able to investigate in some detail the changes undergone by the percopsiforms during their history, and these changes are of great value in an interpretation of the structure of other paracanthopterygian groups in which the fossil record is deficient or lacking.

Before presenting the detailed evidence on the structure and interrelationships of the paracanthopterygians, we should state that our aim is to recognize phylogenetic relationships and to produce a classification containing monophyletic groups, with consequent emphasis on "vertical" divisions. The concept of "horizontal" grades or "levels of organization," although useful, appears to us to be a preliminary and transient stage in deciphering the relationships of organisms—the recognition of grades is essentially the recognition that the representation in those levels of organization is or may be polyphyletic. In the phylogenetic arrangements we have attempted to emphasize groups united by shared specialized characters, and to avoid definition of groups characterized by shared primitive features. The classification of the acanthopterygian fishes as it stands at present is an example of the ultimate futility of using assemblages of primitive characters to express relationship, with large, catch-all basal groups in effect defined arbitrarily by specializations that they do not have (Percoidei), leaving many derived and specialized groups of high rank and of uncertain relationships with one another and with the basal groups.

ACKNOWLEDGMENTS

We owe our greatest thanks to Dr. Bobb Schaeffer, of the Department of Vertebrate Paleontology of the American Museum of Natural History, who provided the original stimulus for this combined neontological and paleontological study by his generous offer of a fine series of Eocene percopsiforms from the Green River Shales, Wyoming. Dr. Schaeffer had himself been working on these fishes for some time, and the specimens and various helpful manuscript notes were turned over to us for our unrestricted use. We are similarly indebted to many other people for advice freely offered and for the loan or gift of large numbers of Recent and fossil specimens: Drs. S. E. Bendix-Almgreen, R. M. Bailey, J. Böhlke, N. Bonde, D. M. Cohen, B. B. Collette, D. H. Dunkle, R. H. Gibbs, Jr., P. C. Goody, P. H. Greenwood, E. A. Lachner, N. B. Marshall, G. W. Mead, B. Patterson, and C. R. Robins, Prof. P. Siegfried, and Drs. C. L. Smith, J. C. Tyler, and N. J. Wilimovsky. Drs. D. M. Cohen, P. H. Greenwood, G. S. Myers, G. J. Nelson, and S. H. Weitzman kindly read and commented on the typescript.

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ABBREVIATIONS

INSTITUTIONAL ABBREVIATIONS

A.M.N.H., the American Museum of Natural History
A.N.S.P., Academy of Natural Sciences of Philadelphia
B.M.N.H., British Museum (Natural History)
G.P.I.M., Geologisch-Paläontologisches Institut, Münster University
M.C.Z., Museum of Comparative Zoology, Harvard University
N.I.O., National Institute of Oceanography, Washington, D. C.
U.F., Florida State Museum, University of Florida
U.M.M.L., University of Miami Marine Laboratory
U.M.M.Z., Museum of Zoology of the University of Michigan
U.S.N.M., United States National Museum, Smithsonian Institution, Washington, D. C.

ANATOMICAL ABBREVIATIONS

A_1, A_2, divisions of adductor mandibulae muscle
aap, adductor arcus palatini muscle
acr, accessory upper pectoral radial
adf, adipose fin
am, adductor mandibulae muscle
ant, antorbital

armx, articular head of maxilla
arpmx, articular process of premaxilla
art, articular
asclac, ascending process of lacrimal
ascpmx, ascending process of premaxilla
aspo, autosphenotic
atfc, anterior opening of trigemino-facialis chamber
bb$_{1-3}$, basibranchials
bbt, basibranchial tooth plates
bcsc, bony cover of supraorbital sensory canal
bcst, bony cover of supratemporal sensory canal
bh, basihyal
B lig, Baudelot's ligament
boc, basioccipital
bocf, basioccipital facet of occipital condyle
cart, cartilage
cb$_{1-5}$, ceratobranchials
cexo, facet of first vertebra joining exoccipital facet
ch, ceratohyal
cl, cleithrum
coden, coronoid process of dentary
cor, coracoid
corpr, posteroventral process of coracoid
csc, caudal scute
ctj, connective tissue in cervical joint
dab, dorsal accessory bone in caudal skeleton
dbb, dermal basibranchial plate
dbbt, basibranchial teeth
dct, dense connective tissue
den, dentary
det, dense pad of supramaxillary tissue
do, dilatator operculi muscle
dspo, dermosphenotic
eb$_{1-4}$, epibranchials
ect, ectopterygoid
eh, epihyal
elms, elevation on maxilla for insertion of levator maxillae superioris muscle
emlig, ethmomaxillary ligament
encl, endocleithrum
end, endopterygoid
ep, epural
epo, epiotic
exo, exoccipital
exof, exocipital facet of occipital condyle
fepsa, foramen of efferent pseudobranchial artery
fhv, foramen of head vein (jugular)
fhyo VII, foramen of hyomandibular trunk of facial nerve
fica, foramen of internal carotid artery
foa, foramen of orbital artery
frcr, frontal crest
fro, frontal
hb$_{1-3}$, hypobranchials
hpp, hypurapophysis
hpu, haemal spine of pre-ural centrum
hyb, hyoid bar
hyo, hyomandibular
hyof, articular surface for hyomandibular
hyp$_{1-6}$, hypurals
icom, commissure between infraorbital and supraorbital sensory canals
ih, interhyal
im, intermuscular bone
inf, infraorbital bone
int, intercalar
iop, interopercular
lac, lacrimal
lap, levator arcus palatini muscle
lat, lateral ethmoid
lhh, lower hypophyal
lms, levator maxillae superioris muscle
md, mandible
mem, dermal bone (or part thereof) that is uncalcified
mes, mesethmoid
met, metapterygoid
mmt, maxillo-mandibular tendon
mx, maxilla
mxam, maxillary division of adductor mandibulae muscle
mxt, maxillary teeth
na, nasal
not, notochordal plug
npu$_{2-5}$, neural spines of pre-ural centra 2–5
npu$_2$a, npu$_2$p, anterior and posterior members of double neural spine on second pre-ural centrum
ns, neural spine
nv$_{1-3}$, neural arches of vertebrae 1–3
op, opercular
opf, outline of pectoral fin
orb, outline of eyeball
otp, outline of tooth patch
pa, parietal
pal, palatine
pas, parasphenoid
pasc, parietal branch of supraorbital sensory canal
pb, pharyngobranchial
pcl, postcleithrum
phyp, parhypural
pl, pleural rib
pmpmx, postmaxillary process of premaxilla
pmx, premaxilla
pop, preopercular
pplig, palato-premaxillary ligament
prbr, projection on head of branchiostegal ray
pro, prootic
ptf, posttemporal fossa
ptfc, posterior opening of trigemino-facialis chamber
pto, pterotic
pts, pterosphenoid
ptt, posttemporal

pu_{1-5}, pre-ural centra
qu, quadrate
rec VII, foramen of recurrent branch of facial nerve
ret, retroarticular
roc, rostral cartilage
sca, scapula
scb, scale bone (supratemporal)
scl, supracleithrum
scom, supraorbital commissure
segpmx, segmented alveolar process of premaxilla
smx, supramaxilla
soc, supraoccipital
sop, subopercular
sos, subocular shelf
sup, supraorbital bone
sym, symplectic
u_{1-3}, ural centra
ud, urodermal
uh, urohyal
uhh, upper hypohyal
un, uroneural
vab, ventral accessory bone in caudal skeleton
vo, vomer
vptt, ventral limb of posttemporal
III, V, VII, IX, X, foramina of cranial nerves

THE PARACANTHOPTERYGIAN CAUDAL SKELETON

THE CENTRAL PARACANTHOPTERYGIANS, the percopsiforms, gadiforms, and batrachoidiforms, are characterized by three features of the caudal skeleton: a large second ural centrum, usually fused with one or more of the upper hypurals, a long, complete neural spine on the second pre-ural centrum, and a maximum of two epurals. In order to assess the significance of these characters, it is necessary to discuss how they arose, and how this type of caudal skeleton is related to the caudal skeletons of the myctophoids and basal acanthopterygians, which are at a similar level of specialization.

In primitive myctophoids such as *Aulopus* and the Cretaceous *Nematonotus* (text figs. 1, 2) the caudal skeleton contains six hypurals, three epurals, two uroneurals, and a free second ural centrum. The first ural and first pre-ural centra have fused into a compound centrum carrying the parhypural and the two lower hypurals. The second pre-ural centrum has a short neural spine, about half as long as its predecessor; there is evidence that this short second pre-ural neural spine is primitive for the teleosts as a whole (Patterson, 1968b, p. 84; see also Monod, 1968, figs. 108, 447, of *Pterothrissus* and *Umbra*).

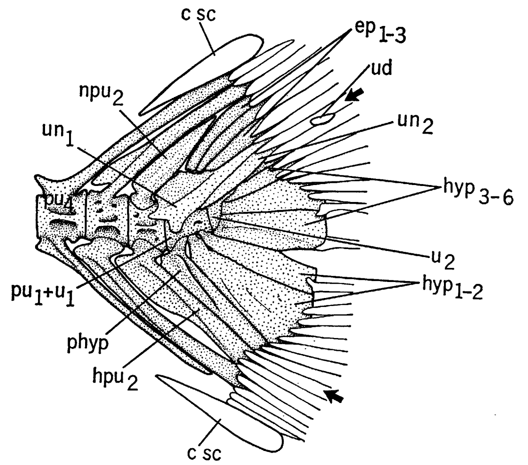

FIG. 1. *Nematonotus longispinus* Davis, Cenomanian, Hajula, Lebanon. Restoration of the caudal skeleton, based mainly on A.M.N.H. No. 3621. Arrows indicate the outermost (unbranched) principal rays.

The most widespread development from this primitive type of caudal skeleton involves fusion of the second ural centrum with the preceding compound centrum, accompanied by a reduction of hypurals to five. These changes take place in advanced myctophoids (*Myctophum*, Rosen, 1964, fig. 23C; present paper, text fig. 2), berycoids (*Melamphaes*, holocentrids, *Diretmus*; Patterson, 1968b), and perciforms (Gosline, 1961b; Monod, 1967, 1968; Patterson, 1968b). In the central paracanthopterygians, percopsiforms (text fig. 16), gadiforms (text fig. 3C, E; Barrington, 1937; Rosen, 1962; Gosline, 1963), and batrachoidiforms (text fig. 4; Regan, 1912), a different type of fusion occurs. The second ural centrum fuses not with the preceding compound centrum but with one or more of the upper hypurals, retaining an intervertebral articulation with the preceding centrum. Apart from the eels and osteoglossomorphs, in which a similar fusion takes place while the first ural and pre-ural centra are still separate, this type of caudal skeleton is known elsewhere only[1] in lampridiforms (Gosline, 1961a, fig. 3D). Within the ophidioid gadiforms, many genera have the upper and lower hypurals emanating from a single centrum, as they do in the Perciformes [but see text fig. 3E and Monod (1968, figs. 714, 715), Poll and van Moll (1966), and van Moll (1967)], and this condition is found in all lophiiforms (text fig. 4E) and gobiesocids (text fig. 4F). In macrourids the caudal skeleton is reduced beyond recognition (Monod, 1968, fig. 567), as it is in most zoarcids (but see Yarberry, 1965, fig. 9).

Although fusion of the upper hypurals with the second ural centrum is characteristic of the central paracanthopterygians, there are

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[1] A caudal skeleton of the myctophoid *Neoscopelus macrolepidotus* showing this condition has been illustrated by Greenwood, Rosen, Weitzman, and Myers (1966, fig. 3), but in fact the upper hypurals are not fused with the second ural centrum in *Neoscopelus* (text fig. 2).

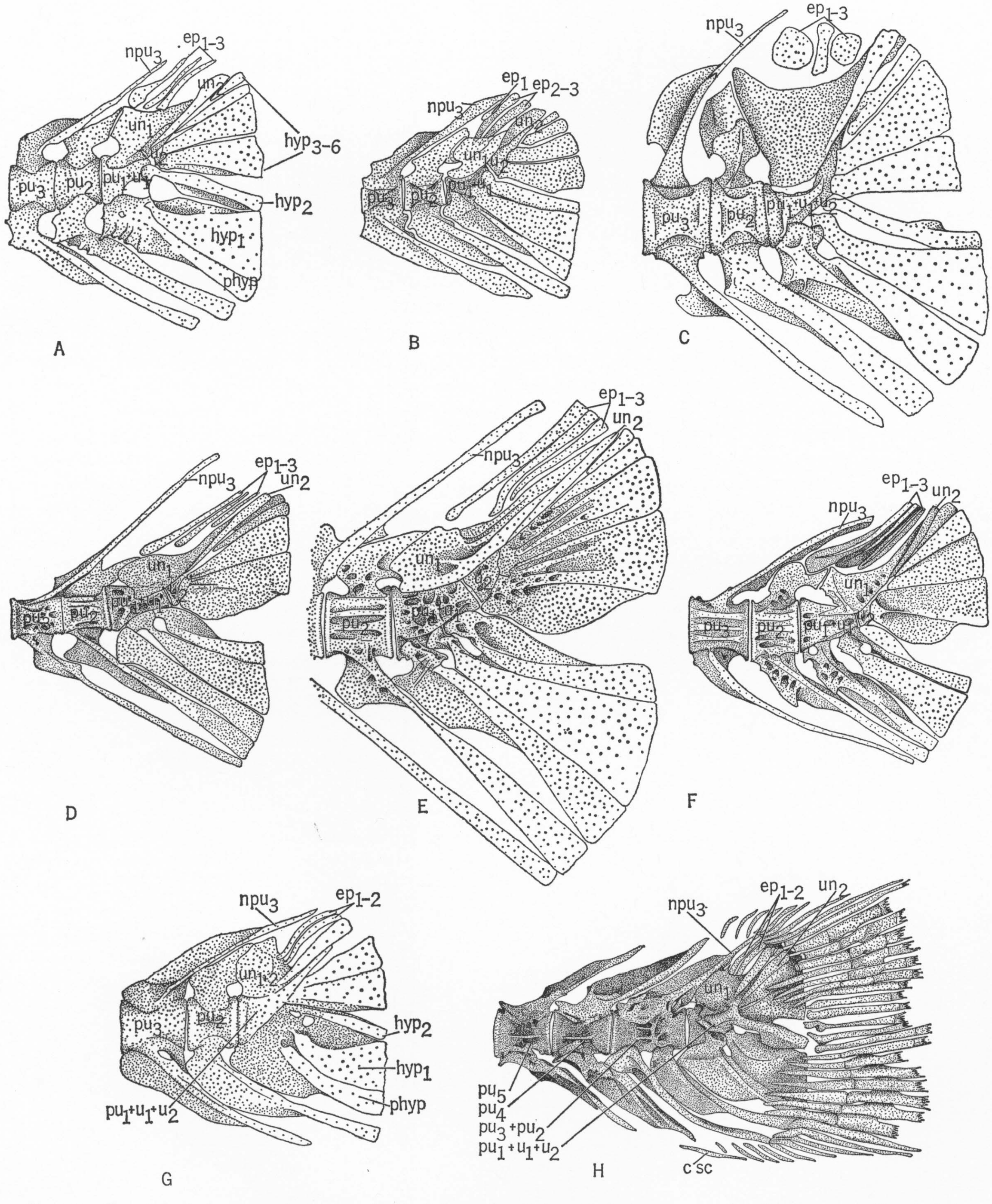

FIG. 2. Caudal skeletons of myctophoid fishes. A. *Chlorophthalmus agassizi* Bonaparte. B. *Aulopus japonicus* Günther. C. *Scopelarchoides nicholsi* Parr. D. *Neoscopelus macrolepidotus* Johnson. E. *Solivomer arenidens* Miller. F. *Scopelengys tristis* Alcock. G, H. *Saurida brasiliensis*, H showing an apparent spine on pu_2 (identified as npu_3) as a result of vertebral fusion.

a few generalized forms in which this fusion has not yet occurred. These include the living morid *Eretmophorus* (text fig. 3D), in which there are five autogenous hypurals, and the fossil percopsiforms *Erismatopterus*, *Amphiplaga* (both Eocene; text figs. 22, 26), and *Sphenocephalus* (Upper Cretaceous; text fig. 35), in all of which there are six hypurals. The condition of the caudal skeleton in these fossil percopsiforms is the most primitive known among paracanthopterygians. These fishes show that Monod (1968) is wrong in interpreting the percopsiforms, gadoids, and *Brotula* as having two free ural centra. The structure interpreted by Monod as the first hypural is the parhypural, and his second hypural is the first and second hypurals fused.

The caudal skeleton of lampridiforms, which shows the typical paracanthopterygian fusion of the upper hypurals with the second ural centrum (Gosline, 1961a), may be distinguished from that of percopsiforms and that of gadiforms by the presence of three epurals and by the neural spine of the second pre-ural centrum, which may be reduced to a low crest (*Lampris*, *Velifer*; Gosline, 1961a, fig. 3D), or may be half as long as its predecessor (*Palaeocentrotus*; Kühne, 1941, fig. 2), but is in no instance fully developed. From the primitive, short, second pre-ural neural spine, as in *Nematonotus*, *Aulopus*, and *Palaeocentrotus*, there are three evolutionary possibilities. The spine may remain about the same height but expand into a plate extending back between the uroneurals; it may decrease in height to a low crest, the first epural coming to lie above it; or it may increase in length into a full neural spine, supporting procurrent fin rays. The first of these is characteristic of myctophoids (text fig. 2); the second, of berycoids and perciforms (Gosline, 1961b; Monod, 1968; Patterson, 1968b); the third, of polymixioids (Gosline, 1961a, p. 14; Patterson, 1968b, figs. 6–9) and all paracanthopterygians. A complete second pre-ural neural spine occurs in many zeiforms, perciforms, and more advanced acanthopterygians, but in these groups there is, almost invariably, clear evidence that this condition is secondary, produced by the fusion of the first epural with a neural crest of normal berycoid or perciform type (see discussion in Patterson, 1968b, p. 89, and Monod, 1968). The sort of evidence involved here is the presence of a low neural crest in the most primitive members of a group, as in *Antigonia* and *Capros* among the zeiforms, *Pristolepis* among the nandids, or *Scomber* among the scombroids, or the presence of a closed joint between the spine and the arch in primitive members of a group, as in *Psettodes* among the pleuronectiforms. There is no evidence that the second pre-ural neural spine of the paracanthopterygians arose in this way, but since these fishes never have more than two epurals, like the various acanthopterygian groups showing a secondary neural spine, it is necessary to consider carefully whether the paracanthopterygian neural spine is primary or secondary. In other words, did the ancestors of early percopsiforms such as *Amphiplaga* and *Sphenocephalus* have a low neural crest on the second pre-ural centrum, with which the first epural later fused, or did they have a short neural spine of primitive type which elongated into a full neural spine, one epural being lost? The non-paracanthopterygian fishes most similar to the basal percopsiforms appear to be the polymixiids, and this similarity is most clearly shown in the caudal skeleton and fin. The percopsiforms (amblyopsids excluded), polymixiids, and the Cretaceous "beryciforms" *Dinopteryx* and *Pycnosteroides* have constantly 18 principal caudal rays with 16 branched, and the caudal skeleton of basal percopsiforms differs from that of polymixiids only in having one less epural. The complete second pre-ural neural spine of polymixiids is certainly primary since it occurs in conjunction with three epurals. Evidently it arose spontaneously by elongation of a short neural spine, as occurs in some specimens of the Cretaceous *Aipichthys* (Patterson, 1968b, fig. 11). The similarity between percopsiforms and polymixiids suggests that their second pre-ural neural spine arose in the same way. It is also worth noting that the earliest percopsiform, the Cretaceous *Sphenocephalus*, appears both too primitive anatomically and too ancient to have developed a second pre-ural neural spine secondarily by fusion of an epural with a neural crest, because this presupposes an ancestral series of forms in which the

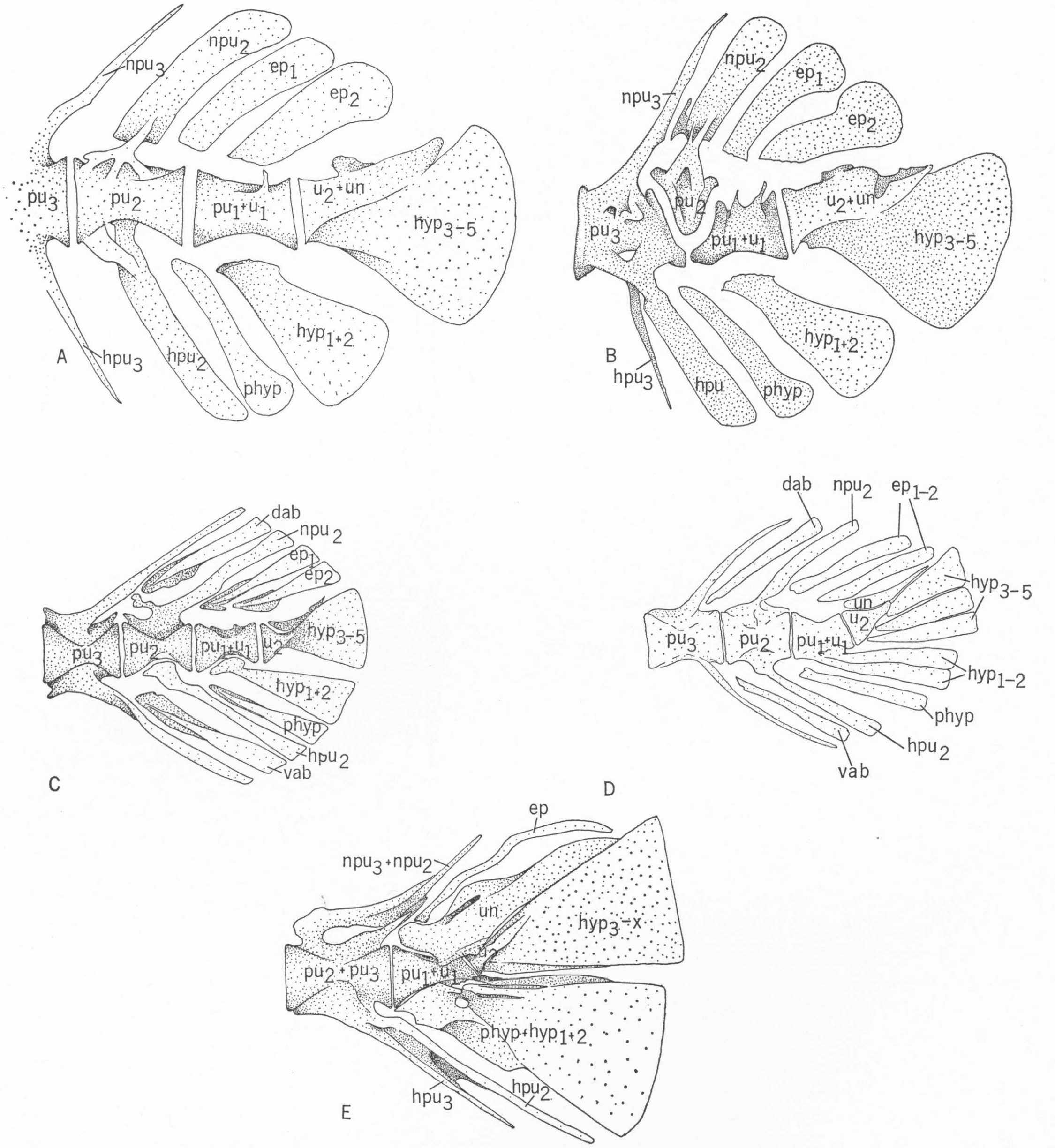

FIG. 3. Caudal skeletons of gadiforms. A, B. *Theragra chalcogramma* (Pallas), B showing partial loss of second pre-ural centrum (pu_2). In B, the spatulate haemal spine (identified as hpu) is believed to be from the second pre-ural centrum (pu_2). Compare haemal spines on pu_3 in B with hpu_2 and hpu_3 in A. C. *Urophycis floridanus* (Bean and Drexel). D. *Eretmophorus kleinenbergi* Giglioli. E. *Ogilbia* sp.

primitive short neural spine was reduced so that the first epural could come to lie above it.

We can conclude with some confidence that the second pre-ural neural spine of paracanthopterygians arose by elongation of a short neural spine, and that the two epurals of paracanthopterygians are due to loss of one epural, not to fusion of an epural with the neural arch of the second preural centrum. Loss of one epural is a common phenomenon in teleosts. In myctophoids it occurs in synodontids (text fig. 2G, H; Gosline, 1961a, p. 11) and is foreshadowed

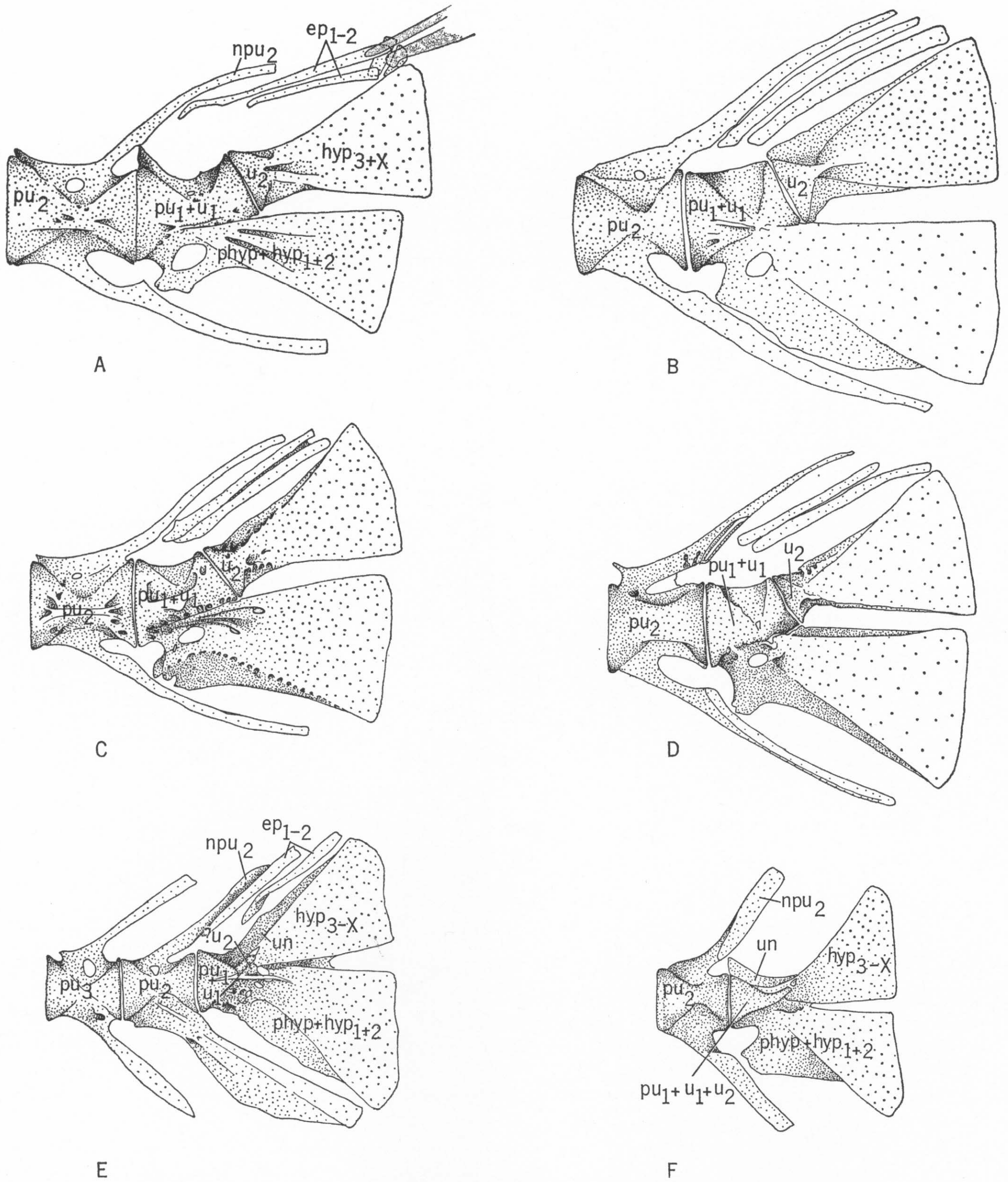

FIG. 4. Caudal skeletons of members of batrachoidiform lineage. A. *Porichthys porosissimus* (Cuvier). B. *Thallasophryne megalops* Bean and Weed. C. *Daector dowi* (Jordan and Gilbert). D. *Opsanus beta* (Goode and Bean). E. *Histrio histrio* (Linnaeus). F. *Gobiesox funebris* Gilbert.

in some specimens of *Aulopus japonicus* (text fig. 2B), producing a condition that could be antecedent to the paracanthopterygian caudal skeleton. Polymixiids normally have three epurals, but in the holotype of the Lower Cenomanian *Omosoma simum* Arambourg, the oldest polymixiid known, there appear to be only two (Niels Bonde, personal communication), and this fish has the basal paracanthopterygian tail fully developed.

The various types of caudal skeleton found in the paracanthopterygians and related groups are summarized in text figure 5.

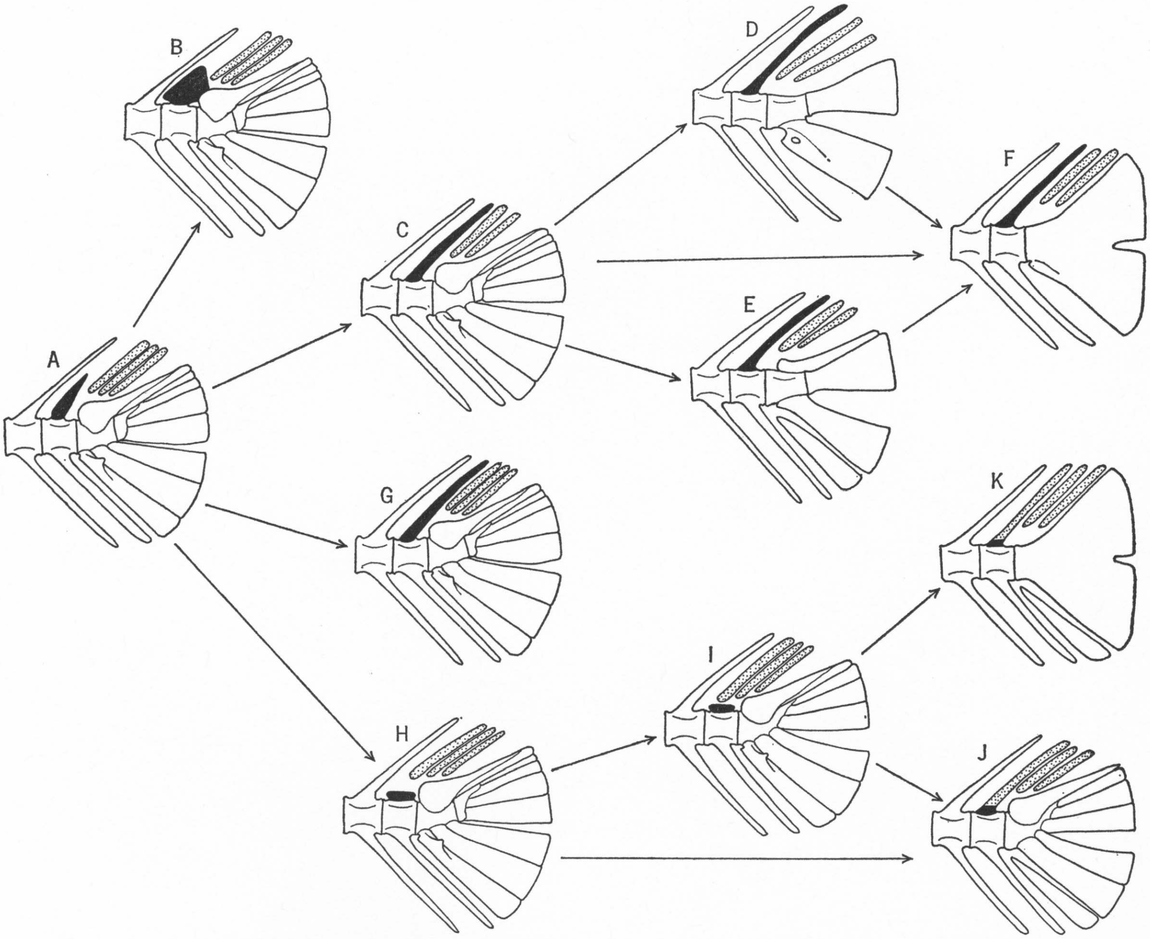

FIG. 5. Diagrams to illustrate changes in the caudal skeleton. A, B. Myctophiformes. C–F. Paracanthopterygii. H–K. Acanthopterygii. The second pre-ural neural arch and spine are solid black; the epurals are stippled. The arrows connecting different types indicate possible structural changes, not phyletic lineages. A. In primitive myctophoids [*Aulopus*, *Nematonotus* (extinct)], the second pre-ural neural spine (npu_2) is short and slender. B. In most myctophoids and in ctenothrissoids, npu_2 is expanded. C. In primitive paracanthopterygians [*Sphenocephalus* (extinct), *Erismatopterus* (extinct), *Amphiplaga* (extinct)], npu_2 is fully developed, and there are only two epurals. D. In ophidioids and batrachoidids, the upper hypurals are fused with the second ural centrum, the lower hypurals are fused with the parhypural, and the uroneurals are lost. E. In advanced percopsiforms (Amblyopsidae) and gadoids, the upper hypurals are fused with the second ural centrum, the lower hypurals are fused, the parhypural has no articulation proximally, and the second uroneural is lost. F. In advanced paracanthopterygians (lophiiforms, gobiesocids; one epural or none in gobiesocids), the hypurals, parhypural, and centra are all fused into a symmetrical plate (cf. K). G. In Polymixioidei, npu_2 is fully developed, and there are three epurals. H. In primitive Berycoidei, npu_2 is reduced to a low crest, the first epural moving forward above it. I. In primitive Perciformes, as in H, but with no free second ural centrum and five hypurals. J. In Zeiformes, Nandidae, Anabantoidei, Pleuronectiformes, as in I, but the first epural is fused with the second pre-ural neural arch, the second uroneural is lost, and the parhypural is free proximally. K. In advanced Scombroidei, Balistoidei, Cottidae, as in J, but the upper and lower hypurals are fused with the supporting centrum into a symmetrical plate (cf. F).

THE PARACANTHOPTERYGIAN FEEDING MECHANISM

THE TAXONOMIC SIGNIFICANCE of jaw-muscle patterns that characterize the Paracanthopterygii was first discussed in a comparison of amblyopsids and aphredoderids (Rosen, 1962). In that study, the critical pattern was described as a combination of a greatly enlarged adductor arcus palatini that fills the floor of the orbit and a more or less cylindrical composite muscle, the levator maxillae superioris, that originates on the palatoquadrate arch and inserts on the maxilla near its palatine articulation. Other muscles of the cheek are not exceptional, that is, there are a normal dilatator operculi and levator arcus palatini, and as many as three distinct divisions of the adductor mandibulae. Of importance, however, are the relative depth relationships of the parts of the adductor mandibulae to the point of aponeurotic origin of the levator maxillae superioris. The depth sequence of these muscles, as given by Rosen (1962) for *Microgadus tomcod*, from the superficial muscles inward, is: A_1, A_2, levator maxillae superioris, A_3. When present in paracanthopterygians, A_1 is invariably feeble and has a tendinous association with the maxillary-mandibular ligament (text fig. 6A, B). It is absent from all examined members of the group save gadids, merlucciids, and percopsids. The major superficial cheek muscle is A_2, and in almost all the many species of paracanthopterygians examined, and more importantly in at least some members of each included family, it is divided into a distinct dorsal and ventral subdivision. The levator maxillae superioris is almost invariably compounded of two parts. In cods and trout perch the two are distinctly subequal. In nearly all other groups, including near cod relatives such as the muraenolepids and macrourids, the inner section enlarges and develops a separate origin on the metapterygoid internal to the insertion of the levator arcus palatini. In no case known to us does the insertion of the levator maxillae superioris ever alter. The innermost cheek muscle, A_3, is invariably present in some form and inserts in the corono-Meckelian fossa of the dentary.

The function of the above muscle pattern was described briefly by Rosen (1962) as exerting some control over maxillary movements while permitting maximum rotational motion of the lower arm of the maxilla. Most paracanthopterygians are able to achieve a nearly circular gape when the mouth is fully opened (pl. 52, figs. 1, 2), and this action depends to a very large extent on a great freedom of movement of the lower maxillary arm, which can be driven forward almost to the vertical. Such an action is made possible by the severe reduction of the external divi-

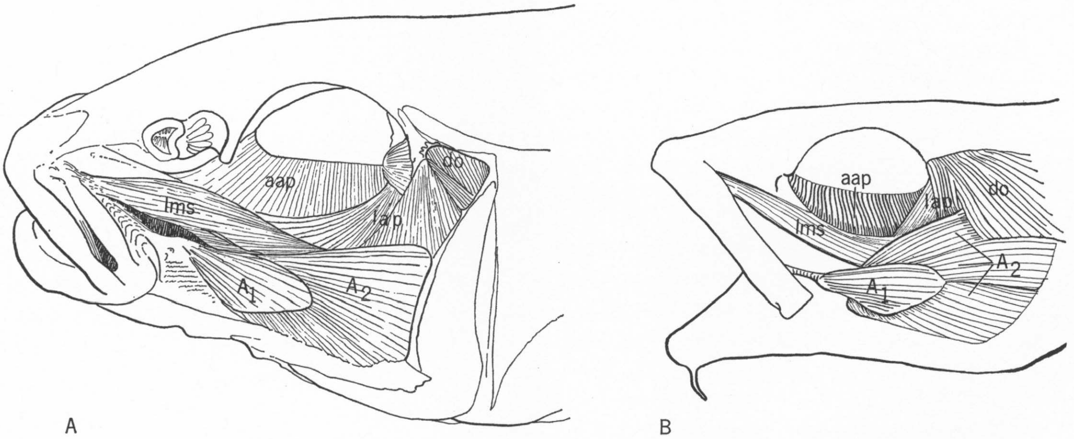

FIG. 6. Diagrammatic representation of the superficial jaw musculature. A. *Percopsis omiscomaycus* (Walbaum). B. *Microgadus tomcod* (Walbaum).

sion (A_1) of the adductor mandibulae, which controls maxillary action in most other fishes and by its replacement with an internal muscle having an insertion near the maxillary fulcrum. The homology of the levator maxillae superioris muscle in teleosts was originally in doubt. In the present studies of myctophoid, berycoid, and perciform fishes, much new evidence has been accumulated which permits a more or less detailed account of the probable mode of origin of the muscle.

The levator maxillae superioris muscle is the crucial component of the paracanthopterygian pattern. That muscle of paracanthopterygians was so named on the basis of its close correspondence in origin, angle, point of insertion, and innervation to the levator maxillae superioris series of *Amia* as described by Allis (1897). In cods and troutperch, as in *Amia*, there are both an anterior and a posterior levator maxillae superioris muscle (text fig. 6A, B), but it is with the anterior one that we are particularly concerned. All other groups of paracanthopterygians appear to be in process of losing, or have already lost, or never have developed, the posterior one. In all cases the levator maxillae superioris muscle forms a cylindrical mass that originates aponeurotically on the palatoquadrate arch and passes forward to a high insertion on the posterior face of the maxillary head, either directly or through a short tendon. Without known exception the fibers are predominantly parallel with the long axis of the entire mass. As thus defined and restricted, the levator maxillae superioris is so far known to occur only in *Amia*, in the Paracanthopterygii, in all members of the family Myctophidae examined, and in some of the Cyclopteridae. Before discussing the myctophid and cyclopterid conditions, we deal with some apparent exceptions to the above generalization.

In surveying a variety of fishes for the possible occurrence of a levator maxillae superioris series, we have come across several instances in which a muscle like the levator maxillae superioris has developed. In the Carangidae, for example, a heavy band of muscle inserts on the maxilla in the levator maxillae superioris position; it originates, however, on the infraorbital bones, about half of it coming directly from the subocular shelf. In *Lampris* the entire outer division of the adductor mandibulae is concentrated on a tendon that inserts in the levator maxillae superioris position. In *Polymixia* the outer division of the adductor mandibulae is divided, as in myctophids, into three sections (pl. 53). The uppermost of these, which is straplike, becomes dissociated anteriorly from the two underlying parts and continues forward and upward along the palatine to insert on the maxilla in the levator maxillae superioris position. In *Gadopsis* (pl. 54; text fig. 7), *Parapercis*, and in a large number of blennies, an inner muscle extends toward the maxilla from the anteroventral margin of the orbit. The fibers run almost at right angles to the maxilla and insert along a wide expanse of the maxillary arm, usually well below the palatine articulation. The resemblance of the blennioid condition to that of the paracanthopterygians is enhanced by the extensive development of the adductor arcus palatini. A similar condition is to be found among many cottoid fishes, as illustrated by Greenwood, Rosen, Weitzman, and Myers (1966).

In contrast to the above, the myctophid arrangement (pl. 55) of the muscle controlling maxillary movement is precisely like that of the paracanthopterygians. The over-all pattern of jaw musculature differs, however, in the small size of the adductor arcus palatini (confined to the rear of the orbit) and the separation of the outer division of the ad-

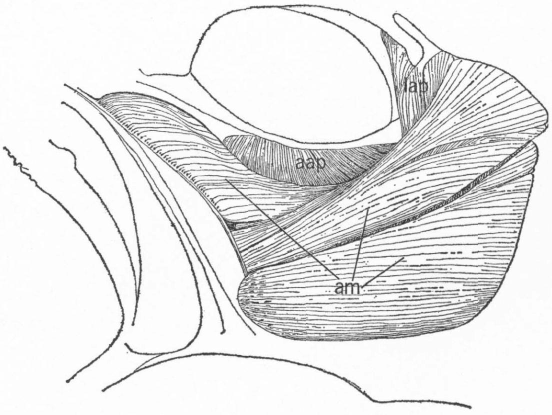

FIG. 7. Diagrammatic representation of the superficial jaw musculature of *Gadopsis marmoratus* Richardson.

ductor mandibulae into three, instead of two, distinct bands. In spite of these differences, a comparison of the jaw musculature of myctophids with that of other myctophoids, with that of the polymixioids and berycoids, and with that of the most generalized paracanthopterygians (gadoids and percopsids) suggests a way in which basic differences in jaw musculature between paracanthopterygians and acanthopterygians may have arisen.

Of all of the myctophoid, paracanthopterygian, and acanthopterygian fishes examined, the aulopids (pl. 56) have the simplest, least-modified arrangement of the jaw muscles. In these fishes the adductor arcus palatini is confined to the rear of the orbit, and the levator arcus palatini is a simple muscle, oval in cross section, that originates on the anterior face of the hyomandibular and sphenotic and inserts on the pterygoid arch. The adductor mandibulae is two-layered, the inner division penetrating the Meckelian fossa, and the superficial division inserting mainly on the coronoid expansion of the lower jaw. The other, and minor, insertion of the outer division of the adductor mandibulae in aulopids consists of a small number of the dorsalmost fibers projecting forward into a large tendon that seems to be a condensation or consolidation of the post-maxillary sheets of ligamentous connective tissues. This maxillary tendon is attached to the maxilla near its connection with the palatine. The neoscopelids *Solivomer* and *Neoscopelus* differ from *Aulopus* only in having the outer division of the adductor mandibulae divided into a dorsal and a ventral band. In the neoscopelid *Scopelengys* (pl. 57), however, the dorsal band extends forward for a considerable distance along the maxillary tendon, so that a major form of maxillary control is achieved. The arrangement of the adductor mandibulae seen in *Scopelengys* was found to be characteristic of all members of the Berycoidei and of the single melamphaeid examined. In about half of the berycoids the adductor arcus palatini is confined to the rear of the orbit; in the others it is large and fills the orbit floor. A further stage in the specialization of the adductor mandibulae muscle is found in the Myctophidae (pl. 55). In all the myctophids examined the muscle inserting on the maxillary tendon is separate and has a deep insertion on the palatoquadrate arch between the superficial and internal divisions of the adductor mandibulae. It is assumed here that this muscle, which at this stage of specialization may be termed "levator maxillae superioris," arose from the dorsalmost band of the outer division of the adductor mandibulae. That supposition is supported in part by the tendency of the myctophid adductor mandibulae to fragment into as many as three separate bands that have independent origins on the preopercular margin. It is also supported by the identity of the tendon on which the levator maxillae superioris inserts, in terms of orientation and point of attachment to the maxilla, with the maxillary tendon of other myctophoids. The extension of the adductor mandibulae onto this tendon in *Scopelengys* rather resembles the preliminary setting for a change to the myctophid pattern.

The most impressive example of the development of a levator maxillae superioris in a group not included in the Paracanthopterygii is provided by the scorpaeniform fishes of the family Cyclopteridae. The generalized scorpaeniforms, the Scorpaenidae (pl. 58), have a jaw-muscle pattern identical with that of some berycoids. The outer division of the adductor mandibulae is a heavy, undivided sheet of muscle that ventrally inserts on the coronoid portion of the mandible and dorsally encroaches moderately on a maxillary tendon. The over-all pattern resembles that of some berycoids, rather than that of *Scopelengys*, because the scorpaeniform adductor arcus palatini appears always to be large and to fill the orbit floor. The pattern is also indistinguishable from one seen in *Epinephelus* (pl. 59). Scorpaeniforms with a somewhat more specialized muscle pattern include the Cottidae in which a dorsomedial part of the adductor mandibulae inserts on the maxillary tendon and has become functionally dissociated from the underlying muscle, which now has developed a major insertion on the maxillary-mandibular ligament. Among the percoid fishes the centropomid *Lates* (pl. 60) shows a similar specialization, and in *Perca* a fully developed external or maxillary division (A_1) of the adductor mandibulae has been developed. The trend in the differentiation of the adductor mandibulae among scorpaeniforms has followed a different course. The most significant changes in jaw musculature have been principally developed in the Cottoidei, and even such extreme forms as triglids show some of the specializations. Among cyclopterids, an inner and an outer part of the adductor series have become associated with the maxilla, but the inner one has been emphasized and the outer part gradually reduced. A morphological series illustrating the transition was discussed by Dietz (1912, fig. 23; 1921, fig. 11) and consisted of different examples of *Liparis vulgaris* (=*L. liparis*) showing initial separation of an inner levator maxillae superioris section, and of *Cyclopterus lumpus*, a more advanced stage in which the levator maxillae superioris has been differentiated fully and in which the A_1 system is incipient. *Cyclopterus*, however, closely resembles *Cottus* (see Greenwood, Rosen, Weitzman, and Myers, 1966, pl. 23), and we would reverse Dietz's *Liparis-Cyclopterus* sequence. Dietz followed the sequence further to show how the cyclopterid mechanism could have given rise to the gadid one. The comparison with gadids is far from the most useful taxonomically that could be made, for the cyclopterid genus *Paraliparis* (pl. 61) itself shows a near-gadoid pattern.

The evolutionary specializations in jaw-muscle patterns among scorpaeniforms provide a known and reasonable morphological sequence for explaining the origin of a paracanthopterygian system. That sequence also, incidentally, may clarify the difference between gadiforms with a large levator maxillae superioris and small A_1 (merlucciids, gadids) and those with two well-separated divisions of the levator maxillae superioris muscle (ophidioids, macrourids, muraenolepoids). The latter arrangement closely resembles the condition of some cyclopterids in which the two muscles become associated with the maxilla and lie side by side. The small A_1 of gadids and the outermost of the two levator maxillae superioris muscles appear to be the same element. Muraenolepoids (pl. 62) show an apparently transitional condition in which the outer member of the paired levator maxillae superioris muscles has a thin layer of superficial fibers that extends outward over the adductor mandibulae and seems to originate in the fascia covering the adductor.

The occurrence of a well-developed levator maxillae superioris system in cyclopterids may seem to provide cause for contesting the taxonomic significance of the pattern in the Paracanthopterygii. It must be noted, however, that but a single family shows this feature in a group that is otherwise typically acanthopterygian. In contrast, all the central paracanthopterygians (or about 150 genera) show the pattern and have a distinctive type of caudal skeleton as well. The integrity of the Paracanthopterygii is not, and could scarcely be expected to be, based on a single structural change, however unusual it might be. The combined evidence is discussed below.

We may assume, as indicated above, that the simplest antecedent condition leading to both the paracanthopterygian and acanthopterygian systems was the *Scopelengys* pattern as outlined above. The pattern is more or less identical with that seen in berycoids and melamphaeids. In those instances, the only change in over-all jaw musculature that would be required is the enlargement of the adductor arcus palatini in melamphaeids and some berycoids. Derivation of the *Polymixia* pattern (pl. 53) from that seen in *Scopelengys* would require only the further encroachment of the upper part of the adductor mandibulae onto the maxillary tendon and the complete separation of that "maxillary" portion from the underlying muscle sheets. The myctophid pattern (pl. 56) appears to be merely one step further in the development of a maxillary muscle and could perhaps be accounted for by an antecedent *Polymixia*-like condition in which the maxillary muscle became additionally subdivided into an anterior "maxillary" part with a deep origin on the palatoquadrate and a posterior "mandibular" part with the original preopercular origin. The principal difference between the condition of the myctophids and that of the paracanthopterygians is probably that, in the ancestral paracanthopterygian, two dorsal and superficial muscles, rather than one, differentiated from the adductor mandibulae and became associated with the maxilla. Of the two probably original maxillary muscles of paracanthopterygians, one was external and the other internal to the main body of the adductor mandibulae.

As noted above and as illustrated in plate 63 and text figure 6A and B, the gadids, merlucciids, and percopsids have a small superficial component of the cheek muscles that originates on fascia from the preopercular margin and inserts on the middle or lower part of the maxillary-mandibular ligament. That small muscle, equivalent in position and insertion, but not size, to the A_1 component of the adductor mandibulae in advanced acanthopterygians, is in process of being lost by *Aphredoderus* and the amblyopsids and is absent from all other paracanthopterygians. It may never have been well developed among the ancestral paracanthopterygians, and perhaps has played no more than a subsidiary role during the early history of these fishes. In fresh specimens of *Merlangus* and *Gadus* the entire body of the small A_1 is drawn forward across the principal mass of the adductor mandibulae when the mouth is fully opened, suggesting that its presence in a more fully developed state would oppose the evolution of a feeding mechanism involving a great forward excursion of the lower maxillary arm. The levator maxillae superioris muscle, which inserts near the maxillary fulcrum, would not oppose a large maxillary excursion forward, and in gadids, merlucciids, and percopsids the existing small A_1 component may serve only as an ancillary means of maxillary retraction and control, which is principally brought about by the levator maxillae superioris muscle. An A_1 component, or its equivalent, certainly seems to be absent from other paracanthopterygians which, nevertheless, possess the same type of feeding mechanism.

The paracanthopterygian feeding mechanism can thus be characterized as a form of jaw protraction in which the upper jaw symphysis undergoes little or no forward movement, but instead serves as a pivotal point around which the maxillary and premaxillary arms undertake a largely unrestricted forward excursion to form a nearly circular gape when the mouth is fully opened. In direct contrast, the acanthopterygian mechanism is characterized by the influence of a large A_1 component of the adductor mandibulae which to a certain extent restricts the amount of forward movement of the lower maxillary arm, but leaves the upper part of the maxilla more or less free to move forward in relation to the ethmoid block. In acanthopterygians the premaxilla is also a much more mobile bone, its symphyseal and alveolar parts being capable of significant forward displacement even in the most generalized forms (see also Schaffer and Rosen, 1961). The development of maxillary control seems to have involved a rather direct derivation of a superficial maxillary muscle (A_1) and the gradual migration ventrad of its tendinous insertion along the maxillary-mandibular ligament.

Associated with the differences in acanthopterygian and paracanthopterygian jaw musculature are differences in the form and function of the maxilla. In acanthopterygians, and in the related atherinomorphs, the maxillary head is relatively more complex in having not only a notch to receive the articular premaxillary process but also a deep, internal hook that acts as a cam to drive the premaxillary head forward when the mouth is opened (Alexander, 1967b). The maxilla is actively rotated on its long axis to produce the outward thrust of its internal hook against the premaxilla. This rotational movement of the maxilla is brought about by the external division of the adductor mandibulae (A_1), the tendon of which inserts mainly on the posterolateral face of the maxillary shaft. In paracanthopterygians the maxillary head has a notch to receive the articular premaxillary process but no enlarged internal hook. The maxilla undergoes very little rotation on its axis, and the premaxillary symphysis is drawn passively forward to a slight extent by the taut connective tissues that bind together the outer borders of the upper and lower jaws. The internal division of the adductor mandibulae (levator maxillae superioris), which controls maxillary movement in paracanthopterygians, usually has a broad insertion directly on the posterior face of the maxilla near its palatine articulation. During opening of the mouth, the maxilla is rotated slightly on its axis as a simple result of its mechanical connections to the lower jaw.

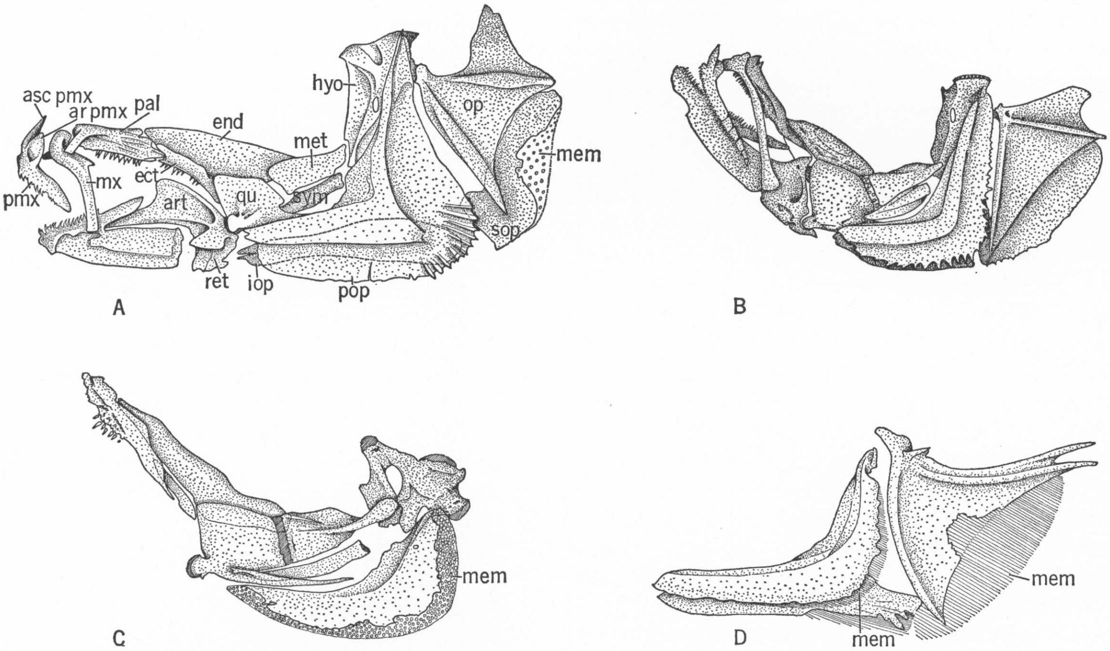

FIG. 8. Opercular apparatus and jaw suspension in percopsiforms. A. *Percopsis transmontana* (Eigenmann and Eigenmann). B. *Aphredoderus sayanus* (Gilliams). C. *Amblyopsis spelaea* DeKay. D. *Typhlichthys subterraneus* Girard. B–D, after Rosen (1962).

The levator maxillae superioris, which, because of its extensive contact with the palatoquadrate arch, has limited extensibility, probably acts as a tensor, or muscle of orientation, to restrain and correctly position the maxilla during mandibular abduction. If this muscle produces any specific maxillary movement, that movement probably would occur during mandibular adduction when the maxillary head is rotated inward toward the rostrum. It is therefore likely that the acanthopterygian and paracanthopterygian sections of the adductor mandibulae that affect maxillary motion have antagonistic actions, the acanthopterygian A_1 rotating the internal part of the maxilla outward during jaw protrusion and the paracanthopterygian levator maxillae superioris positioning the maxilla during protrusion and bringing its internal part inward toward the midline during jaw retraction. It is also evident that the development of an enlarged internal cam on the head of the acanthopterygian maxilla is related to a positive protrusility of the premaxilla, whereas protrusility in paracanthopterygians is both slight and passive in the absence of a specific mechanism of this sort.

In a few paracanthopterygians in which the levator maxillae superioris has been lost (e.g., lophiids and gobiesocids), the acanthopterygian mechanism has been simulated by the development of an internal maxillary lever of distinctive shape and by the broad insertion of the superficial division of the adductor mandibulae onto the maxillary-mandibular ligament (Field, 1966). On the other hand, in various perciforms (e.g., haemulonids and lutjanids) positive clockwise and counterclockwise axial rotation of the maxilla has been achieved by the division of the A_1-maxillary tendon into a lateral and a medial branch. That specialization, or one very much like it, probably was antecedent to the gerrid protrusion system in which the maxillary heads are rotated inward, rather than outward, to form a slip-ring for conducting forward the enormously enlarged ascending premaxillary processes (Schaeffer and Rosen, 1961).

The seemingly opposite means of achieving maxillary control, which have resulted in the principal protrusile component of the upper jaw being either ventral (in paracanthopterygians) or dorsal (in acanthopterygians), are correlated with a host of differences in basic syncranial architecture. A comparison of the generalized percopsiforms, gadiforms, and batrachoidiforms with primitive and generalized acanthopterygians (berycoids and centropomids) reveals that an average difference exists between the two groups in height and breadth of head. The paracanthopterygian skull is, in almost all cases, nearly as wide as or wider than high. The skull of acanthopterygians (at least the more primitive types) tends to be rather deep and laterally compressed. The difference is reflected osteologically in the presence of a high supraoccipital crest and rather deep jaw suspension with a more or less straight or only slightly curved opercular margin in acanthopterygians, and a much lower crest, shallow jaw suspension, and a very sharply angular opercular margin in paracanthopterygians. The extreme angularity of the gill cover in the paracanthopterygians has been brought about by dorsoventral compression of the head and the consequent reduction in the expanse of the lateral surface of the branchial chamber that is covered by the relatively stiff opercular. The characteristically thin, flexible, and in many cases partly membranous subopercular has grown upward and backward at a rather sharp angle toward the posterodorsal tip of the opercular and forms the principal component of the para-

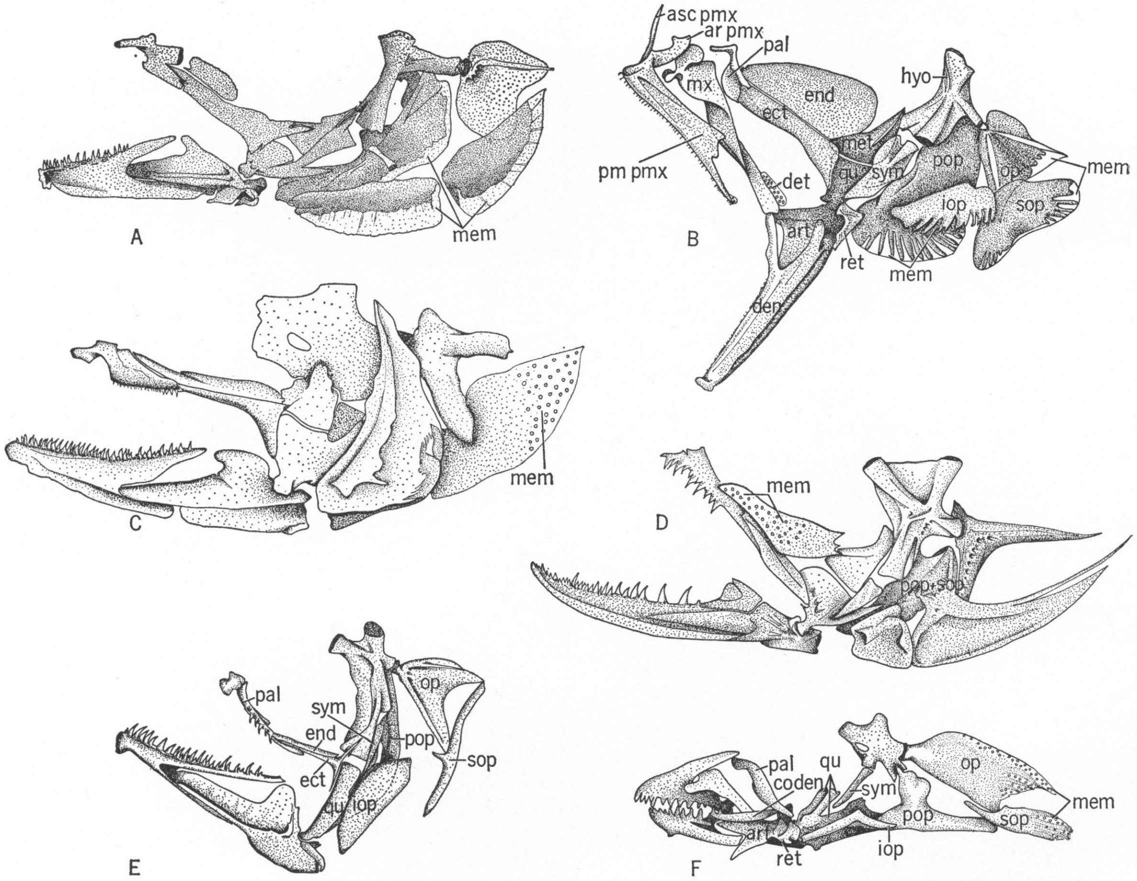

FIG. 9. Opercular apparatus and jaw suspension in some paracanthopterygians. A. *Pollachius virens* (Linnaeus). B. *Hymenocephalus cavernosus* (Goode and Bean). C. *Dinematichthys* sp. D. *Porichthys porosissimus* (Cuvier). E. *Histrio histrio* (Linnaeus). F. *Gobiesox funebris* Gilbert.

canthopterygian gill cover (text figs. 8, 9). In primitive acanthopterygians the situation is reversed, with the opercular being the dominant bone.

The relatively greater width of the paracanthopterygian head is necessarily also correlated with the development of the hyobranchial apparatus which, at rest, is broad and shallow and displaced forward so that the basihyal (glossohyal) is very near the mandibular symphysis. The hyoid bars tend to be rather long. Full extension of the jaws in the paracanthopterygian, without a simultaneous maximum expansion of the branchial chamber, clearly would force the anterior part of the hyoid apparatus downward to a much greater extent than it would in fishes with a more posterior basihyal, shorter hyoid

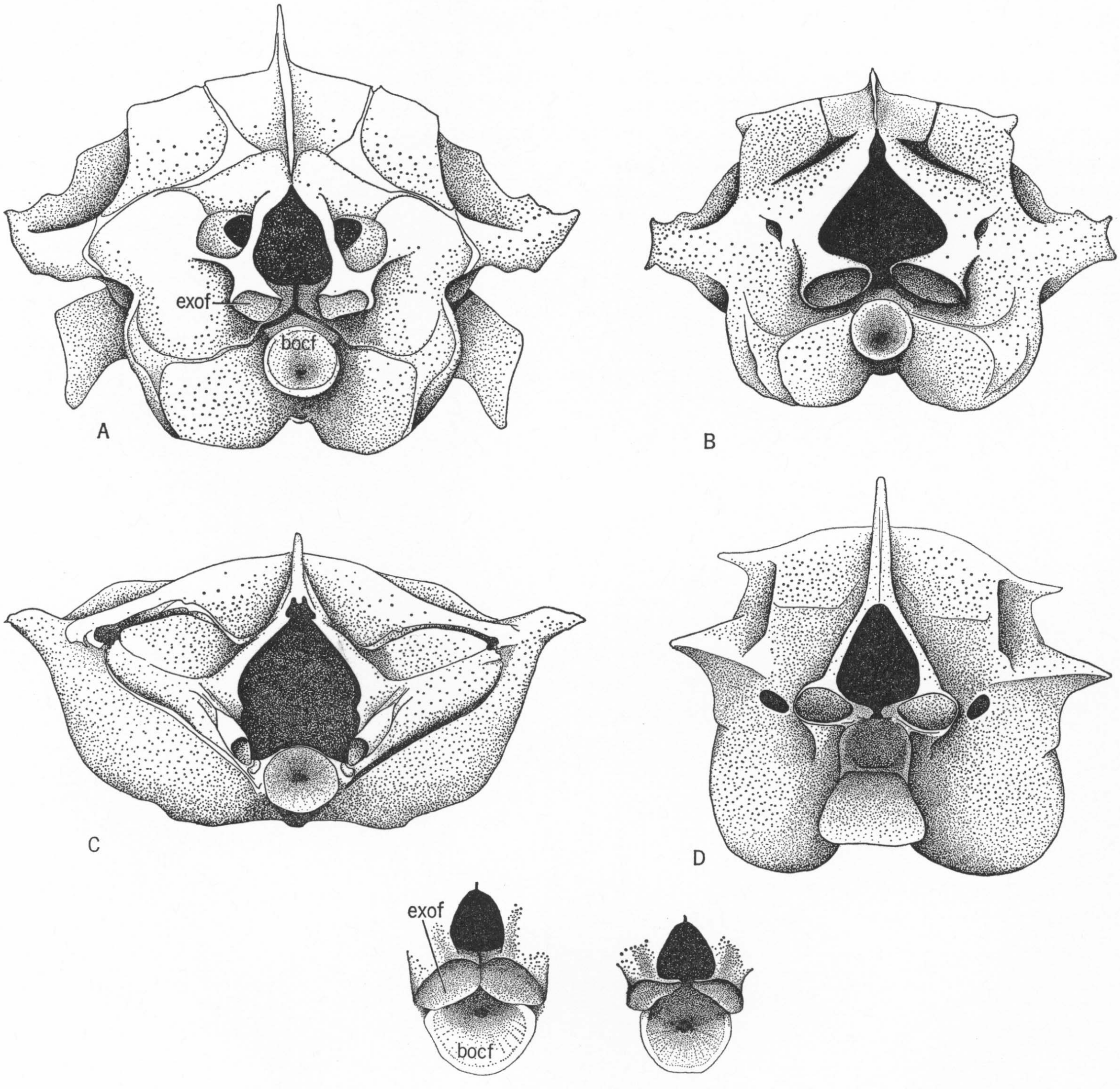

FIG. 10. Occipital region of neurocrania to show form of exoccipital and basioccipital facets. A. *Percopsis omiscomaycus* (Walbaum). B. *Aphredoderus sayanus* (Gilliams). C. *Porichthys porosissimus* (Cuvier). D. *Dinematichthys* sp. E. The beryciform *Hoplostethus japonicus* to the left, and a typical percoid to the right; after Starks (1904).

bars, and a deeper and narrower head (i.e., the acanthopterygians). Fossil percopsiforms and gadiforms (as well as Recent ones that have died) often show an exaggerated hyoid displacement (see pl. 65, fig. 2, and pl. 68, fig. 1). Whereas kineticism in the paracanthopterygian skull affects principally the hyobranchial and opercular apparatus, in the acanthopterygian the most striking kinetic features center around the upper jawbones and the palatoquadrate arch. The deeper skull of the acanthopterygians would also imply less movement of the head in relation to the body axis than in the less deep-headed paracanthopterygians. Raising of the head on a cervical pivot during mouth protrusion is, in fact, a characteristic feature of aphredoderids, gadids, and at least some ophidioids (but probably most paracanthopterygians), and this difference in head mobility is reflected in differences in the occipital joint with the vertebral column (text fig. 10A–D). This cervical joint tends to have a vertical emphasis in acanthopterygians, with the exoccipital articular surfaces aligned together above the basioccipital facet (text fig. 10E, F). In paracanthopterygians the joint is distinctly horizontal, with the exoccipital surfaces displaced laterally away from the foramen magnum and only slightly above the plane of the basioccipital facet. Finally, the more generalized acanthopterygians differ from paracanthopterygians in having a subocular shelf on the infraorbital bones, and perhaps this difference also is related to differences in the feeding mechanism. A subocular shelf is otherwise restricted in occurrence among teleosts to the members of the family Myctophidae (text fig. 11) and the osteoglossomorph genus *Notopterus*.

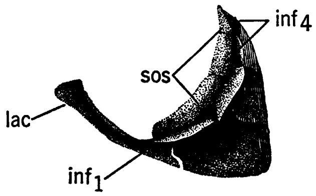

FIG. 11. Left infraorbital bones of *Symbolophorus californiense* (Eigenmann and Eigenmann), showing the extensive development of a subocular shelf. Parallel lines indicate membrane.

In summary, primitive acanthopterygians and paracanthopterygians differ in a multitude of syncranial characters, and most, if not all, of the differences are related to basic dissimilarities in the feeding mechanism. The acanthopterygian mechanism is based on muscular control of the maxilla via an external division of the adductor mandibulae, and on a highly protrusile premaxilla. The paracanthopterygian system is based on muscular control of the maxilla via an internal division of the adductor mandibulae, the levator maxillae superioris, that is associated with limited premaxillary protrusility but that allows a very much greater excursion forward of the lower maxillary arm than in generalized acanthopterygians.

SYSTEMATIC AND COMPARATIVE ANALYSIS

ORDER PERCOPSIFORMES

LIVING PERCOPSIFORMS

Accounts of the anatomy of the living percopsiforms *Percopsis* and *Aphredoderus* have been given by Regan (1911), Rosen (1962), and Gosline (1963). Rosen and Gosline both concluded that the closest relatives of these two genera are the Amblyopsidae. Gosline held that the amblyopsids should remain in the Cyprinodontiformes, but Rosen found that the resemblances between amblyopsids and cyprinodonts are not indicative of relationship (see also Rosen, 1964), and he made the amblyopsids the only members of an order Amblyopsiformes "adjoining the order Percopsiformes." Later (Greenwood, Rosen, Weitzman, and Myers, 1966) the amblyopsids were included within the order Percopsiformes, which now contains three suborders: Percopsoidei, Aphredoderoidei, and Amblyopsoidei.

The osteology of *Percopsis*, *Aphredoderus*, and the amblyopsids is illustrated in plate 64, plate 65 (fig. 1), and text figures 8, 10, and 12–16. Some significant characters common to all three groups are the following:

1. Levator maxillae superioris muscle developed.
2. Adductor arcus palatini fills floor of orbit.
3. Supraoccipital crest confined to posterior face of neurocranium.
4. Parietals large and flat, separated by supraoccipital, no supratemporal fossa.
5. Anterior part of supraorbital sensory canal not bone enclosed, running in a broad trough on frontal.
6. Orbitosphenoid and basisphenoid absent.
7. Pars jugularis with only two openings.
8. Intercalar large.
9. Exoccipital condyles large and distinct from basioccipital condyle.
10. Lacrimal with large ascending process in front of lateral ethmoid.
11. No subocular shelf.
12. Maxilla excluded from gape by premaxilla, premaxilla with ascending and articular processes, crossed ligaments joining heads of maxilla and premaxilla to ethmoid and palatine.
13. No supramaxillae.
14. Palatine toothed.
15. Six branchiostegals in "percoid" arrangement.
16. Basibranchial teeth present.
17. Baudelot's ligament to first vertebra.
18. Epineurals absent.
19. Ribs inserted high on centra, above parapophyses.
20. A complete neural spine on second preural centrum.
21. Upper hypurals fused with second ural centrum.
22. Upper and lower postcleithra fused.
23. No pelvic spine.
24. Dorsal and anal fin spines present (a single dorsal spine in *Typhlichthys* and as many as two dorsal and anal spines in *Amblyopsis* among amblyopsids).
25. A single supraneural.

Of these characters, 1, 2, 5–10, 13, 19–22 are advanced, together defining the order, 12, 15, 18, and 24 are common to many groups at about this level of evolution, and 11, 14, 16, 17, and 23 are primitive. The only character that needs discussion is 25, the single supraneural. There seem to be two different sets of median bones above the vertebrae in front of the actinopterygian dorsal fin. In primitive actinopterygians there is a series of metameric bones above the neural arches which appear to be detached neural spines, the supraneurals. Supraneurals are primitively numerous and have no connection with the dorsal fin supports, because in *Lepisosteus*, many fossil holosteans, and the teleost *Thaumaturus* the two series overlap. There are many supraneurals in chondrosteans, most holosteans, and primitive teleosteans (elopoids, osteoglossoids, salmonoids, and others), the series becoming reduced to one or two bones above the foremost vertebrae in such fishes as the myctophoids *Aulopus*, *Chlorophthalmus*, and *Synodus*, and all supraneurals being lost in many teleost groups. In advanced teleosts, at and near the percoid level, there is a series of bones above the neural spines in front of the first dorsal radial. Smith and Bailey (1961) have demonstrated convincingly that in percoids these bones, the predorsals, are the leading radials of the dorsal fin which have ceased to carry fin rays. Primitively the predorsals are few in number, but up to seven occur in some centrarchids. Thus in one or more teleost lineages, the supraneurals appear to have been lost, their place later being taken by the predorsals. The question to be answered here is whether the single bone that lies above the first or second neural spine in percopsiforms is the last supraneural or the first predorsal. No conclusive answer can yet be given to this question, but, because the bone invariably lies over the foremost vertebrae and is separated from the first dorsal radial by a distinct interspace, usually of several vertebrae, and is platelike, with a small central cavity, resembling the supraneural of *Chlorophthalmus* and *Synodus* rather than the rodlike predorsals of Beryci-

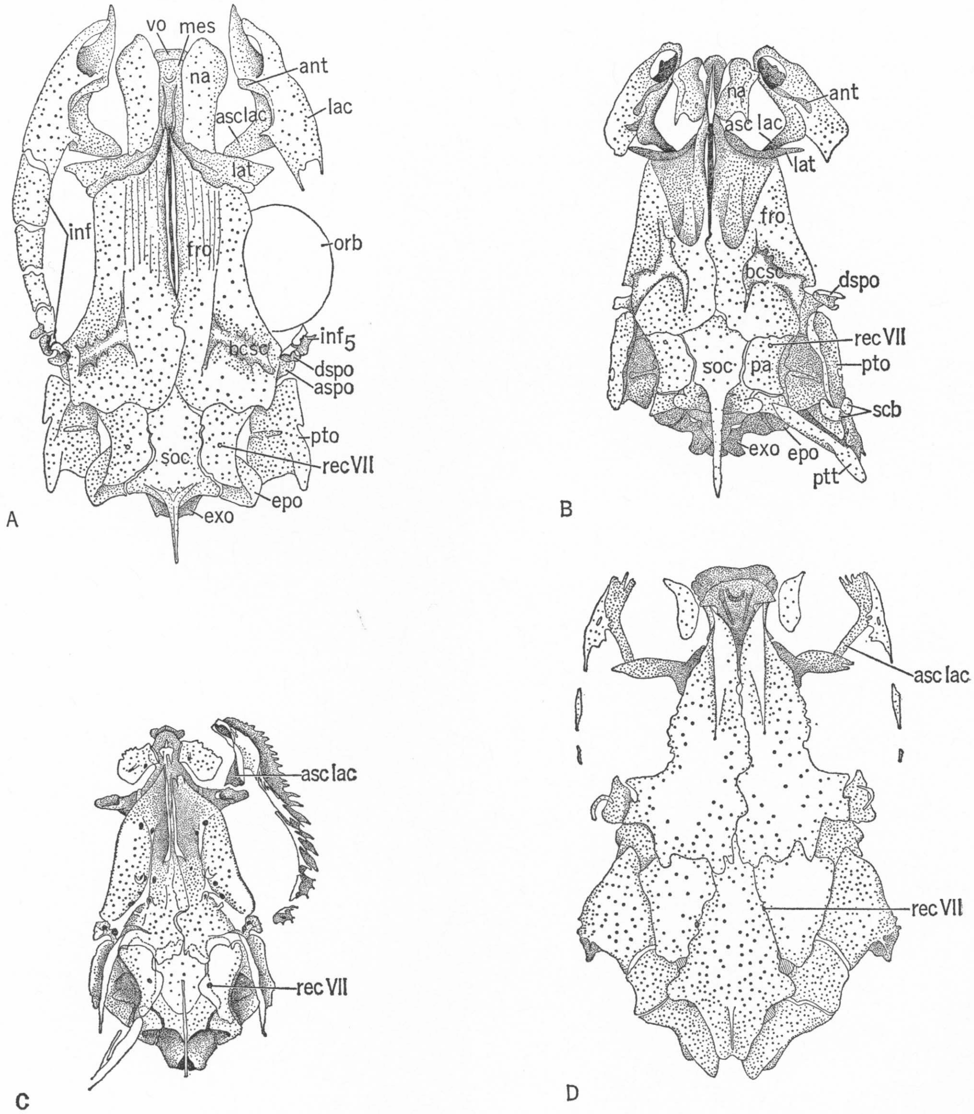

FIG. 12. Dorsicrania in percopsiforms. A. *Percopsis omiscomaycus* (Walbaum). B. *Percopsis transmontana* (Eigenmann and Eigenmann). C. *Aphredoderus sayanus* (Gilliams). D. *Amblyopsis spelaea* DeKay.

TABLE 1

Anatomical Similarities and Differences Among Living Percopsiforms

		Percopsidae	Aphredoderidae	Amblyopsidae
1	Frontals	Truncated anteriorly	Tapering anteriorly	—[a]
2	Supraorbital sensory canal	Bone-enclosed posterolaterally	Not bone-enclosed	—
3	Supraoccipital crest	Moderately large, thickened dorsally	Smaller	Reduced
4	Posttemporal fossa	Not extending onto frontal, not scale-covered	Extending onto frontal, scale-covered	Ill defined
5	Vomer	Toothless	Toothed	—
6	Pterosphenoid-parasphenoid contact	Absent	—	Present
7	Ectopterygoid	Toothed in *P. transmontana*	Toothed	Toothless
8	Endopterygoid	Toothless	Toothed	Toothless
9	Alveolar process of premaxilla	Normal	Segmented distally	—
10	Postmaxillary process of premaxilla	Present, low	Absent	—
11	Dorsal process on shaft of maxilla	Present	Absent	—
12	Levator maxillae superioris muscle	Double	Single	—
13	External division of adductor mandibulae	Remnant present	Absent	—
14	Infraorbitals	4	—	2 or 3
15	Lacrimal and infraorbitals	Smooth or very weak serrations	Spiny	Smooth
16	Antorbital	Present	Absent	—
17	Parasphenoid	Narrow	—	Expanded
18	Opercular	Excavated dorsally	Truncated anterodorsally	Not ossified dorsally
19	Opercular scales	Absent	Present	Absent
20	Preopercular	Weakly serrate at angle	Spiny at angle	Smooth
21	Olfactory bulb	Near olfactory organ	Near forebrain	—
22	Basibranchial teeth	2 patches	2 patches confluent	2 patches

TABLE 1—(*Continued*)

		Percopsidae	Aphredoderidae	Amblyopsidae
23	Tooth plates on dorsal edge of ceratohyal	Along entire margin	Present posteriorly	Absent
24	Branchiostegals	Projection on head of 4th	Projections on heads of 4th+5th	No projections
25	Vertebrae	33–35	28–29	27–35
26	Epipleurals	On first 3 or 4 vertebrae only	—	On all abdominal vertebrae in *Amblyopsis* and *Typhlichthys*
27	Parhypural	Articulated with centrum	Free	—
28	Second hypural	Distinct	Fused with first	—
29	Epurals	2	2	1 or 2
30	Free upper hypurals	Often 2	1	None
31	Uroneurals	2	1	—
32	Branched caudal rays	16[b]	—	9–16, modally 10–14[c]
33	Procurrent caudal rays	8–10, 4 or 5 spinous	7–10, 4–7 spinous	8–12
34	Dorsal fin	I–II, 9–12	III–IV, 10–11	0–II, 7–12
35	Adipose fin	Present	Absent	—
36	Anal fin	I–II, 6–7	II–III, 5–7	0–II, 7–11
37	Postcleithrum	Upper plate very large	Upper plate reduced	Reduced or absent
38	Pelvic fin	Subthoracic, girdle free, 8 rays, 1st unbranched	Subthoracic, girdle attached to postcleithrum, 7 rays, 1st branched	Abdominal, 0–6 rays, 1st unbranched
39	Pelvic splint	Present	—	Absent
40	Anus	Abdominal	Jugular in adult	—
41	Scales	Weakly ctenoid	Strongly ctenoid	Traces of ctenii in *Chologaster*
42	Lateral line	Complete	Interrupted	Absent
43	Caudal fin	Forked	Truncate	Rounded
44	Eyes	Normal	—	Reduced or absent

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[a] Condition as in preceding column.

[b] Regan (1911) described *Percopsis* as having 19 principal caudal rays, one more than *Aphredoderus*, and this number has been accepted by later workers, but in all the specimens we have examined there are 18 principal rays.

[c] Woods and Inger (1957).

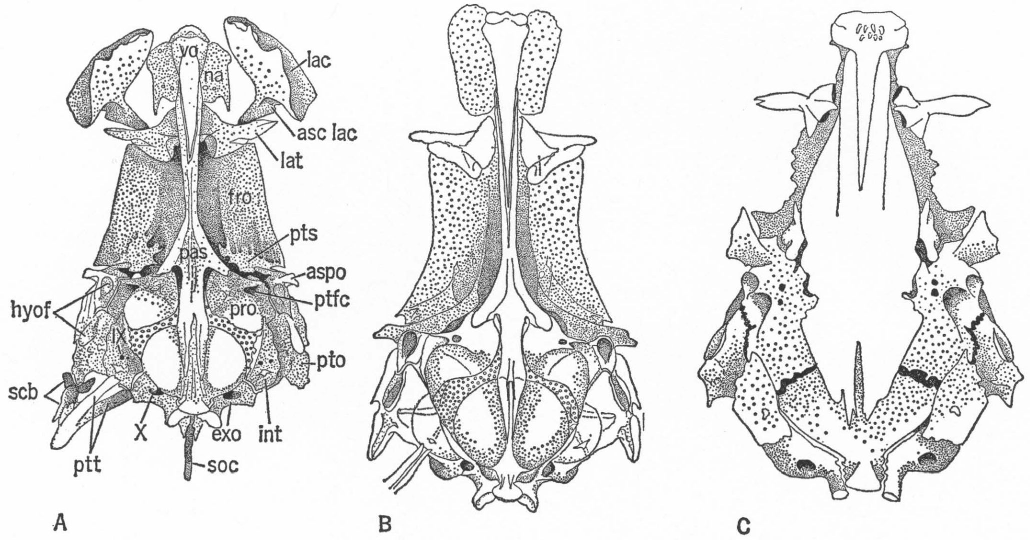

FIG. 13. Basicrania in percopsiforms. A. *Percopsis transmontana* (Eigenmann and Eigenmann). B. *Percopsis omiscomaycus* (Walbaum). C. *Amblyopsis spelaea* DeKay.

formes and Perciformes, we think it probable that the bone is a supraneural, not a predorsal.

Table 1 shows the main anatomical differences among the living percopsiforms. To review these various similarities and differences, the Percopsidae are the most primitive of the three families in characters 2, 9, 12, 13, 16, 27, 28, 30, 31, 35, 40, 42, and 43. The fossil percopsiforms described below demonstrate that *Percopsis* also retains the primitive condition in characters 1, 3, 4, 10, and possibly in 23 (see p. 409). Advanced characters of *Percopsis* are found in the maxilla (11) and olfactory bulb (21). *Percopsis* and *Aphredoderus* differ from amblyopsids in retaining the primitive condition in characters 6, 7, 14, 17, 29, 32, 39, and 44, but there seem to be no advanced characters in which *Percopsis* and *Aphredoderus* resemble each other and differ from the amblyopsids (the abdominal pelvics, the reduction of fin spines,[1] and the cycloid scales of amblyopsids are secondarily developed; pp. 390, 409). *Aphredoderus* is the most primitive of the three in the palatal dentition (5, 8), and the structure of the fossil forms suggests that it also retains the primitive percopsiform condition in characters 15, 19, 20, 24, 38, and 41 and in the more numerous dorsal and anal spines (34, 36). The amblyopsids are the most advanced group in almost every character. The resemblances between *Aphredoderus* and the amblyopsids in specialized characters, especially those of the pre-

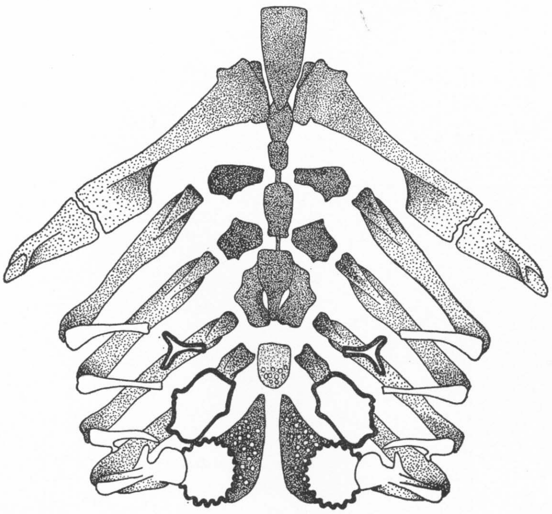

FIG. 14. Diagrammatic representation of the hyobranchial apparatus of *Amblyopsis spelaea* DeKay.

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[1] In contrast to percopsids and aphredoderids, amblyopsids were believed to have no dorsal and anal fin spines. In large examples of *Amblyopsis spelaea* we have, however, found as many as two dorsal and two anal spines.

maxilla (9, 10), caudal skeleton and fin, the position of the vent, and the reduced lateral line, indicate that the closest relative of the amblyopsids is *Aphredoderus*.

The interrelationships of living percopsiforms can be summarized by the statement that the Aphredoderidae and Amblyopsidae are more closely related to each other than either is to the more primitive, and generalized, Percopsidae. In taxonomic terms, the order Percopsiformes appears to contain two living suborders, Percopsoidei (Percopsidae only) and Aphredoderoidei (Aphredoderidae and Amblyopsidae).

FOSSIL PERCOPSIFORMS

Four genera of fossil percopsiforms have been described: *Trichophanes* Cope (1872), Oligocene–Miocene; and *Erismatopterus* Cope (1871), *Amphiplaga* Cope (1877), and *Asineops* Cope (1870), all Middle Eocene. Like the living Percopsiformes, all are known only from fresh-water deposits on the North American continent. Cope placed *Trichophanes*, *Erismatopterus*, and *Amphiplaga* in the Aphredoderidae, and *Asineops* in the Asineopidae, a monotypic family said to be close to the Aphredoderidae. Apart from a few comments on *Trichophanes* by Cockerell (1908, 1913) no work has been done on these supposed percopsiforms since Cope's original brief descriptions, and they are very poorly known. In order to assess their relationships, these four genera are described in detail below, and the Upper Cretaceous marine genus *Sphenocephalus*, which proves to be related to the percopsiforms, is also described.

FAMILY **APHREDODERIDAE**

GENUS **TRICHOPHANES** COPE

Trichophanes.—COPE, 1872, p. 479.

DIAGNOSIS: Oligocene and Miocene Aphredoderidae differing from *Aphredoderus* in having stronger spines on infraorbitals and

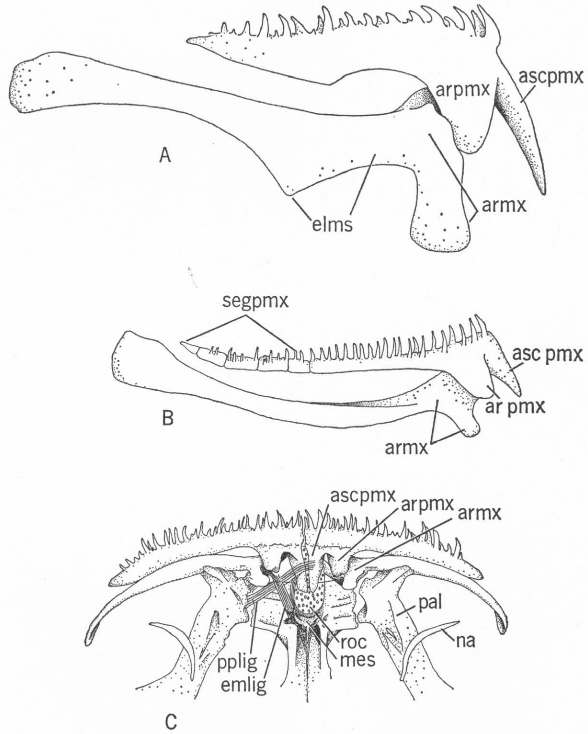

FIG. 15. Upper jawbones in percopsiforms. A. *Percopsis omiscomaycus* (Walbaum). B. *Aphredoderus sayanus* (Gilliams). C. *Typhlichthys subterraneus* Girard. All after Rosen (1962).

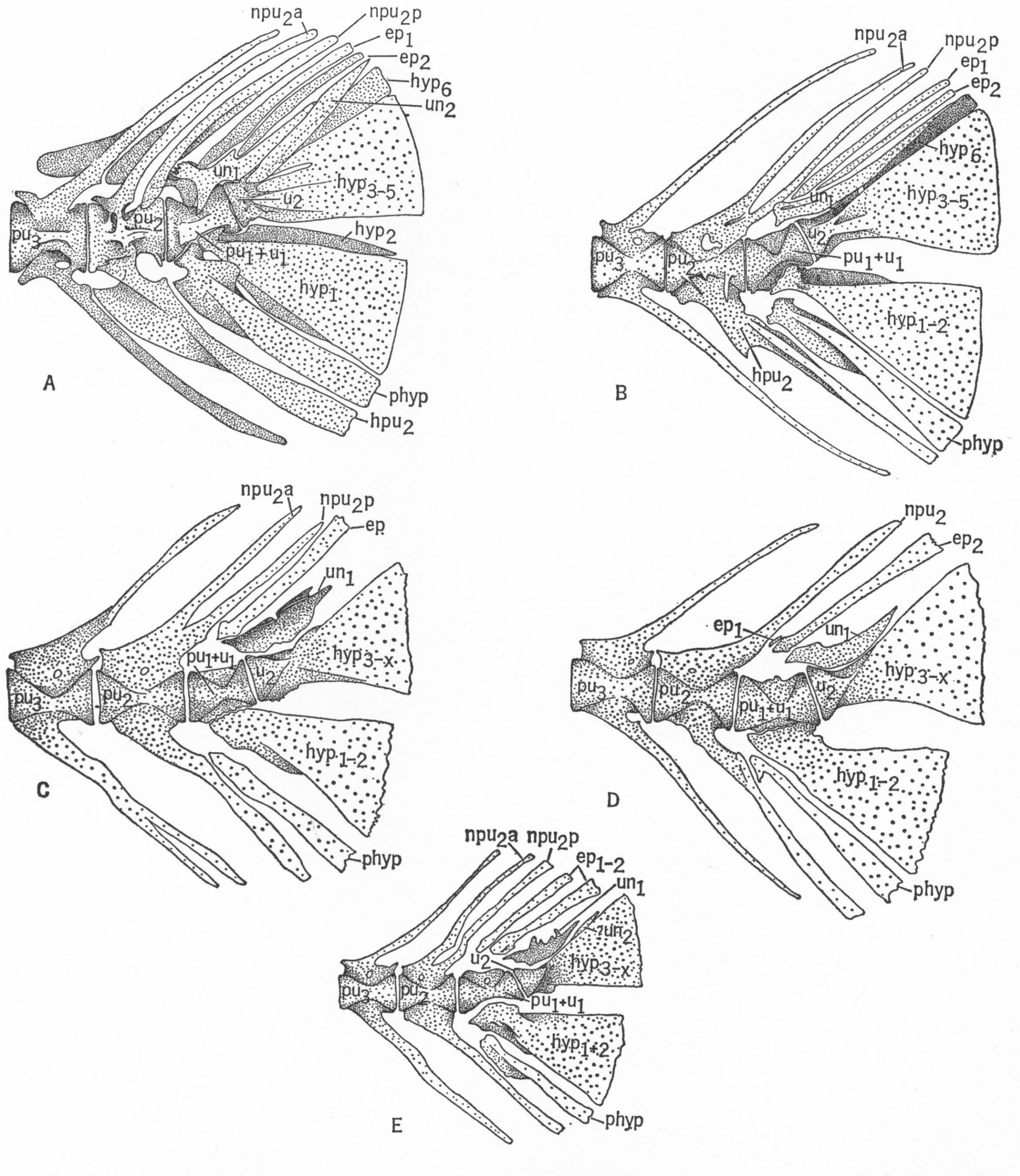

FIG. 16. Caudal skeletons of percopsiforms. A. *Percopsis omiscomaycus* (Walbaum). B. *Aphredoderus sayanus* (Gilliams). C. *Chologaster agassizi* Putnam. D. *Typhlichthys subterraneus* Girard. E. *Amblyopsis spelaea* DeKay. All after Rosen (1962).

preopercular, parasphenoid expanded, 30–31 vertebrae, a second uroneural, parhypural articulating with supporting centrum, caudal fin forked and with eight or nine procurrent spines above and below, eight pelvic rays, and scales with long, slender ctenii.

TYPE SPECIES: *Trichophanes hians* Cope (1872, p. 480).

REMARKS: Three species have been described in *Trichophanes*. *Trichophanes hians*, from lignites of supposed Miocene age at Osino, Nevada, is known only from the holotype (U.S.N.M. No. 4060). *Trichophanes foliarum* Cope and *T. copei* Osborn, Scott, and Speir (1878, p. 98) are from the Florissant lake beds, Florissant, Colorado. *Trichophanes copei* is known only from the holotype (at Princeton), which has never been figured or redescribed, and there is nothing in the original brief description to distinguish it from *T. foliarum*; probably it is a synonym of this species.

The generic diagnosis above is based on *T. foliarum*, because almost nothing is known of *T. hians*. Cope said that in *T. hians* the preopercular is not serrated and that there are only two dorsal and anal spines, but the preopercular is not visible in the specimen, the dorsal spines cannot be counted, and there are three anal spines. The scales of *T. hians* are very like those of *T. foliarum*, and there is no reason to doubt that the two species are congeneric, although the fish is so preserved that it yields very little information.

Trichophanes foliarum Cope

Plate 65, figure 2; text figures 17–19

Trichophanes foliarum.—COPE, 1878, p. 73 (original description; Florissant lake beds, Florissant, Colorado). COPE, 1884, p. 753, fig. 4. COCKERELL, 1908, p. 571, figs. 1, 2. COCKERELL, 1913, p. 152.

Trichophanes copei.—OSBORN, SCOTT, AND SPEIR, 1878, p. 98 (original description; Florissant lake beds, Florissant, Colorado).

DIAGNOSIS: *Trichophanes* reaching about 110 mm. in standard length, length of head and depth of trunk about 30 per cent and 25 per cent of standard length, respectively, 13+17–18 vertebrae; D IV, 11–12; A III, 6–7; P 13–14; V 8; C x–xi, I, 8, 8, I, ix; about 25 scales in a transverse series on the trunk.

HOLOTYPE: U.S.N.M. No. 4058, a fish lacking the caudal region.

MATERIAL: A.M.N.H. No. 18924, B.M.-N.H. Nos. P.10631, P.12506–P.12508.

HORIZON AND LOCALITY: Florissant lake beds, Florissant, Colorado; those beds have usually been considered to be of Miocene age, but the evidence for such an allocation is weak. Recent opinion (Keroher *et al.*, 1966) favors a Middle Oligocene age.

DESCRIPTION: The specimens are preserved as natural molds in fine-grained shale and have been studied principally by means of latex casts.

The dimensions of two complete specimens are given in table 2.

Cope's holotype appears to be the largest recorded specimen; although incomplete, the measurements given by Cope indicate that it would have been about 110 mm. in standard length.

The skull roof is not completely preserved in any specimen, but the visible parts resemble those of *Aphredoderus* very closely, with the scales extending forward over the posttemporal fossa to a low, semicircular crest on the frontals at the hind edge of the

TABLE 2

PROPORTIONAL MEASUREMENTS OF TWO SPECIMENS OF *Trichophanes*

	A.M.N.H. No. 18924	B.M.N.H. No. 12506
Standard length (mm.)	70	56
Total length, in per cent of standard length	121	120
Head length, in per cent of standard length	29	30
Trunk depth, in per cent of standard length	24	23
Predorsal length, in per cent of standard length	41	45
Preanal length, in per cent of standard length	67	66

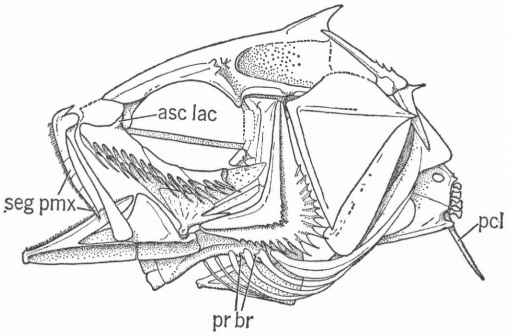

FIG. 17. *Trichophanes foliarum* Cope, Oligocene, Florissant lake beds, Florissant, Colorado. Restoration of skull and pectoral girdle.

orbit that limits this fossa, no part of the supraorbital sensory canal bone-enclosed, but small processes forming incomplete bridges at the origin of the parietal and anterolateral branches, and the frontals tapering anteriorly. Nothing can be seen of the ethmoid or postorbital regions of the neurocranium, but A.M.N.H. No. 18924 shows that the parasphenoid was considerably expanded below the orbit, being much broader than in *Aphredoderus*.

As in *Aphredoderus*, the lacrimal and infraorbitals are spiny, but the spines are larger than in the living genus. On the lacrimal and first two infraorbitals there is a comblike fringe of long, slender spines both on the ventral edge of the bones and on the flange overhanging the groove for the sensory canal.

Both A.M.N.H. No. 18924 and B.M.N.H. No. P.12506 show that the alveolar process of the premaxilla was broken up into three or four separate segments, as in *Aphredoderus*, and the size of the jaws, the shape of the premaxilla and maxilla, and the visible parts of the palate are all just as in *Aphredoderus*. B.M.N.H. No. P.12506 shows that the vomer and palatine were toothed.

There are six branchiostegals, with "percopsoid projections" (McAllister, 1968, p. 6) on the heads of the fourth and fifth, as in *Aphredoderus*. The ceratohyal is imperforate, and in A.M.N.H. No. 18924 and B.M.N.H. No. P.12507 there are indications that tooth plates were present on the posterior part of the upper margin of the ceratohyal, another resemblance to *Aphredoderus* (in *Percopsis* there are tooth plates along the whole upper edge of the ceratohyal).

The preopercular has a long horizontal limb, and around the angle in the bone there are 12–15 spines, the longest at the angle; these spines are stronger and less numerous than those in *Aphredoderus*. The opercular has a single spine opposite the point of suspension, with no evidence of a second spine above it as there is in *Aphredoderus*, but the bone is truncated anterodorsally, as in *Aphredoderus*, not excavated as in *Percopsis*. The opercular, subopercular, and cheek are all completely scale-covered, another resemblance to *Aphredoderus* rather than to *Percopsis*.

There are 13 abdominal vertebrae, 17–18 caudal vertebrae, and a free second ural centrum, two or three more than in *Aphredoderus*. The first ribs are borne on the third

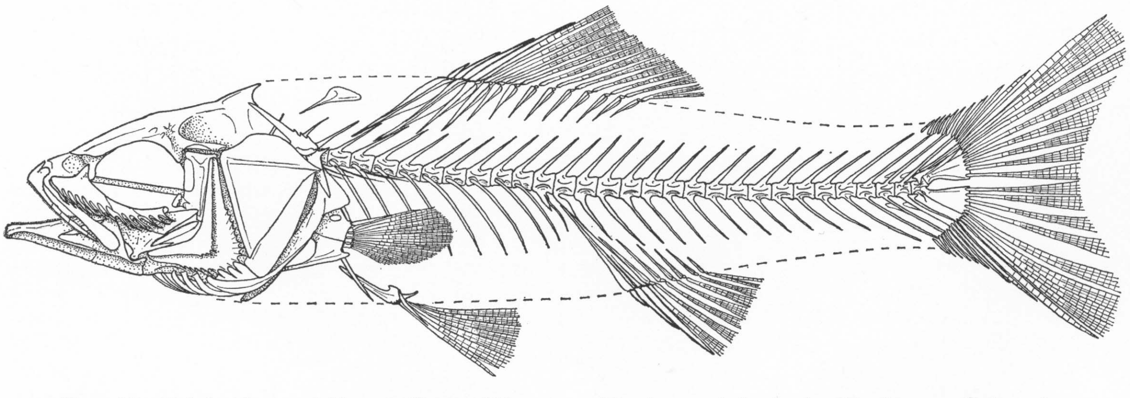

FIG. 18. *Trichophanes foliarum* Cope, Oligocene, Florissant lake beds, Florissant, Colorado. Restoration, scales omitted.

vertebra, and the ribs are inserted on the centrum above the parapophyses on the third to the twelfth vertebrae, the thirteenth having small ribs inserted on a ventral process. There are epipleural bones on the first five vertebrae. The first haemal spine is expanded into a transverse plate which lies behind the proximal ends of the first two anal radials.

The caudal skeleton (text fig. 19) is of normal percopsiform type, with two epurals, a complete neural spine on the second preural centrum, and the second ural centrum fused with all but the uppermost (the sixth) of the upper hypurals. The caudal skeleton resembles that of *Percopsis* rather than that of *Aphredoderus* in having an articulation between the parhypural and the supporting centrum, a moderately large first uroneural with a saddle-like articulation on the centrum, and a second uroneural, but it resembles that of *Aphredoderus* rather than that of *Percopsis* in having the second hypural fused with the first, although not reduced to a short crest as it is in *Aphredoderus*. In the upper hypurals *Trichophanes* seems to be intermediate between *Percopsis*, in which the fifth hypural is often autogenous, and *Aphredoderus*, in which it is indistinguishably fused with the third and fourth, for the fifth hypural is fused with those below it but can be recognized by surface ridges. No specimen of *Trichophanes* shows any doubling of the neural and haemal spines on the last few preural vertebrae, a common feature in *Aphredoderus*.

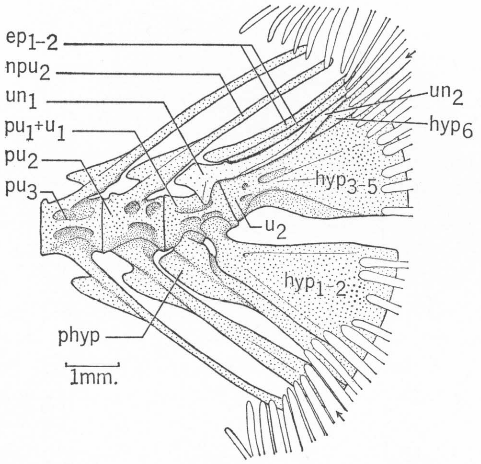

FIG. 19. *Trichophanes foliarum* Cope, Oligocene, Florissant lake beds, Florissant, Colorado. Caudal skeleton of B.M.N.H. No. P.12506. Arrows indicate the outermost (unbranched) principal fin rays.

The caudal fin is emarginate or weakly forked, not truncate as in *Aphredoderus*, and contains 18 principal rays with 16 branched. There are 10 or 11 upper procurrent rays, all but the last apparently spinous, and nine lower procurrent rays, all but the last spinous. The foremost procurrent rays lie in front of the fourth pre-ural neural and haemal spines.

In the pectoral girdle there is a spine on the hind edge of the supracleithrum, as in *Aphredoderus*. In other respects the girdle shows no significant differences from the girdle of *Percopsis* and that of *Aphredoderus*. There are four pectoral radials, and the upper and lower postcleithra are fused. The pectoral fin contains 13 or 14 rays.

The pelvic girdle is crossed by the tips of the postcleithra, and the pelvic fin contains a splint and eight rays, all branched. *Trichophanes foliarum* resembles *Percopsis* in the number of pelvic rays, and *Aphredoderus* in having a branched first ray.

The dorsal fin contains four spines, the first very small, and 11 or 12 soft rays, supported by 13–15 radials. The first dorsal radial lies behind the third neural spine, and there is a single supraneural lying behind the first neural spine. The fourth dorsal spine is equal in length to about 55 per cent of the maximum depth of the trunk. There is no sign of an adipose fin.

The anal fin contains three spines and six or seven soft rays supported by seven to nine radials. The third anal spine is equal to about 50 per cent of the depth of the trunk.

The scales are strongly ctenoid (Cockerell, 1908, p. 572, referred to them as "ultra-ctenoid"), with long, bristle-like ctenii. The scales, although more strongly ctenoid than those of *Aphredoderus*, are similar in size, with about 25 in a transverse series on the trunk. As in *Aphredoderus*, there is no sign of a lateral line.

Although in many fossil teleosts the position of the anus can be inferred from fossilized gut contents, the available specimens of *Trichophanes* show no evidence to indicate whether the vent was jugular, as in adult

Aphredoderus, or abdominal, as in *Percopsis*.

RELATIONSHIPS OF *Trichophanes*

Placed in the Aphredoderidae by Cope (1872, 1878, 1884), *Trichophanes* was made the type of a monotypic family, Trichophanidae, by Cockerell (1908, p. 573) on the grounds that, although similar to *Aphredoderus*, it was intermediate between the Aphredoderidae and Percopsidae, resembling *Percopsis* and especially *Columbia* in the "shape of the dorsal fin" and the forked caudal fin. Later (1913, p. 152) Cockerell decided that these features were insufficient for familial distinction and relegated *Trichophanes* to a subfamily, Trichophaninae, of the Aphredoderidae. More detailed information on the structure of *Trichophanes foliarum* shows that it is undoubtedly very closely related to *Aphredoderus*. Important characters in which it resembles this genus and differs from the Percopsidae include the large, scale-covered posttemporal fossa, the open supraorbital sensory canal, the premaxilla without a postmaxillary process and with a segmented alveolar process, the maxilla without a dorsal process on the shaft, the spiny infraorbitals, the second hypural fused with the first, the branched first pelvic ray, the dorsal fin with four spines, and the anal with three. The differences between *Trichophanes* and *Aphredoderus* (the stronger spines on the infraorbitals and preopercular, the expanded parasphenoid, the presence of two or three more vertebrae and procurrent caudal spines, a second uroneural, a parhypural articulating with the supporting centrum, a forked caudal fin, one more pelvic ray, and more strongly ctenoid scales) are relatively trivial, and *Trichophanes* can certainly be included in the Aphredoderidae. There seems to be no need to distinguish *Aphredoderus* and *Trichophanes* at the subfamilial level as Cockerell proposed. Further, in many of the characters in which it differs from *Aphredoderus* (the more numerous vertebrae, second uroneural, parhypural, forked caudal) *Trichophanes* is the more primitive, resembling the Percopsidae, and the strong infraorbital and preopercular spines may also be primitive for the Percopsiformes (see *Sphenocephalus*, p. 407). Only one character of *Trichophanes*, the expanded parasphenoid, differs substantially from the condition in *Aphredoderus*. An expanded parasphenoid is, however, characteristic of the Amblyopsidae, the closest living relatives of *Aphredoderus*, which raises the question of whether *Trichophanes* is closer to *Aphredoderus* or to the amblyopsids. Many of the characters in which the amblyopsids appear to be more primitive than the Aphredoderidae, such as the cycloid scales, abdominal pelvics, and the absence of fin spines, are probably secondarily acquired (cf. the reappearance of these characters in the Stephanoberycoidei among the Beryciformes), and nothing seems to be known in the amblyopsids that definitely opposes their derivation from such a fish as *Trichophanes*.

FAMILY **PERCOPSIDAE**

GENUS **AMPHIPLAGA** COPE

Amphiplaga.—Cope, 1877, p. 388.

DIAGNOSIS: Eocene percopsid fishes with well-developed marginal and pharyngeal dentition, preopercular spiny at the angle, operculum scaled, 31 or 32 vertebrae, prezygapophyses of posterior abdominal vertebrae enlarged, six autogenous hypurals, pelvics eight-rayed, dorsal and anal each with three spines.

TYPE AND ONLY SPECIES: *Amphiplaga brachyptera* Cope.

Amphiplaga brachyptera Cope

Plate 66, plate 68, figure 1, text figures 20–22

Amphiplaga brachyptera.—COPE, 1877, p. 812 (original description; Green River Shales, Wyoming). COPE, 1884, p. 87, pl. 7, fig. 5, pl. 12, fig. 4.

Erismatopterus endlichi.—COPE, 1877, p. 812 (original description; Green River Shales, Wyoming). COPE, 1884, p. 82, pl. 12, fig. 5.

DIAGNOSIS: As for the genus, only species: reaching about 90 mm. in standard length; D III, 9–10; A III, 7; P 14; V 8; C x–xii, I, 8, 8, I, viii–xi.

HOLOTYPE: U.S.N.M. No. 3996 (Cope, 1884, pl. 12, fig. 4), a fish lacking the head.

MATERIAL: In addition to the holotype, U.S.N.M. No. 4011 (Cope, 1884, pl. 7, fig. 5), U.S.N.M. No. 3997 (holotype of *E. endlichi*, Cope, 1884, pl. 12, fig. 5), U.S.N.M. No. 18133 (pl. 68, fig. 1), U.S.N.M. No. 19878, U.S.N.M. No. 19882.

HORIZON AND LOCALITY: Middle Eocene,

Green River Shales, Twin Creek, Wyoming. The species occurs only in light-colored limestones and marls.

DESCRIPTION: The dimensions of five specimens are given in table 3.

The skull roof is partially visible in U.S.N.M. Nos. 4011, 18133, and 19882, and is of normal percopsid type, closely resembling the skull roofs of *Percopsis* and *Erismatopterus*. The supraoccipital crest is rather long, with a strongly thickened upper edge. The parietals are invariably disturbed and in U.S.N.M. No. 4011 appear to meet medially, but probably they were separated by the supraoccipital as in *Percopsis*. A large foramen for the lateralis accessorius branch of the facial nerve is visible in U.S.N.M. No. 4011; it lies almost at the midpoint of the parietal, as in *Aphredoderus*. The posttemporal fossa resembles that of *Percopsis* in size. The frontals are broad, troughlike, and abruptly truncated anteriorly, as in *Percopsis* and *Erismatopterus*. The supraorbital sensory canal was bone-enclosed only in the posterolateral part of the frontal, where it ran through a broad tunnel, as in *Percopsis* and *Erismatopterus*. Nothing can be seen of the neurocranium except that the parasphenoid was slender and there were prominent exoccipital condyles (U.S.N.M. No. 18133).

The lacrimal is of typical percopsiform type, with a spikelike ascending process on the dorsal margin. The ventral edge of the lacrimal is smooth, and in this respect and in size and shape the bone resembles that of *Percopsis* rather than that of *Aphredoderus*. There is no clear evidence of an antorbital.

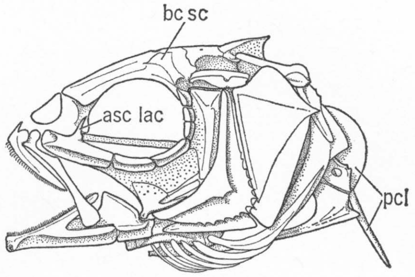

FIG. 20. *Amphiplaga brachyptera* Cope, Middle Eocene, Green River Shales, Wyoming. Restoration of skull and pectoral girdle.

The infraorbitals are shallow bones, without marginal serrations, as in *Percopsis*. The premaxilla has a low ascending process, only slightly higher than the articular process, and no postmaxillary process, in these features resembling *Aphredoderus*, but the alveolar process is not segmented distally. The maxilla is more than half as long again as the premaxilla and has a low dorsal process above the middle part of the alveolar process of the maxilla—resemblances to *Percopsis* in both features. There is no supramaxilla. The mandible is moderately deep, with the sensory canal running in an open groove except at the tip of the dentary. The teeth on the premaxilla and dentary are rather large, perhaps a little larger than those of *Percopsis*.

The hyomandibular is broad and vertical, but as in *Percopsis* and *Aphredoderus* the symplectic is elongate and strongly inclined forward, so that the condyle of the quadrate lies below the center of the orbit. The palatine is toothed, but both the endopterygoid and ectopterygoid appear to be without

TABLE 3

PROPORTIONAL MEASUREMENTS OF FIVE SPECIMENS OF *Amphiplaga brachyptera* COPE

U.S.N.M. Specimens	Standard Length, Mm.	As Per Cent of Standard Length					
		Total Length	Head Length	Trunk Depth	Predorsal Length	Preanal Length	Peduncle Depth
No. 18133	33.5	120	28.5	21	42	66	12
No. 3997	48	118	33	22	45	69	13
No. 19878	52	122	31	20	46	72	11
No. 19882	48.5	—	29	22	46	72	—
No. 4011	90	117	29	23	44.5	70	13
Mean		119	30	21.5	44.5	70	12

teeth, as in *Percopsis*.

The ceratohyal is rather shallow, as in *Percopsis* and *Aphredoderus*, and there is no sign of a fenestra in the bone. In U.S.N.M. Nos. 4011 and 19878 there is evidence of a series of tooth plates along the dorsal margin of the ceratohyal. There are two hypohyals and a large triangular urohyal. The six branchiostegals are arranged as in *Percopsis* and *Aphredoderus*, the two slender anterior rays inserted on the ventral edge of the ceratohyal and the last of the four broad posterior rays lying on the epihyal. There appear to be no "percopsoid projections" on the heads of the branchiostegals. The teeth on the upper and lower pharyngeals are large and conspicuous.

The preopercular resembles that of *Percopsis* rather than that of *Aphredoderus* in being very broad at the angle, but the horizontal limb is not so long as it is in *Percopsis*, and there are about a dozen spines on the hind edge of the preopercular around the angle, the spines being relatively larger in smaller specimens. The opercular has a single prominent spine connected by a ridge with the point of suspension. The upper part of the opercular is more completely ossified than it is in *Percopsis* and *Aphredoderus*. The subopercular is long, as in *Percopsis* and *Aphredoderus*, with a broad, blunt process at the tip of the opercular. Both the opercular and subopercular were probably completely scale-covered. The interopercular is an elongate triangle largely covered by the preopercular.

The vertebral column contains 14 abdominal vertebrae, 16–17 caudal vertebrae, and a free second ural centrum. As in *Percopsis* and *Aphredoderus*, the transverse processes on the abdominal vertebrae project almost horizontally, and, although the mode of articulation of the ribs is not clearly visible, they probably articulated with the upper faces of the transverse processes, as in the living genera. On the posterior abdominal vertebrae (about the eighth to fourteenth vertebrae) the prezygapophyses are greatly enlarged, projecting anterodorsally as conspicuous spines. The ribs are stout and occupy about two-thirds of the depth of the abdominal cavity. The first rib is inserted on the third vertebra. The only traces of intermuscular bones are slender epipleurals on the second (and probably also the first) vertebra of U.S.N.M. No. 18133. The first haemal spine is short and expanded laterally into a triangular plate which lies behind the first anal radial.

The caudal skeleton resembles that of *Percopsis* in the complete neural spine on the second pre-ural centrum, the presence of flanges on the proximal parts of the second and third pre-ural haemal and neural spines, the two epurals, two uroneurals, and the articulation between the parhypural and the supporting centrum. The caudal skeleton is more primitive than that of *Percopsis* in having six autogenous hypurals, none fused with the second ural centrum, and the second hypural fully developed. The second uroneural in some cases has a broad, trun-

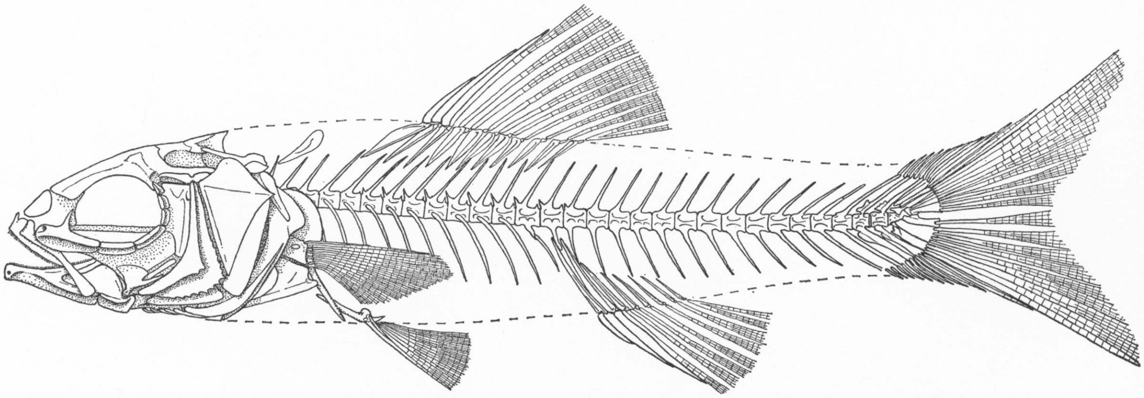

FIG. 21. *Amphiplaga brachyptera* Cope, Middle Eocene, Green River Shales, Wyoming. Restoration, scales omitted.

cated proximal end (U.S.N.M. No. 19882), but in the smallest specimen, U.S.N.M. No. 18133 (text fig. 22B), it ends proximally in a small half centrum articulating with a complete second ural centrum. The fifth and sixth hypurals articulate with this third ural centrum. A third ural centrum occasionally occurs as a transient stage in ontogeny or even in the adult of such primitive teleosts as the elopoids (Hollister, 1936, figs. 18, 22–24) and may occur in the myctophoid *Trachinocephalus* (Hollister, 1937, fig. 2), but the condition in this individual of *Amphiplaga*, in which the centrum is fused with the second uroneural, appears to be unique. Possibly it may be explained by the origin, in phylogeny, of the second uroneural, which is probably formed by fusion of the fourth and fifth ural neural arches (Patterson, 1968a, p. 226). The fourth ural neural arch would correspond with a third ural centrum (since the first ural centrum supports two hypurals and is compound), and it seems possible that it could occasionally induce the appearance of a third ural centrum, even in moderately advanced teleosts such as the Percopsiformes.

The caudal fin is forked and contains 18 principal rays with 16 branched, with 10–12 upper procurrent rays, the first six to eight spinous, and eight to 11 lower procurrent rays, the first five to seven spinous. The foremost procurrent rays articulate with the neural spine of the third (three specimens) or fourth (three specimens) pre-ural centrum above, the haemal spine of the fourth (five specimens) or fifth (U.S.N.M. No. 18133) pre-ural centrum below. In U.S.N.M. No. 4011 the first upper procurrent spine (text fig. 22A), which is very short and would not have projected through the skin, has a horizontal, leaf-shaped expansion at the tip; probably this is the last vestige of the caudal scute of more primitive teleosts.

In the shoulder girdle, U.S.N.M. No. 3997 indicates that there was a small, U-shaped supratemporal, resembling that of living percopsiforms. The posttemporal and supracleithrum are exactly as in *Percopsis*, the posttemporal with a long epiotic limb, a stout intercalar limb, a projecting flange which carried the sensory canal on the outer face of the bone, and one or two weak serrations posterodorsally in some specimens, the supracleithrum long, stout, and without ornament. The cleithrum resembles that of *Percopsis* rather than that of *Aphredoderus* in having a large posterodorsal plate. The scapula and coracoid were evidently embedded in cartilage, as in *Aphredoderus*, since in U.S.N.M. No. 4011 both bones have drifted away from the cleithra. The scapula and coracoid resemble those of *Percopsis* in shape. As in living percopsiforms, the upper

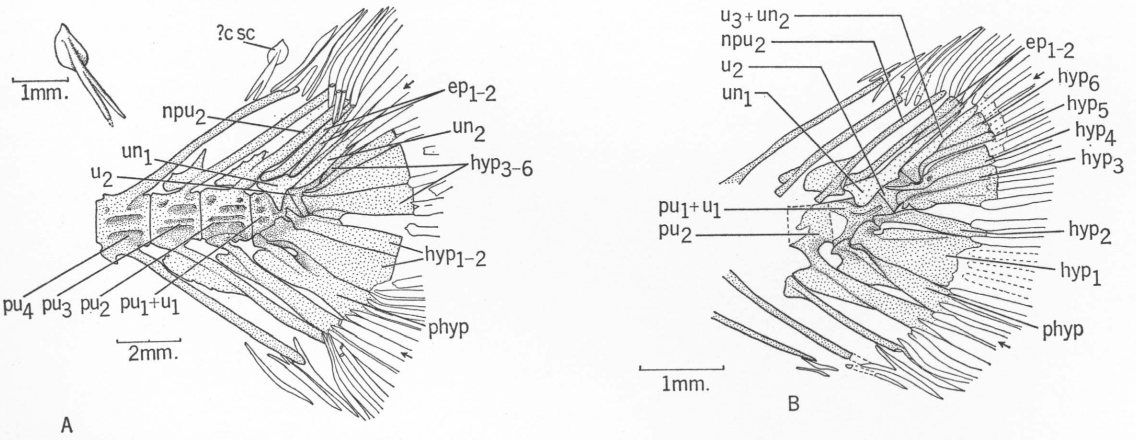

FIG. 22. *Amphiplaga brachyptera* Cope, Middle Eocene, Green River Shales, Wyoming. A. Caudal skeleton of U.S.N.M. No. 4011, reversed left to right. Insert above is an enlarged view of the first upper procurrent ray, as preserved. B. Caudal skeleton of U.S.N.M. No. 18133, an abnormal individual with a third ural centrum. Arrows mark the outermost (unbranched) principal rays in both figures.

and lower postcleithra are fused into a single bone, rodlike below, scalelike above. The upper, scalelike plate is very large, as in *Percopsis*. The pectoral fin is inserted rather low on the flank and is large, with 14 rays.

The pelvic fins are subthoracic, the fin originating just behind the tip of the postcleithrum and the pelvic girdle lying well behind the cleithral symphysis. The postcleithra cross the pelvic bones, but whether there was any attachment between the two, as in *Aphredoderus*, or the girdle lay free, as in *Percopsis*, is an open question. The pelvic bones appear to be identical with those of *Erismatopterus* (text fig. 27). The pelvic fin contains a splint and eight rays, the first unbranched, as in *Percopsis*.

The dorsal fin originates behind the pelvics, the first radial lying behind the fourth neural spine. The fin contains three stout, smooth spines and nine to 10 soft rays, supported by 10–11 radials. The third dorsal spine is equal to about 90 per cent of the maximum depth of the trunk in the smallest specimens, this ratio decreasing to about 80 per cent in the largest specimens. A single supraneural lies between the second and third neural spines. There is no trace of an adipose fin in any specimen, but, since exceptional conditions of preservation are necessary before this fin can be detected in fossils, it is quite possible that *Amphiplaga* had one. The anal fin contains three stout spines and seven soft rays, supported by eight radials. The third anal spine is equal in length to 85–90 per cent of the third dorsal spine.

The scales (pl. 66) are thin, with concentric circuli, and strongly but finely ctenoid, the ctenii being about as numerous as in *Percopsis* but larger. The lateral line appears to be uninterrupted. There are about 19 scales in a transverse series on the trunk, with nine above and nine below the lateral-line scale, as in *Percopsis*. Scales cover the bases of the caudal fin rays, the opercular and subopercular, but not the preopercular, the skull roof, or, apparently, the cheek.

RELATIONSHIPS

The relationships of *Amphiplaga* are discussed below (p. 397), together with those of *Erismatopterus*.

GENUS **ERISMATOPTERUS** COPE

Erismatopterus.—COPE, 1871, p. 428.

DIAGNOSIS: Eocene percopsid fishes with marginal and pharyngeal dentition reduced, preopercular smooth or with three or four weak serrations at angle, opercular squamation much reduced or absent, 30 vertebrae, six autogenous hypurals, pelvics seven-rayed, dorsal and anal each with two spines.

TYPE SPECIES: *Cyprinodon levatus* Cope (1870, p. 382).

REMARKS: Cope described three species in this genus: *E. levatus*, *E. rickseckeri*, and *E. endlichi*, all from the Green River Shales. Reexamination of the type material shows that *E. rickseckeri* is a synonym of *E. levatus*; *E. endlichi*, of *Amphiplaga brachyptera*.

Erismatopterus levatus (Cope)

Plate 68, figure 2; text figures 23–27

Cyprinodon levatus.—COPE, 1870, p. 382 (original description; Green River Shales, Wyoming).
Erismatopterus levatus.—COPE, 1871, p. 428. COPE, 1884, p. 80, pl. 9, figs. 6, 7.

Erismatopterus rickseckeri.—COPE, 1871, p. 428 (original description: Green River Shales, Wyoming). COPE, 1884, p. 81, pl. 6, fig. 2.

DIAGNOSIS: As for the genus, only species: reaching about 70 mm. in standard length; D II, 6–7; A II, 7; P 14; V 7; C x–xi, I, 8, 8, I, viii–x.

SYNTYPES: A.M.N.H. No. 2526, two headless fishes on a single slab.

MATERIAL: In addition to the syntypes, A.M.N.H. No. 2696 (Cope, 1884, pl. 9, fig, 7), A.M.N.H. No. 2800 (two fishes on a slab. syntypes of *E. rickseckeri*, one figured by Cope, 1884, pl. 6, fig, 2), and a series of specimens in the American Museum of Natural History collected by B. Schaeffer in 1948, especially A.M.N.H. Nos. 3993–3999.

HORIZON AND LOCALITY: Middle Eocene, Green River Shales; Green River Cut and Fish Cut, Wyoming. The species occurs only in dark, bituminous shales.

DESCRIPTION: The dimensions of five specimens are given in table 4.

The skull roof is more or less completely preserved in several specimens, and a composite restoration is shown in text figure 23. This skull roof differs from the skull roofs of *Percopsis* and *Aphredoderus* only in minor details, showing all the features common to both living genera. The large supraoccipital crest, thickened dorsally, resembles the crests of *Percopsis* and *Amphiplaga* rather than the reduced crest of *Aphredoderus*. The parietals are separated by the supraoccipital but are a little closer to each other than in the living genera. The foramen of the ramus lateralis facialis lies near the anterior edge of the parietal, as in *Percopsis*. Laterally, the parietal forms the medial wall of a large, open, posttemporal fossa. The pterotic carried the temporal sensory canal forward in a broad, open groove, with a lateral notch through which the preopercular canal passed ventrally. The autosphenotic is small and does not project laterally. The dilatator fossa and hyomandibular facet on the pterotic and autosphenotic are as in *Percopsis* and *Aphredoderus*. The frontals resemble those of *Percopsis* and *Amphiplaga* in being truncated anteriorly, in having a broad tunnel enclosing the posterior part of the supraorbital sensory canal, and in lacking the curved crest at the posterolateral corner of the frontal which in *Aphredoderus* and *Trichophanes* marks the limit of the enlarged posttemporal fossa. Anteriorly, the supraorbital sensory canal ran in a broad, shallow trough, limited medially by a low crest on each frontal, as in *Percopsis* and *Aphredoderus*. The nasals are invariably poorly preserved, but appear to have been moderately large triangular bones, rolled upward medially, as in *Percopsis*. The lateral ethmoids are large, squarish bones, deeper than in *Aphredoderus* and perhaps deeper than in *Percopsis*. The vomer is not visible. The parasphenoid is straight and slender. Nothing has been seen of the otic and occipital regions of the neurocranium except that A.M.N.H. No. 2800 shows that these were large exoccipital condyles.

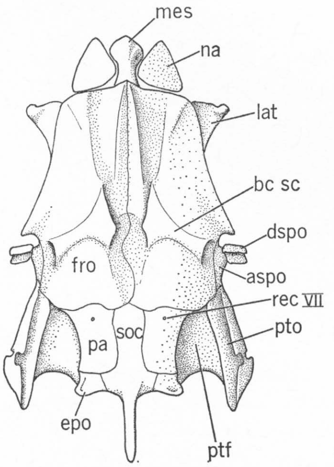

FIG. 23. *Erismatopterus levatus* (Cope), Middle Eocene, Green River Shales, Wyoming. Restoration of skull roof.

The lacrimal is identical with the lacrimals of *Percopsis* and *Amphiplaga*. As in *Amphiplaga*, there is no evidence of an antorbital. There are four smooth, troughlike infraorbitals, resembling those of *Percopsis*, and a dermosphenotic overlying the autosphenotic. There is no subocular shelf.

In the jaws and palate there are no discernible differences between *E. levatus* and *Amphiplaga*, except that the teeth on the dentary and premaxilla appear to be much

TABLE 4

PROPORTIONAL MEASUREMENTS OF FIVE SPECIMENS OF *Erismatopterus levatus* (COPE)

A.M.N.H. Specimens	Standard Length, Mm.	As Per Cent of Standard Length					
		Total Length	Head Length	Trunk Depth	Predorsal Length	Preanal Length	Peduncle Depth
No. 2696	43[a]	119	—	23	51	67	10
No. 2800	61	—	29.5	26	46	70	—
No. 3999	54	122	31	22	46	68.5	12
No. 3993	63	—	29	23	46	70	—
No. 3994	69[a]	—	30	22.5	47	69.5	12
Mean		120	30	23	47	69	11

[a] Estimated.

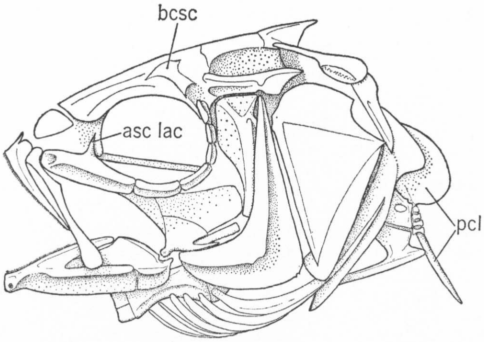

FIG. 24. *Erismatopterus levatus* (Cope), Middle Eocene, Green River Shales, Wyoming. Restoration of skull and pectoral girdle.

smaller in *E. levatus* and the tooth patch on the dentary covers only about half of the margin of the bone. No teeth are visible on the palate in *E. levatus*, possibly owing to the mode of preservation.

There are six branchiostegals, arranged as in *Amphiplaga*, with no signs of anterior projections on the heads of the four posterior rays. The hyoid arch resembles that of *A. brachyptera* except that there is no trace of tooth plates on the upper edge of the ceratohyal; possibly they were absent. Although every specimen of *A. brachyptera* shows large, conspicuous pharyngeal teeth, no pharyngeal teeth are visible in any specimen of *E. levatus*, and certainly the pharyngeal dentition was more feebly developed.

The preopercular is shaped as in *A. brachyptera*, but only in one specimen (A.M.N.H. No. 2800) is there any sign of serrations on the hind edge of the bone. In this specimen there are three or four very weak serrations at the angle of the bone, but in other specimens it appears quite smooth. The opercular has a single spine opposite the point of suspension, with a weaker spine above, and is slightly truncated anterodorsally, resembling that of *Aphredoderus* in shape. The subopercular and interopercular appear to be like those in *Amphiplaga*. Whereas in *Amphiplaga* the opercular and subopercular are completely scaled, in *E. levatus* the only trace of opercular squamation is a single very thin cycloid scale near the point of suspension in one specimen.

There are 30 vertebrae, 13–14 abdominal, 15–16 caudal, and a free second ural centrum. There are epipleural bones on the second vertebra (and probably also on the first) and short, stout ribs inserted on the centrum above the transverse process on the remaining abdominal vertebrae except the last, which has slender ribs inserted on a ventral process. The prezygapophyses of the posterior abdominal vertebrae are not enlarged as they are in *Amphiplaga*. The first haemal spine lies behind the proximal ends of the first two anal radials. The caudal skeleton (text fig. 26) is identical with that of normal individuals of *Amphiplaga brachyptera* (text fig.

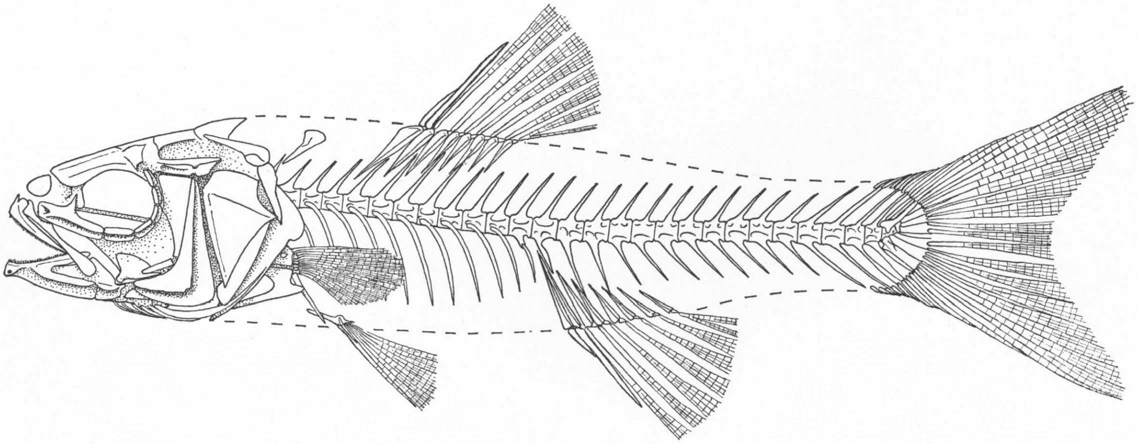

FIG. 25. *Erismatopterus levatus* (Cope), Middle Eocene, Green River Shales, Wyoming. Restoration, scales omitted.

22A). The forked caudal fin contains 18 principal rays with 16 branched. There are nine to 11 upper procurrent rays, the last two or three segmented and the foremost inserted on the third or fourth pre-ural neural spine, and eight to 10 lower procurrent rays, the last two or three segmented and the foremost inserted on the fourth or fifth pre-ural haemal spine. The foremost procurrent rays appear to be spinous.

In the shoulder girdle there is a small, triradiate supratemporal, resembling that of *Percopsis*. The remainder of the shoulder girdle shows no differences from that of *Amphiplaga*, except that there is no evidence of serrations on the posttemporal. The upper and lower postcleithra are fused. The pectoral fin contains 14 rays supported by four radials of the usual hourglass shape.

The pelvic girdle is crossed by the tips of the postcleithra, but it shows no sign of processes or thickenings to indicate that there were ligamentous connections between the bones. The pelvic girdle (text fig. 27) resembles that of *Percopsis* very closely. The pelvic fin contains a splint and seven rays, the first unbranched, one fewer than in *Amphiplaga* and *Percopsis*.

The dorsal fin contains two smooth spines and six or seven soft rays, supported by seven or eight radials. The first dorsal radial lies behind the fifth neural spine. The second dorsal spine is equal in length to about 60 per cent of the maximum depth of the trunk. There is a single predorsal bone, lying behind the second neural spine. There is no clear evidence of an adipose fin, possibly only owing to imperfect preservation.

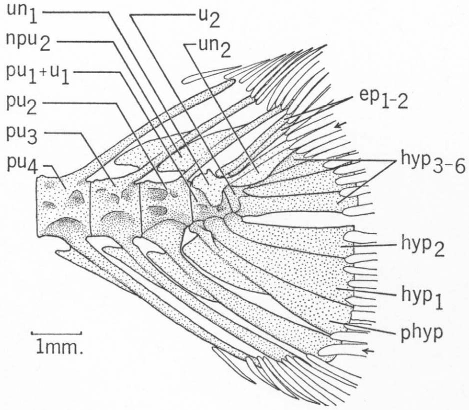

FIG. 26. *Erismatopterus levatus* (Cope), Middle Eocene, Green River Shales, Wyoming. Caudal skeleton of A.M.N.H. No. 3999. Arrows mark the outermost principal (unbranched) fin rays.

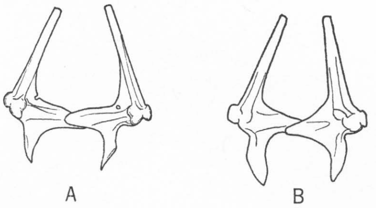

FIG. 27. Pelvic girdles in ventral view. A. *Percopsis omiscomaycus* (Walbaum). B. *Erismatopterus levatus* (Cope), Middle Eocene, Green River Shales, Wyoming, restored from A.M.N.H. No. 3995.

The anal fin contains two spines and seven soft rays supported by eight radials. The second anal spine is equal in length to about 90 per cent of the second dorsal spine.

The scales are almost invariably poorly preserved and were evidently very thin, but in two or three specimens it is possible to see that they were finely ctenoid. It is not possible to count the scales accurately, but they appear to be very similar to those of *Amphiplaga* in size. No lateral line is visible.

RELATIONSHIPS OF *Amphiplaga* AND *Erismatopterus*

Amphiplaga and *Erismatopterus* were placed in the Aphredoderidae (then thought to be a perciform group) by Cope (1884) and have been retained in this family by all later authors except Jordan (1905, p. 242), who came nearer the truth in erecting a family Erismatopteridae which he placed next to the Percopsidae, although later (1923, p. 165) he reverted to Cope's view.

The differences between *Amphiplaga* and *Erismatopterus* are given in table 5.

In those features in table 5 in which there is a distinction between *Percopsis* and *Aphredoderus*, *Amphiplaga* resembles *Percopsis* in respect to 10, *Aphredoderus* in respect to 2, 6, 7, 11, and 14, whereas *Erismatopterus* resembles *Percopsis* in respect to 2, 6, 7, 11, 12, and 14, and *Aphredoderus* in respect to 8 and 10. There is a suggestion here that *Amphiplaga* is closer to *Aphredoderus*, and *Erismatopterus* to *Percopsis*, but this seems to be due largely to the retention in *Amphiplaga* and *Aphredoderus* of the primitive

TABLE 5

DIFFERENCES BETWEEN *Amphiplaga* AND *Erismatopterus*

		Amphiplaga	*Erismatopterus*
1	Occurrence	Pale limestones and marls	Dark, bituminous shales
2	Foramen of lateralis accessorius nerve in parietal	Central	Anterior
3	Teeth in premaxilla and dentary	Moderately large	Small
4	Tooth plates on upper edge of ceratohyal	Present	Probably absent
5	Pharyngeal teeth	Large and conspicuous	Small
6	Preopercular	Spiny at angle	Smooth in most individuals
7	Operculum	Completely scaled	Opercular squamation much reduced or absent
8	Vertebrae	$30–31+u_2$	$29+u_2$
9	Prezygapophyses on posterior abdominal vertebrae	Enlarged	Normal
10	Pelvic fin rays	i, 7	i, 6
11	Dorsal fin rays	III, 9–10	II, 6–7
12	First dorsal radial	Behind 4th neural spine	Behind 5th neural spine
13	Longest dorsal spine	80–90% depth of trunk	*Ca.* 60% depth of trunk
14	Anal fin rays	III, 7	II, 7

percopsiform condition in the spiny preopercular (6), scaled operculum (7), and more numerous fin spines (11, 14) (see p. 407). Differences between *Amphiplaga* and *Erismatopterus* in the dentition (3–5) and perhaps also in the abdominal prezygapophyses (9) (the enlarged zygapophyses of *Amphiplaga* may be due to the insertion on the vertebral column of hypertrophied retractores arcuum branchialium muscles, controlling the enlarged pharyngeals) are probably correlated with differences in habitat (1).

Apart from these differences, the two fossil genera are very similar in proportions, in many details of the skull, caudal skeleton, and fin, and it is evident that they are more closely related to each other than to either *Percopsis* or the Aphredoderidae. The best evidence of this is in the primitive caudal skeleton and the upper jaw, both identical in the two genera, the jaw resembling that of *Percopsis* in the dorsal process on the maxilla and the relatively short premaxilla, and that of *Aphredoderus* in the absence of a postmaxillary process and the short ascending process of the premaxilla. Taken together, the affinities of *Amphiplaga* and *Erismatopterus* are with *Percopsis* rather than with the Aphredoderidae. Resemblances are shown not only in primitive features, such as the shape of the frontals, supraoccipital crest, and posttemporal fossa, the bone-enclosed posterior part of the supraorbital sensory canal, the large dorsal plate on the postcleithrum, the uninterrupted lateral line, fully developed second hypural, and forked caudal fin, but by characters that in this lineage are advanced, such as the dorsal process on the maxilla, the short premaxilla, the toothless ectopterygoid, and the smooth lacrimal and infraorbitals. *Erismatopterus*, in particular, is close to *Percopsis* in the scaleless operculum, smooth preopercular, and reduced number of dorsal and anal spines, although it appears too advanced in the reduced dentition, apparent loss of ceratohyal tooth plates, and the reduced number of dorsal fin rays to have been very close to the ancestor of the living genus. In the absence of definite information on the antorbital and adipose fin, what is known of *Amphiplaga* indicates that it may have been closer to the ancestry of *Percopsis*.

There remains the question of whether *Amphiplaga* and *Erismatopterus* should be included in the Percopsidae. The only characters of the fossil genera which oppose such an assignment are the short ascending processes of the premaxillae, the smaller vertebral number, and the six autogenous hypurals. These are insufficient grounds for familial separation.

FAMILY SPHENOCEPHALIDAE

Sphenocephalidae.—PATTERSON, 1964, p. 383.

AMENDED DIAGNOSIS: Deep-bodied, marine, Cretaceous percopsiform fishes with about five dorsal and anal spines; a pair of large crests, diverging anteriorly, on frontals, as in merlucciid gadiforms; infraorbitals, preopercular, and opercular spiny, operculum scaled; gape large, premaxilla long, with notched postmaxillary process; ceratohyal deep and perforate; anterior vertebrae compressed; upper and lower postcleithra not fused; pelvics seven-rayed, 16 branched caudal rays; scales ctenoid, lateral line uninterrupted; antorbital, one supramaxilla, endopterygoid teeth, pelvic splint, and adipose fin present.

GENUS SPHENOCEPHALUS AGASSIZ

Sphenocephalus.—AGASSIZ, 1838 [1833–1844, vol. 4], p. 4.

DIAGNOSIS: As for the family; only genus.

REMARKS: This genus has previously been known only from the type species, *S. fissicaudus*, from the Campanian of Westphalia (a second species, *S. cataphractus*, was transferred to the trachichthyid genus *Tubantia* by Patterson, 1964, p. 413). The type material of *S. fissicaudus* and all the specimens available to von der Marck (1885, p. 240) were from the buff-colored sandy limestone of Baumberg, but one specimen (B.M.N.H. No. P.2100) is from the blue-gray limestone of Sendenhorst. Smith Woodward (1901, p. 388) wrote of this specimen, "apparently of this species [*S. fissicaudus*] but, if so, with dorsal and anal fins incomplete behind." Smith Woodward referred to the fact that the dorsal and anal fins contain eight and seven soft rays, respectively, compared with 11 and eight in typical *S. fissicaudus*. The fins of B.M.N.H. No. P.2100 are certainly complete, and now that a larger series of *S. fissicaudus* from Baumberg is available for comparison, B.M.N.H. No. P.2100 can be shown to differ in other characters. Although there is only a single specimen, it seems best to describe the Sendenhorst form as a new species (p. 404), if only to draw attention to the existence of a second member of this important genus.

Sphenocephalus fissicaudus Agassiz

Plate 69, figure 1, plate 70, figure 1, text figures 28–33

Sphenocephalus fissicaudus.—AGASSIZ, 1839 [1833–1844, vol. 4], p. 129, pl. 17, figs. 3–5 (original description; Baumberg, Westphalia). PATTERSON, 1964, p. 383, fig. 78 (list of previous references).

DIAGNOSIS: *Sphenocephalus* reaching about 170 mm. in standard length, length of head about 38 per cent of standard length, depth of trunk slightly less (37%); vertebrae $12+18+u_2$; D V, 11; A V, 8; P 15; V i, 6: C x–xii, I, 8, 8, I, viii–xi; longest dorsal and anal spines approximately equal in length; about 20 scales in a transverse series on trunk.

MATERIAL: B.M.N.H. Nos. P.3932, P.8772–P.8774, and P.9059, and five speci-

TABLE 6

PROPORTIONAL MEASUREMENTS OF SEVEN SPECIMENS OF *Sphenocephalus fissicaudus* AGASSIZ

Specimens	Standard Length, Mm.	As Per Cent of Standard Length					
		Total Length	Head Length	Trunk Depth	Predorsal Length	Preanal Length	Peduncle Depth
G.P.I.M. No. A.14	90	130	37	37	54	68	14
G.P.I.M. No. 935	91	—	37	37	53	72	13
G.P.I.M. No. 8772	98	130	40	38	55	76	14
B.M.N.H. No. P.8773	107	122	35	36	50	73	15
G.P.I.M. No. 934	113	128	37	36	53	71	14
G.P.I.M. No. 8778	116	131	41	36	54	72	12
B.M.N.H. No. P.9059	168	125	41	39	50	75	13
Mean		128	38	37	53	72	13.5

mens on loan from the Geologisch-Paläontologisches Institut, Münster University (G.P.I.M. Nos. 934, 935, 8772, 8778, and A.14).

Horizon and Locality: Campanian, Baumberg, Westphalia.

Description: The dimensions of seven specimens are given in table 6.

Since the maximum depth of the trunk is almost 40 per cent of the standard length, *Sphenocephalus* was a much deeper and more laterally compressed fish than the Tertiary and living percopsiforms. One consequence is that the skull is always preserved in lateral view, with the skull roof crushed horizontally. The account and restoration (text fig. 28) of the skull roof are therefore less complete and more speculative than those for *Erismatopterus* and *Amphiplaga*.

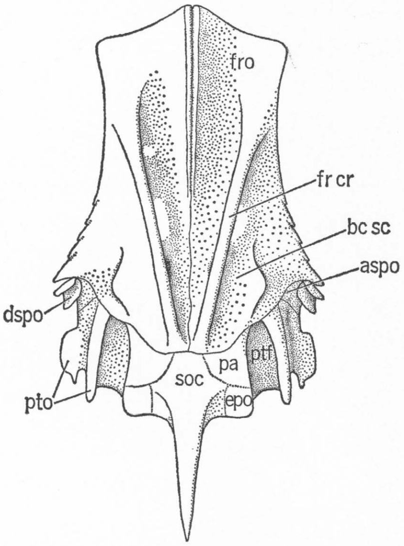

Fig. 28. *Sphenocephalus fissicaudus* Agassiz, Campanian, Baumberg, Westphalia. Restoration of skull roof.

The supraoccipital crest is triangular, with a thickened upper edge, and is larger than in other percopsiforms, projecting above the skull roof as a consequence of the deeper trunk. The parietals are not visible in any specimen, but several specimens (B.M.N.H. Nos. P.9059 and P.8774, and G.P.I.M. No. 8778) show the supraoccipital crest bounded anteriorly by a low transverse crest which is not part of the frontals. This is possibly a mere artifact caused by horizontal crushing of parietals of normal percopsiform type, but it could equally well indicate that the parietals were in contact medially for a short distance, forming a low transverse crest as in *Ctenothrissa* (Patterson, 1964, fig. 2), or the crest may have been minimally interrupted by the supraoccipital, as in the polymixiid *Berycopsis* (Patterson, 1964, fig. 24). In any case, the size of the supraoccipital crest indicates that the trunk musculature probably extended onto the skull roof in greater bulk than it does in living percopsiforms, and a transverse parietal crest would not be out of place as a site of origin of this muscle. The frontals are broad posteriorly, troughlike and sharply truncated anteriorly. The most conspicuous feature of the frontals is a pair of high, stout crests or struts, originating near the midline of the posterior part of the frontals and diverging anteriorly to end on the anterolateral part of the supraorbital flange. Above the posterior part of the orbit there is a large oval opening through the crest, which forms a strut above it. The supraorbital sensory canal, reaching the frontal from the pterotic, passed through a foramen below a raised flange at the posterolateral corner of the bone and emerged in the median cavity between the paired frontal crests. These crests must have delimited a large, deep, mucous cavity which contained both the supraorbital commissure of the sensory canals and their forward continuation to the nasals, running in the troughlike anterior parts of the frontals. The large hole through the crest above the orbit must have transmitted a branch of the sensory canal to the supraorbital flange. The frontals and the pattern of the supraorbital sensory canal in *Percopsis*, *Amphiplaga*, and *Erismatopterus* differ from those of *Sphenocephalus* in that the frontal crests are much lower and shorter, without a forward extension with a hole below it; they can be derived from *Sphenocephalus* by reduction of the frontal crests. The pattern in *Sphenocephalus* is exactly duplicated in the merlucciid *Macruronus*, but *Merluccius* and *Rhinocephalus* (text fig. 50) differ only in having the large pore beneath the frontal crest and the opening transmitting the sensory canal into the median mucous cavity confluent, as they are in most gadoids. In gadoids the anterior part of the supraorbital canal on the frontal is also often bone-enclosed, but this condition is achieved during ontogeny by the upgrowth of laminae from the medial and lateral parts of the frontal (Svetovidov, 1948).

Along the posterior part of the supraorbital margin of the frontal in *Sphenocephalus* there are three or four weak ridges ending in small spines. The autosphenotic is small and does not project laterally. The dermosphenotic is a scroll-like bone, not fused with the autosphenotic. The pterotic is rather short and carries the main cephalic sensory canal on a broad, projecting ledge. The preopercular sensory canal passed downward in a notch behind this ledge, and the infraorbital canal passed to the dermosphenotic in front of it. The posttemporal fossa appears to agree with the fossa of percopsids in shape and size. The nasals are moderately large triangular bones, probably carrying the sensory canal in an open trough. The mesethmoid is not visible in any specimen. The vomer bears a large D-shaped patch of teeth. The parasphenoid is slender, without teeth, and must have extended back below the basioccipital. The triangular ascending process of the parasphenoid was perforated by the internal carotid artery in the usual way. Nothing can be seen of the otic and occipital parts of the neurocranium except for the occipital condyle, which was tripartite, with very large exoccipital condyles distinct from each other and from the basioccipital condyle. In the size and differentiation of the exoccipital condyles, which are reflected in the deep, highly modified first vertebra, *Sphenocephalus* differs markedly from polymixiids and berycoids. There is no sign of an orbitosphenoid or basisphenoid in any specimen.

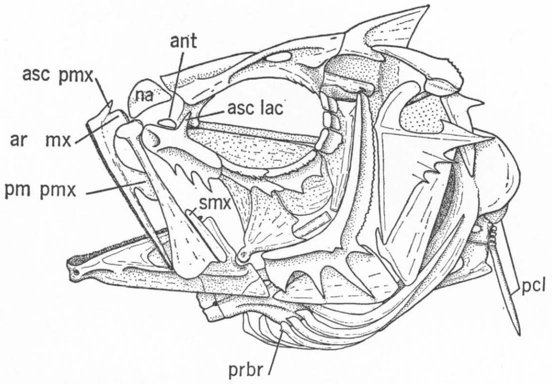

FIG. 29. *Sphenocephalus fissicaudus* Agassiz, Campanian, Baumberg, Westphalia. Restoration of skull and pectoral girdle.

The infraorbital series contains seven bones: antorbital, lacrimal, four infraorbitals, and dermosphenotic. The lacrimal is long, slightly deeper than the infraorbitals, and has three large spines on its ventral edge. On the dorsal margin of the bone, just in front of the midpoint, there is a strong, splintlike, ascending process lying in front of the lateral ethmoid, as in other percopsiforms. In the angle between this process and the anterodorsal part of the lacrimal there is a small bone, thickened ventrally where it meets the lacrimal, which is clearly an antorbital, similar to the antorbitals of *Percopsis* and *Polymixia*. The first and second infraorbitals are moderately long, with two large spines on the ventral edge of each and a few spines along the edge of the flange overhanging the sensory canal. The third and fourth infraorbitals are small; the third has two spines on its margin. There is no subocular shelf.

The mouth is large, the jaws extending back to the level of the center of the orbit and the preorbital region being rather long. The ascending process of the premaxilla is small, shorter than the articular process behind it. The alveolar process of the premaxilla is very long, ending just in front of the tip of the maxilla, and, although very slender, it bears a band of teeth to its tip. The posterior part of the alveolar process is usually disturbed in the fossils. Although such dislocation may be only because of its fragility, one specimen (G.P.I.M. No. 8778) strongly suggests that it was segmented distally, as in *Trichophanes*, *Aphredoderus*, and some amblyopsids. In G.P.I.M. No. 8772, however, the alveolar process is solid and unsegmented to its tip. In front of the midpoint of the alveolar process, there is a high postmaxillary process with a deep notch (the "gadoid notch") in its posterior edge. The long, toothless maxilla is rodlike anteriorly, but behind the level of the postmaxillary process of the premaxilla it widens steadily to its broad posterior end. The posterior edge of the maxilla is concave dor-

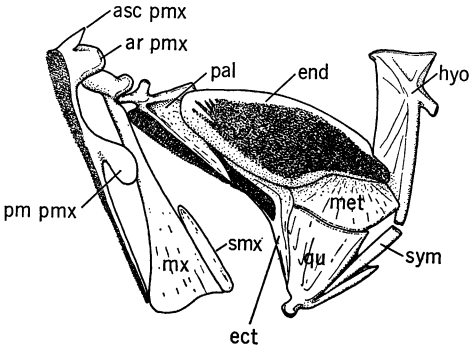

FIG. 30. *Sphenocephalus fissicaudus* Agassiz, Campanian, Baumberg, Westphalia. Restoration of palate and jaws of right side in medial view.

sally. There is a single supramaxilla, slender but long.

In the mandible the toothed margin of the dentary is long, extending back to the level of the suture between the dentary and articular in the ventral part of the jaw. There is a large, triangular retroarticular, projecting posteriorly. The mandibular sensory canal ran in a broad groove which appears to have been open throughout its length, except for a narrow bridge in the anterior half of the dentary and a bone-enclosed portion at the tip of the dentary. There are no spines or ornament on any of the jawbones.

The hyomandibular has a single head and is long and slightly inclined forward. The symplectic is not elongated but inclines forward so that the condyle of the quadrate lies below the center of the orbit. The endopterygoid is very large, extending back across the medial surface of the metapterygoid toward the hyomandibular. Except for a narrow marginal band, the entire medial surface of the endopterygoid is covered with teeth, the teeth becoming denser posteriorly. Both the palatine and ectopterygoid are also toothed along their oral margins. The palatine and ectopterygoid were not sutured together. The palatine has an ossified maxillary process, fitting in a groove near the head of the maxilla in the normal way.

The hyoid arch is suspended from the junction of the hyomandibular and symplectic by a stout interhyal. The epihyal and ceratohyal were not sutured together. The ceratohyal is very deep and of beryciform type, with an oval fenestra (the "beryciform foramen" of McAllister, 1968, p. 6) crossed by the groove for the hyoidean artery. There are two hypohyals. Specimen B.M.N.H. No. P.9059 shows that there were tooth plates along the upper edge of the epihyal and at least the posterior part of the ceratohyal.

There are six branchiostegals, the two foremost inserted on the inner or ventral surface of the ceratohyal, the four posterior ones on the outer face of the ceratohyal. On the heads of the four posterior branchiostegals there are anterior projections (the "percopsoid projections" of McAllister, 1968) which increase in size from front to rear. The sixth branchiostegal is inserted on or just behind the junction of the epihyal and ceratohyal. There is a large, triangular urohyal.

Parts of the branchial skeleton are visible in several specimens, but they show only that both the upper and lower pharyngeals were large and well toothed, and that the gill arches were provided with flat or stumplike tooth plates and with a few long, toothed gillrakers. The basibranchials are not visible in any specimen.

The preopercular is weakly angulate, turning through about 60 degrees, and the ventral limb of the bone is only just over one-third of the length of the vertical limb. The sensory canal ran in an open groove, covered laterally by a flange which is smooth except for a single short spine at the angle. The posterior edge of the vertical limb is serrated along its whole length, the serrations growing stronger downward. At the angle of the bone there is a straight spine, and along the ventral margin three more spines, increasing in size from front to rear, the last very long, stout, and gently curved. The shape of the opercular is unusual and characteristic. Running back from the point of suspension of

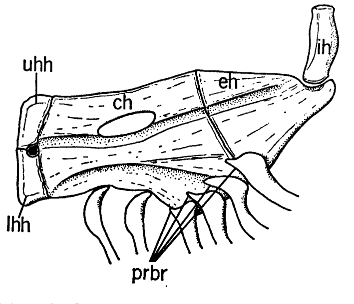

FIG. 31. *Sphenocephalus fissicaudus* Agassiz, Campanian, Baumberg, Westphalia. Restoration of left hyoid arch and branchiostegals.

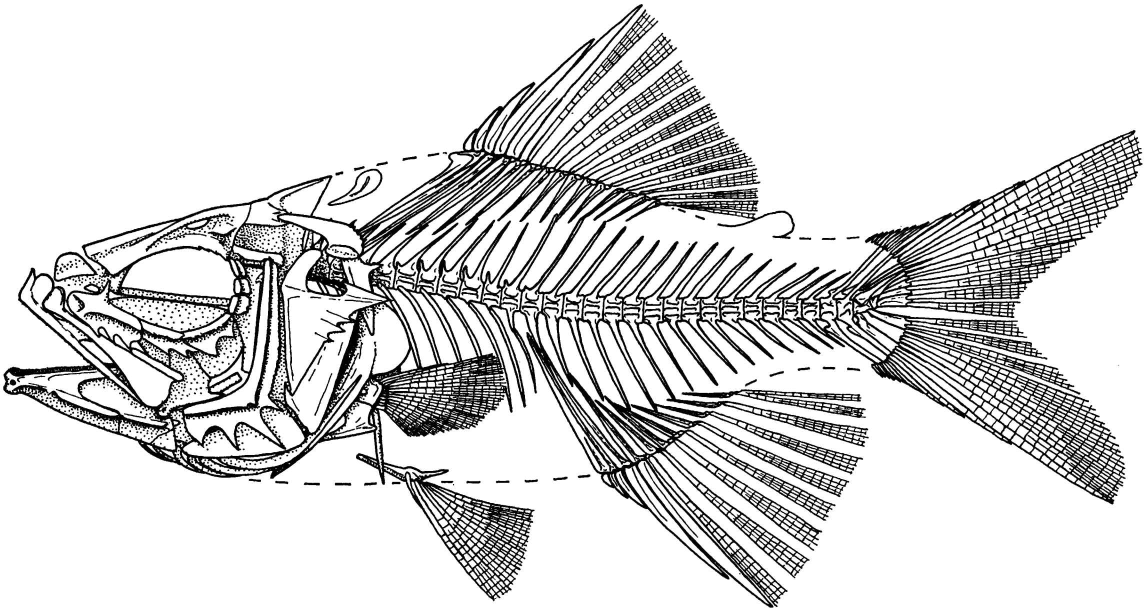

FIG. 32. *Sphenocephalus fissicaudus* Agassiz, Campanian, Baumberg, Westphalia. Restoration, scales omitted.

the bone there is a strong horizontal crest on the medial surface which ends in a long, slender spine. There is a deep, ovoid excavation in the upper margin, surrounded by thick bone, extending down to this horizontal crest. Spaced out below the principal spine there are three smaller spines, decreasing in size downward, which project across the upper part of the subopercular. The subopercular is long, covering the whole posteroventral edge of the opercular, but is thin, flimsy, and without spines. At the anterodorsal corner of the subopercular there is a strong dorsally directed spike, not a blunt process as there is in Tertiary and living percopsiforms. The interopercular is a rather short but deep triangular bone with a smooth lower edge. The opercular and subopercular are covered by scales.

There are 12 abdominal vertebrae, 18 caudal vertebrae, and a free second ural centrum. The first five vertebrae are compressed anteroposteriorly and deeper than long (text fig. 33). The first vertebra is particularly highly modified, with a pair of high, anterodorsal facets that articulate with the exoccipital condyles, a deep, short centrum and a pair of short, thick, ventral processes, probably giving origin to Baudelot's ligament, as in amblyopsids (Woods and Inger, 1957, p. 246). The first rib is inserted on the third vertebra, and the ribs are borne on transverse processes on the last four abdominal vertebrae. The ribs are short and slender, occupying only about half of the depth of the abdominal cavity. There are traces of slender epipleurals on the first four or five vertebrae, but no epineurals. The prezygapophyses of the last five or six abdominal vertebrae and the first caudal vertebra are enlarged, projecting anterodorsally against the hind edge of the preceding neural spine, as in *Amphiplaga*. On the more anterior abdominal vertebrae the neural arches and the bases of the neural spines are expanded anteroposteriorly.

The caudal skeleton is identical with that of *S. brachypterygius* (text fig. 35; Patterson, 1968b, p. 61, fig. 10) and does not differ from the caudal skeletons of the Eocene percopsids *Amphiplaga* and *Erismatopterus*. The caudal fin is deeply forked and contains 18 principal rays with 16 branched. There are 10–12 upper procurrent rays (normally 11 or 12), the last two or three segmented, and eight to 11 lower procurrent rays (normally 10), the last three segmented. The foremost procurrent rays are inserted on the neural

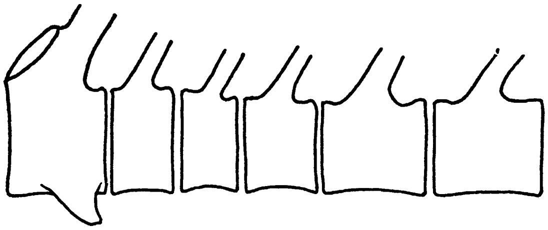

FIG. 33. *Sphenocephalus fissicaudus* Agassiz, Campanian, Baumberg, Westphalia. Sketch to show the relative proportions of the first six vertebral centra.

and haemal spines of the third pre-ural centrum and are paired structures, not spines.

In the shoulder girdle there is no clear evidence of a supratemporal. The posttemporal is large, with a broad epiotic limb and a stout intercalar limb. The lateral line was carried on a broad horizontal flange projecting from the lateral surface of the posttemporal, and there are a few coarse serrations on the posterodorsal corner of the bone. The supracleithrum has a large spine on its posterior edge just above the point of entry of the lateral line. The cleithrum is long, with a large, thick posterior plate. The scapula and coracoid are sutured together, not separated by cartilage. The scapular foramen lies in the center of the scapula. The coracoid is of moderate size, the anterior process arching forward to meet the cleithrum well above the cleithral symphysis. In contrast to Tertiary and living percopsiforms, the upper and lower postcleithra are not fused together. The upper, scalelike postcleithrum is rather small and is covered by the posterior plate of the cleithrum. The lower postcleithrum is long, reaching the ventral border of the trunk. There are four pectoral radials of the usual hourglass shape. The pectoral fin contains 15 rays and is about as large as the pelvic fin.

The pelvic girdle (text fig. 34) is very like that of *Percopsis* and that of *Erismatopterus* (text fig. 27), with stout medial processes, the right lying dorsal to the left, and long, pointed, posterior processes. The anterior process of the pelvic bone crosses the lower postcleithrum, but there is no sign of any articulation between the two. The pelvic fin contains a splint and seven soft rays, the first unbranched. When pressed against the trunk, the pelvic fin would have ended just in front of the origin of the anal.

The dorsal fin contains five stout spines, the first very small and the fifth ranging in length from about 55 per cent of the depth of the trunk in the largest specimens to about 65 per cent in the smallest, and 11 soft rays. There are 14 dorsal radials, the enlarged first radial lying behind the third neural spine. There is a single supraneural, resembling the supraneurals of the percopsids in shape, lying above the second and third neural spines. There is a large, scale-covered adipose fin, clearly visible in several specimens [B.M.N.H. Nos. P.9059 (pl. 62, fig. 2), P.8773, P.8774; G.P.I.M. Nos. 934, 8772].

The anal fin contains five stout spines, almost identical with the dorsal spines in size, and eight soft rays. There are 10 anal radials.

The scales are strongly ctenoid, as are those of *Amphiplaga* and *Aphredoderus*. The scales are rarely well preserved and are difficult to count, but there appear to be about 20 in transverse series on the trunk, with the conspicuous, uninterrupted lateral line passing through the seventh from the top. Scales cover the cheek and operculum.

Sphenocephalus brachypterygius, new species

Text figure 35

Sphenocephalus fissicaudus.—SMITH WOODWARD, 1901, p. 338 (in part). PATTERSON, 1968b, fig. 10.

DIAGNOSIS: *Sphenocephalus* reaching at least 90 mm. in standard length; proportions

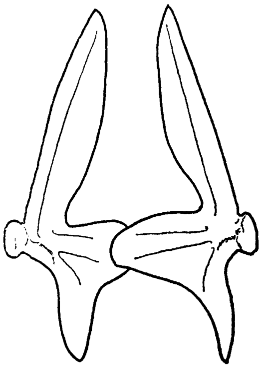

FIG. 34. *Sphenocephalus fissicaudus* Agassiz, Campanian, Baumberg, Westphalia. Pelvic girdle in ventral view, restored from B.M.N.H. No. P.9059.

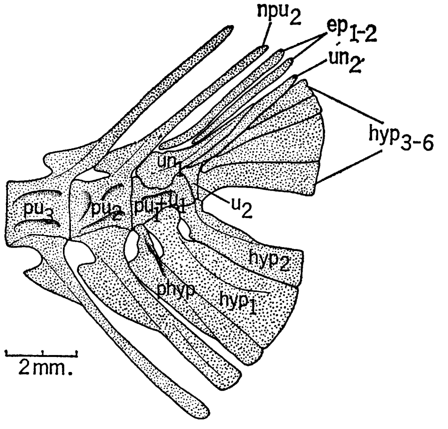

FIG. 35. *Sphenocephalus brachypterygius*, new species, Campanian, Sendenhorst, Westphalia. Caudal skeleton of B.M.N.H. No. P.2100. Outermost (unbranched) principal rays as in percopsids.

as in *S. fissicaudus* but differing from that species in having two fewer caudal vertebrae (vertebrae $12+16+u_2$); D IV, 8; A V, 7; anal fin originating behind last dorsal ray, longest dorsal spine shorter than longest anal spine, first pelvic ray branched.

HOLOTYPE: B.M.N.H. No. P.2100, a complete fish, mainly preserved as a natural mold.

MATERIAL: The holotype only.

HORIZON AND LOCALITY: Campanian, Sendenhorst, Westphalia.

DESCRIPTION: The specimen is 92 mm. in standard length. Other dimensions, expressed as per cent of standard length, are: total length, 122; head length, 40; trunk depth, 37; predorsal length, 52; preanal length, 74; caudal peduncle depth, 15. These proportions do not differ significantly from those of *S. fissicaudus*, and there is nothing in the visible parts of the skull to distinguish the specimen from the latter. The abdominal vertebrae are not completely visible, but there are 10 pairs of ribs, suggesting that there were 12 abdominal vertebrae, as in *S. fissicaudus*. There are 16 caudal vertebrae and a free second ural centrum, two fewer than in *S. fissicaudus*. The prezygapophyses are enlarged on the last five abdominal vertebrae and the first caudal vertebra, as in *S. fissicaudus*. The caudal skeleton and fin (text fig. 35) have already been described (Patterson, 1968b, p. 61, fig. 10). The pectoral and pelvic girdles do not appear to differ from those of *S. fissicaudus*. The pectoral fin contains 16 rays; the pelvic seven, with the first branched, a difference from *S. fissicaudus* (and it appears to be a little smaller than the pelvic fin in that species). The dorsal fin contains four spines and eight soft rays, supported by 10 radials (V, 11 with 14 radials in *S. fissicaudus*) and the last dorsal spine is equal in length to only about 45 per cent of the depth of the trunk (55–65% in *S. fissicaudus*). An adipose fin is present. The anal fin contains five spines and seven soft rays supported by nine radials (V, 8 with 10 radials in *S. fissicaudus*) and originates behind the last dorsal ray. The longest anal spine is equal in length to about 53 per cent of the depth of the trunk, being much longer than the dorsal spines. No scales are preserved.

RELATIONSHIPS OF *Sphenocephalus*

Sphenocephalus, previously placed in the Trachichthyidae, was made the type of a monotypic family, Sphenocephalidae, by Patterson (1964, p. 385), the family being included in the beryciform suborder Polymixioidei. Then very incompletely known, *Sphenocephalus* was found to resemble the Polymixiidae principally in having subthoracic pelvics without a spine, 16 branched caudal rays, and a toothed endopterygoid. Later (Patterson, 1968b, p. 61, fig. 10) *Sphenocephalus* was shown to agree with the Polymixiidae in all the details of the caudal skeleton except that there are only two epurals (three in polymixiids). *Sphenocephalus* was found to differ from the Polymixiidae in the short supraoccipital crest, thickened anterodorsally, the absence of epineurals, the presence of a pelvic splint, and the short dorsal and anal fins, with at least 10 rays fewer than any polymixiid. Now that *Percopsis* is known to have 16 branched caudal rays, as does *Aphredoderus*, *Sphenocephalus* agrees with these Percopsiformes not only in those characters in which it resembles the Polymixiidae (endopterygoid teeth are present in *Aphredoderus*) but also in all those in which it differs from this family. The much more complete information on *Sphenocephalus* now available shows that it also resembles the Percopsiformes in the ascending process on the lacrimal, the enlarged, separate exoccipital condyles, the six branchiostegals with "percopsoid projections" on the heads of the large posterior rays, the presence of tooth plates on the upper margin of the ceratohyal, the excavated upper part of the opercular and the long subopercular, the enlarged prezygapophyses on the posterior abdominal vertebrae (as in the Eocene *Amphiplaga*), the structure of the pelvic girdle, the presence of an adipose fin (*Sphenocephalus* and *Percopsis* are the only known "spiny-rayed" fishes with an adipose), the single supraneural, and the numerous procurrent caudal rays (eight to 12, cf. seven to 10 in *Percopsis* and *Aphredoderus*, eight to 12 in Eocene percopsids).

Recognition of these similarities between *Sphenocephalus* and the Percopsiformes, which are certainly indicative of relationship, suggests two alternatives. Either *Sphenocephalus* must be transferred to the Percopsiformes, the Percopsiformes and Polymixiidae being kept separate, or the Percopsiformes and Polymixioidei must be combined. The resemblances between *Sphenocephalus* and the Percopsiformes are not only more numerous but clearly more significant than those between *Sphenocephalus* and the polymixiids. The specialized characters in which *Sphenocephalus* resembles the Percopsiformes and differs from the Polymixiidae are particularly striking: the ascending process on the lacrimal, the fact that the supraorbital and mandibular sensory canals lie in open troughs anteriorly (bone-enclosed in all polymixiids), the separate exoccipital condyles (a simple tripartite condyle in all polymixiids), the single supramaxilla (two in polymixiids), six branchiostegals (eight in polymixiids), excavated dorsal part of the opercular, enlarged abdominal prezygapophyses, absence of epineurals, single supraneural (three predorsals in polymixiids, as in most percoids), two epurals, and numerous procurrent caudal rays. The form of the posterior part of the skull roof, the absence of a subocular shelf, the presence of ceratohyal tooth plates, of an adipose fin, of a pelvic splint, and of short dorsal and anal fins are primitive characters in *Sphenocephalus* and the Percopsiformes, and are conditions not found in the Polymixiidae. In contrast, the majority of the resemblances between *Sphenocephalus* and the Polymixiidae are in primitive characters [toothed endopterygoid, antorbital, supramaxilla, perforate ceratohyal (see p. 408), free second ural centrum and six hypurals, subthoracic, spineless pelvics, separate upper and lower postcleithra, few dorsal and anal spines]. Two features of the caudal skeleton, however, the complete neural spine on the second pre-ural centrum and the 18 principal caudal rays, are found together only in percopsiforms, polymixiids, and the Cretaceous "beryciforms" *Dinopteryx* and *Pycnosteroides*. Advanced characters in which the Polymixiidae differ from *Sphenocephalus* and the percopsiforms include the long supraoccipital crest, thickened centrally rather than anteriorly, the large supratemporal fossa, the subocular shelf on all the infraorbitals, and the three predorsal bones. Although few, these characters are significant, for they emphasize the fact that the Polymixiidae are involved in evolutionary trends found in the Berycoidei and Perciformes rather than in the Percopsiformes.

The conclusions to be drawn from these comparisons are that *Sphenocephalus* belongs with the Percopsiformes, and that the Percopsiformes are to be distinguished from the Polymixiidae because of a suite of advanced characters which (as is shown below) relate them to the Gadiformes, whereas the Polymixiidae are linked with the Berycoidei and Perciformes by a different set of advanced characters. Nevertheless, in addition to the unique similarities between percopsiforms and polymixiids in the caudal skeleton and caudal ray number, *Sphenocephalus*, as the most primitive percopsiform known, provides further indications of percopsiform-polymixiid relationships which are not evident in Tertiary and living percopsiforms. These include the marine Tethyan habitat, the rather large supraoccipital crest (the occipital part of the skull roof of *Sphenocephalus* seems to be intermediate between that of other percopsiforms, with a low crest and no supratemporal fossa, and that of the polymixiid *Berycopsis*, in which the supratemporal fossa and supraoccipital crest are much shorter than in other polymixiids), the large gape and long jaws, the large supramaxilla, deep, "berycoid" type of ceratohyal, deep trunk, and the number of fin spines (five in both dorsal and anal). These suggest that the percopsiforms and polymixiids could have shared a common ancestry in Cretaceous seas in a deep-bodied fish with the short supraoccipital crest, pelvic splint, short dorsal and anal fins, and adipose of *Sphenocephalus*, and the bone-enclosed sensory canals, simple occipital condyle, two supramaxillae, eight branchiostegals, and three epurals of the Polymixiidae.

Finally, there is a suite of characters in which *Sphenocephalus* resembles neither the known percopsiforms nor the polymixiids. These include the high, anteriorly diverging crests on the frontals, the very long alveolar process of the premaxilla and the large postmaxillary process with a notch in its hind edge, the very large spines on the preopercular and the spiny opercular, the compressed anterior vertebrae, and modified first vertebra. The preopercular spines recall the trachichthyid *Acrogaster*, the scorpaenids, and others, but these resemblances are clearly fortuitous, and the preopercular and opercular spines are evidently a peculiarity of *Sphenocephalus* (more numerous and less prominent preopercular spines occur in the Oligocene aphredoderid *Trichophanes*). The diverging crests on the frontals, the long alveolar process and notched postmaxillary process of the premaxilla, and the compressed anterior vertebrae resemble characters of the gadiforms (in which an ascending process on the lacrimal also occurs). The significance of these gadiform resemblances is discussed further below (p. 435).

There remains to be settled the systematic position of the Sphenocephalidae within the Percopsiformes. In reference to the list of percopsiform characters on page 380, *Sphenocephalus* agrees with other percopsiforms in the majority of characters in which its structure is known, but differs in the form of the supraoccipital crest, probably in the form of the parietals, and in the presence of a supramaxilla and separate upper and lower postcleithra. Comparison of *Sphenocephalus* with the Percopsidae, Aphredoderidae, and Amblyopsidae (table 1) shows that it resembles the Percopsidae in the majority of its known characters (all of these probably primitive), but agrees with the Aphredoderidae in the extensive palatal dentition, the absence of a dorsal process on the maxilla, the spiny infraorbitals and preopercular, and the scaly opercular. Two of these aphredoderid characters, the spiny infraorbitals and scaly operculum, also occur in fossil Percopsidae (*Amphiplaga*) and are probably primitive for the order. This combination of characters shows that *Sphenocephalus*, although apparently closer to the Percopsidae, cannot definitely be placed in either the Percopsoidei or the Aphredoderoidei at this time. It appears in many ways to be more primitive than the members of both suborders. The Sphenocephalidae are best placed provisionally in a third suborder of the Percopsiformes, Sphenocephaloidei.

EVOLUTIONARY TRENDS IN THE PERCOPSIFORMES

The evidence now available from fossil and living percopsiforms allows us to visualize the order as containing two lineages, the Percopsoidei (*Amphiplaga* and *Erismatopterus*, Middle Eocene; *Percopsis*, extant) and the Aphredoderoidei (*Trichophanes*, Oligocene–Miocene; *Aphredoderus*, Amblyopsidae, extant), which diverged, probably in fresh water during the early Tertiary, from originally marine, *Sphenocephalus*-like ancestors. Making the assumption that *Sphenocephalus* is morphologically close to the hypothetical ancestral percopsiform group, we can recognize a number of trends in percopsiform evolution, apart from simple loss of structures such as the supramaxilla, antorbital, pelvic splint, and adipose fin:

1. Migration from marine (*Sphenocephalus*) to fresh-water (Percopsidae, Aphredoderidae) and eventually troglodytic (Amblyopsidae) habitats.
2. Reduction in the depth of the head and trunk, culminating in the slender, broad-headed amblyopsids. Decrease in the depth of the head is reflected in the reduction of the supraoccipital crest and in amblyopsids by the development of pterosphenoid-parasphenoid contacts.
3. Decrease in the number of dorsal fin spines in the sequence: 5 (*Sphenocephalus fissicaudus*); 4 (*S. brachypterygius*, *Trichophanes*); 3 (*Amphiplaga*, *Aphredoderus*); 2 (*Erismatopterus*, *Percopsis*, *Amblyopsis*); 1 (*Typhlichthys*, *Amblyopsis*); 0 (*Amblyopsis*, *Chologaster*). Decrease in the number of anal spines in the sequence: 5 (*Sphenocephalus*); 3 (*Trichophanes*, *Amphiplaga*, *Aphredoderus*); 2 (*Erismatopterus*, *Percopsis trans-*

montana, Amblyopsis); 1 (*Percopsis omiscomaycus, Amblyopsis*); 0 (Amblyopsidae).

4. Reduction in the gape, involving shortening of the maxilla, the alveolar process of the premaxilla, and the toothed border of the dentary, but without modification of the suspensorium. The size of the gape decreases in the sequence *Sphenocephalus*, Aphredoderidae, Amblyopsidae, Percopsidae. Other modifications of the jaws include reduction or loss of the postmaxillary process of the premaxilla in all Tertiary and recent percopsiforms, segmentation of the alveolar process of the premaxilla in the Aphredoderidae and some of the Amblyopsidae, and development of a dorsal process on the maxilla for insertion of the levator maxillae superioris in the Percopsidae.

5. Reduction in the buccal dentition. *Sphenocephalus* has the most extensive buccal dentition; endopterygoid teeth are reduced in the Aphredoderidae and lost in other groups; ectopterygoid teeth are lost in the Amblyopsidae and *Erismatopterus*; *Percopsis omiscomaycus* has also lost the vomerine and palatine teeth.

6. Reduction in the spination of the infraorbitals, preopercular, opercular, and scales. Once again, *Sphenocephalus* shows the greatest development of spiny ornament, except for the "ultractenoid" scales and comblike infraorbital and preopercular spines in *Trichophanes*. Infraorbital and preopercular spines are lost in the Percopsidae and Amblyopsidae (except for a few preopercular spines in *Amphiplaga*), and the ctenii of the scales are reduced in *Erismatopterus* and *Percopsis* and lost in the Amblyopsidae (but see Rosen, 1962, fig. 23). Concomitant with reduction in spination, the opercular squamation is reduced and lost. The operculum is completely scaled in all forms with a serrated preopercular (*Sphenocephalus*, Aphredoderidae, *Amphiplaga*), the squamation being much reduced in *Erismatopterus* and lost from *Percopsis* and the Amblyopsidae. Scaling of the operculum is an advanced character in teleosts (Patterson, 1967a, p. 107), but the scales are secondarily lost in many lineages. Usually, such loss is accompanied by increasing ornamentation of the bones of the skull, as in the Ctenothrissoidei and Berycoidei (Patterson, *loc. cit.*), but in percopsiforms the opposite trend occurs.

7. Reduction in the bony cover of the sensory canals on the head. In *Sphenocephalus* the cephalic sensory canals are already almost entirely exposed, the only remnants of the primitive bony covering of the canals being the large frontal crests, the enclosure of the supraorbital canal in the posterolateral part of the frontal, and a short bridge over the mandibular canal in the dentary. The frontal crests and the bridge across the mandibular canal are lost from all Tertiary and living percopsiforms, and the posterior part of the supraorbital canal is exposed in the Aphredoderidae and Amblyopsidae. Reduction (Aphredoderidae) and loss (Amblyopsidae) of the lateral line are perhaps related to exposure of the cephalic sensory canals.

8. In *Sphenocephalus* the ceratohyal is deep, with a large central fenestra, the upper edge of the hyoid bar bears tooth plates, and there are anterior projections on the heads of the four posterior branchiostegals. In *Percopsis* the ceratohyal is shallower but in some cases has a small fenestra near the upper edge (McAllister, 1968, p. 125), there are tooth plates on both the ceratohyal and epihyal, and there is an anterior projection on the foremost of the large posterior branchiostegals (McAllister, *loc. cit.*). In the Aphredoderidae the ceratohyal has no fenestra, tooth plates occur only on the epihyal and the posterior part of the ceratohyal, and the fourth and fifth branchiostegals have anterior projections (McAllister, 1968, p. 124). In the Amblyopsidae the ceratohyal is shallow and imperforate, and there are no hyoid tooth plates and no projections on the heads of the branchiostegals.

McAllister (1968, p. 6) considered a fenestra in the ceratohyal ("beryciform foramen") to be characteristic of the beryciforms and their close relatives, but the evidence of fossil teleosts indicates that a deep, perforate ceratohyal is primitive for most lower teleosts. A ceratohyal of this type occurs in *Leptolepis* (Rayner, 1937, fig. 6; Smith Woodward, 1895, pl. 14, fig. 6), *Allothrissops* and *Pachythrissops* (Nybelin, 1964, pl. 9, fig. 4), *Anaethalion* (Nybelin, 1967, pl. 6, fig. 2) *Ichthyodectes* (Bardack, 1965, p. 59), the clupeoid *Diplomystus*, and in *Ctenothrissa* and *Aulolepis* (Patterson, 1964, figs. 10, 20). As this list includes the most primitive of all teleosts (*Leptolepis*) and primitive members of the Elopomorpha (*Anaethalion*), Clupeomorpha (*Diplomystus*), Osteoglossomorpha (*Allothrissops, Ichthyodectes*), and Protacanthopterygii (ctenothrissoids), and, as the fenestra is largest in *Leptolepis*, decreasing in size in more advanced forms, the conclusion is certainly justifiable that a ceratohyal fenestra is a feature primitive for teleosts. The occurrence of a perforate ceratohyal in *Sphenocephalus* (or any other fish) is therefore not evidence of relationship with the Beryciformes but only an indication of primitive conditions. The trend toward a shallow imperforate ceratohyal in percopsiforms is one that has occurred in almost every teleost group.

The tooth plates along the upper margin of the hyoid bar in percopsids and aphredoderids are a puzzling feature. Among living teleosts such tooth plates are otherwise known only in *Elops*, some engraulids, the trichiurid *Eupleurogrammus*, and in *Rachycentron*, in the last of which they are secondarily redeveloped (G. J. Nelson, personal communication) and also secondarily in the stomiatoid *Neonesthes capensis* (S. H. Weitzman, personal communication). In *Amia* there are a few tooth plates on the epihyal and the posterior part of the ceratohyal, about as in *Aphredoderus*. Among fossil fishes hyoid tooth plates seem to have been described only in *Eusthenopteron* (Jarvik, 1954). The occurrence of these tooth plates in *Eusthenopteron*, *Amia*, and *Elops*, together with the probability that all the visceral arches were originally toothed, indicates that ceratohyal tooth plates are a primitive feature in teleostomes. The absence of ceratohyal tooth plates from myctophoids and salmoniforms generally suggests at first that the percopsiforms developed ceratohyal teeth secondarily, as does *Rachycentron*. But the presence of the tooth plates in *Amphiplaga* and *Sphenocephalus*, showing that percopsiforms have retained them at least since the Cretaceous, together with the trend toward reduction and loss of the teeth in the Aphredoderidae and Amblyopsidae, makes it at least possible that the tooth plates are a primitive feature, retained by the percopsiforms alone among living euteleosteans (see Greenwood, Myers, Rosen, and Weitzman, 1967).

Anterior projections on the heads of the large posterior branchiostegals were first noticed by McAllister (1968). He referred to them as "percopsoid projections" and found them on the middle five (of seven) branchiostegals in the Ophidiidae and Brotulidae, and on the foremost large ray in the Moridae, Gadidae, and Macrouridae. Such projections seem to be absent from other teleosts. In the Percopsiformes the trend is toward reduction from the ophidioid condition (*Sphenocephalus*) through the gadoid and macrouroid condition (*Percopsis*) to the absence of the projections (Amblyopsidae). This suggests that the occurrence of projections on all the large posterior rays is the primitive condition in paracanthopterygians, that the presence of a projection on the fourth branchiostegal in gadoids and macrouroids is evidence that these fishes are related to the ophidioids and percopsiforms, but that the absence of projections, as in amblyopsids, is not evidence against paracanthopterygian relationships.

9. If the vertebral number in *Sphenocephalus* ($12+16-18+u_2$) is primitive for percopsiforms, a reasonable assumption since this is similar to the vertebral number in the Polymixiidae ($10-13+14-19+u_2$), then Tertiary and living percopsiforms show an increase in the number of abdominal vertebrae relative to the number of caudals (Aphredoderidae, $12-13+16-18+u_2$; *Amphiplaga*, $14+16-17+u_2$; *Erismatopterus*, $13-14+15-16+u_2$; *Percopsis*, $17-19+15-17+u_2$; *Amblyopsis*, *Typhlichthys*, $12+16-18+u_2$; *Chologaster*, $17-18+17-18+u_2$).

10. The caudal skeleton in *Sphenocephalus*, *Amphiplaga*, and *Erismatopterus* differs from that of the Polymixiidae only in having one less epural. In *Percopsis* hypurals 3 and 4 are normally fused with the second ural centrum. In *Aphredoderus* hypurals 3, 4, and 5 are fused with the second ural centrum, the second hypural is fused into the first, the parhypural has no basal articulation, and the second uroneural is lost. The Amblyopsidae differ from *Aphredoderus* only in having no free upper hypurals. Concurrent with these endoskeletal changes in the tail, the caudal fin changes from forked (*Sphenocephalus*, Percopsidae) to emarginate (*Trichophanes*) or truncate (*Aphredoderus*), finally becoming rounded in the Amblyopsidae, in which the number of principal caudal rays (18 in other percopsiforms) is reduced to 12–17.

11. In *Sphenocephalus* the procurrent caudal rays are longitudinally divided, but in both the Percopsidae and the Aphredoderidae they become spinous. The development of procurrent caudal spines is characteristic of several groups near the basal acanthopterygian level of organization (Myctophidae, Ctenothrissoidei, Polymixiidae, Berycoidei; Patterson, 1968b).

12. The pelvic fins are subthoracic in *Sphenocephalus*, the Percopsidae, and the Aphredoderidae. In *Aphredoderus* the pelvic bones are attached to the postcleithra by ligaments, but in *Percopsis* the pelvic girdle lies free. In the Amblyopsidae the postcleithra are reduced, and the pelvic fins (present only in *Amblyopsis*

spelaea) revert to the abdominal position. The pelvic fins have eight rays in *Percopsis*, *Amphiplaga*, and *Trichophanes*, seven in *Sphenocephalus*, *Erismatopterus*, and *Aphredoderus*, and none to six in the Amblyopsidae.

In *Polymixia* the tip of the postcleithrum is attached by ligament to the posterolateral corner of the pelvic bone, as in *Aphredoderus* (Gosline, 1963, p. 11), and in the primitive polymixiid *Berycopsis* the pelvic girdle was also attached to the postcleithra (Patterson, 1964, p. 278). Such attachments suggest that the condition in *Aphredoderus* is primitive for the percopsiforms, *Percopsis* and the Amblyopsidae representing stages in the retreat of the pelvic girdle, a change that is known also to occur during ontogeny in melamphaeids (Ebeling, 1962).

In regard to the number of pelvic fin rays, the Polymixiidae have seven or eight, as do the Percopsidae, but *Polymixia* normally has seven, as do the most primitive members of the family, *Omosoma* and *Berycopsis*. Because there is evidence (p. 432) that seven-rayed pelvics are also primitive for the Gadiformes, it is probable that the pelvic fins of *Sphenocephalus*, *Erismatopterus*, and *Aphredoderus* show the primitive percopsiform condition (aside from the branching of the first ray in *Sphenocephalus brachypterygius* and aphredoderids), with *Amphiplaga*, *Percopsis*, and *Trichophanes* showing a secondary increase in the number of rays.

Trends in percopsiform evolution that cannot be studied in fossils are changes in the levator maxillae superioris muscle, reduction in the external division of the adductor mandibulae, and forward migration of the anus.

To summarize this section, we can recognize several categories of percopsiform evolutionary trends. Some, such as reduction in the gape and buccal dentition (4, 5) and shallowing of the hyoid (8), are not confined to this group but occur in many lineages. Migration into fresh water (1) and the change from a forked to a rounded tail (10) that often accompanies it are also found in many lineages, especially among the protacanthopterygians and acanthopterygians. The percopsiforms are the only paracanthopterygian group now confined to fresh water, all other paracanthopterygians remaining primarily marine. Other percopsiform trends are particularly characteristic of paracanthopterygians, especially the reduction of the bony cover of the cephalic sensory canals (7) and the sequence of fusions in the caudal skeleton that results in support of the caudal fin by two large hypural plates borne on separate centra (10). Finally, there is a set of features in which the percopsiform trend is the reverse of that characteristic of generalized acanthopterygians. These include a decrease in the depth of the head and trunk (2), a reduction and eventual loss of median fin spines (3), a reduction in spiny ornament on the bones of the cheek and operculum, accompanied by loss of the scale covering of the operculum (4), an increase in the number of abdominal vertebrae relative to the caudals (5), and the posterior migration and increase in fin-ray number of the pelvic fins (12) (cf. Patterson, 1964, pp. 449–459). These trends are essentially the key to the problem of paracanthopterygian origins. They show that the percopsiforms are neither "an offshoot of a primitive scopeliform or protoscopeliform stock" (Gosline, 1961a, p. 36), nor are they and the beryciforms "two distinct and quite independent radiations from the salmoniform level" (Greenwood, Rosen, Weitzman, and Myers, 1966, p. 388). Greenwood and his coauthors (1966) wrote that "the Paracanthopterygii have clearly trended toward the acanthopterygian form," but in fact the converse is true. From ancestors of basal acanthopterygian type the paracanthopterygians have diverged along lines involving the suppression of acanthopterygian features. This conclusion is the most important to emerge from the present analysis of percopsiform history.

FAMILY **ASINEOPIDAE**, INCERTAE SEDIS

Asineopidae.—COPE, 1884, p. 85.

DIAGNOSIS: Eocene North American, freshwater fishes of uncertain ordinal position (possibly related to Percopsiformes, Polymixiiformes, Lampridiformes, or Perciformes) with head large (length greater than depth of trunk) and almost completely covered by scales; a long dorsal fin with eight or nine spines, no adipose fin, two anal spines; pelvics subthoracic, eight-rayed, with no spine or splint; scales thick, cycloid, lateral line normal; caudal skeleton like that in percopsiforms and with upper hypurals fused to u_2, but haemal spine of pu_2 invariably double, neural spine of this centrum invariably single; caudal fin rounded, with 12 branched rays and few procurrent rays; $12–14+13–15$ vertebrae, epipleurals present but no epineurals, ribs on transverse processes on last few abdominal vertebrae; cephalic sensory canals bone-enclosed, skull bones without ornament or serrations; supraoccipital crest long, low, thickened centrally; no basisphenoid, trigemino-facialis chamber with only two external openings; lacrimal large, no other infraorbital bones present, no antorbital; premaxilla with very long ascending process, maxilla expanded behind premaxilla, no supramaxillae; teeth on vomer, palatine, ectopterygoid, premaxilla, dentary, and basihyal; hyomandibular double-headed; six branchiostegals, ceratohyal slender, lower hypohyal enlarged.

GENUS **ASINEOPS** COPE

Asineops.—COPE, 1870, p. 381.

DIAGNOSIS: As for the family; only genus.

REMARKS: Cope described three species in this genus: *A. squamifrons* (see below), *A. viridensis* (1871, p. 426), and *A. pauciradiatus* (1877, p. 813; 1884, p. 87, pl. 14, fig. 1). *Asineops viridensis* he later (1884, p. 87) found to be a synonym of *A. squamifrons*. *Asineops pauciradiatus* is known only from the holotype (U.S.N.M. No. 4045). Cope found that this specimen differed from *A. squamifrons* in having fewer dorsal and anal soft rays, fewer vertebrae, shorter dorsal fin spines, and a deeper trunk. Examination of the specimen shows that the dorsal fin and vertebrae are like those in *A. squamifrons*, but the depth of the trunk is about 44 per cent of the standard length (mean 33% in *A. squamifrons*) and that the longest dorsal spines are equal in length to six caudal vertebrae compared with seven in *A. squamifrons*. These differences may be due only to the very large size of the fish (standard length *ca.* 205 mm.; *A. squamifrons* reaches about 150 mm.). The anal fin appears to contain seven or eight soft rays, compared with nine to 11 in *A. squamifrons*. The caudal skeleton, caudal formula, and scale structure are like those in *A. squamifrons*. This single specimen does not allow a decision on whether it is merely a large individual of *A. squamifrons* or a second species, but the latter is more probable. The head is incomplete, and the only point of interest it shows is a large toothed bone which appears to be the endopterygoid, toothless in *A. squamifrons*.

Asineops squamifrons Cope

Plate 67, plate 69, figure 2, plate 70, figure 2,
text figures 36–40

Asineops squamifrons.—COPE, 1870, p. 381 (original description; Green River Shales, Wyoming). COPE, 1871, p. 426. COPE, 1884, p. 85, pl. 9, fig. 5, pl. 10. COCKERELL, 1914, p. 191.

Asineops viridensis.—COPE, 1871, p. 426 (original description; Green River Shales, Wyoming).

DIAGNOSIS: *Asineops* reaching about 15 cm. in standard length, depth of trunk and length of head about 33 per cent and 39 per cent, respectively, of standard length; vertebrae $12-14+13-15+u_2$; D VIII–IX, 11–

TABLE 7

PROPORTIONAL MEASUREMENTS OF FIVE SPECIMENS OF *Asineops squamifrons* COPE

Specimens	Standard Length, Mm.	As Per Cent of Standard Length					
		Total Length	Head Length	Trunk Depth	Predorsal Length	Preanal Length	Peduncle Depth
M.C.Z. No. 2837	37	127	36.5	30	43	72	15
A.M.N.H. No. 3992	51	126	37	30	45	73	15
U.S.N.M. No. 19873	68	125	37	37	48.5	75	17
A.M.N.H. No. 781G	102	129	45	35	48	—	18.5
U.S.N.M. No. 11111	106	—	40	35	46	—	—
Mean		127	39	33	46	73	16

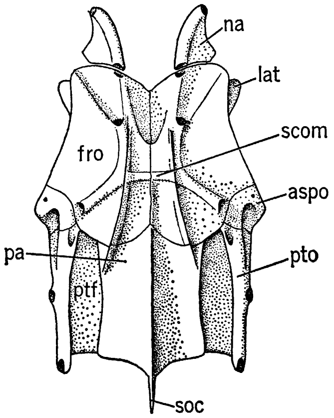

FIG. 36. *Asineops squamifrons* Cope, Middle Eocene, Green River Shales, Wyoming. Tentative restoration of skull roof.

12; A II–III, 9–11; P 17; V i, 7; C v, I, 6, 6, I, v; about 18 scales in a transverse series on trunk, lateral line passing through eighth from top.

HOLOTYPE: U.S.N.M. No. 4009 (Cope, 1884, pl. 9, fig. 5), a fish lacking the head.

MATERIAL: Eleven specimens: U.S.N.M. Nos. 11109, 11111, 11112, 19678, 19681, 19873; A.M.N.H. Nos. 781G, 2530, 2691, 3992; M.C.Z. No. 2837.

HORIZON AND LOCALITY: Middle Eocene, Green River Shales; Green River Cut, Fish Cut, and Twin Creek, Wyoming.

DESCRIPTION: The dimensions of five specimens are given in table 7.

The large, broad head was almost completely covered with thick scales. On the skull roof scales extend forward to the tips of the ascending processes of the premaxillae, on the cheek they reach the hind end of the lacrimal, and they cover the articular in the mandible. Because of the breadth of the head, the skull is crushed differently in every specimen, and this fact and the thick covering of scales make it difficult to reconstruct the skull accurately. Further, the bones of the neurocranium were joined only by cartilage, not by suture (A.M.N.H. No. 2530), so that the braincase has invariably disintegrated to some extent. In U.S.N.M. Nos. 11111 and 19678 it has been possible to dissect away most of the scales covering the skull roof, and the tentative restoration shown in text figure 36 is based mainly on these two specimens.

The skull roof was flat and broad, with a long postorbital division; the autosphenotic is closer to the tip of the frontals than to the hind end of the pterotic. The posterior part of the skull roof is not clearly visible in any specimen, and the relative extent of the parietal and supraoccipital cannot be made out. There was a low, triangular, supraoccipital crest projecting back from the skull roof, and the crest appears to have continued forward onto the frontals, indicating that the parietals were separated by the supraoccipital. The supraoccipital crest has a strengthening ridge in its center, not along its anterior edge as in percopsiforms. The frontals are short, ending just behind the orbit, about at the level of the sphenotic-pterotic suture, so the parietals were probably large. Anteriorly there is a broad median groove on the frontals, the rostral fossa, which must have accommodated the long ascending processes of the premaxillae. Running back from near this groove on the frontals there is a pair of low crests, diverging posteriorly and continued back by the parietals toward the posttemporal fossa. The presence of these crests and the forward extension of the supraoccipital crest and squamation suggest that the trunk muscles extended forward onto the frontals. The supraorbital sensory canal was bone-enclosed in the frontals, in contrast to the percopsiforms. Passing on to the posterolateral corner of the frontal from the pterotic, the supraorbital canal entered a tube in the bone which runs anteromedially, gives off a bone-enclosed supraorbital commissure, and then passes forward to the an-

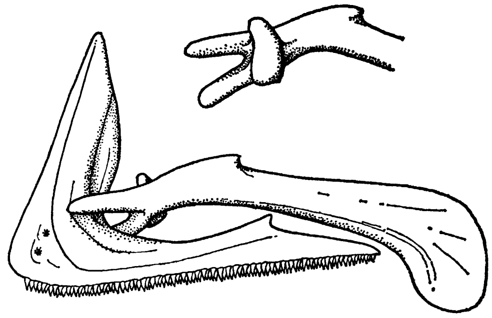

FIG. 37. *Asineops squamifrons* Cope, Middle Eocene, Green River Shales, Wyoming. Left upper jaw in lateral view, and (above) head of left maxilla in medial view.

terior end of the frontal, giving off a branch to a groove in the anterolateral part of the bone through a raised pore en route.

The nasals are moderately large curved bones, transmitting the supraorbital sensory canal through a tube at the medial edge. The sphenotic is large, projecting laterally in a broad postorbital process. The pterotic is long, carrying the temporal sensory canal in a closed tube from which the preopercular canal was given off through a pore midway along the bone. The hyomandibular is double-headed, the elongate facet for the bone on the pterotic and the rounded socket on the sphenotic being clearly separated. The dilatator fossa above the hyomandibular facet appears to be similarly subdivided.

The prootic is partially visible in A.M.N.H. No. 2530. The trigemino-facialis chamber has only two openings, the posterior opening transmitting both the jugular vein and the hyomandibular trunk of the facial nerve, as in living percopsiforms and most perciforms. A.M.N.H. No. 2530 also indicates that there was no basisphenoid, and there is no sign of either an orbitosphenoid or a pterosphenoid in any specimen. A.M.N.H. No. 781G shows that there were large exoccipital condyles, their surfaces at a slight angle to the basioccipital condyle but lying on the same vertical plane. It is not possible to see to what extent the exoccipital condyles were separated from each other. The vomer is toothed, but the broad parasphenoid is toothless. The lateral ethmoids are thick, spongy, and heavily ossified.

The lacrimal appears to be the only infraorbital bone present; there is no trace of a dermosphenotic, antorbital, or any other infraorbital in any specimen, the normal position of the infraorbitals being occupied by thick scales. The lacrimal is large and elongate, resembling lacrimals of the Percopsidae in size, with a smooth ventral edge and a dorsal process articulating with the lateral ethmoid. This dorsal process is not splint-like, as is the ascending process of the lacrimal in the Percopsiformes, but it is much larger and more prominent than the articular facet that occurs in the Beryciformes and Perciformes.

The head of the hyomandibular is double, as mentioned above, and the bone is short but extremely broad. The hyomandibular lies almost vertically, but, as in percopsiforms, the large symplectic is inclined forward so that the condyle of the quadrate lies below the center of the orbit. The endopterygoid is slender and apparently toothless (M.C.Z. No. 2837), but both the ectopterygoid and the palatine are toothed. There is no clear evidence of a metapterygoid in any specimen, and this bone may have been absent, its place being taken by the broad hyomandibular. The palatine has a long, stout maxillary process articulating with the lateral part of the head of the maxilla.

The premaxilla has a very long ascending process, equal in length to about 70 per cent of the alveolar process. There is no distinct articular process on the premaxilla, the articular process being represented only by a ridge on the posterolateral surface of the ascending process, as in the cichlid *Pterophyllum* (Alexander, 1967a, fig. 5). Just behind the midpoint of the alveolar process of the premaxilla there is a small postmaxillary process with a concave hind edge. The alveolar process of the premaxilla bears a broad band of rather large, recurved teeth to its tip. The maxilla is about 15 per cent longer than the premaxilla and is strongly expanded behind the latter. The head of the maxilla is produced into two well-separated processes: a dorsolateral one which fits against the posterolateral surface of the ascending process of the premaxilla and articulates with

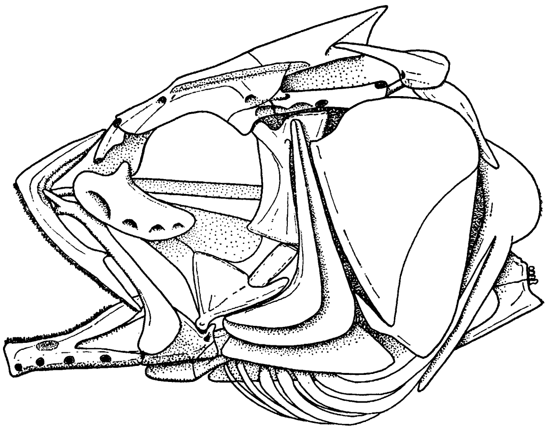

FIG. 38. *Asineops squamifrons* Cope, Middle Eocene, Green River Shales, Wyoming. Restoration of skull and pectoral girdle.

the maxillary process of the palatine, and a ventromedial one which fits against the medial face of the ascending process of the premaxilla. At the junction of these two processes [the "lateral part of the head" and the premaxillary condyle in Alexander's (1967a, p. 46) terminology] is the knoblike cranial condyle, passing medially to articulate with the vomer. On the anterior part of the shaft of the maxilla there is a dorsal thickening or low process, much as in the Percopsidae. There is no supramaxilla. The jaws of *Asineops* were clearly protrusile. They agree with Alexander's (1967a) account of protrusile perciform jaws rather than with those of atherinomorphs (Alexander, 1967b), closely resembling the jaws of the cichlid *Pterophyllum*, the nandids, and others.

The mandible is long and moderately deep, with the oral border of the dentary toothed for about three-quarters of its length. There is a small independent retroarticular; this and the ventrolateral surface of the articular are covered by scales. The mandibular sensory canal ran in a tube which is closed in the articular and opens through four pores spaced along the dentary.

All the opercular bones are completely scale-covered and without ornament or serrations. The vertical limb of the preopercular is almost twice as long as the horizontal limb, and the angle in the bone is about 80 degrees. The opercular is very broad, the maximum breadth being about 80 per cent of the depth. The anterodorsal corner of the bone is truncated, and the dorsal margin hardly rises above the point of articulation with the hyomandibular. The subopercular is long and deep, with a large spike at its anterodorsal corner. The interopercular is a large triangular bone extending well below the preopercular.

There are six branchiostegal rays, as in percopsiforms, the two anterior ones articulating with the ventral edge of the ceratohyal, the four posterior ones with its lateral surface, as in all higher teleosts. There are no anterior projections on the heads of the branchiostegals. The epihyal is not visible. The ceratohyal is shallow, with no fenestra and no groove on its lateral surface. The large, triangular, lower hypohyal occupies the entire anterior end of the ceratohyal. The upper hypohyal may be absent or may be squeezed out dorsally, as in the nandids. Between the hypohyals, and often projecting below the mandible in the fossils, there is a long basihyal, broadest anteriorly, where it bears a small patch of rounded teeth. The lower pharyngeals are visible in U.S.N.M. No. 19873 and are large and covered with long, pointed teeth, largest anteriorly.

The vertebrae are difficult to count anteriorly where they are covered by the skull bones, but they appear to vary in number. There are 12–14 abdominal vertebrae (nor-

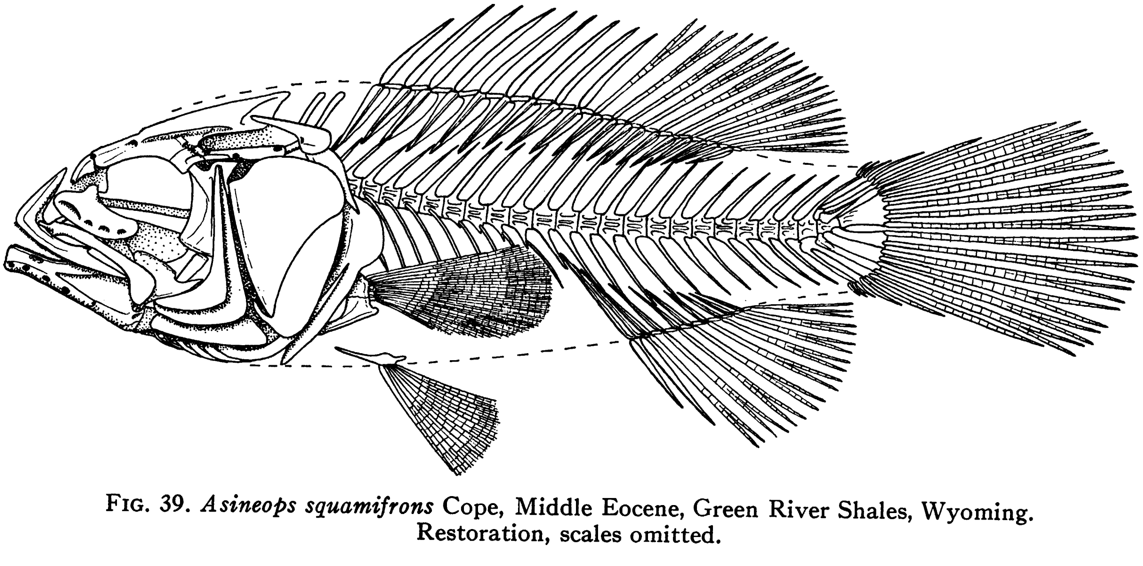

FIG. 39. *Asineops squamifrons* Cope, Middle Eocene, Green River Shales, Wyoming. Restoration, scales omitted.

mally 12), 13–15 caudal vertebrae (normally 14), and a free second ural centrum, the total number of vertebrae (including u_2) ranging from 27 to 29. The first centrum is deepened and modified to fit the tripartite occipital condyle, and the second is anteroposteriorly compressed. There are 11 or 12 pairs of stout, short ribs. The ribs seem to be inserted on the centrum above short transverse processes, as in percopsiforms, except on the last three or four abdominal vertebrae where they insert on the hind faces of ventrally directed processes. There are epipleurals on the first seven or eight vertebrae but no epineurals.

The caudal skeleton (text fig. 40) resembles that of living percopsiforms in having a complete neural spine on the second pre-ural centrum, only two epurals, and the upper hypurals fused with the second ural centrum. The first uroneural has a saddle-like articulation with the fused first ural and pre-ural centra, as in the Percopsidae. Between this uroneural and the upper hypural plate there is a bone which may be a second uroneural (as in the Percopsidae) or a free upper hypural (as in *Aphredoderus*), but the preservation is not sufficiently good to show whether the bone is paired (uroneural) or median (hypural). As in the Percopsidae, the parhypural and two lower hypurals are separate and autogenous. The haemal spine of the second pre-ural centrum is invariably double, suggesting that the centrum may be compound in origin. In one specimen (U.S.N.M. No. 11111; text fig. 40B) the second pre-ural vertebra is clearly formed by fusion of two centra and here the haemal spine is triple, although the neural spine is still single. In two other specimens (U.S.N.M. Nos. 11109 and 19681) the second pre-ural centrum is apparently single, but the haemal spine is triple and the neural spine is double. The caudal fin is large and rounded and contains only 14 principal rays with 12 branched. There are five procurrent rays above and below, only the last segmented, the foremost procurrent rays articulating with the neural and haemal spine of the second pre-ural centrum.

In the shoulder girdle there is some indication (A.M.N.H. No. 3992) of a small, thin supratemporal, but no details of the bone are visible. The posttemporal is large, with a long epiotic limb and a stout intercalar limb. The supracleithrum is broad and short. The cleithrum has a broad, smooth, posterior plate. The coracoid is of moderate size, the anterior process attaching to the cleithrum well above the cleithral symphysis. U.S.N.M. No. 19873 and A.M.N.H. No. 2691 suggest that the upper scalelike postcleithrum and the lower rodlike postcleithrum were not fused as they are in Tertiary percopsiforms. There are four pectoral radials. The pectoral fin is large and contains 17 rays.

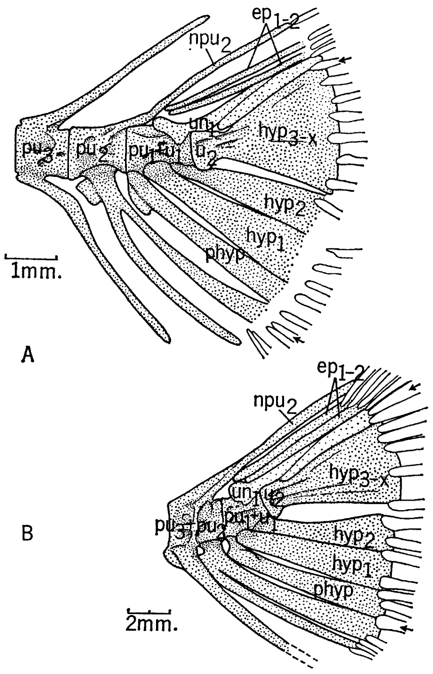

FIG. 40. *Asineops squamifrons* Cope, Middle Eocene, Green River Shales, Wyoming. Caudal skeletons. A. A.M.N.H. No. 3992. B. U.S.N.M. No. 11111. Arrows indicate the outermost (unbranched) principal rays.

The pelvic fins are subthoracic, the fins originating behind the tips of the lower postcleithra and the girdle having no contact with the cleithra. The pelvic bones have medial processes which probably met in the midline, but both these and the posterior processes are shorter than those in percopsiforms. The pelvic fin contains eight rays, the first unbranched. There is no pelvic splint.

The dorsal fin contains eight (one specimen) or nine (all other specimens) spines and 11 (normally) or 12 soft rays, supported by 19 or 20 radials. The dorsal spines are alternately inclined to right and left, as they are in many acanthopterygians. There is some variability in the dorsal spines, but the third to eighth are normally equal in length, the ninth being a little shorter. The longest dorsal spines are equal to about 50 per cent of the depth of the trunk. The spine-bearing radials are well spaced, with long, ossified middle segments linking their tips; U.S.N.M. No. 11112 shows that these middle segments are fused with the proximal segments at least on the first five radials. The first dorsal radial lies behind the second or third neural spine. Two predorsals lie behind the first and second neural spines. These bones are rodlike, as are the predorsals of acanthopterygians, not platelike as is the single supraneural of percopsiforms. The bases of the dorsal fin rays, both soft and spinous, are scale-covered. There is no adipose, the elongate dorsal occupying the position of this fin.

The anal fin contains two (normally) or three (U.S.N.M. No. 11112) spines and nine (normally) to 11 (U.S.N.M. No. 11112) soft rays supported by 10–13 radials. The second anal spine is equal in length to about 85 per cent of the longest dorsal spines. The base of the anal fin is scale-covered to the same extent as the dorsal.

The scales are cycloid, with strongly marked circuli which become sinuous posteriorly. On the outer surface of the scales there are small pustules or tubercles which tend to lie in radial rows (pl. 67). There are about 18 scales in a transverse series on the trunk, with the conspicuous, uninterrupted lateral line passing through the eighth scale from the top, and about 32 scales along the lateral line.

RELATIONSHIPS OF *Asineops*

Cope (1884, p. 85) placed *Asineops* in a family Asineopidae, "differing from the Aphredoderidae in the simple pubes." Cope thought that *Pygaeus*, from the Middle Eocene of Monte Bolca, might also belong in the Asineopidae, but this fish has spiny head bones, no extension of the scales over the head, thoracic pelvics with a spine, a caudal skeleton of basal perciform type, and 15 branched caudal rays; it seems to be correctly placed in the Acanthuroidei. The family Asineopidae is thus monotypic. Later authors have followed Cope in placing the Asineopidae next to the Aphredoderidae or have included *Asineops* in the Aphredoderidae. Cope's comparison of *Asineops* with the aphredoderids was an inspired guess, for the fish is superficially very different, and the only character he mentioned indicative of percopsiform relationships was the number of pelvic rays. It is a tribute to Cope's insight that today, with far more information on the fossil and a more coherent system of classification, we cannot do much to improve on his decision.

The area in which relatives of *Asineops* are to be sought is indicated primarily by the structure of the upper jaw, dorsal fin, pelvic fins, and caudal skeleton. The upper jaw is of advanced perciform type. The dorsal fin, with a long spinous portion, the spines inclined to right and left, supported by radials with well-developed middle segments, is of primitive acanthopterygian type, as in holocentrids and various generalized perciforms. The subthoracic, spineless, eight-rayed pelvics resemble those of percopsiforms, the Polymixiidae, some Cretaceous "beryciforms" (*Aipichthys*, *Pharmacichthys*), and the Lampridiformes (Veliferidae). The caudal skeleton is of percopsiform type. These characters indicate that *Asineops* lies near the borderline between the Paracanthopterygii and the Acanthopterygii, and may be related to the Percopsiformes, to the Lampridiformes (with which *Aipichthys* and *Pharmacichthys* are included in this discussion; these Cretaceous forms show striking resemblances to the Lampridiformes and could well represent the ancestral stock of the order; see Patterson, 1968b, p. 97) or to the Polymixiidae.

Resemblance between *Asineops* and the Percopsiformes include:

1. Occurrence in North American fresh-water deposits, together with percopsiform fishes (all known polymixiids and lampridiforms are marine).
2. Basisphenoid absent, orbitosphenoid also probably absent (both present in polymixiids and lampridiforms).
3. Only two openings in the pars jugularis of the trigemino-facialis chamber (a separate opening for the hyomandibular nerve in polymixiids and lampridiforms).

4. The dorsal process on the lacrimal, although smaller than the splintlike ascending process of percopsiforms, is larger than the condyle that articulates with the lateral ethmoid in polymixiids and lampridiforms.

5. Supramaxillae absent (two present in polymixiids, none in lampridiforms).

6. Six branchiostegals (eight in polymixiids, six or fewer in lampridiforms).

7. Epineurals absent (present in Polymixiidae and in the lampridiform *Velifer*).

8. Neural spine on second pre-ural centrum complete (short or much reduced in lampridiforms), two epurals (three in polymixiids and lampridiforms).

9. Anal fin short (long in polymixiids and generalized lampridiforms).

This list of resemblances[1] is impressive, but other characters clearly oppose the inclusion of *Asineops* in the Percopsiformes. As preamble, it should be noted that *Asineops* is more primitive than any percopsiform, even *Sphenocephalus*, in having the supraorbital, temporal, and mandibular sensory canals bone enclosed and in the few procurrent caudal rays. *Asineops* is also more primitive than any Tertiary or living percopsiform, resembling *Sphenocephalus* and generalized acanthopterygians, in the spike on the anterodorsal corner of the subopercular (a blunt process in percopsiforms), the insertion of the last three or four pairs of ribs on ventrally directed processes, and the separate upper and lower postcleithra. On the other hand, *Asineops* differs markedly from all percopsiforms, and is more advanced than them, in the long postorbital division of the braincase, the long supraoccipital crest and crests for muscle insertion on the frontals, the protrusile jaws and highly specialized premaxilla, the absence of infraorbital bones, double-headed hyomandibular, single hypohyal, long dorsal fin with nine spines, the presence of two predorsals, and the extension of the scales over the head. All these characters throw doubt on a close relationship between *Asineops* and the percopsiforms. In addition, two of the most important anatomical indications of such a relationship, the dorsal process on the lacrimal and the caudal skeleton, are not entirely convincing; the lacrimal because the dorsal process might be a hypertrophied articular condyle rather than an ascending process, the caudal skeleton because of the possibility that the second pre-ural centrum is compound in origin. In *Asineops* the haemal spine of the second pre-ural centrum is invariably double; in percopsiforms the neural spine of this centrum is frequently double, but the haemal spine is rarely so (Rosen, 1962, p. 9). In *Asineops* the neural spine of the second pre-ural centrum may remain single even when the haemal spine is triple (text fig. 40b), which raises the possibility that the second pre-ural centrum in *Asineops* is compound in origin, having arisen by fusion of the second and third pre-ural centra, the single neural spine representing that of the third pre-ural centrum. This would indicate that in the ancestors of *Asineops* the second pre-ural neural spine was reduced or lost, as it is in the Lampridiformes (Patterson, 1968b, p. 97).

Evidence in favor of a relationship between *Asineops* and the Lampridiformes or the Polymixiidae is rather scanty. The skull roof, with a long, low supraoccipital crest, thickened centrally, paired crests for muscle insertion on the frontals and parietals, and the sensory canals bone-enclosed, agrees well with that of the Polymixiidae. Generalized lampridiforms have a similar skull roof but with the supraoccipital crest hypertrophied. The occipital condyle, which has large exoccipital components in the same vertical plane as the basioccipital condyle, could well be of polymixiid and lampridiform type, as it is not known whether the exoccipital condyles are widely separated as they are in percopsiforms. The thick, spongy bones of the neurocranium, separated by cartilage, resemble those of *Lampris* and *Velifer*. The specialized, protrusile upper jaw of *Asineops*, with no supramaxillae, resembles that of *Lampris* and that of *Velifer* rather closely, but the jaws are toothless in these lampridiforms and there is no maxillary process on the palatine (Regan, 1907, p. 639). The absence of ornament from the skull bones and the presence of six branchiostegals are also resemblances to lampridiforms. The caudal

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[1] Many of the resemblances are in features that are generally distributed in the higher teleosts. Hennig (1965) has correctly pointed out that "... it is not the extent of resemblance or difference ... that is of significance [in determining] phylogenetic relationship, but the connection of the agreeing or divergent characters with earlier conditions."

skeleton of *Asineops* could develop from the polymixiid type by fusion of the upper hypurals with the second ural centrum and loss of one epural (if the second pre-ural centrum is not compound), or from the lampridiform type by the loss of one epural and the fusion of the second and third pre-ural centra (if pu_2 is compound). A long, spinous, dorsal fin, similar to that of *Asineops*, occurs in both the Polymixiidae (*Homonotichthys*) and the Veliferidae (*Palaeocentrotus*, *Velifer multispinosus* Smith, 1951), predorsals occur in both these groups, and the scales tend to cover the bases of the median fins. In *Velifer* scales also cover the head, much as in *Asineops*. The scales of *Asineops* show some resemblance to the spinous or tuberculate scales of the polymixiid *Pycnosterinx dubius*, and are especially like those of *Dinopteryx*, which, although ctenoid, resemble those of *Asineops* in shape, size, texture, and in their tendency to extend onto the head. *Dinopteryx* is still very poorly known, but in many other features (body shape, shape of maxilla, texture of skull bones, dentition, and shape of operculum) it is very like *Asineops*. It is difficult to be more precise about these resemblances, some of which are due to nuances of bone texture and the way in which the skulls disintegrate during fossilization, but of all fossil teleosts we have seen, *Dinopteryx* is the one that most definitely resembles *Asineops*. *Dinopteryx*, previously the type of a heterogeneous suborder Dinopterygoidei of Cretaceous Beryciformes, is perhaps only a relative of the polymixiids that has developed a pelvic spine, for, so far as is known, this character is the only one in which it differs from the polymixiids (Patterson, 1964, p. 388; 1968b, p. 87). Provisionally, we regard the Dinopterygidae (*Dinopteryx* only) and Pycnosteroididae (*Pycnosteroides*) as members of the Polymixioidei (see p. 447). The possibility exists that *Asineops* is a specialized derivative of this polymixiid-dinopterygid stock that has entered fresh water. Although such a hypothesis may appear unlikely, one point in favor of such a migration is the occurrence in the Green River Shales, alongside *Asineops*, of *Diplomystus*, a clupeoid that also occurs with the marine Cretaceous polymixiids and *Dinopteryx*.

Finally, it is necessary to consider a third possibility, that *Asineops* is related to fishes now included in the Perciformes. Although the caudal skeleton of *Asineops* is clearly more primitive than that of any perciform, it could give rise to a perciform type by fusion of u_2 with the preceding centrum. The subthoracic, eight-rayed pelvics of *Asineops* also appear to be more primitive than those of perciforms, but subthoracic pelvics are re-acquired in several groups that appear to be perciform derivatives (anabantoids, mugiloids), whereas the pelvic spine is also often lost and the number of pelvic rays may secondarily increase (as in pleuronectiforms). These possibilities are mentioned because of certain striking resemblances between *Asineops* and the Nandidae (placed in the Percoidei by Greenwood, Rosen, Weitzman, and Myers, 1966), the Anabantoidei (placed in the Perciformes by Greenwood and his co-authors), and the Channiformes (a separate pre-perciform order, according to Greenwood and his co-authors). The question of whether or not these three groups are related is still open. Among recent workers, Liem (1963) concluded that anabantoids and the Channiformes were convergent, not related; Gosline (1968) found that these two groups were related, but he remained undecided about the proximity of the nandids; Monod (1967) and Patterson (1968b) thought that the structure of the caudal skeleton indicated that the three groups were related; and Nelson (in press) reached the same conclusion from a study of the gill arches. These various opinions need not be discussed here; they reflect uncertainties about the significance of the parasphenoid teeth, subthoracic pelvics, and aspinous fins that occur in some of these fishes. *Asineops* resembles the nandids closely in the skull roof; the rostral fossa and the form and distribution of the crests and bone-enclosed sensory canals are exactly as in *Pristolepis*, except that the rostral fossa of *Asineops* is larger, although intermediate in size between that of *Pristolepis* and that of *Polycentrus*. The upper jaw of *Asineops* is also like that of the nandids. The hyoid bar of *Asineops*, which has a slender ceratohyal, its tip occupied only by the lower hypohyal, six branchiostegals, and a long, spatulate basihyal with a patch of teeth at its tip, is also like that in nandids. In anabantoids the head is completely scaled, as in *Asineops*; in both anabantoids and channiforms the pelvic fins may be subthoracic, as in *Asineops*; and in channiforms there is no pelvic spine. The caudal skeleton and fin of *Asineops* are strikingly like those of nandids, anabantoids, and channiforms (Monod, 1968, figs. 654, 655, 789–793; Patterson, 1968b, p. 89; Gosline, 1968, fig. 2), even to the number of fin rays and the doubling of the second pre-ural haemal spine (frequent in nandids), except that in *Asineops* the second ural centrum is not fused to its predecessor as it is in the other groups. *Asineops* cannot be said to resemble any one of these three groups (nandids, anabantoids, channiforms) more closely than the others. Rather it exhibits a mosaic of the characters of all three, and the significance of these characters is far from clear.

The extended discussion of the possible relationships of *Asineops* is necessary because of the apparent intermediate position of the fish between the paracanthopterygians and acanthopterygians. If *Asineops* is a paracanthopterygian, it differs from all others in its percoid-like upper jaw and dorsal fin, suggesting a possibility of relationship between the paracanthopterygians and various groups now classified in or near the Perciformes. If *Asineops* is related to the polymixiids or lampridiforms, its occurrence with and resemblances to Eocene percopsiforms are important evidence on the relationships and origin of the paracanthopterygians. If *Asineops* is related to the nandid-anabantoid-channiform assemblage, it provides important evidence on the origins of these groups. The evidence for each of these three hypotheses is presented in the foregoing discussion. On the available evidence, we believe that no conclusion can be reached, so we leave the Asineopidae as a family *incertae sedis*.

ORDER GADIFORMES

LIVING GADIFORMS (GADOIDEI, MURAENOLEPOIDEI, MACROUROIDEI,[1] OPHIDIOIDEI, ZOARCOIDEI)

In order to deal effectively with the questions of the composition of the Gadiformes and the relationships of the order, it is essential to clarify some anatomical misconceptions relating especially to the tail skeleton. Most of what has been written on the gadiform caudal skeleton has been based on species of the genus *Gadus*. The *Gadus* tail is relatively specialized, however, showing a high degree of consolidation and reduction of hypural elements. By some workers (Boulenger, 1902, p. 295; Regan, 1903, p. 466) it was thought not to contain hypural elements but to be composed entirely of the reduced neural and haemal spines of the posterior vertebrae and of the modified interneural and interhaemal bones of now-missing median fin elements. That view was based on the idea that gadids were derived from fishes like the "tailless" macrourids. In a study of the development of the *Gadus* caudal skeleton, Barrington (1937) presented evidence that relates the individual structures in the tail region to a typical pattern of teleostean hypural and epural bones. Although Barrington's terminology is different from that now in use (neural and haemal spines, for example, are referred to as epurals and hypurals, respectively), his meaning is clear: ". . .the tail of *Gadus* resembles in various details both of its structure and development a normal homocercal tail." Barrington also concluded, however, that the two hypural plates of *Gadus* can be strictly homologized with the more numerous hypurals of other fishes only if one supposes that the two elements in *Gadus* represent compound hypurals. He objected to such an interpretation on the grounds that fusion probably would not ". . .have occurred without leaving some trace of compound origin in the development of the hypural." In contrast to this view Gosline (1961a) believed the caudal skeleton of gadoids ". . .to be far more aberrant than even that of the eels. . ." and that ". . .its parts cannot easily be homologized with those

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[1] As indicated by Marshall (1965, 1966) and by our own observations, the Macrouroidei cannot be distinguished satisfactorily from the Gadoidei. We retain the term here only for convenience in discussion.

of any. . ." of a variety of diverse teleostean groups. This statement was later elaborated (Gosline, 1963), following an initial report (Rosen, 1962) that the gadiform, percopsiform, and amblyopsid fishes show many striking similarities of the skull and tail structure. Gosline believed that "The caudal skeleton of the lampridiform, percopsiform, gadiform, and amblyopsoid fishes appears to be of a highly unusual, if not unique, nature." He amended that interpretation with the remark that ". . .the groups under consideration represent a rather different lineage of sequential fusion of parts. . .from that which has led to the type of caudal skeleton found in. . .most other higher teleosts." We agree that differences in the sequence of fusion of parts of the caudal skeleton are what differentiate the paracanthopterygians from the acanthopterygians (see our discussion of the caudal skeleton, above). The essential point, however, is that the gadiform structure (text fig. 3C), no matter how much it may have become specialized by reduction in caudal peduncle depth, is, as Barrington has said, a fundamentally normal homocercal tail. This fact can be established by study of such gadoid genera as *Melanonus* (Melanonidae), *Antimora*, *Eretmophorus*, and *Salilota* (Moridae). In all there are five distinct hypurals distributed on two centra: the customary two hypurals on compound centrum pu_1+u_1 and three hypurals on u_2. There is also a distinct parhypural, a single uroneural, two epurals, and a full neural spine on pu_2 (text fig. 3D). The pattern is similar to that of some Recent percopsids. Study of the morid genera makes it evident that the basic gadiform caudal skeleton is not exceptional in any way, and shows that Monod's interpretation (1968, pp. 497, 610, figs. 568–576) of the gadoid tail as having two free ural centra is due to his mistaking the parhypural for the first hypural.

There are in the tail region of many gadoids, however, one or more dorsal and ventral accessory bones between the neural and haemal spines that have contributed to the confusion about the origin of the cod tail. As noted above, these structures were interpreted by Boulenger and Regan as relicts of dorsal- and anal-fin pterygiophores of a once diphycercal tail. Barrington (1937), although not explicit, also apparently believed that the accessory bones (and the parhypural and two epurals as well) are relict pterygiophores (radials). A simpler interpretation of these elements, however, is that they are the remnants of neural and haemal spines of vertebrae that have been lost in connection with a shortening of the caudal axis. The tendency of percopsiforms and gadiforms to have supernumerary neural and haemal spines is well marked (text fig. 3A–D) and is commonly indicated by the presence of an apparently bifurcate spine (see also Barrington's figure of *Gadus merlangus*, 1937, p. 458; and Monod's figure of *Pollachius virens*, 1968, fig. 575). Our specimens of *Theragra chalcogramma* (text fig. 3A, B) show the development of a supernumerary spine on pu_3 during incomplete, and therefore evident, vertebral loss. The upper part of the obsolescent centrum of pu_2, with its attached neural arch and spine, is still present, and the usual haemal spine of pu_2, identifiable by its distinctive shape, is now joined at the base with the normal haemal spine of pu_3. In specimens of *Percopsis* (pl. 64, and text fig. 16A) it can be seen that remnant neural spines are not invariably ankylosed with the associated replacement centrum (note the free arch at the base of the posterior neural spine on the now second pre-ural centrum), and it seems clear to us from the fact that these accessory bones in gadoids are in some cases autogenous and in others ankylosed to normal elements that the so-called gadoid caudal pterygiophores of authors are no more than the remnant haemal and neural spines resulting from vertebral loss (see also Monod, 1968, p. 497).

The above evidence for vertebral subtraction also may explain the tendency in gadoids, muraenolepoids, and ophidioids for the posterior dorsal and anal fin pterygiophores to be more numerous than the caudal body segments. Posteriorly there may be as many as three pterygiophores per segment, although this inequality gradually disappears anteriorly where a one-to-one relationship is typical.

Certain anatomical peculiarities of gadiforms, other than the caudal skeleton, also are in need of clarification. One of these, the position of the scapular foramen between the scapula and coracoid rather than within the scapula, has received considerable attention. As noted by Boulenger (1901) and later remarked on by Svetovidov (1948), a similar position of the foramen can be found also in trachinids, callionymids, and nototheniids. In addition, the foramen has a more normal position within the scapula in some macrouroids (Regan, 1903; Svetovidov, 1948). The general occurrence in gadiforms of the levator maxillae superioris muscle is another feature that merits a moment's attention because of Gosline's (1968, p. 19) recent statement, "In *Merluccius*, which differs from most gadoids in having a prognathous lower jaw, [I can] find no 'levator maxillae superioris.'" We have seen the levator maxillae superioris well developed in all our *Merluccius* material (pl. 63), and Dietz (1921) had previously illustrated the muscle in *Merluccius vulgaris*. The alveolar process of the gadiform premaxilla was implied also by Gosline (1968, p. 23) to be notably shorter than the maxilla. This dentigerous posterior extension of the premaxilla is greatly enlarged in many gadiforms, however, as in the Lower Eocene and Recent members of the Merlucciidae (pls. 71, 72, text fig. 52) and in the Bregmacerotidae. The distinctive anterior position near the olfactory capsule of the olfactory lobe of the brain is not found in *Melanonus*, and some merlucciids (Marshall, 1966), and the route taken through the orbit by the olfactory tracts is characteristic not only of gadids but also of various other teleosts. A survey of the otophysic and neuroanatomical specializations of some gadiforms was presented by Svetovidov (1948). The fact that the hyomandibular of gadoids has but a single head (text fig. 9A, B) was given some importance (Gosline, 1968, p. 23) but this feature, too, is of questionable significance if one considers that among myctophoid fishes (text. fig. 41A–C) and within the family Holocentridae the hyomandibular head may be either simple or bifid. Finally, the absence of a lateral commissure enclosing the pars jugularis of gadoids and macrouroids and the presence of a commissure defining a well-developed

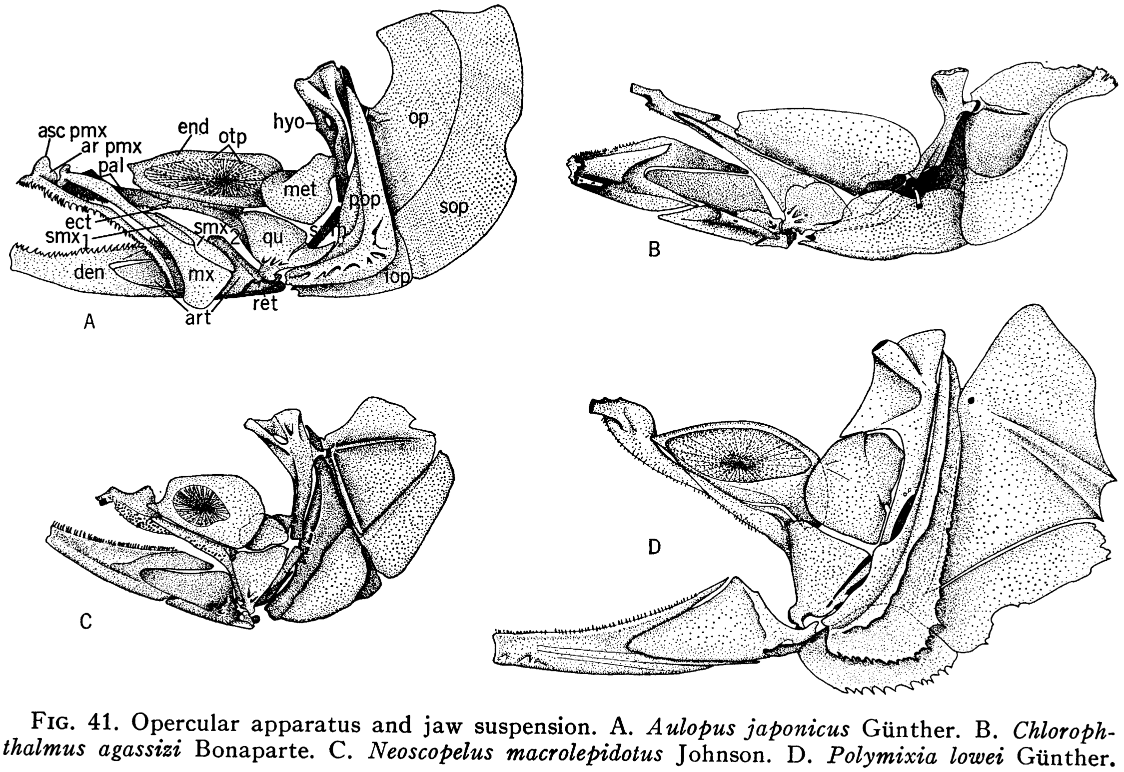

FIG. 41. Opercular apparatus and jaw suspension. A. *Aulopus japonicus* Günther. B. *Chlorophthalmus agassizi* Bonaparte. C. *Neoscopelus macrolepidotus* Johnson. D. *Polymixia lowei* Günther.

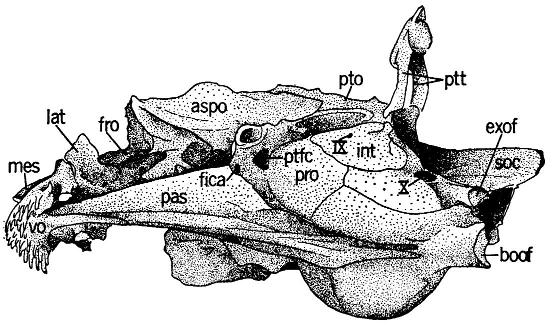

FIG. 42. *Ogilbia* sp., neurocranium in ventral three-quarter view.

trigeminofacialis recess in ophidioids (text fig. 42) were suggested by Gosline (1968, p. 23) as two of many reasons for excluding the latter from relationship with gadiforms. In this connection it is noteworthy that within the Scorpaeniformes may be found an entire spectrum of development of the trigeminofacialis recess, from the well-developed percoid type of recess of scorpaenids to the near cod condition of some cottoids in which the lateral commissure is no more than a slender ligament.

The question of the composition of the Gadiformes, or at least of a gadiform lineage, may conveniently be begun with a consideration of the inclusion of the Ophidioidei which has recently been contested by Gosline (1968). Gosline believed that ophidioids should be included instead in the Perciformes because, in common with percoids, they possess a pelvic spine, and because, according to information compiled by Regan (1903), the ophidioid jaw suspension is more like that of *Gadopsis* than that of gadiforms, especially in its divided hyomandibular head. The objection to an ophidioid placement in or near the gadiforms based on differences in jaw suspension we find to be unacceptable, for reasons illustrated by text figure 9. The fact that ophidioids retain a generalized trigemino-facialis opening in the pars jugularis, as compared with the reduction and loss of the lateral commissure in gadiforms, formed another of his arguments. A final anatomical argument presented by Gosline (1968) for placing ophidioids near the percoids and not in or near the Gadiformes was that ophidioids have the scapular foramen in the scapula and gadiforms have it between the scapula and coracoid. Except for the presence of a pelvic spine in ophidioids, all the other points are dealt with above. Even were gadoids to be consistently different from ophidioids in the various features emphasized by Gosline, this evidence would still not warrant exclusion of the ophidioids, since the presence, for example, of a lateral commissure is a condition that occurs also in other paracanthopterygians as well as in almost all generalized teleosts.

Because considerable phylogenetic importance has been attributed to the pelvic spine in evaluations of the relationships of the ophidioid fishes, we have attempted a brief survey of pelvic-fin structure in a variety of acanthopterygians and paracanthopterygians. In certain acanthopterygians examined (berycoids, serranoid-like fishes, and generalized blennioids) the pelvic spine (text fig. 43A, C) consists of a pungent, cylindrical spine shaft and a complex, somewhat asymmetrical base consisting of two lateral flanges that resemble the paired elements of the ray bases and a central, slightly medially directed ventral extension of the spine shaft that has a direct hingelike articulation with the pelvic girdle. The central process has the appearance of a somewhat inwardly bent thumb emerging from the forward edge of the spine between the lateral articular

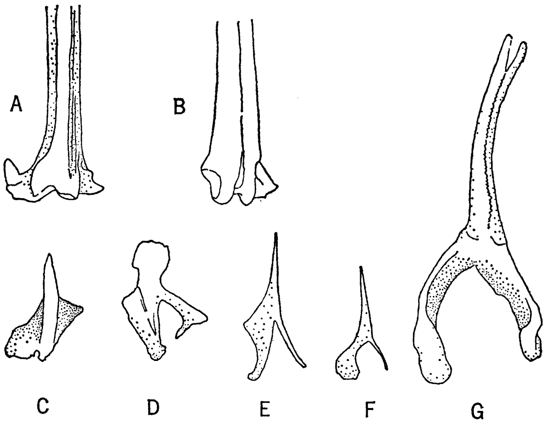

FIG. 43. Right pelvic spines in various advanced euteleosteans, anterior view to show form of basal articular structures. A. *Holocentrus*. B. *Siganus*. C. Blenniid. D. Gobiesocid. E. Antennariid. F. Ophidiid and batrachoidid. G. *Gadopsis*. Spine base only shown in A and B.

surfaces. The complex, and invariably characteristic, tripartite spine base was found to be fully developed no matter how reduced the spine itself may have become (text fig. 43C). In the acanthuroid genus *Siganus* (text fig. 43B) the pelvic fin consists of a spine followed by three rays and another spine. The anterior spine is clearly a paired structure in which the two unsegmented halves have become fused together. No median basal structure is present. The posterior pelvic spine in *Siganus* is more complex, and only at its base is there a sign of its paired origin. The shaft is complexly folded and ridged. In centrarchids the pelvic spine has a simple, raylike base and a cylindrical, pungent shaft. There is an exceedingly small and peculiar first pelvic-fin element in *Gadopsis* (text fig. 43G) unlike any others we have seen. Its base is composed of two subequal articular surfaces, the inner being the larger as in the bases of the fin rays that follow. The two articular surfaces come together to form a cylindrical shaft which is traversed longitudinally by an irregular median line of light-refracting material. The shaft divides bilaterally at its tip to form two small, finger-like processes. The whole structure has the appearance of an obsolescent fin ray that retains indications of an original bilateral nature in the paired proximal and distal components and in the light-refracting material that runs longitudinally along the center of the median shaft. The entire element is composed of a rubbery substance of granular appearance, which picks up a small amount of alizarin dye, suggesting incomplete or diffuse ossification. In paracanthopterygians the pelvic spinelet, when present, is notably asymmetrical (text fig. 43D–F). The structure has a divided base in which the outer half is invariably large and triangular and the inner half slender and slightly recurved. The spinelet appears to have been derived from a simple ray in which the base and a small part of the shaft of the outer ray-half form the bulk of the structure and in which the inner ray-half contributes only its slender, sliver-like base. In young gobiesocids of the genus *Acyrtus*, the spinelet also consists of two parts: an outer section with the typically enlarged base that is continuous with a hollow, cylindrical, open-ended shaft; and a small, slender inner part. When present in ophidioids, the spinelet either resembles that of batrachoidids and antennariids or is reduced to a minute, inverted, V-shaped fragment. The tentative conclusion we reach from these observations is that a variety of pelvic spinelike structures occurs in the higher teleosts and that some of them are the result of ankylosis of a simple ray (e.g., *Siganus*). The paracanthopterygian spinelet gives every indication of being simply a greatly reduced ray, the inner half of which has been severely degraded and fused with its opposite member. It is greatly different from the pelvic "spine" of *Gadopsis*, the nature and probable origin of which are obscure.

Gosline (1968, p. 18) has convincingly shown that ophidioids and gadiforms have a similar sensory apparatus and mode of life, and that both are rather similar ecologically to *Gadopsis* and some blennioids in a preference for, and the use of, the substrate environment. He attributed the ophidioid-gadiform similarities to convergence due to similar habitus. We agree that the question of convergence is indeed at issue in such a

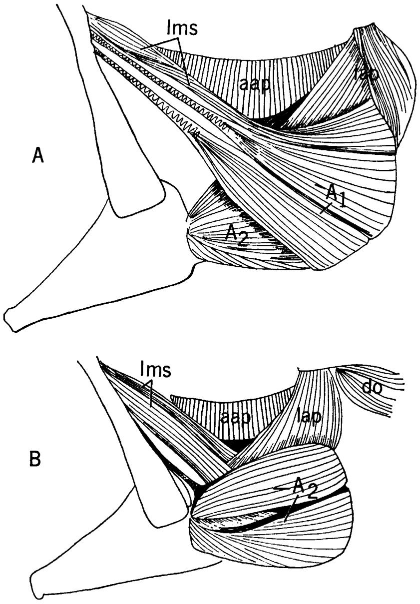

FIG. 44. Diagrammatic representation of superficial jaw musculature in some gadiforms. A. Pattern in *Steindachneria* and *Malacocephalus*. B. Pattern in *Rissola* and *Lepophidium*.

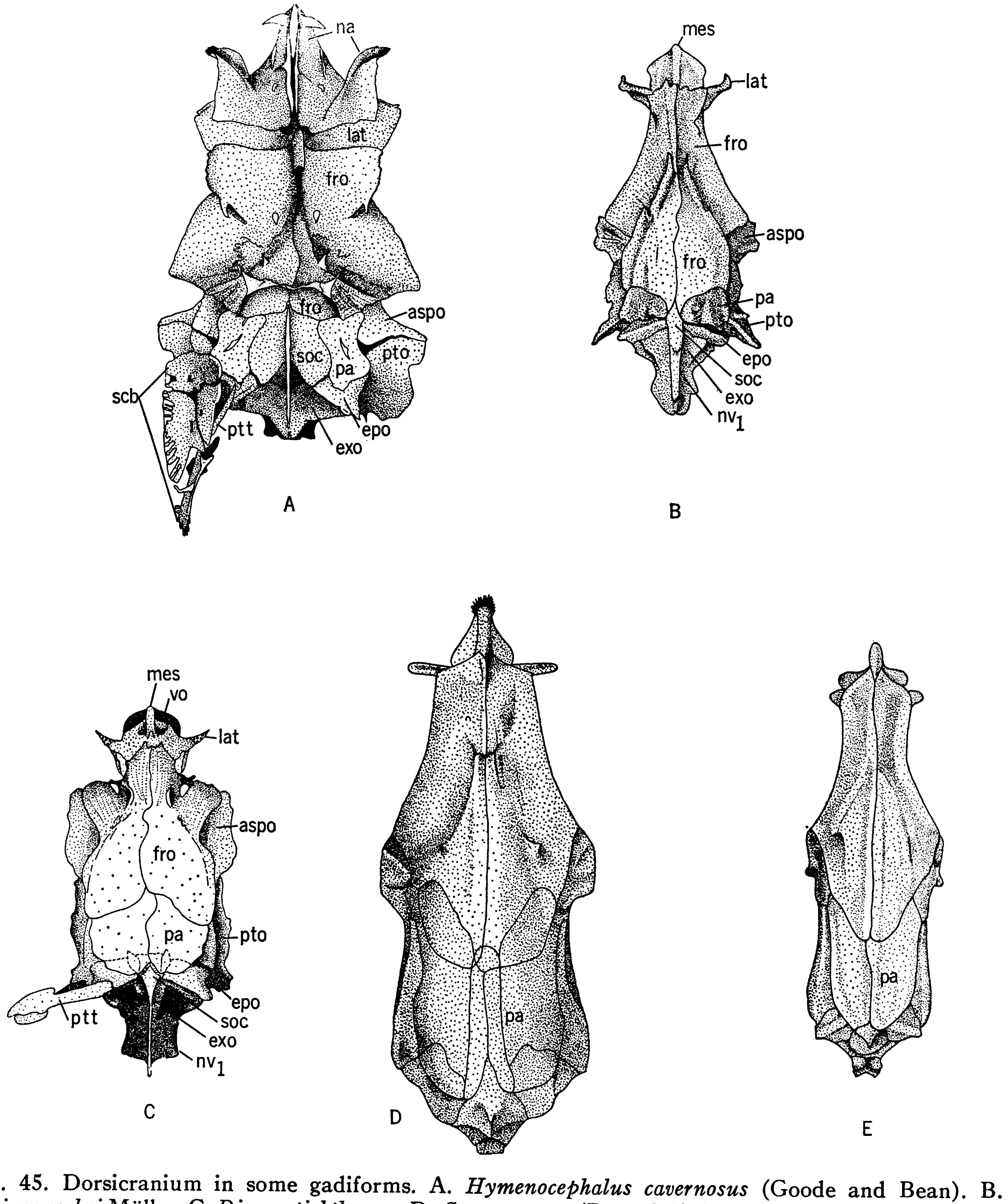

FIG. 45. Dorsicranium in some gadiforms. A. *Hymenocephalus cavernosus* (Goode and Bean). B. *Ophidium rochei* Müller. C. *Dinematichthys* sp. D. *Carapus acus* (Brünnich). E. *Carapus dentatus* (Cuvier). B, D, and E after Emery (1880).

comparison, but conclude that the evidence points to the convergence of ophidioids with *Gadopsis* and the blennioids, and phyletic relationship to the gadiforms.

In the course of comparisons of ophidioids with a variety of elongate benthic teleosts, including *Gadopsis*, *Parapercis*, and numerous blennioids, we have been struck by the fact that all the above except the ophidioids have either a typical percoid caudal skeleton or one that could be derived from a percoid pattern and have the jaw muscles very similarly specialized (see discussion of *Gadopsis* above in the section on feeding mechanisms, and pl. 54 and text fig. 7). On the basis of these comparisons we suggest tentatively that *Gadopsis* is more closely related to the Trachinoidei and the Blennioidei than is indicated by its present position in the Percoidei. We have found that trachinoids and some of the Blennioidei and Gobioidei (see Dietz, 1914, pp. 129–133) possess the same distinctive pattern of cheek musculature.

Comparisons of the ophidioids need not be so negative, however, for they are very close in many ways to the muraenolepids, for example, in jaw musculature (pls. 62, 73, 74, and text fig. 44B), body form, fin arrangements, and particularly in the possession of peculiar, minute, embedded, eel-like scales (in some ophidioids only) that lie in the dermis at right angles to one another in an open cross-hatched pattern. Moreover, ophidioids show specializations of the swim bladder and of the abdominal part of the axial skeleton rather like those of some gadoids and macrouroids, there are similarities between ophidioids and gadiforms in various parts of the skull (see Greenwood, Rosen, Weitzmann, and Myers, 1966, and text figs. 42, 45), and the caudal skeleton of some tailed ophidioids is of a basic paracanthopterygian type (text fig. 3E; Monod, 1968, figs. 714, 715).

Excluding for the moment the highly modified carapids, ophidioids can be distinguished from gadiforms chiefly by the presence of a small supramaxilla,[1] the development of a complex basioccipital joint with the first vertebra, involving the formation of a bony arch between the foramen magnum and the basioccipital facet (text fig. 10D), and by the development of closely segmented and much-thickened pelvic rays which in many species are preceded by a minute, embedded spinelet. Pelvic fins in gadiforms, although frequently reduced in size and ray number, generally are neither enlarged nor closely

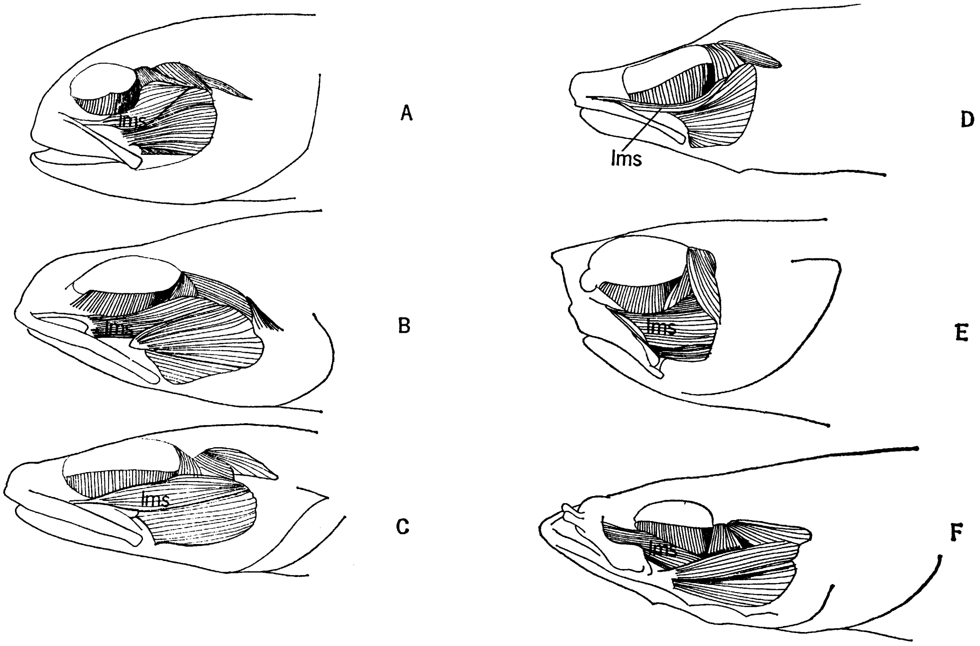

FIG. 46. Diagrammatic representation of superficial jaw musculature in some paracanthopterygians. A. *Zoarces viviparus* (Linnaeus). B. *Lycodes reticulatus* Reinhardt. C. *Lycodopsis pacifica* (Collett). D. *Lycodapus dermatinus* Gilbert. E. *Lionurus liolepis* (Gilbert). F. *Chologaster cornuta* Agassiz.

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[1] In the gadoid genus *Melanonus*, there is developed on the lower maxillary arm a stiff, apparently nonosseous structure that resembles a supramaxilla in position and shape. Whether it represents a membranous supramaxilla or simply an enlarged, reinforced ligament similar to the one present in ophidioids we cannot say.

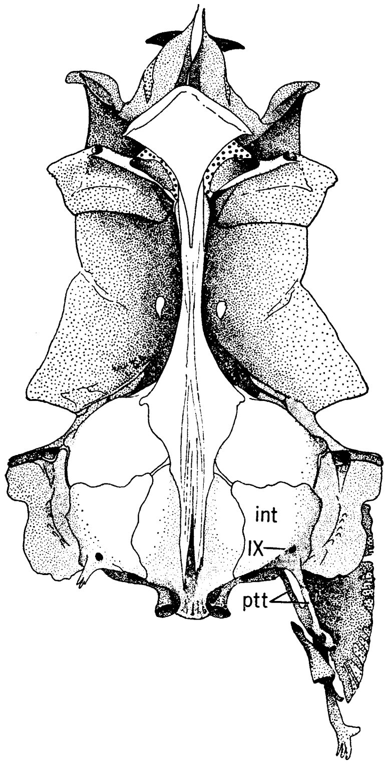

FIG. 47. Basicranium of *Hymenocephalus cavernosus* (Goode and Bean).

segmented, and are not preceded by a spinelet. But the enlarged first three pelvic rays of the gadoid *Bregmaceros* and the first two of *Enchelyopus* are very much thickened and are closely segmented. The pelvics of batrachoidids and gobiesocids show all the ophidioid modifications. In the antennarioid lophiiforms the pelvic fins are like those of gadoids, but are preceded by a spinelet, and in the zoarcoid fishes, here included in the gadiform lineage, the pelvic rays are reduced in number, in many cases are closely segmented and thickened, but are not preceded by a spinelet. [Gosline (1968, p. 24) claimed to have found a spinelet in zoarcids; we have been unable to verify this report, although we examined the same and many other species as well.]

The relationship of the zoarcids to the gadiform lineage is the least well documented of relationships of the five included suborders. Although we are now able to point to striking similarities between the jaw musculature of zoarcids (text fig. 46) and that of macrourids (pl. 75), the most critically needed evidence, that of the caudal skeleton, obviously is unavailable in these "tailless" fishes. However, in a recent report Yarberry (1965, pp. 460–461, fig. 9) described and illustrated the distinctly gadoid-like tail skeleton in representatives of the zoarcid genus *Melanostigma*, one of which had a distinct, free, second ural centrum. The remaining evidence, which in our opinion warrants their tentative inclusion here, was presented by Greenwood, Rosen, Weitzman, and Myers (1966).

All the other suborders seem to us solidly joined together in a subgroup of the Paracanthopterygii, the uniting specializations of which include the form of the cheek muscles and caudal skeleton, the presence of a posteriorly notched postmaxillary process on the premaxilla (pls. 71, 72, pl. 76, fig. 1, and text fig. 48), a greatly enlarged intercalar (text fig. 47), the frequent development of "percopsoid projections" on one or more of the anterior, bladelike branchiostegals (McAllister, 1968), and the formation of small, tubelike, exoccipital facets (pl. 77). All members of the group are elongate fishes, often of the deeper and colder dysphotic marine environments, with the tail reduced or confluent with the dorsal and anal fins, which are long, many-rayed, and in many cases secondarily subdivided (see Svetovidov, 1948), and a tendency to develop jugular pelvic fins and mental or circummental barbels.

It is apparent that the higher classification of the gadiform fishes is at present in an unsatisfactory state and that a great deal more anatomical work is needed before familial and subordinal relationships can be clarified. We have been able, however, to reaffirm the distinctiveness of certain of the family-level

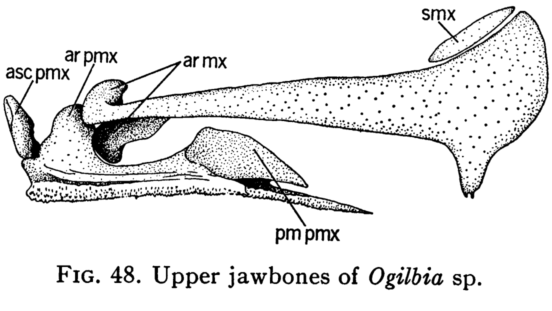

FIG. 48. Upper jawbones of *Ogilbia* sp.

and subordinal groupings and to question others, using chiefly details of the feeding mechanism and caudal skeleton.

In the Gadidae the hypurals are consolidated into two plates (text fig. 3A–C), one on the compound centrum (pu_1+u_1) and one on the second ural (u_2). In the jaw mechanism of gadids, the premaxilla has an exceedingly short alveolar process (pl. 76, fig. 1), and the maxilla is controlled not only by the robust and extensive levator maxillae superioris muscle but also by a peculiar and reduced superficial division of the adductor mandibulae (A_1) that originates on the fascia covering the main mass of the adductor (A_2). The caudal skeleton of merlucciids is like that of the gadids, but the jaw mechanism shows some consistent differences. In merlucciids the premaxillary alveolar process is long (pls. 71, 72), extending almost to the tip of the maxilla, and, although the maxilla has dual muscular control as in gadids, the levator maxillae superioris is a flatter, less robust muscle, and is constricted by a transverse tendon halfway along its length near the dorsal edge of the quadrate (pl. 63). In the Moridae, a small superficial division of the adductor mandibulae (A_1) is not present, and the main mass of the adductor is greatly reduced or absent. The levator of morids, however, resembles that of merlucciids in having a transverse tendon constricting the muscle above the quadrate and the gadids in having the levator maxillae superioris very well developed and extensive. Morids differ from other gadiforms, however, in having the hypurals unconsolidated in some genera (text fig. 3D); there usually are five separate and distinct elements (two hypurals on pu_1+u_1 and three on u_2). The uroneural of morids also is somewhat larger than that of other gadiforms.

We have found the Bregmacerotidae to be fundamentally different myologically and osteologically from other gadoids. The affinity of these small, large-scaled fishes to other gadoids is indicated by the position of the scapular foramen near the coracoidal margin, the *Gaidropsarus-Ciliata-Enchelyopus* dorsal and anal fin pattern, the distinctly notched postmaxillary process of the premaxillary, and the expanded parapophyses on the abdominal vertebrae. The bregmacerotids are decidedly peculiar as gadoids, however, in lacking exoccipital facets, in having very small, laterally displaced parietals, modified scales along the dorsal midline to convey a branch of the lateral-line canal system, jaw muscles closely resembling those of zoarcoids and some macrourids (the main superficial part of the adductor mandibulae being greatly reduced), two pectoral radials, a large, posteriorly toothed, myctophoid-like, dermal-basibranchial tooth plate (text fig.

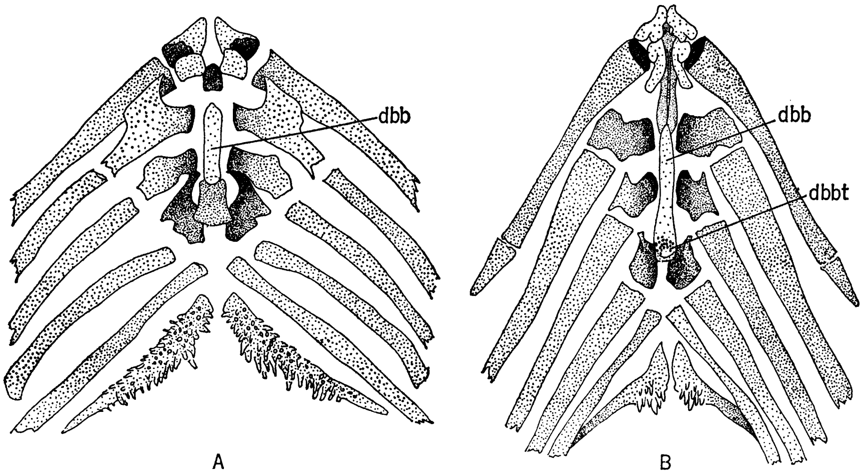

FIG. 49. Hyobranchial apparatus. A. *Muraenolepis marmoratus* Günther. B. *Bregmaceros macclellandi* Thompson. Note presence of dermal basibranchial plates, with a posterior tooth patch in *Bregmaceros*.

49B) between the first three gill arches, and no second or third basibranchial ossifications in the copula below, the first three pelvic rays greatly thickened and closely segmented as in ophidioids, and, in the caudal skeleton, the hypural plate on the second ural centrum greatly enlarged, dorsoventrally symmetrical, and having the chief role in caudal fin support, and the hypural plate of the compound centrum (pu_1+u_1) reduced and displaced ventrally. That the bregmacerotid caudal skeleton is nevertheless of the gadiform type is clear from the fact that all basic components are present, viz., a free second ural centrum, an autogenous parhypural, two epurals, a full spine on pu_2, and the gadoid accessory bones between the neural and haemal spines of pu_2 and pu_3. A general account of the Bregmacerotidae was given by d'Ancona and Cavinato (1965).

The muraenolepids, by contrast, have a more normal gadoid skull roof and occipital region, and the caudal skeleton, although reduced, has the characteristic gadoid dorsoventral asymmetry. As in bregmacerotids, a dermal basibranchial plate is present between the first three branchial arches, although it is edentulous (text fig. 49A). The very numerous, rodlike pectoral radials of muraenolepids are not found in other gadiforms, but the jaw muscles closely resemble those of ophidioids and some macrouroids (see p. 425).

The macrouroid fishes are of two general types: those that resemble morids in the jaw mechanism (text fig. 44A), and those with a basically muraenolepid-ophidiid pattern of jaw muscles (text fig. 44B). No attempt has been made to correlate types of jaw musculature with differences in the position of the scapular foramen, the number and type of pectoral radials, or other features that are known to vary within the Macrouroidei. The group appears to us, however, to be far from homogeneous, and we would even go so far at this time as to suggest the possibility that the Macrouroidei contain convergently modified gadoids and ophidioids.

The ophidioids are discussed in some detail above. They form a rather closely knit group of fishes, and even the highly modified carapids show most of the group characters. Emery's (1880) account of carapid osteology is somewhat oversimplified and does not include certain important features, for example, the presence of a well-developed, postmaxillary process of the premaxillary which is notched posteriorly in typical paracanthopterygian fashion. He did illustrate for *Carapus acus*, however, the typical basibranchial tooth plate that is found in many other ophidioids and in muraenolepids and bregmacerotids. Of special interest are his descriptions and figures of the shoulder girdle in *Carapus acus* and *C. dentatus*, in which he noted the presence of a basal cartilage that lies above and parallel with the pectoral radials. This elongate cartilage is in the position of the accessory or fifth radial in members of the batrachoidiform lineage, especially in such forms as *Batrachoides didactylus* and *Gigantactis longicirra* in which that radial is represented entirely as cartilage. The formation of supernumerary pectoral radials in various gadoids and in batrachoidiforms may all very well originate as secondary ossifications of such basal cartilages. In the development of a supernumerary radial, the frequent cases of elongation of the radials, and the development of a ventral, spikelike process of the coracoid, the primary shoulder girdle of ophidioids closely resembles that of batrachoidids and lophiiforms. Various ophidioids also resemble bregmacerotids and merlucciids in the development of greatly expanded transverse processes that are closely associated with the swim bladder. Carapids lack the small supramaxilla and ventral maxillary process of other ophidioids (text fig. 48), but they are the only members of the suborder known to have the peculiar vexillifer larva.

Some zoarcids and macrouroids retain remnants of the typical paracanthopterygian caudal skeleton. In the macrouroid *Trachyrhynchus trachyrhynchus* (N. B. Marshall, personal communication) and in the zoarcid genus *Melanostigma* two offset hypural plates emanating from a single centrum are evident. As noted above, Yarberry (1965) found a representative of *Melanostigma* in which the two hypural plates originated on separate centra, which may be taken as at least an indication that the usual macrouroid and zoarcoid form of the caudal skeleton may have been derived by the loss of the second ural centrum from a more generalized gadiform pattern.

Whether the suborders assembled here (Gadoidei, Muraenolepoidei, Macrouroidei, Ophidioidei, and Zoarcoidei) should be grouped in one, two, or three orders is problematical, and will remain so until more information is available on the over-all morphological diversity in some of the groups and until more is known of their early developmental history, especially of such stages as the vexillifer larva of the ophidioid fishes. For the present, we follow the arrangement of them in a single order, Gadiformes, as proposed by Greenwood, Rosen, Weitzman, and Myers (1966).

FOSSIL GADIFORMS (GADOIDEI, MACROUROIDEI, AND OPHIDIOIDEI)

Fossil gadoids are abundant in the Palearctic Tertiary, especially in the Oligocene and Miocene of Russia and Europe (for general reviews, see Svetovidov, 1948, pp. 32–35; Danil'chenko, 1964, pp. 430–433). In the Maikop beds of the Caucasus (Oligocene-Miocene) studied by Danil'chenko (1947, 1949, 1950, 1953, 1957, 1960), four of the seven living gadoid families are already present: Gadidae (*Raniceps*, *Palaeomolva*), Moridae (*Lotella* [a gadoid, but definitely not *Lotella*; D. M. Cohen, personal communication], *Onobrosmius*), Merlucciidae (*Palaeogadus*, *Merluccius*), and Bregmacerotidae (*Bregmaceros*, *Bregmacerina*). The Melanonidae (*Melanonus*) occur in the Oligocene of the Caucasus and Carpathians (Danil'chenko, 1953), and the Macrouridae (*Hymenocephalus*) have been identified (with some doubt) in the Oligocene of the Carpathians (Gorbach, 1961). The only other records of macrourid skeletons are in the Upper Miocene: *Bolbocara* (Jordan, 1927) in the Lompoc beds of California (see also David, 1943, p. 128), a doubtful record, and *Trichiurichthys* (Sauvage, 1873) from Licata, Sicily. But David (1956) has erected no fewer than 11 new genera of Macrouridae (two in the Bathygadinae, nine in the Macrourinae) on isolated scales from the Oligocene and Miocene of California, Oregon, and Washington. *Eclipes* (Jordan and Gilbert, 1919; Jordan, 1921; David, 1943) from the Miocene of California is a morid, according to Svetovidov (1948) and Danil'chenko (1960), but David's (1943, p. 127) account of the tail suggests that the relationship is distant. Outside the Holarctic Region, the only recorded fossil gadoids from the Oligocene and Miocene are *Bregmaceros* from the Oligocene of Iran (Arambourg, 1967) and otoliths from Australia and New Zealand referred to the Merlucciidae, Gadidae, Bregmacerotidae and Macrouridae (Frost, 1924, 1928, 1933; Stinton, 1957, 1958).

In the Eocene, gadoids are much less common. Skeletal remains recorded include *Bregmaceros* from the Paleogene (Eocene or Oligocene) of the Caucasus (Danil'chenko, 1962; David, 1946a, 1956, has described scales of *Bregmaceros* from the Upper Eocene of California), *Palaeogadus* (Merlucciidae) from the Middle Eocene of Syria (Signeux, 1959), *Rhinocephalus* (Merlucciidae) from the Lower Eocene London Clay (Casier, 1966), and from the basal Eocene Mo-clay of Denmark an undescribed *Rhinocephalus* and fishes with fins resembling those of *Merluccius* (Bonde, 1966). Although skeletal evidence of Eocene gadoids is rare, otoliths have been described in abundance. In southeastern England, for example, the London Clay contains otoliths of *Palaeogadus* and four gadid genera (Stinton, 1966), and the basal Eocene and Paleocene strata below the London Clay contain *Palaeogadus*, six gadid genera, four of which are extinct and absent from the London Clay, and two extinct macrourid genera (Stinton, 1965). We are not qualified to comment on the significance of these otoliths.

The earliest undoubted gadoid is a fish collected by A. Rosenkrantz in the Lower Danian (basal Paleocene) of West Greenland, to be described by Dr. S. E. Bendix-Almgreen, Copenhagen, to whom we are indebted for permission to mention observations made on the specimen in 1967.

The only records of Cretaceous gadoids are Dunkle's description (1958) of isolated scales from the Campanian Blair Formation, Wyoming, as belonging to a new gadid genus, *Paractichthys*, and David's account (1946b) of macrouroid-like scales, *Rankinia*, from the Panoche Formation (Santonian-Campanian) of California. In our opinion these scales

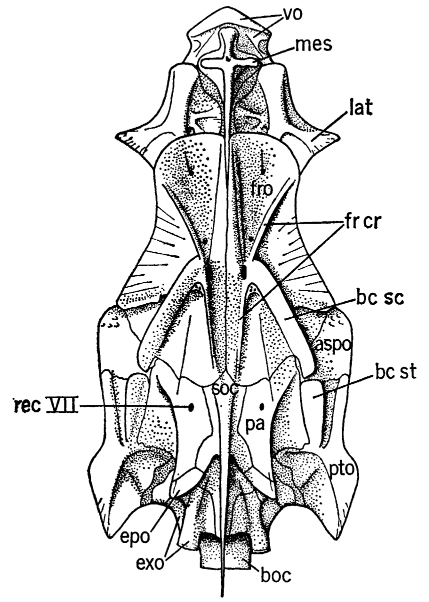

FIG. 50. *Rhinocephalus planiceps* Casier, Lower Eocene, London Clay. Restoration of skull roof, nasals and dermosphenotic omitted.

yield no information useful in the present context.

The Oligocene and Miocene gadoids have been thoroughly dealt with by Danil'chenko. He found (1950) that the widespread merlucciid genus *Palaeogadus* probably included the ancestors of the Gadinae, Lotinae, and *Merluccius*, these groups having branched off in the Oligocene. Within the genus *Palaeogadus*, Danil'chenko found that secular trends can be recognized in at least three lineages, involving increase in the number of vertebrae and median fin rays, decrease in the size and increase in the number of scales, increase in the number of vertebrae supporting caudal fin rays, and decrease in thickness accompanied by increase in the segmentation of the anterior rays of both dorsal fins and the anal fin. He wrote, "In the Lower Oligocene representatives of this genus the anterior rays of the median fins. . .are quite similar in shape to the spiny rays of Beryciformes and Perciformes." These observations are of importance as pointers to the structure of the ancestral gadoids.

The most important of the early fossil gadoids is *Rhinocephalus planiceps* from the Lower Eocene (Ypresian) London Clay, because of its age and because it is known by large, almost uncrushed skulls. Casier (1966, p. 318, pls. 55, 56, text figs. 74, 76) has recently described this species, but further preparation of the material with an "Airbrasive" has brought to light considerable additional information.

Casier described and restored the skull roof of *Rhinocephalus*, but in all the specimens available to him the crests on the frontals and pterotics are severely abraded. In a specimen collected at Sheppey in 1967 by Dr. S. D. Garner of Orpington, Kent (now in his private collection), it has been possible to prepare part of an unabraded skull roof. This shows (text fig. 50) that the crests or flanges that covered the supraorbital and temporal sensory canals on the pterotic and posterolateral part of the frontal are large and extend outward, as in morids and most gadids, giving the "deux étages" structure that Casier (1966, p. 325) thought to be absent from *Rhinocephalus*, as it is from *Merluccius*. The skull roof of *Rhinocephalus* shows many features common to morids, merlucciids, gadids, and macrourids, such as the massive rostral region, with a long, crested mesethmoid, broad lateral ethmoids, and long, troughlike nasals, the open sensory canals, open, shallow posttemporal fossa, supratemporal fossa extending forward onto the frontal, long, low supraoccipital crest, and projecting epiotics and pterotics. The lateral ethmoids of *Rhinocephalus* are in the form of hollow cones, open posteriorly, as in *Merluccius* and gadids. In morids and macrourids the lateral ethmoids are vertical laminae, like those of generalized teleosts. Running forward from the supraoccipital crest there is a pair of crests on the frontals, diverging anteriorly, which enclose a deep, median, mucous cavity between them. The supraorbital sensory canal entered this cavity through a pore at the junction of this crest and the flange covering the posterior part of the canal. Diverging frontal crests of this type are present only in the Merlucciidae among gadoids (Regan, 1903; Marshall, 1966, p. 276), although remnants of the crests are recognizable in macrourids and morids. Similar crests occur in *Sphenocephalus* (text fig. 28).

The neurocranium of *Rhinocephalus* (text

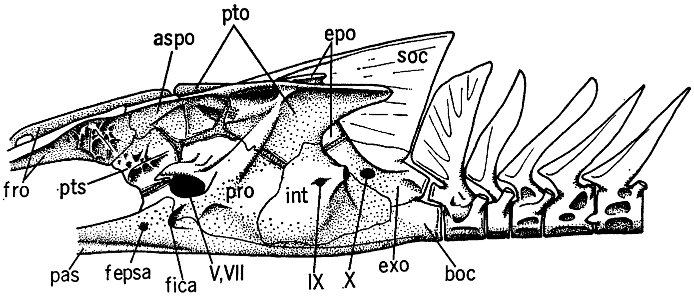

FIG. 51. *Rhinocephalus planiceps* Casier, Lower Eocene, London Clay. Restoration of posterior part of neurocranium and first five vertebrae.

fig. 51) is of typical gadoid form. Gosline (1968, p. 23) wrote: "The most peculiar feature of the Gadiformes is the course of the hyomandibular branch of the facial nerve. In most teleosts. . .the hyomandibular branch and the main trunk of the facialis nerve exit from the cranium by separate openings, . . . the hyomandibular branch enters the medial face of the hyomandibular bone and passes downward within it. In the gadoids. . .the hyomandibular branch has the same cranial exit as the main facialis trunk, after which it swings backward and penetrates the front of the hyomandibular bone." *Rhinocephalus* shows that the reduction and modification of the trigemino-facialis chamber responsible for this gadoid feature were complete in the Lower Eocene. In front of the trigemino-facialis foramen there is a moderately large pterosphenoid, larger than in living macrourids, gadids, and merlucciids but resembling this bone in some morids. The intercalar is very large and contains the glossopharyngeal foramen, as is usual in gadoids. The exoccipital condyles are large and well separated, with the basioccipital condyle projecting beyond them, as in merlucciids and many gadids. The first vertebra is about as long as deep, the second is very short, the third a little longer, and the fourth and succeeding vertebrae longer than deep—a typical gadoid pattern. The first vertebra and neural spine lie close behind the skull, but there is no sign of the fusion that occurs in many gadoids. The first rib inserts on the third vertebra, the third, fourth, and fifth vertebrae bearing short, horizontal, anterolaterally directed ribs (Casier, 1966, pl. 55, fig. 2), as in *Merluccius*. The vertebrae are not known behind the fifth, but presumably

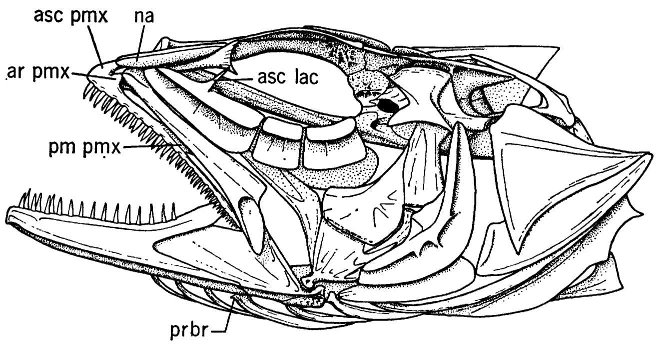

FIG. 52. *Rhinocephalus planiceps* Casier, Lower Eocene, London Clay. Restoration of skull and pectoral girdle. The posterior infraorbitals and supratemporal ossicles (scale bones) are omitted.

the parapophyses were normal, as in *Palaeogadus*, not expanded as they are in *Merluccius*.

The infraorbitals are deep, flimsy bones of normal gadoid type. The elongate lacrimal has a high, splintlike, ascending process, as in *Merluccius* (pl. 72) and percopsiforms.

The jaws have been described by Casier, and are very like those of *Merluccius*, long, with large, enamel-capped teeth, the lower jaw projecting beyond the upper, the premaxilla with a small ascending process, shorter than the articular process, and the maxilla expanded behind the premaxilla. There is no supramaxilla. The postmaxillary process of the premaxilla is large and has a deep notch in its hind margin. There is a deep, pocket-like excavation in the posterior part of the maxilla, as in merlucciids (pls. 71, 72), morids, and gadids. The teeth consist of vasodentine, as in living gadoids (Tomes, 1899). Both the vomer and palatine are toothed; in the toothed palatine *Rhinocephalus* is more primitive than living merlucciids and gadids, but in some morids (*Mora*) the palatine is toothed. The hyomandibular has a posteroventral process articulating with the head of the preopercular, and at the angle of the preopercular there is an anterodorsal process which articulates with the tip of the hyomandibular. The symplectic is expanded dorsally. The preopercular ends well below the pterotic, and there is no notch in the edge of the pterotic above it, indicating that the preopercular sensory canal ended blindly above. All these features of the hyomandibular, symplectic, and preopercular are typically gadoid.

The hyoid bar is long and slender, with no fenestra and no groove on its lateral surface, and the lower hypohyal is enlarged, as usual in gadoids. There are seven branchiostegals, three slender rays articulating with the ventral face of the ceratohyal, and four broad posterior rays articulating with the lateral face of the hyoid bar. There are "percopsoid projections" (McAllister, 1968) on the heads of the first three large posterior rays, as in *Merluccius*.

In the shoulder girdle, there are four sensory canal ossicles overlying the posttemporal fossa in front of the posttemporal, as in other gadoids. There is a spine on the hind edge of the cleithrum, as in *Merluccius*, and the ventral part of the cleithrum is drawn out forward, ending at the level of the mandibular articulation, as in other gadoids. The coracoid is short and slender. In one specimen the pelvic girdle and the base of one pelvic fin are preserved. The girdle resembles that of gadids and that of macrourids, not that of merlucciids, in having medial processes (Gosline, 1963, p. 12), and these processes appear to have met and overlapped in the midline, as they do in percopsiforms. The pelvic fins were inserted below the anterior part of the opercular and must have lain well in front of the pectorals, but there were no direct attachments between the pelvic girdle and the cleithrum. The pelvic fin contains seven rays.

The only scales preserved are those on the operculum in one or two specimens. These scales are small, cycloid, and ovoid, with a central nucleus and strongly marked circuli.

The trunk and fins are not preserved in *Rhinocephalus planiceps*, but in the basal Eocene Mo-clay of Denmark there occur large skulls of an undescribed species of *Rhinocephalus*, together with many complete juvenile gadoids and at least one larger form (Bonde, 1966). In this larger fish the dorsal and anal fins are like those of *Merluccius*, the caudal skeleton (Bonde, personal communication) is like that of *Mora* and *Merluccius*, and the foremost caudal rays are inserted on the neural and haemal spines of the ninth pre-ural centrum, just as in these genera.

The oldest known gadoid is the complete specimen from the Lower Danian (Kangilia Formation) of West Greenland, mentioned above, which is to be described in detail in a forthcoming publication by Dr. S. E. Bendix-Almgreen, of Copenhagen. This fish is about 17 cm. in standard length and is of typical gadoid form. It is slender, with elongate dorsal and anal fins extending back almost to the caudal fin, which has very numerous procurrent rays. The foremost procurrent rays of the dorsal fin lie in front of the eighth pre-ural neural and haemal spines. The distal parts of the dorsal and anal fins are not preserved, but the anal fin appears to be single, and the dorsal fin to be divided into a short anterior portion and a long posterior portion, as in the Merlucciidae. The caudal skeleton is similar to that of morids (text fig. 3D). The skull roof appears to be similar to that of *Rhinocephalus* (text fig. 50), and the premaxilla and lacrimal are like those of *Rhinocephalus* (text fig. 52) and *Sphenocephalus* (text fig. 30). The symplectic and preopercular bones are of gadoid type (see, for comparison, text figs. 9A and 52). The teeth are small, as in morids and macrourids, not enlarged as they are in *Rhinocephalus* and other merlucciids.

The only fossil ophidioid fishes in which the skeleton is known are *Protobrotula sobijevi* (Danil'chenko, 1960), from the Lower Oligocene Maikop beds of the Caucasus, and *Propteridium douvillei* (Priem), from the Oligocene of Elam, Iran (see Arambourg, 1967). *Protobrotula* appears to be an ophidioid, and *Propteridium* is certainly a brotulid (D. M. Cohen, personal communication), but the published descriptions of these fishes do not yield much useful phylogenetic information.

Ophidioid otoliths have been described from the Oligocene and Miocene of Australia and New Zealand (Frost, 1924; Stinton, 1957, 1958; Ophidiidae, Carapidae), the East Indies, and Europe. Eocene ophidiid otoliths are recorded from North America (Frizzell and Dante, 1965, erected three new ophidiid genera for otoliths from the Middle and Lower Eocene of Texas) and Europe (Frizzell and Dante transferred many of the European Eocene species to their new genus *Bauzaia*). In the London Clay Stinton (1966) recorded six living ophidiid genera, and in the Paleocene Thanetian one extinct ophidiid genus (Stinton, 1965). *Carapus* otoliths have been described by Frizzell and Dante in the Middle Eocene of Texas.

We have considered the possibility that *Ampheristus* from the Lower Eocene London Clay, placed in the Scorpaenidae by Casier (1966), is an ophidioid. This fish is known only from the skull, vertebral column, and paired fins. The otoliths are of ophidioid type (Stinton, 1966, p. 456), and many features of the skull, such as the form of the skull roof (Casier, 1966, fig. 77), the large intercalar which is penetrated by the glossopharyngeal nerve, and the occipital condyle (Casier, 1966, fig. 79), are of gadoid or ophidioid structure. The scorpaenids share some of these features, but in *Ampheristus* the parapophyses are expanded, as in ophidioids. The pelvic fins, however, contain a spine and several rays, there appears to be no supramaxilla, the lacrimal is of scorpaenid type, and there are eight branchiostegals inserted on a deep, perforate ceratohyal of beryciform type. In the absence of information on the median fins and caudal skeleton and the presence or absence of an infraorbital-preopercular stay, no final decision is possible.

Apart from the evidence of otoliths that the ophidioids were already numerous and widely distributed in the Lower Eocene, the fossils are of little value in an analysis of the relationships of the Ophidioidei.

No fossil zoarcoids are known.

EVOLUTIONARY TRENDS IN THE GADIFORMES

In the Gadoidei, Muraenolepoidei, and Macrouroidei, the most significant evidence from living forms can be summarized as follows:

1. According to Marshall (1965, 1966), *Melanonus* is more primitive than other living gadoids on the grounds that *Melanonus* is a morid-like fish, but lacks the otophysic connection of morids and has the olfactory lobes at the forebrain.
2. In the caudal skeleton, the most primitive condition is found in morids (text fig. 3D). In jaw musculature, merlucciids show the most generalized condition (pl. 63), combining gadid features (external division of A_1 present) and morid features (midpoint of levator maxillae superioris constricted by a tendon).
3. *Bregmaceros* and *Muraenolepis* are more primitive than other gadoids in retaining a dermal basibranchial plate, toothed in *Bregmaceros* (text fig. 49).
4. The macrouroids are of questionable status, exhibiting a tangle, at present inextricable, of morid, merlucciid, and ophidioid features.
5. *Muraenolepis* is distinct from the morids, merlucciids, and gadids, resembling the ophidioids in many ways.
6. *Bregmaceros* is sharply distinguished from other gadoids by features of the skull and caudal skeleton, which is dorsoventrally symmetrical

and carries caudal fin rays only on five or six vertebrae (not three or four, as Danil'chenko, 1960, wrote).

On paleontological evidence, Danil'chenko (1960) concluded that the Moridae are "probably the oldest family" of the Gadoidei, because of the variety of morids in Oligocene rocks. But the variety of Oligocene morids is reduced by the removal of *Melanonus* to a separate family (Marshall, 1965), and the diagnostic feature of the Moridae, the otophysic connection, must exclude the family from the ancestry of other gadoids. Danil'chenko's conclusion must also be modified because of subsequent discoveries of merlucciids in Eocene and Paleocene rocks; apart from *Bregmaceros* in the Upper Eocene, the only gadoids known from skeletons in the Eocene are merlucciids. Danil'chenko found that the Eocene-Oligocene merlucciid *Palaeogadus* could have given rise both to living merlucciids and to gadine and lotine gadids. In turn, the Lower Eocene *Rhinocephalus* could well have been ancestral to *Palaeogadus*, and, as is shown above, it exhibits several morid and macrourid characters that are absent from later merlucciids and gadids. *Rhinocephalus* is already, however, aligned with gadids and later merlucciids by such specializations as the shape of the lateral ethmoids, the marginal dentition, the occipital condyle, and the anterior ribs, and for this reason the morid and macrourid lines must be as ancient as *Rhinocephalus*. But the Lower Paleocene gadoid from West Greenland, which resembles *Rhinocephalus* in many ways and has a merlucciid fin pattern, has a type of organization that might be expected in the common ancestor of both the morid-macrourid and the merlucciid-gadid lineages.

The distinctive features of *Bregmaceros* are perhaps not of great phylogenetic importance, since Danil'chenko (1960) found that the Lower Miocene bregmacerotid *Bregmacerina* suggested a link between this family and the Moridae, resembling the latter in several ways, especially in having the caudal fin rays extending forward to the twelfth vertebra.

Muraenolepoids have no fossil record, and we cannot evaluate the significance of the characters in which the single living genus differs from gadoids.

The combination of the neontological and paleontological evidence on gadoid and macrouroid interrelationships thus indicates that there are two principal lineages—merlucciid-gadid and morid-macrourid (in part)—the second probably including bregmacerotids, whereas the muraenolepoids are of uncertain relationships. The basal Eocene merlucciid *Rhinocephalus* shows that those two lineages must have been separate in the Paleocene, the basal Paleocene fish from Greenland lying near the common stem of the two. The common ancestor of gadoids and muraenolepoids must therefore have been a Cretaceous fish exhibiting the following characters: a moderately elongate trunk, probably containing about 40 vertebrae with 12 abdominal (the Greenland fish has a few more caudals); short ribs from the third vertebra; long dorsal and anal fins, approaching but not confluent with a forked caudal fin having many procurrent rays extending over eight to 10 vertebrae; the dorsal fin with a partially or completely separate anterior portion, the first one or two rays of which were spinous (as in many macrourids and merlucciids); the caudal skeleton with five autogenous hypurals, a single uroneural and one pair of accessory bones in front of the second pre-ural neural and haemal spines; the pelvic fins lying close behind or below the pectorals [the abdominal position of the pelvics in the merlucciid *Lyconodes* (Marshall, 1966, p. 277) is presumably secondary] and containing seven rays; the skull roof and neurocranium resembling those of *Rhinocephalus* (text figs. 50–52); the cephalic sensory canals not bone-enclosed except for the posterior part of the supraorbital canal, where it passes below the main frontal crest, the RLA of Freihofer's (1963) pattern 7; the olfactory lobes at the forebrain; the exoccipital condyles prominent; the first vertebra enlarged and carrying Baudelot's ligament, the second very short; the lacrimal with an ascending process; the gape large, with no supramaxilla and a deep notch behind the postmaxillary process of the premaxilla; the premaxilla, dentary, vomer, palatine, and basibranchials bearing small teeth; the ceratohyal shallow and carrying seven branchiostegal rays, with "percopsoid projections" on the first three external rays; the opercular scale-covered and with a spine; the subopercular large; and the scales probably cycloid.

If we turn now to the Ophidioidei and Zoarcoidei, the only conclusion to be drawn from fossils is that the occurrence of the distinctive ophidioid type of otolith in the Paleocene suggests that the group is as ancient as the Gadoidei. This conclusion is supported by the features in which living ophidioids are more primitive than any known gadoid: the presence of a lateral commissure and a supramaxilla and the absence of accessory bones from the caudal skeleton. The postulated common ancestor of Gadiformes must therefore have existed in the Cretaceous, and there is at present no good evidence against the hypothesis that this fish differed from the ancestral gadoid constructed above only in having a lateral commissure, a supramaxilla, no caudal accessory bones, and the caudal fin confined to the last three or four vertebrae. The ophidioids agree with gadoids in many of the characters assigned to this fish (distribution of dentition, "percopsoid projections," and branchiostegal and vertebral count), but there is no evidence in ophidioids of a divided dorsal, an ascending process on the lacrimal, a forked tail, or the original condition of the skull roof.

As a possible Cretaceous ancestor of the Gadiformes, Danil'chenko (1960) suggested the Cenomanian *Protobrama*, which resembles gadoids in the elongate dorsal and anal fins, separated by a short gap from a caudal fin occupying 10–12 vertebrae. But subsequent study of *Protobrama* (Patterson, 1967b) has shown that this fish is a highly specialized relative of the Plethodontidae and can have no relationship to the Gadiformes. There is no known Cretaceous fish showing any sign of the characteristic specializations of the Gadiformes, possibly because of the boreal Atlantic origin of the group (Svetovidov, 1948, developed this conclusion only for the gadoids and muraenolepoids, but it is not contradicted by the distribution of fossil and living ophidioids and zoarcoids and is supported by the absence of any gadiform from the very large Eocene Tethyan fauna known from Monte Bolca). The occurrence of the earliest gadoid in Greenland is also significant in this connection. It is likely that exploration of the almost unknown marine vertebrate fauna of the Cretaceous of Greenland and Arctic Canada will provide evidence of early gadiforms. But in the absence of such Cretaceous fossils, adequate evidence on the origin of gadiforms can be derived from a comparison between living and fossil gadiforms and percopsiforms, tabulated below.

Resemblances between percopsiforms and gadiforms are:

1. Among the characters of living percopsiforms listed on page 380, gadiforms agree in 1 (lms muscle), 2 (adductor arcus palatini fills floor of orbit except in *Melanonus*), 5 (anterior part of supraorbital canal open), 6 (orbitosphenoid and basisphenoid absent, except perhaps for a remnant of the basisphenoid in the zoarcoid *Melanostigma*; Yarberry, 1965), 8 (intercalar large), 9 (exoccipital condyles large and distinct, except in *Bregmaceros*), 10 (lacrimal with ascending process in generalized gadoids), 11 (no subocular shelf), 12 (upper jaw similar), 14 (palatine toothed in primitive gadiforms), 16 (basibranchial teeth in ophidioids and *Bregmaceros*), 17 (Baudelot's ligament to first vertebra in gadoids and zoarcoids), 18 (epineurals absent), 20 (full neural spine on pu_2), 21 (upper hypurals fused with u_2, except in some gadoids), 22 (upper and lower postcleithra fused in most gadoids; Svetovidov, 1948; ?ophidioids), 25 (a single supraneural, but more than one in some ophidioids).
2. Earliest percopsiforms marine, gadiforms marine.
3. Skull roof very similar in earliest percopsiforms (text fig. 28) and gadiforms (text fig. 50).
4. Olfactory lobe at olfactory organ in most gadoids and in *Percopsis*.
5. A remnant of the external division of the adductor mandibulae present in gadids, merlucciids, and percopsids.
6. One supramaxilla in the earliest percopsiforms (*Sphenocephalus*) and in ophidioids.
7. "Percopsoid projections" on all four external branchiostegals in *Sphenocephalus* and on the first three in ophidioids and merlucciids.
8. Pterosphenoid-parasphenoid contacts develop in amblyopsids, gadoids, and ophidioids.
9. A deep notch behind the postmaxillary process of the premaxilla in *Sphenocephalus*, gadoids, and ophidioids.
10. Opercular scale-covered, excavated dorsally, and with a spine in generalized percopsiforms and gadiforms.
11. Pelvic girdle not directly attached to cleithrum, pelvics with seven rays in generalized percopsiforms and many gadoids.

12. Anus jugular in aphredoderoids, some gadoids, and ophidioids.

Ten out of the 20 differences listed in table 8—3 (antorbital), 5 (endopterygoid teeth), 6 (ectopterygoid teeth), 7 (ceratohyal), 11 (hypurals), 12 (uroneurals), 13 (caudal rays), 16 (adipose fin), 18 (pelvic position), and 19 (pelvic splint)—are due only to the loss of primitive characters in gadiforms. More significant is the fact that these features are almost identical with those separating the Beryciformes and the Perciformes (except for the absence of an adipose and pelvic splint from the Beryciformes, and the persistence of endopterygoid and ectopterygoid teeth and a second uroneural in some of the Perciformes). Of the remaining differences, 4 (loss of serrations on dermal bones), 10 (parhypural), 14 (loss of fin spines), and 20 (loss of ctenii on scales) involve changes that also occur during percopsiform evolution (see p. 407) and are therefore to be expected in the transition between primitive percopsiforms and gadiforms. Character 8 (the branchiostegal count) seems to be the only one in which percopsiforms are more advanced than gadiforms, excluding known percopsiforms from the direct ancestry of gadiforms and enabling one to recognize them as a monophyletic unit. Characters 9 (vertebral number), and 15 and 17 (dorsal and anal fins), are the essential differences between the two orders; these rather profound

TABLE 8

Differences Between Gadiformes and Percopsiformes

		Percopsiformes	Gadiformes
1	Supratemporal fossa	Not developed, except possibly in *Sphenocephalus*	Well developed in gadoids
2	Supraoccipital crest	Short	Long in gadoids
3	Antorbital	Present except in aphredoderoids	Absent
4	Lacrimal, infraorbitals, and preopercular	Serrated except in advanced forms	Smooth
5	Endopterygoid	Toothed in *Sphenocephalus* and *Aphredoderus*	Toothless
6	Ectopterygoid	Toothed	Toothless
7	Ceratohyal	Deep, perforate, with tooth plates on upper margin in primitive forms	Shallow, imperforate, not toothed
8	Branchiostegals	6	Primitively 7
9	Vertebrae	Primitively 12+16–18	Primitively 12+*ca.* 30
10	Parhypural	Autogenous, articulates with centrum in primitive forms	Free in gadoids, fused with lower hypurals in ophidioids[a]
11	Hypurals	Primitively 6	Primitively 5
12	Uroneurals	Primitively 2	Primitively 1
13	Branched caudal rays	16	No fixed number, fewer in ophidioids, more in gadoids
14	Fin spines	D IV-V, A V in *Sphenocephalus*	D I-II in macrourids and merlucciids, no anal spines
15	Dorsal fin	About 15 rays	Many rays
16	Adipose fin	Present in *Sphenocephalus* and percopsoids	Absent
17	Anal fin	About 12 rays	Many rays
18	Pelvic fins	Well behind pectorals	Below or in front of pectorals
19	Pelvic splint	Present	Absent
20	Scales	Ctenoid except in amblyopsids	Cycloid except in macrourids

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[a] But see Monod (1968, figs. 714, 715).

changes in the external form of the fish, although certainly correlated with changes in the mode of locomotion, cannot yet be satisfactorily explained in functional terms.

The conclusions to be drawn from these comparisons are that the gadiforms are very closely related to the percopsiforms, and originated from a Cretaceous fish resembling *Sphenocephalus* but with seven branchiostegals, primarily by elongation of the trunk and median fins, accompanied by reduction of spination in the dermal bones, scales, and median fins. Subsequent evolutionary trends in gadiforms apparently were associated with a reduction of the caudal region (macrourids and morids) and a shortening of the caudal axis by vertebral subtraction (gadids; see discussion above, p. 420).

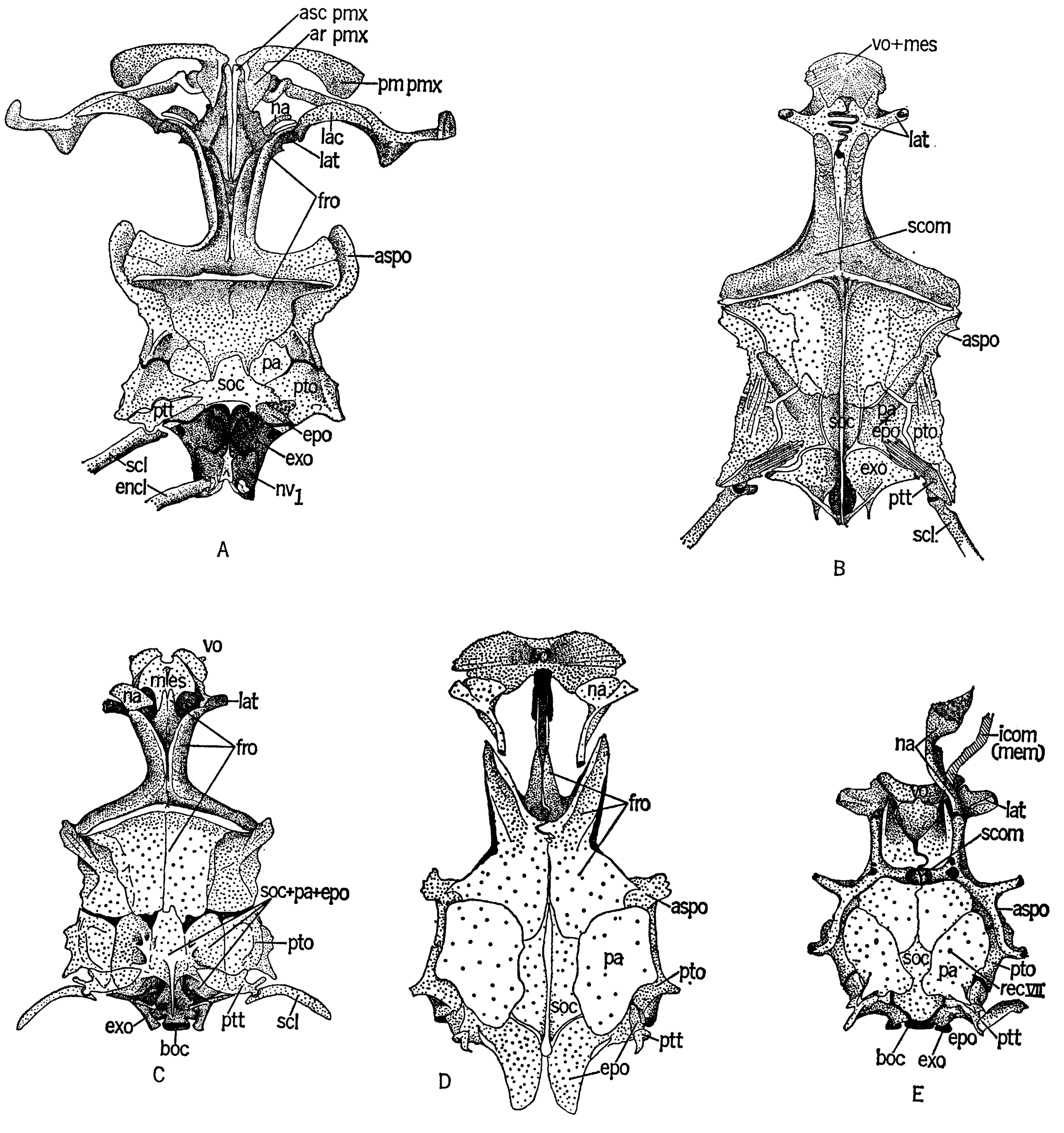

FIG. 53. Dorsicranium in members of the batrachoidiform lineage. A. *Thalassophryne megalops* Bean and Weed. B. *Opsanus beta* (Goode and Bean). C. *Porichthys porosissimus* (Cuvier). D. *Histrio histrio* (Linnaeus). E. *Gobiesox funebris* Gilbert.

THE BATRACHOIDIFORM LINEAGE (BATRACHOIDIFORMES, LOPHIIFORMES, AND GOBIESOCIFORMES)

The original alignment of the lophiiforms with the batrachoidiforms was proposed by Regan (1912); and of the gobiesociforms with the batrachoidiforms, by Starks (1905). That evidence was summarized by Greenwood, Rosen, Weitzman, and Myers (1966). In spite of the seemingly trivial bases on which the original allocations were made, for example, Starks's comparison of the gobiesociform adhesive disc with the adhesive egg plate of batrachoidiforms, the three groups can be shown to be tied together by a host of shared anatomical specializations. These may conveniently be listed, as follows (refer to pl. 78, and text figs. 4, 9, 10C, 53–59), with the understanding that the comparisons generally do not take into consideration the more bizarrely modified ceratioid fishes or the lophiids. The lophiiform characters listed below have been drawn from the antennarioid fishes and the less-specialized of the closely related ceratioids.

1. Skull roof greatly flattened.
2. Supraorbital commissure present and broadly continuous with supraorbital lateral-line canal, in a deep-walled groove (batrachoidiforms) or in bone-enclosed canals (gobiesociforms).
3. Anterior margins of frontals sharply or bluntly pointed and diverging, dorsally concave, and housing supraorbital lateral-line canals.
4. Parietals present, large and superficial in gobiesociforms and lophiiforms, and variable in size and shape and separate, fused with the epiotics, or fused with the epiotics and supraoccipital in batrachoidiforms.
5. Posttemporal greatly reduced in size and without an ossified lower arm.
6. Vomer broad anteriorly and notched medially in gobiesociforms, lophiiforms, and generalized batrachoidiforms.
7. Parasphenoid sutured anteroventrally to frontals in batrachoidiforms and lophiiforms, with broad lateral extensions that approach frontals in gobiesociforms.
8. Sphenotics very large and flaring forward and laterally in all groups.
9. Intercalar absent.
10. Exoccipital condyles distinct, well developed, and arising lateral to the basioccipital condyle.
11. Infraorbital series represented only by lacrimal.
12. Levator maxillae superioris muscle present in batrachoidiforms (text fig. 55) and most lophiiforms.
13. Ascending process of premaxilla very well developed (text fig. 56).
14. Marked trend in reduction of pterygoid

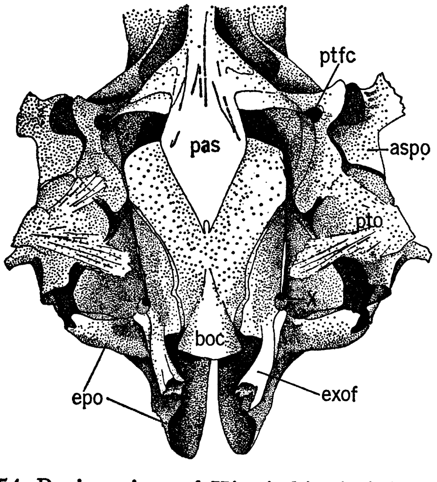

FIG. 54. Basicranium of *Histrio histrio* (Linnaeus).

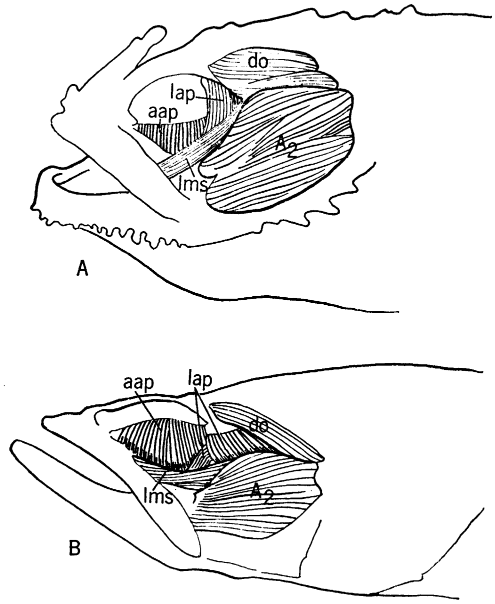

FIG. 55. Diagrammatic representation of superficial jaw musculature in batrachoidids. A. *Opsanus tau* (Linnaeus). B. *Porichthys porosissimus* (Cuvier).

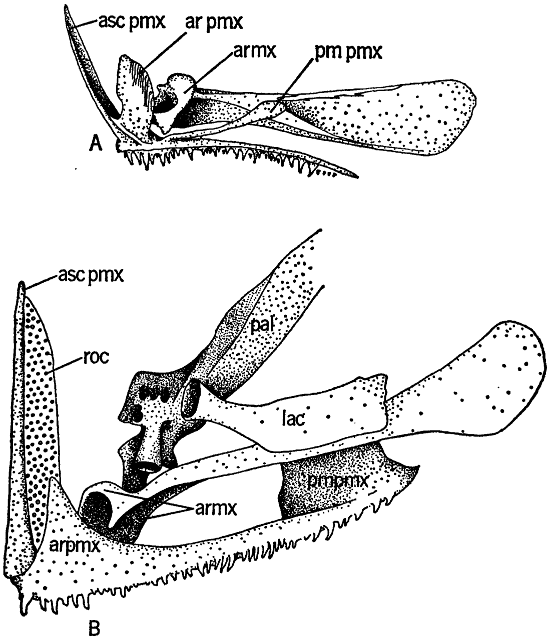

FIG. 56. Upper jawbones. A. *Histrio histrio* (Linnaeus). B. *Porichthys porosissimus* (Cuvier).

ossifications, as follows: failure of endopterygoid to ossify completely in some batrachoidiforms; severe reduction of all pterygoid bones and fusion of metapterygoid with hyomandibular in lophiiforms; loss of all pterygoid bones in gobiesociforms (text fig. 9).

15. Ankylosis of hyomandibular with preopercular in batrachoidiforms and some lophiiforms, or joining of the two bones by interdigitating suture in gobiesociforms.

16. Upper hypohyal elongate and extending backward over dorsal surface of ceratohyal (text fig. 57) (lower hypohyal probably fused with upper in gobiesociforms; McAllister, 1968).

17. Some or all of the four large, posterior branchiostegals cylindrical in cross section along part of their length.

18. Branchiostegals six in number in batrachoidiforms, generalized lophiiforms, and gobiesociforms.

19. Upper end of preopercular well below upper edge of hyomandibular.

20. Posterior margin of opercular deeply excavated in batrachoidiforms and lophiiforms (shallowly excavated in gobiesociforms).

21. Subopercular very long and slender and extending backward and upward to posterior tip of opercular in batrachoidiforms and lophiiforms.

22. Reduction of basibranchial ossifications (in batrachoidiforms) or their loss (in lophiiforms and gobiesociforms) (text fig. 58).

23. Elongation of anterior hypobranchials.

24. Conjunction, without ankylosis, of third and fourth epibranchials.

25. Caudal skeleton with two hypural plates, parhypural fused with lower, with a neural spine on pu_2, and with two epurals in batrachoidiforms and some lophiiforms (epurals are reduced to one or to none in some lophiiforms and in gobiesociforms).

26. Pectoral radials elongate, lowermost in-

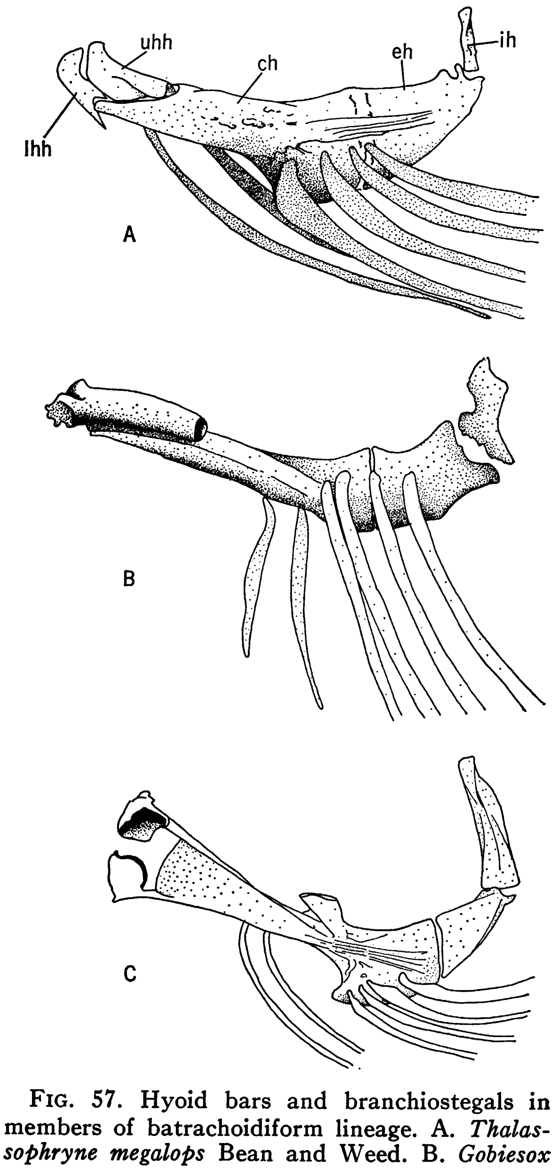

FIG. 57. Hyoid bars and branchiostegals in members of batrachoidiform lineage. A. *Thalassophryne megalops* Bean and Weed. B. *Gobiesox funebris* Gilbert. C. *Histrio histrio* (Linnaeus).

variably enlarged, five in number in batrachoidiforms (in *Batrachoides didactylus*, upper radial slender and cartilaginous), two to five in number in lophiiforms (when five, in *Gigantactis longicirra*, upper radial cartilaginous as in *B. didactylus*), apparently five in gobiesociforms (apparent upper fifth radial fused with scapula) (text fig. 59).

27. Coracoid with a posteroventral prong that, in batrachoidiforms and lophiiforms, is tipped with cartilage.

28. Pelvic fin preceded by a concealed, minute, spinelike ray.

29. Pelvic rays reduced in number and thickened, or lost.

30. An anterior spinous dorsal in some batrachoidiforms and lophiiforms.

31. Caudal fin truncate or rounded, with a greatly reduced ray number.

32. Scales absent or small and embedded.

The three groups differ in a number of features concerned with feeding and locomotion. Most evident are the "lure" apparatus of the lophiiforms and the ventral adhesive organ of the gobiesociforms. The gobiesociforms exhibit also an extreme condition of dorsoventral flattening of the head and body which has very much modified the orientation and, to some extent, the shape of bones in the jaw suspension and opercular apparatus. The jaws of gobiesociforms are also somewhat simplified in terms of the number of maxillary and premaxillary processes, and the teeth and direction of the gape seem to be adapted principally to the cutting and scraping of short adherent vegetation. Presumably most of their peculiarities as a group are closely related to their ecological preferences for regions characterized by rapid water exchange, such as the intertidal zone and steeply descending freshwater streams. Perhaps the almost complete bony covering of their cephalic lateral-line canals is also related to life in rapidly moving water.

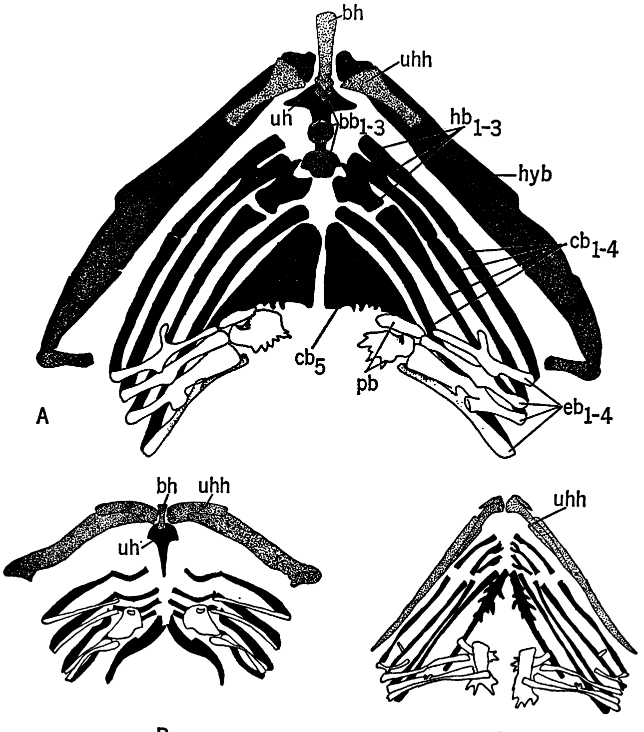

FIG. 58. Pharyngobranchial apparatus in members of the batrachoidiform lineage. A. *Thalassophryne megalops* Bean and Weed. B. *Gobiesox funebris* Gilbert. C. *Histrio histrio* (Linnaeus).

Among lophiiforms the absence of a supraorbital lateral-line commissure is probably related to the migration during ontogeny of the illicial and postillicial fin components onto the head. Among scorpaeniform fishes, a similar loss of the temporal commissure and the separation of the parietals in which the commissure runs are related to the migration of the spinous dorsal onto the temporal region. Whereas lophioids have lost the postmaxillary process of the premaxilla, that process has become enormously developed in antennarioids (text fig. 56B) and some ceratioids. The postmaxillary process in many cases takes the form of a spatulate or oblanceolate process on a long, posteriorly directed pedicel. We are aware of the development of a postmaxillary process of this sort elsewhere among fishes only in some macrourids. Most of the major specializations of lophiiforms concern the feeding mechanism which, in general, is adapted to the taking in of exceedingly large prey. Presumably the hyperdevelopment of the grasping and swallowing apparatus is related to the migration of the gill opening backward to the postaxillary position. The principal method of feeding, perhaps the exclusive one, among lophiiforms is indicated by the presence of the "lure." The predator remains more or less stationary and attracts prey to it. Such behavior is probably more true of lophiids and some antennarioids than it is of ceratioids, for the ceratioid shoulder girdle appears to be of a fairly normal type. The pectoral girdle of lophiids is greatly modified in accordance with extreme flatness of body, and that of some antennarioids in accordance with the development of a prehensile apparatus or of a "walking" mechanism in the wholly benthonic types.

Some important differences among the batrachoidiforms, lophiiforms, and gobiesociforms concern the jaw muscles and caudal skeleton. Among batrachoidiforms and antennarioids the levator maxillae superioris system of maxillary control is fully developed. Among ceratioids it is variously reduced or modified, but the modifications of their cheek muscles are similar to those of the more specialized zoarcoids and macrouroids, viz., the superficial part of the adductor mandibulae is reduced or virtually eliminated to expose most or all of the levator maxillae superioris. In contrast, the adductor mandibulae is enlarged, and often complexly folded, and the levator maxillae superioris completely absent, in the extremely flattened lophiids and gobiesociforms. In both of these cases in which the levator maxillae superioris is wanting, the maxilla is without direct muscular control, its action depending instead on its mechanical connections with the mandible. The adductor mandibulae serves only the lower jaw (see Field, 1966).

The caudal skeleton of lophiiforms and gobiesociforms (Monod, 1968, figs. 806, 843, 844) differs from the generalized paracanthopterygian condition primarily in having u_2 fused with pu_1+u_1 and thereby in having

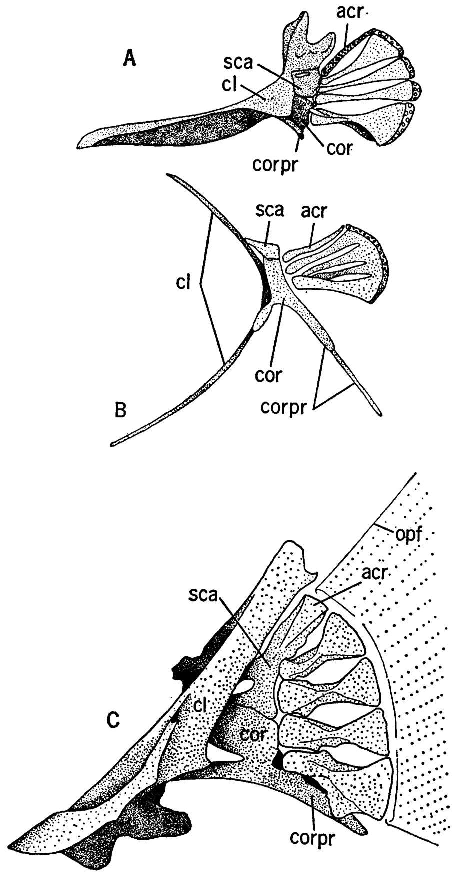

FIG. 59. Shoulder girdle in members of the batrachoidiform lineage. A. *Batrachoides didactylus* (Bloch and Schneider), after Monod (1960). B. *Gigantactis longicirra* Waterman, after Waterman (1948). C. *Gobiesox funebris* Gilbert.

the two hypural plates emanating from a single, complex half-centrum (text fig. 4E, F). In view of the large number of other similarities between these two groups and the batrachoidids it would seem reasonable to assume that the single centrum support arose from a dual centrum of the type seen in batrachoidids. Both lophiiforms and gobiesociforms show a type of parhypural fusion characteristic of batrachoidids, both have a neural spine on pu_2, and neither has more than two epurals.

The reductional trends in both jaw muscles and in the caudal skeleton are in general very similar to the comparable reductional trends that occur within the gadiform lineage.

Fossil evidence bearing on the problem of batrachoidiform, lophiiform, and gobiesociform relationships is almost non-existent. No fossil gobiesociforms have yet been recognized, and the single batrachoidiform so far identified, from the Lower Pliocene of Algeria, is placed in the living species *Batrachoides didactylus* (Arambourg, 1927).

Apart from isolated teeth and jawbones referred to *Lophius* (without good reason), the only fossil lophiiforms known are *Lophius brachysomus* Agassiz, from the Middle Eocene of Monte Bolca, Italy, *Lophius budegassa* Arambourg (1927), from the Lower Pliocene of Algeria, and *Histionotophorus bassanii* (de Zigno) from Monte Bolca. *Lophius brachysomus* is known only from the type specimen, in Paris, and has not been redescribed since Agassiz' work. It appears, however, to be a genuine lophiid, and, according to Arambourg (1927, p. 216), it is close to the Indo-Pacific *Lophiomus*. *Histionotophorus bassanii* was briefly redescribed by Eastman (1904), who placed it in the Lophiidae. Gill (1904), on the basis of Eastman's figures, considered the fish to be an antennariid, close to or even to be included in *Pterophryne.* Eastman (1905) replied that in antennariids there are three pectoral radials, whereas *Histionotophorus* has only two, as in lophiids. Tate Regan, in a manuscript note with the British Museum (Natural History) specimen of *Histionotophorus*, compared it with the Australian antennarioid *Brachionichthys* (Brachionichthyidae), which has only two pectoral radials and also has the second and third dorsal spines connected by membrane throughout their length, as in *Histionotophorus* (pl. 76, fig. 2). In *Histionotophorus*, however, there are only 18 vertebrae and 13 soft dorsal rays, compared with 23 vertebrae and 15–20 soft dorsal rays in *Brachionichthys* (Regan, 1912, p. 283). The caudal skeleton of *Histionotophorus* (text fig. 60) is extremely specialized in having no epurals, and in this respect and the presence of only two pectoral radials (cf. Monod, 1960, fig. 80) the fish is certainly more advanced than the antennariids, which must therefore have been in existence before the Middle Eocene. This conclusion, that the Lophiiformes are of considerable antiquity, is all that can be gained at present from the fossils.

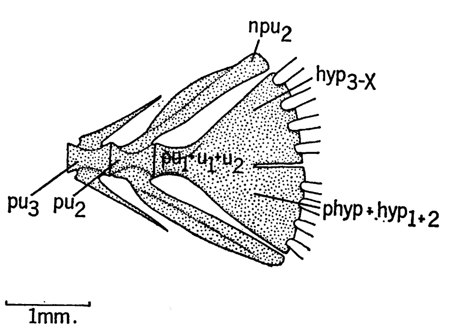

FIG. 60. *Histionotophorus bassanii* (de Zigno), Middle Eocene, Monte Bolca, Italy. Caudal skeleton, based on B.M.N.H. No. P.19060.

In any consideration of the relationships of the batrachoid lineage (Batrachoidiformes, Gobiesociformes, Lophiiformes), the first question that must be answered is whether the existing evidence favors an alignment within the Paracanthopterygii or the Acanthopterygii. To consider the second possibility first, it is immediately apparent that the batrachoidids bear a striking superficial resemblance to various acanthopterygians, namely, to the trachinoid perciforms and to the Scorpaeniformes. As an example of the fallacy of deriving one Recent group from another, it can be quickly established that living batrachoidids could not have given rise either to trachinoids or scorpaeniforms. For example, no batrachoidid has more than two epurals in the caudal skeleton, and a subocular shelf is lacking on the infraorbital bones. Trachinoids and scorpaeniforms usually have three epurals, and the generalized members of those groups have a normal acanthopterygian subocular shelf. The question can be reversed to ask if batrachoidids could themselves have been derived from some similar acanthopterygian group, as had long been supposed. Again a negative answer is easily given. In trachinoids and scorpaeniforms, as in all perciforms and derivative groups, the first pre-ural and the first and second ural centra are consolidated into a single half-centrum unit which supports the parhypural and all hypural bones. In batrachoidids, the upper hypurals are fused to the reduced second ural centrum which maintains a definite intervertebral joint with the combined first ural and pre-ural centrum carrying the lower hypurals and the parhypural. This condition is certainly more primitive and could not have been derived from the trachinoid, scorpaeniform, or perciform condition. A more reasonable question than either of the above is whether batrachoidiform and scorpaeniform fishes could have come from a common early acanthopterygian ancestor in which the second ural centrum had not yet fused with the preceding element and in which there was a low crest on the second pre-ural centrum, and three epurals. From such a hypothetical ancestor the scorpaeniforms could have arisen simply by fusion of the second ural centrum (u_2) with the preceding pu_1+u_1. Batrachoidiforms could have followed a somewhat different course and have retained u_2 while fusing the anteriormost epural with the low crest on pu_2 to give the characteristic paracanthopterygian pu_2 neural spine. Although neural spines, when formed in this way in perciforms, generally leave a visible suture or some other structural sign of epural fusion, the change may have been very old and the imprint of its origin obliterated. The batrachoidids could also have lost the subocular shelf and the anal and pelvic spines which a hypothetical common ancestor might have been expected to possess. The batrachoidids and scorpaeniforms show many similarities, however, in the possession of venom glands, a horseshoe-shaped swim bladder with drumming muscles (only in scorpaenids among scorpaeniforms), and a levator maxillae superioris muscle (only in cyclopterids among scorpaeniforms). Also favoring a common ancestry of these groups is the occurrence in the reduced pelvics of batrachoidids of a minute, embedded, first, spinelike element (text fig. 43F), an asymmetry in the two scorpaeniform hypural plates that suggests derivation from a two-centrum hypural support, a reduced number of caudal rays, and the presence of an endocleithrum-like epineural rib on the first vertebra of a few scorpaenids (see Greenwood, Rosen, Weitzman, and Myers, 1966, pp. 391–392). The answer to the question of a possible common descent of the two groups is clearly affirmative, if allowance is made for individual group specializations in the hyobranchial apparatus, fin structure, infraorbital and roofing bones, and upper jawbones to arise in one or the other assemblage.

As against the above conclusion that batrachoidids and scorpaeniforms could have had a common ancestor, there is no evidence that precludes batrachoidid derivation from somewhere near the stem of the Gadiformes and Percopsiformes. In the case of the second hypothesis, and the one advocated in this study, the structural specializations that would be required to differentiate the three main paracanthopterygian groups are: flattening of the dorsicranium and loss of the intercalar in batrachoidids; reduction of pelvic number and the formation of a minute, embedded, spinelike element in batrachoidids and ophidioid gadiforms; increase in the number of pectoral radials in batrachoids and many gadiforms; reduction in caudal peduncle depth and caudal ray number in batrachoidids and in some gadiforms; elongation of the anterior hypobranchials in batrachoidids and gadiforms; conjunction of the third and fourth epibranchials and development of cylindrical posterior branchiostegals in batrachoidids; development of jugular pelvics in batrachoidids and gadiforms and of a mental barbel in gadiforms; contrasting specializations of the swim bladder in batrachoidids and gadiforms; loss of the pelvic splint in batrachoidids and gadiforms; and loss of the antorbital bone and the adipose fin in all groups except percopsids. The peculiar bunched appearance of the anterior abdominal vertebrae in batrachoidids and gadiforms, and the invariable occurrence of special features of the jaws, jaw suspension, opercular apparatus, the levator maxillae superioris system of maxillary control, and, in the caudal skeleton, of a full spine on pu_2, no more than two epurals, and a separate u_2 that becomes fused with the upper hypurals in batrachoidiforms, gadiforms, and percopsiforms, provide additional reasons for regarding the three groups as members of a monophyletic group. Also noteworthy is the large number of parallelisms evident in the batrachoidid and gadiform lineages. We cannot, of course, summarily dismiss the idea of convergence and polyphyly, but at this time the concept of the Paracanthopterygii as a monophyletic group seems to us to be the interpretation that is simplest and most consistent with the sum of the presently known evidence.

The features that relate the members of the gadiform and batrachoidiform lineages are as follows:

1. Supraorbital part of frontal with a deep groove for cephalic lateral-line canal.
2. Frontals fused into an undivided plate in some members of both groups.
3. Parasphenoid suturally united to frontals in batrachoidiforms and some gadiforms.
4. Exoccipital condyles laterally displaced on each side of basioccipital condyle.
5. Alveolar process of premaxilla in many cases greatly reduced or absent.
6. Postmaxillary process with a notch posteriorly in gadiforms and in antennarioids and ceratioids; greatly elongate and spatulate in some macrouroids, antennarioids, and ceratioids.
7. Levator maxillae superioris muscle well developed.
8. Opercular reduced, usually deeply excavated posteriorly; subopercular large, forming most of distinctly angular gill cover and extending upward and backward to posterodorsal tip of opercular.
9. Basibranchial copula greatly constricted anteroposteriorly, gill arches converging on a relatively short span.
10. Anterior hypobranchials much longer than posterior element.
11. Anterior vertebrae extremely crowded and joined together via overlapping prezygapophyses and postzygapophyses, their pungent neural spines slightly diverging.
12. Caudal skeleton in all generalized forms consisting of a separate u_2 bearing upper hypurals and a complex pu_1+u_1 carrying lower hypurals, uroneural greatly reduced or wanting; with two epurals, and with a full neural spine on pu_2.
13. Branched caudal fin rays not exceeding 16 in number, reduced to 11 or fewer in most cases.
14. Caudal peduncle rather shallow, especially near caudal fin base.
15. Pectoral radials in numerous cases more than four in number.
16. Pelvic fin rays reduced in number and greatly thickened and closely segmented in ophidioids, zoarcoids, some gadoids, and in batrachoidiforms.
17. Median fins long and many-rayed; confluent with caudal or joined to caudal by a membrane in various members of both lineages.
18. Scales usually greatly reduced, embedded, or absent.

THE RELATIONSHIPS OF THE PARACANTHOPTERYGII

THE EVIDENCE PRESENTED ABOVE points to the conclusion that the paracanthopterygians are a monophyletic group which originated in Cretaceous seas and of which the most primitive members are the percopsiforms. The ancestral paracanthopterygian must therefore have had the following primitive characters which occur in percopsiforms: a free second ural centrum, six autogenous hypurals, two uroneurals, a forked caudal fin, an adipose fin, a pelvic splint, an antorbital, endopterygoid teeth, a deep, perforate ceratohyal with tooth plates[1] on the upper margin, a large tooth plate on the basibranchials, and Baudelot's ligament to the first vertebra. The advanced characters that would enable one to recognize this ancestral form must include the presence of (or evidence of potentiality to develop): a full neural spine on the

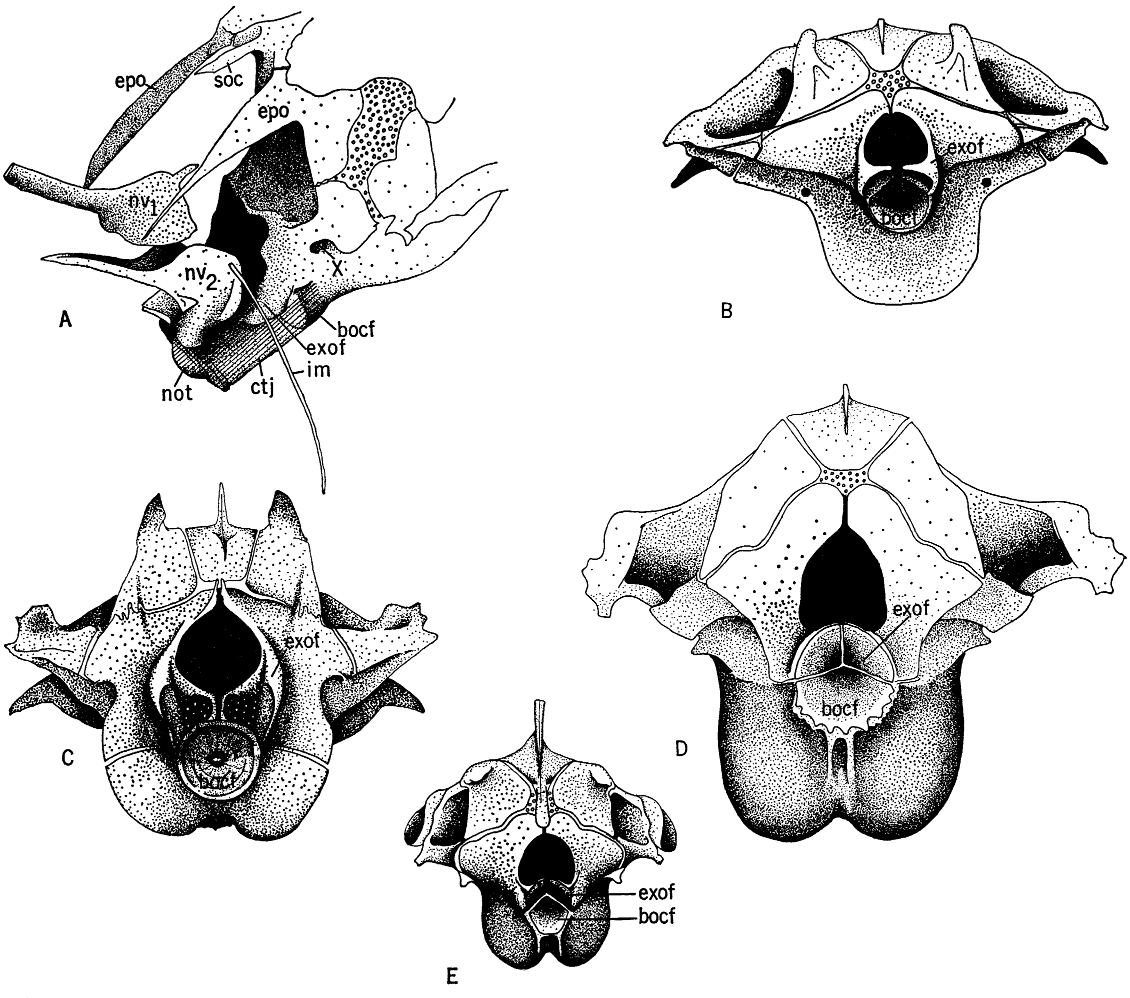

FIG. 61. Occipital region of neurocranium, showing form of the basioccipital and exoccipital facets. A, C. *Neoscopelus macrolepidotus* Johnson. B. *Aulopus japonicus* Günther. D. *Myctophum affine* (Lütken). E. *Polymixia lowei* Günther.

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[1] Ceratohyal tooth plates, an ascending process on the lacrimal, and a "gadoid notch" behind the postmaxillary process are not known to occur in any of the groups that are here compared with paracanthopterygians, and are not mentioned in these comparisons.

second pre-ural centrum, reduction of the number of epurals to two and of branched caudal rays to 16, about five dorsal and anal fin spines, subthoracic pelvics, the pelvic girdle articulated with the lower postcleithrum or lying close to it, an ascending process on the lacrimal, a notch behind the postmaxillary process of the premaxilla, only one supramaxilla, a deep subdivision of the adductor mandibulae muscle (the levator maxillae superioris) inserting on the maxilla near the maxillo-palatine articulation, and well-defined exoccipital condyles. Features of the jaws that are present in all paracanthopterygians, the exclusion of the maxilla from the gape and the presence of ascending and articular processes on the premaxilla and of crossed ligaments joining the maxilla and premaxilla to the ethmoid and palatine, limit the area in which close relatives of the primitive paracanthopterygians are to be sought to other primitive groups exhibiting those specializations (myctophoids, polymixioids, berycoids) or the potentiality to develop them (ctenothrissoids). Before the evidence for relationship between paracanthopterygians and each of these groups is discussed, it is perhaps necessary to emphasize that at the level at which any direct relationships exist, among extremely generalized Cretaceous fishes, very few characters will serve as decisive evidence of relationship, and even these may be of limited value because of lack of knowledge of the relevant fossil forms.

If the polymixioids be taken first (represented by one living genus, a few Tertiary fossils, and half a dozen Cretaceous genera), they have all the primitive characters of the ancestral paracanthopterygian (an antorbital occurs in all three living species of *Polymixia*) except for the adipose fin and pelvic splint. In respect to the advanced characters of percopsiforms, they have the neural spine on pu_2, the 16 branched caudal rays, the dorsal and anal fin spines, subthoracic pelvics, and

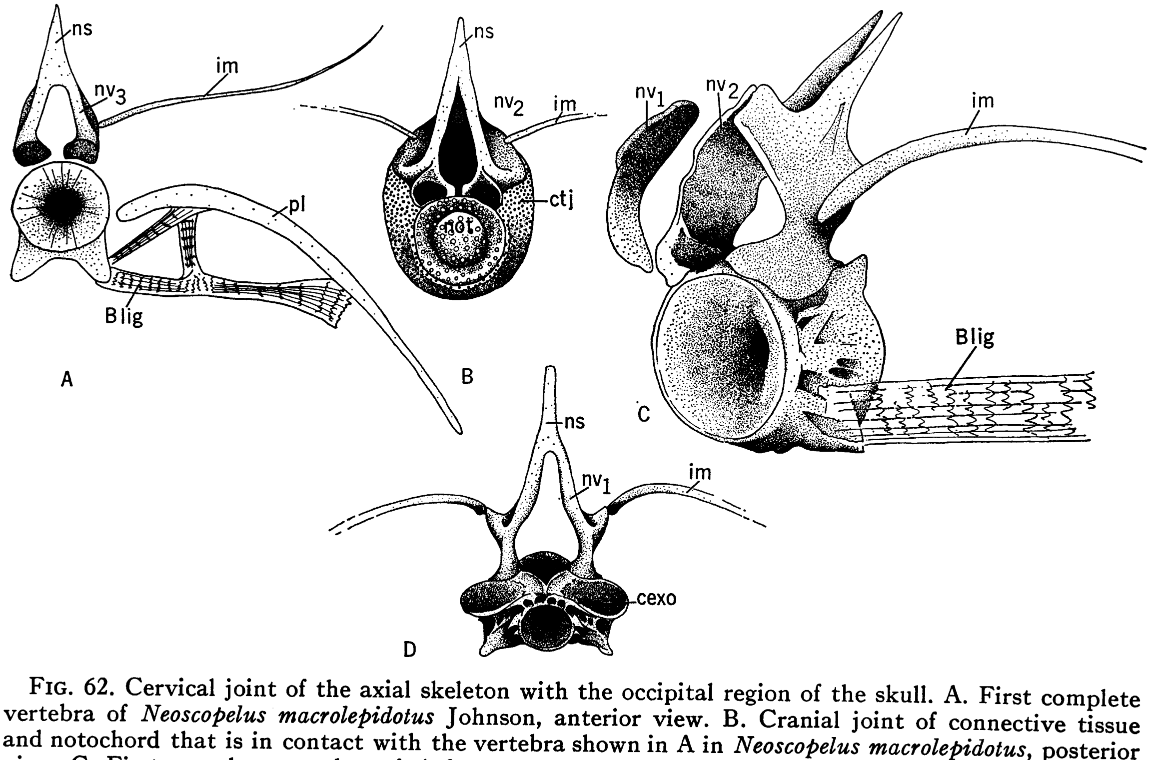

FIG. 62. Cervical joint of the axial skeleton with the occipital region of the skull. A. First complete vertebra of *Neoscopelus macrolepidotus* Johnson, anterior view. B. Cranial joint of connective tissue and notochord that is in contact with the vertebra shown in A in *Neoscopelus macrolepidotus*, posterior view. C. First complete vertebra of *Aulopus japonicus* Günther that is in contact with a narrow connective tissue cranial joint under the first neural arch (nv_1) of which only the right half is illustrated, anterior three-quarter view. D. First vertebra of *Aphredoderus sayanus* (Gilliams), in anterodorsal view.

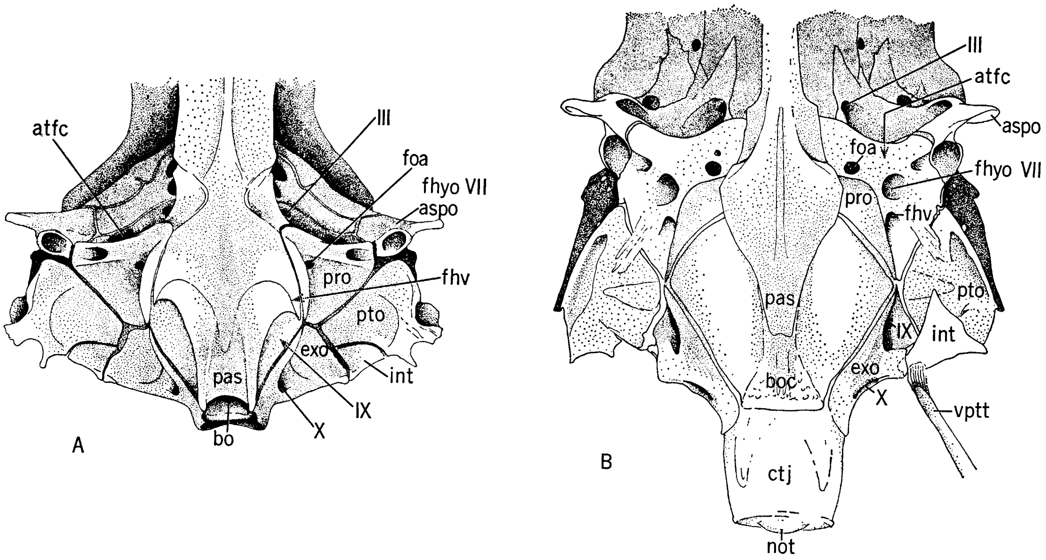

FIG. 63. Basicranium in myctophoids. A. *Aulopus japonicus* Günther. B. *Neoscopelus macrolepidotus* Johnson.

they have a muscle somewhat resembling the levator maxillae superioris (pl. 53). They invariably have the primitive three epurals, so far as is known they have two supramaxillae (in some Cretaceous forms only one has been seen, possibly owing to imperfections of the material), and the occipital condyle is a simple circular structure with a central pit (*Polymixia*, text fig. 61E) or has the exoccipital condyles very slightly differentiated (*Berycopsis*, *Homonotichthys*; Patterson, 1964, figs, 26, 37). Further differentiating the polymixioids from the paracanthopterygians is the occurrence of a primitive type of subocular shelf on all the infraorbitals, and of three predorsals, characters that link them with the acanthopterygians (p. 406). Finally, there is the probability that a large pelvic spine, another acanthopterygian feature, has developed in polymixioids, since such a structure is present in two Cretaceous genera, *Dinopteryx* and *Pycnosteroides*, which are known to differ from the Polymixiidae only in this character and are here provisionally aligned with the polymixioids (see p. 418).

In comparing the Myctophoidei with basal paracanthopterygians, we are handicapped by lack of knowledge of the interrelationships of the wide range of forms at present included in this group. In the most recent treatment of the group (Gosline, Marshall, and Mead, 1966), two lineages were distinguished, the "alepisauroid inioms" (Paralepididae, Anotopteridae, Alepisauridae, Omosudidae, Scopelarchidae, Evermannellidae) and "myctophoid inioms" (Aulopidae, Synodontidae, Bathysauridae, Harpadontidae, Bathypteroidae, Ipnopidae, Chlorophthalmidae, Myctophidae, Neoscopelidae, Scopelosauridae). The alepisauroids are slender, elongate fishes, characterized by absence of the swim bladder, reduction in ossification of the skeleton, and reduction in the squamation. They are thought to have originated, through the scaled paralepidids, from near the Chlorophthalmidae. The alepisauroid characters mentioned above, and others, such as the absence of teeth from the pterygoids, show that the alepisauroids can have no connection with the problem of paracanthopterygian origins and they are not mentioned herein again. The "myctophoids," as envisaged by Gosline, Marshall, and Mead, contain a basal group, the aulopids, which gave rise to two lineages, one containing the synodontids, bathysaurids, and harpadontids (all slender fishes, without supramaxilla or pterygoid teeth), and one containing the six remaining families. These families in turn are regarded as comprising three lineages diverging from chlorophthalmid-like ancestors: the bathypteroid lineage (Bathypteroidae and Ipnopidae, slender, deep-sea fishes, with the eyes reduced, without swim bladder or pterygoid teeth, the adipose fin absent except in *Bathypterois*), the Scopelosauridae (slender, without swim bladder or pterygoid teeth), and the myctophid lineage (Myctophidae and Neoscopelidae). Clearly, the only myctophoids that need to be considered in a comparison with generalized paracanthopterygians are the four most generalized families—the Aulopidae, Chlorophthalmidae, Myctophidae, and Neoscopelidae.

It appears to us that the Aulopidae, Chlorophthalmidae, and Neoscopelidae form a related group in which the last two families are the more specialized. The peculiar cervical joint of the Chlorophthalmidae and Neoscopelidae (text figs. 61–63) is present in a somewhat simpler form in the aulopids. Whereas synodontids and harpadontids appear to be still further specializations of the aulopid lineage, the consolidation of the upper jawbones being their most notable feature, the Myctophidae seem to us to be well separated from all the other myctophoid groups examined here. They are distinctive in the great lateral compression of body, the occasional presence of median fin spines, the spiny operculum (text fig. 64), the peculiar appearance of the epurals (text fig. 2C), the presence of a levator maxillae superioris muscle (pl. 55) and subocular shelf (text fig. 11), and especially in the primitive condition of the occipital condyle as a tripartite structure with a central pit (text fig. 61D) as in *Polymixia* (text fig. 61E) and in the specimens of *Salmo* and *Hiodon* that we have examined. The members of the aulopid and myctophid lineages have had a long independent history; all four families can be recognized in the Cretaceous (Aulopidae: *Nematonotus*, *"Sardinioides" illustrans*; Chlo-

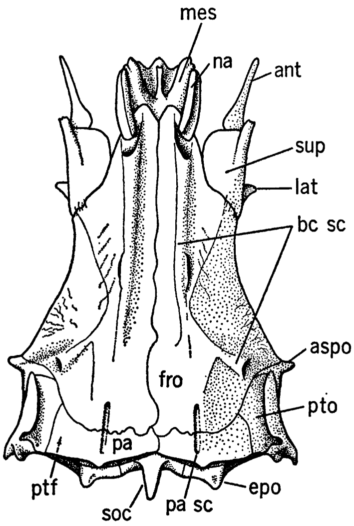

FIG. 65. *Nematonotus longispinus* Davis, Cenomanian, Hajula, Lebanon. Restoration of skull roof.

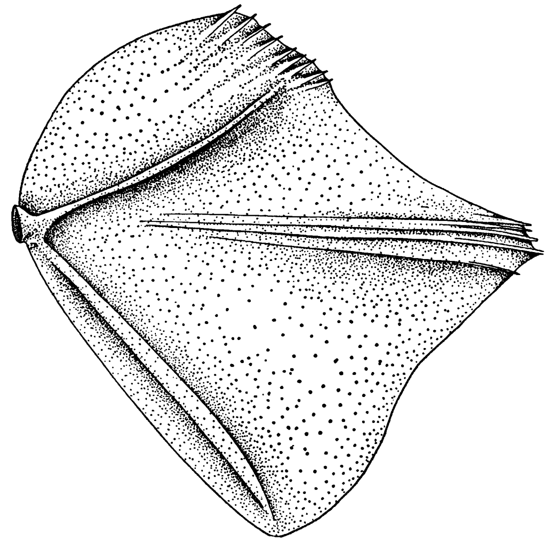

FIG. 64. Opercular of the myctophid *Diaphus theta* Eigenmann and Eigenmann, showing the sinuous and dentate posterodorsal margin.

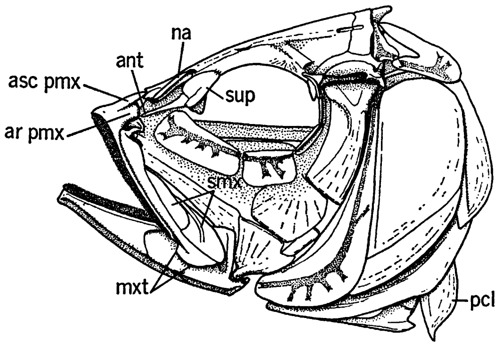

FIG. 66. *Nematonotus longispinus* Davis, Cenomanian, Hajula, Lebanon. Restoration of skull and pectoral girdle.

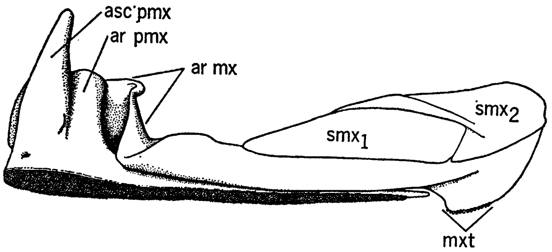

FIG. 67. *Nematonotus longispinus* Davis, Cenomanian, Hajula, Lebanon. Restoration of left upper jaw.

rophthalmidae: *Acrognathus*; Neoscopelidae: *Sardinioides*; Myctophidae: *Sardinius*). In order to gain some idea of the primitive condition in this group, we have prepared preliminary reconstructions of the Cenomanian *Nematonotus longispinus* (text figs. 1, 65–69). This fish resembles *Aulopus* (text fig. 70) in the extremely primitive architecture of the skull roof, with small, flat parietals in contact medially and carrying a parietal branch of the supraorbital canal (the anterior pit-line), a fully roofed posttemporal fossa, a large supraorbital and antorbital, two large supramaxillae (text fig. 67), and large caudal scutes (text fig. 1). It is, however, more primitive than *Aulopus* or any other living myctophoid in having a small patch of teeth on the posterior expansion of the maxilla, the first uroneural forked proximally (as in *Elops*, *Alepocephalus*, and *Clupavus*), and a urodermal (as in *Elops*, *Coregonus*, *Osmerus*, and *Argentina*, text fig. 71, alone among living teleosts). Also, the pectorals of *Nematonotus* are inserted very low on the flank, as in alepisauroids, which in this feature seem more primitive than aulopids. *Nematonotus*, although specialized in the elongate third dorsal ray and the thickened, closely segmented anterior rays of the paired fins, is therefore the most primitive myctophoid known. The hyoid bar of *Nematonotus* (text fig. 69) is imperforate, but seems to exhibit the basic acanthopterygian pattern (Hubbs, 1919) in the deepening of the posterior part of the ceratohyal and the enlarged bases and lateral position of the last four (of 10) branchiostegals. In *Aulopus* (text fig. 72)

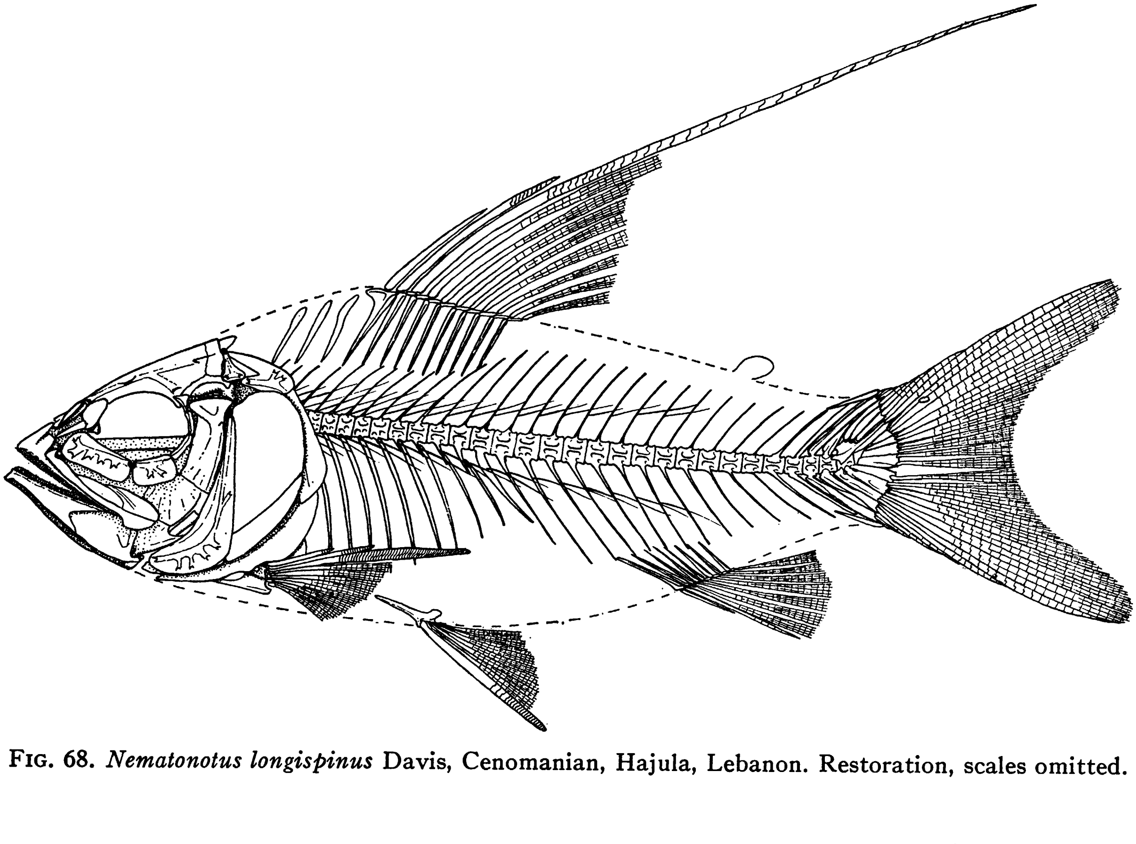

FIG. 68. *Nematonotus longispinus* Davis, Cenomanian, Hajula, Lebanon. Restoration, scales omitted.

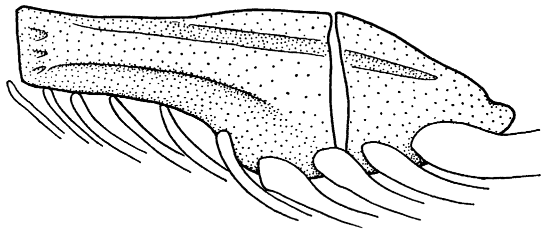

FIG. 69. *Nematonotus longispinus* Davis, Cenomanian, Hajula, Lebanon. Left hyoid bar and branchiostegals, restored from B.M.N.H. No. P. 47514.

there are about 15 branchiostegals, the last few rays being more slender than their predecessors, thus reversing the normal (and primitive) condition of progressive increase in size of the branchiostegals from front to rear.

Despite the presence of maxillary teeth, which is not surprising in view of Berry's (1964) discovery that larval *Scopelosaurus* have an extensive maxillary dentition, the heads of the maxilla and premaxilla in *Nematonotus* (text fig. 66) are highly advanced, the premaxilla with a high ascending process and an articular process embraced by the lateral part of the maxillary head. The swim bladder is absent or greatly reduced in living aulopids and chlorophthalmids, but there is no reason to believe that such was the case in the more generalized Cretaceous forms.

With this background on myctophoid structure and interrelationships, we can now compare generalized myctophoids with the most primitive paracanthopterygians. Myctophoids exhibit all the primitive characters found in paracanthopterygians except one, the perforation of the ceratohyal. Advanced paracanthopterygian characters found among myctophoids include the development of a levator maxillae superioris (in Myctophidae; pl. 55), the tendency to lose the anterior supramaxilla (present in Aulopidae only), and the development of large, separate, exoccipital condyles, especially in the Neoscopelidae (Gosline, Marshall, and Mead, 1966, fig. 5; present paper, text fig. 62B). This development appears to be associated with the support of a flexible tubular structure of connective tissue and unrestricted notochord that is interpolated between the occiput and the first fully developed vertebra. A very similar structure is present also in chlorophthalmids, and a slightly developed

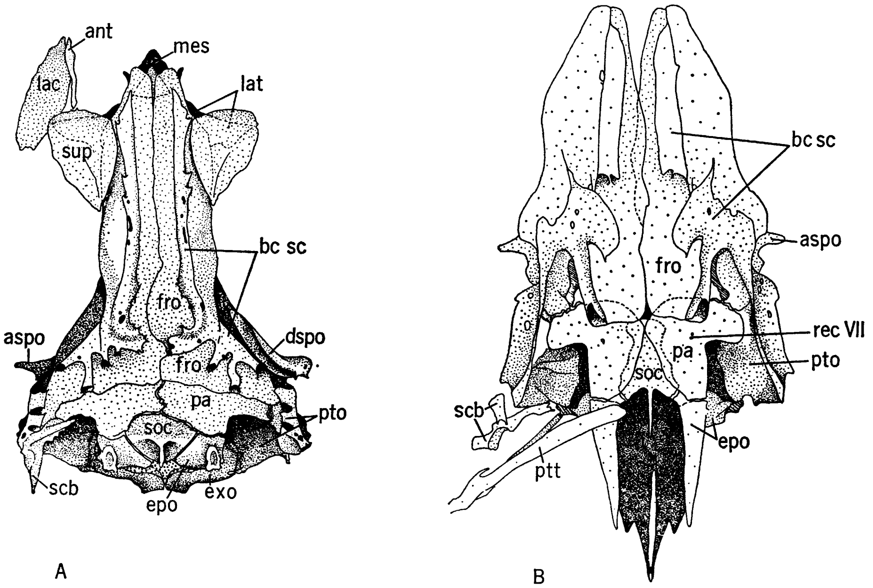

FIG. 70. Dorsicranium in myctophoids. A. *Aulopus japonicus* Günther. B. *Neoscopelus macrolepidotus* Johnson, lacrimal, antorbital, and supraorbital omitted.

form of this non-osseous cervical joint is present in aulopids (text fig. 62). It is clear from the presence in the cervical region of neoscopelids of two free neural arches and spines above the notochordal joint that at least two cervical centra have been lost. It is true, of course, that this non-osseous joint is a specialization probably associated with increased cranial mobility in these wholly predatory groups, but its early development may have been associated with the full differentiation of separate, laterally displaced, exoccipital facets that characterize the flexibly jointed crania of the generalized predatory paracanthopterygians (note the great similarity in the first vertebral joint of neoscopelids and aphredoderids, text fig. 62, and see discussion of feeding mechanisms, above). In the caudal skeleton, myctophoids retain the primitive 19 caudal rays and the short neural spine on pu_2, in many cases expanding this into a plate (text fig. 2). Where an apparent second pre-ural neural spine occurs in myctophoids, as in the specimen of *Saurida brasiliensis* illustrated in text figure 2H, it is produced by fusion of the second and third pre-ural centra. Advanced myctophoids do tend, however, to reduce the number of epurals to two, as in synodontids (Hollister, 1937; present paper, text fig. 2G), and even in aulopids the first epural may be very small (text fig. 2B). The second ural centrum fuses with the preceding centrum, not the upper hypurals, in advanced forms (text fig. 2C, H). Further evidence of the advanced structure of some myctophoids is the occurrence of a single dorsal and anal spine in at least one species of the myctophid genus *Lampanyctus*, and the presence in all the myctophid genera examined of a well-developed subocular shelf on all the infraorbitals, as in polymixiids and holocentrids (text fig. 11). The pelvic fins of myctophoids may be inserted relatively close behind the pectorals, but the pelvic girdle does not seem to articulate with the postcleithrum (short in most myctophoids), as it does in percopsiforms, polymixioids, and primitive berycoids.

The berycoids are represented by about 10 living families, two of which, the Trachichthyidae and Holocentridae, extend back into the Cretaceous and intergrade there. The most generalized members of this group, Cretaceous genera such as *Lissoberyx* and *Caproberyx* (Patterson, 1967a), do not have an adipose fin, a pelvic splint, basibranchial, or endopterygoid teeth—primitive characters present in early percopsiforms. Endopterygoid teeth occur, however, in living *Monocentris*. Advanced basal paracanthopterygian features present in berycoids include a similar pattern of spines in the median fins and subthoracic pelvics (but invariably with a spine). Berycoids retain the primitive 19 caudal rays, as do myctophoids. The second pre-ural neural spine in berycoids is primitively short and becomes further reduced during evolution. In a single specimen of *Monocentris* (Patterson, 1968b, fig. 14), a full neural spine is developed. There are invariably three epurals, and, in advanced forms, the second ural centrum fuses with the preceding centrum, not with the upper hypurals. There is no sign of a levator maxillae superioris or anything resembling it in berycoids, and the exoccipital condyles are undifferentiated or only slightly distinct (text fig. 10E).

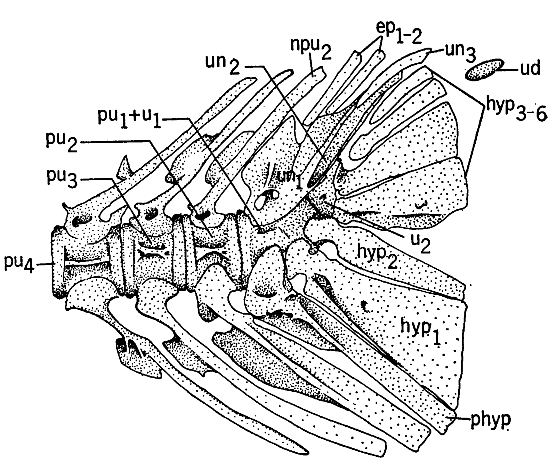

FIG. 71. Caudal skeleton of *Argentina striata* Goode and Bean.

The ctenothrissoids are represented by only three Cretaceous genera, *Ctenothrissa*, *Aulolepis*, and *Pateroperca*, the last very incompletely known. They differ from generalized paracanthopterygians (and resemble the berycoids) in having no adipose fin (all available specimens examined), but exhibit all the other primitive characters of these fishes. In the caudal skeleton, *Ctenothrissa* and

Aulolepis agree with primitive myctophoids, having caudal scutes and a short neural spine on the second pre-ural centrum, but *Pateroperca* (in the one specimen showing these structures) has a full neural spine, as in polymixioids and paracanthopterygians (Patterson, 1968b, figs. 1–5). There are three epurals in all. Ctenothrissoids are without fin spines, have two large supramaxillae, and the exoccipital condyles undifferentiated (*Ctenothrissa*) or feebly developed (*Aulolepis*). Myological evidence, of course, is lacking.

Finally, it is perhaps necessary to compare the lampridiforms with primitive paracanthopterygians, since these fishes develop a similar upper hypural structure (Gosline, 1961a) and seem to be related to the polymixioids and berycoids rather than to any higher group. The lampridiforms, represented today by a series of highly modified forms of which *Velifer* is the least specialized, can be traced back through basal Eocene forms (Bonde, 1966) to the Lower Paleocene *Bathysoma*, and seem to have originated from near the Cretaceous fishes *Aipichthys* and *Pharmacichthys* (Patterson, 1968b, p. 97), which can well be included in the order. Detailed osteological evidence is lacking for many lampridiforms, especially the fossil forms, but so far as is known they differ from primitive paracanthopterygians in having no adipose fin, no pelvic splint, unmodified occipital condyles, a short or reduced second pre-ural neural spine, three epurals, 19 principal caudal rays (except in trachipteroids and stylephorids, which have greatly reduced tails), and no levator maxillae superioris muscle.

To express these comparisons in terms of formal taxonomy is no easy task. The traditional "string-of-beads" concept, criticized by Gosline (1961a), is easily applied, leading to the arrangement of the major groups under consideration in the sequence Myctophoidei-Paracanthopterygii-Polymixioidei-Berycoidei, with the Ctenothrissoidei to be placed probably next to the myctophoids, the lampridiforms between the polymixioids and berycoids. In such a sequence the progressive loss of primitive features such as the adipose fin and pelvic splint and the acquisition of advanced characters such as median and pelvic fin spines are easily demonstrated. But one of the main conclusions to be drawn from recent work on teleost phylogeny is that such an approach is valueless and doomed to failure. What we find is a mosaic

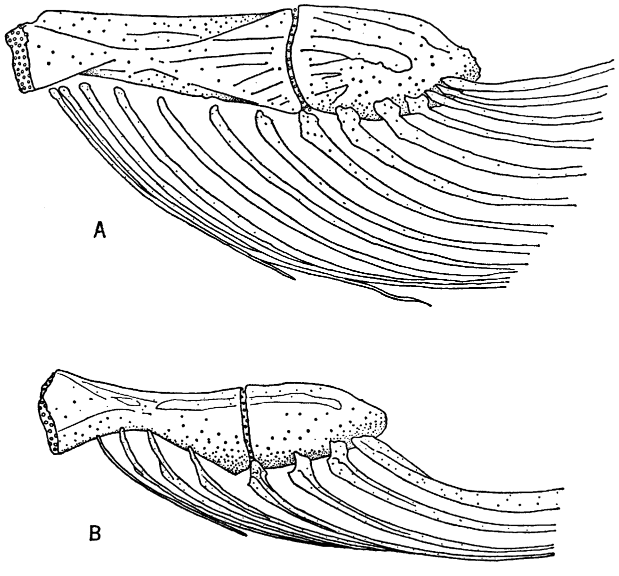

FIG. 72. Hyoid bar and branchiostegal rays in myctophoids. A. *Aulopus japonicus* Günther. B. *Chlorophthalmus agassizi* Bonaparte.

of primitive and advanced features, the first lost and the second acquired in different lineages in a pattern that can be disentangled in a number of ways depending on the weight attached to the various characters. We may start from the proposition that the fishes under consideration comprise three major radiations (a myctophoid radiation, a paracanthopterygian radiation, and an acanthopterygian radiation), each of which can be traced back to Cretaceous fishes of very generalized type. The distinction among these radiations is blurred by the discovery in each of characters previously thought to be characteristic of others and by the occurrence of small groups, of equal antiquity, not easily included in any one of these main radiations: the ctenothrissoids, intermediate in many ways between myctophoids and berycoids; the polymixioids, intermediate between paracanthopterygians and acanthopterygians; the lampridiforms, intermediate between polymixioids and acanthopterygians; and the paradoxical asineopids.

The myctophoid lineage includes fishes that are the most primitive of the whole complex. There seems to be only a single advanced character that unites all the known forms and enables one to recognize the lineage—the shallowing and loss of the fenestra in the ceratohyal (text figs. 69, 72). The myctophoids can then be envisaged as a series of radiations from very primitive, aulopid-like fishes. Their resemblances to paracanthopterygians (levator maxillae superioris in myctophids, exoccipital condyles in neoscopelids, two epurals in synodontids) and to acanthopterygians (subocular shelf and the median fin spines of some myctophids) must have arisen independently within the myctophoids. These parallel developments are therefore evidence of relationships with paracanthopterygians and acanthopterygians which emphasize the advanced level reached by some branches of the myctophoid radiation, but do not indicate that paracanthopterygians originated from myctophoid fishes.

The enormous acanthopterygian radiation has its basis in berycoid-like fishes, characterized by advanced features in the caudal skeleton (reduction of the second pre-ural neural spine), pelvic fins (a large spine), and the skull (absence of basibranchial teeth, development of a subocular shelf), as well as by negative features such as the loss of the adipose fin and pelvic splint and the absence of a levator maxillae superioris, which differentiate them from the paracanthopterygians at their first appearance.

The polymixioids can be distinguished by two advanced characters, the subocular shelf and three predorsals, which relate them to the acanthopterygians, and by three negative characters, the loss of the pelvic splint and adipose fin (presumably a

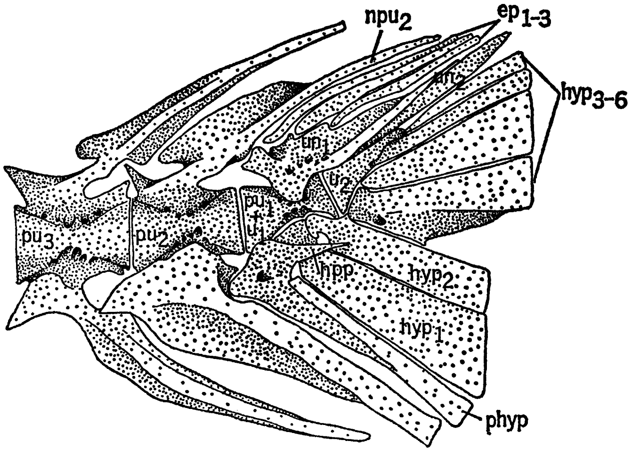

FIG. 73. Caudal skeleton of *Polymixia lowei* Günther.

consequence of elongation of the dorsal fin) and absence of a true levator maxillae superioris. A further link with the acanthopterygians is perhaps provided by the development of a pelvic spine within the group, in *Dinopteryx* and *Pycnosteroides*. There seems to be nothing else to distinguish the polymixioids from the early percopsiforms. Although the polymixioids appear in the fossil record some 10 million years before the percopsiforms, there is no possibility that any fish strongly resembling a Cretaceous or Recent polymixioid was the common ancestor of the paracanthopterygians, since all known polymixioids have elongate median fins and can have had no adipose fin. The fact that we have had to make the necessary search to confirm this statement is sufficient indication of the existence of a close relationship between percopsiforms and polymixioids. The question to be answered is whether the evidence of relationship between percopsiforms and polymixioids [caudal skeleton differing only in the loss of one epural (text fig. 73), caudal fin with 16 branched rays, and an attempt at a levator maxillae superioris] is of greater or lesser significance than the evidence of relationship between polymixioids and acanthopterygians (subocular shelf, predorsal bones, parallel development of a pelvic spine). Our opinion is that, although the caudal specializations linking polymixioids and percopsiforms are unique, those characters that link polymixioids and acanthopterygians consist of one feature also developed in myctophids (subocular shelf), one parallel development (pelvic spine), and one of dubious significance (predorsal bones; the difficulty of distinguishing between these and supraneurals is discussed above, p. 380), and that therefore the polymixioids can tentatively be viewed as the closest relatives of the paracanthopterygians.

The Lampridiformes are probably an ancient lineage, because *Aipichthys*, the most primitive member, is more primitive than either berycoids or polymixioids in the caudal skeleton and fin (Patterson, 1968b, p. 87), and the lineage can at present be recognized by only one advanced character, "hypurostegy" of the caudal rays, other characters (absence of an adipose, pelvic splint, and subocular shelf) being found in neighboring groups. Trends followed during the evolution of the group such as fusion of the upper hypurals with the second ural centrum (as in paracanthopterygians), reduction of the second pre-ural neural spine to a low crest, and development of thoracic pelvics and numerous fin spines in some forms (all as in acanthopterygians), reduction in the dentition, specialization of the jaws, and the bizarre modifications of the trunk and fins in stylephorids and trachipteroids, provide no coherent picture of parallel development with other groups, and at present we can only place them between the polymixioids and berycoids, having no good reason to align them more closely with one than the other.

The problem of the position of the ctenothrissoids is to be solved with reference to the acanthopterygians, myctophoids, and more primitive teleosts, not the paracanthopterygians, to which they show little resemblance (only the polymixiid-like caudal skeleton of *Pateroperca* and the ctenothrissoid skull-roof pattern, in which the open posttemporal fossa is enlarged and the supratemporal fossa is very small or undeveloped, as in percopsiforms). There seem to be no specialized features common to the three known genera of ctenothrissoids which will enable one to characterize them as a monophyletic group, whereas the differences between *Aulolepis* and *Ctenothrissa*, both well-known genera, coupled with the different type of caudal skeleton in the poorly known *Pateroperca*, suggest considerable diversity in the group. The ctenothrissoids resemble the acanthopterygians in the absence of an adipose fin, the structure of the upper jaw, which is not unlike that of some Cretaceous berycoids (Patterson, 1967a, fig. 6, but see also Berry, 1964, fig. 6, larval *Scopelosaurus* jaws), the perforate ceratohyal (imperforate in all myctophoids), the subthoracic or thoracic pelvics, and the presence of procurrent caudal spines (as in all berycoids, but among myctophoids only in the Myctophidae). For these reasons we feel inclined to reject the hypothesis that ctenothrissoids are merely myctophoids, and place them on the acanthopterygian side of the divergence from the common ancestor of myctophoids and acanthopterygians. This conclusion may be modified if Marshall (1961) was correct in relating the living *Macristium* (Macristiidae) to the ctenothrissoids, and if Berry and Robins (1967) were right in placing their new genus *Macristiella* in the Macristiidae, for this fish (a single postlarval specimen known) has an adipose fin and has 16 branchiostegals, many more than *Macristium* (10) and ctenothrissoids (nine). The premaxillae of *Macristiella* appear to us to meet in the midline and to bear a single dorsal process (shown by Berry and Robins, 1964, fig. 2 but not fig. 3) which is laterally placed, in relation to the complex maxillary head, and is therefore an articular process, not an ascending process. No conclusions on the macristiids can be drawn until adult specimens are available.

The possibility that the Macristiidae (*Macristium* and *Macristiella*) are living relatives of the Cretaceous ctenothrissoids has led us to an examination of other protacanthopterygian groups of uncertain affinities that were placed by Greenwood, Rosen, Weitzman, and Myers (1966) in the Cetomimiformes adjacent to the Ctenothrissiformes. The Cetomimiformes contain four suborders, the Cetomimoidei (Cetomimidae, Rondeletiidae, Barbourisiidae), the Ateleopoidei (Ateleopidae), the Mirapinnatoidei (Mirapinnidae, Eutaeniophoridae, Kasidoroidae), and the Giganturoidei (Giganturidae, Rosauridae). Myers and Freihofer (1966) added a fifth suborder, Megalomycteroidei (Megalomycteridae). We have examined representatives of all these families except the Mirapinnidae and Megalomycteridae.

Walters (1964) placed the Giganturidae near the myctophoid fishes, but believed an affinity with the "...subiniomous teleosts [to be suggested by] their maxillae which border on the gape, and by the presence of a muscle [found in *Esox* and *Argentina*, but not in myctophoids] passing through a gap between the hyomandibular and the preopercular to insert on the lower jaw." Walters' view of giganturid relationships accords well with a suggestion by Tucker (1954) that the only other giganturoid group, represented by the genus *Rosaura*, may be related to the stomiatoids. The differences between giganturids and rosaurids are considerable, since the latter is evidently based on a larval form, but we noted similarities in the structure of the caudal skeleton which, in *Bathyleptus* and *Rosaura*, consists of a series of closely fitted plates rather than of separate hypural and epural elements. *Rosaura* resembles the larvae of certain myctophoid groups such as the Paralepididae, but it is deeper-bodied and has much shorter jaws. An adipose fin is present in *Rosaura* and absent from giganturids. The information currently available on these bizarre fishes does not permit a firm decision on their taxonomic placement. In agreement with the views of Walters and Tucker, we recommend their provisional allocation as a suborder in the protacanthopterygian order Salmoniformes.

Whereas the giganturoids appear to be "subiniomous fishes," the remaining cetomimiforms show definite resemblances to various groups of higher fishes. Superficial dissections and brief comparisons of *Ateleopus indicus* (*ca.* 300 mm.) with *Trachypterus rexsalmonorum*, *Desmodema* sp., and *Regalecus glesne* (*ca.* 150–200 mm.) reveal a number of striking similarities in the details of the upper jaw, the entire jaw musculature, and in the details of the caudal skeleton to those features of lampridiforms. In all, the premaxilla excludes the maxilla from the gape and has a high, broad, ascending process, but no articular or postmaxillary processes. The maxilla has a complex and deeply folded articular head and a shaft that is broadly oblanceolate. Living lampridiforms have no supramaxilla, but *Ateleopus* has a single leaf-shaped supramaxilla of moderate size. The cheek musculature in *Trachypterus* and *Ateleopus* is sheetlike and divided into an upper and a lower section, the upper somewhat the larger and having a principal insertion on the coronoid process of the lower jaw, but with superficial tendinous attachments also to the posterior face of the maxilla. The levator arcus palatini has an oblique forward insertion on the palato-pterygoid, and the adductor arcus palatini fills the floor of the orbit. The caudal skeleton of our specimens of *Trachypterus*, *Desmodema*, and *Ateleopus* is wholly cartilaginous and consists of a large, undivided, upper plate that is fused with a well-developed second ural centrum, in the manner of the upper hypural-u_2 fusion in *Lampris* and *Velifer*. Two lower hypurals and a distinct parhypural are present and articulate with an elongate compound centrum (pu_1+u_1). No dorsal structures are clearly evident, although a single cartilaginous nodule was found above the upper hypural in *Ateleopus*. The neural and haemal spines of the fourth and fifth preural centra are osseous. Those of more posterior centra are flexible and show no distinct signs of ossification. We are struck by the resemblances between *Trachypterus* and the mirapinnoid fishes in the over-all configuration of the head and particularly in the form of the jaws as illustrated by Bertelsen and Marshall (1956), and we presume from the illustrated structure of the caudal fin in *Mirapinna* (Bertelsen and Marshall, 1956, fig. 1), in which the upper lobe originates somewhat behind the lower and is well separated from it, that the internal structure of the tail is likely to be very similar to what we have seen in *Trachypterus*, in which the two lobes are also independent of each other. In the single small specimen of *Eutaeniophorus festivus* that we have seen the upper and lower hypural complexes are well separated and offset, but no centra are present. Its upper jaw bones and jaw musculature are like those of ateleopids, regalecids, and trachypterids, as described above, but we could find no supramaxilla. Although we have seen no examples of *Mirapinna* and *Megalomycter*, we note the general similarity in the configuration of the head, body, and fins to those features in the Eutaeniophoridae. Bertelsen and Marshall have pointed out many of the resemblances between the ateleopids and the mirapinnoid fishes, and we do not doubt the phyletic significance of these similarities. The various similarities noted above among trachypteroid, ateleopoid, mirapinnid, and eutaeniophorid fishes appear to warrant the removal of the last three groups from the Protacanthopterygii and their inclusion in the Acanthopterygii in or near the Lampridiformes.

The remaining mirapinnoid family is the Kasidoroidae (*Kasidoron edom* only; Robins and de Sylva, 1965; Robins, 1966). From illustrations of this fish and a brief examination of the holotype we are convinced that it is very closely related to, and may be only the larva of, the beryciform *Gibberichthys pumilus*, with which it agrees in almost every character (see Parr, 1933, 1934, and note especially the differences between his 32-mm. and 91-mm. specimens of *Gibberichthys* in relation to the differences between the smaller specimen and the 21-mm. *Kasidoron* illustrated by Robins and de Sylva). *Kasidoron* is therefore a beryciform, and this is also probably the correct position of the Cetomimoidei. The three cetomimoid families, Cetomimidae, Barbourisiidae, and Rondeletiidae (the last two monotypic), seem to form a related group (Harry, 1952; Rofen, 1959), members of which have, in the past, been placed simultaneously in the Beryciformes and Myctophoidei (Parr, 1929, 1946). From an examination of specimens of *Rondeletia*, *Barbourisia*, *Cetomimus*, and *Gyrinomimus* and from information in the literature (Parr, 1929, 1934, 1945; Harry, 1952; Rofen, 1959) it seems clear that *Rondeletia* is the most generalized form, with *Barbourisia* and the cetomimids representing progressive, if somewhat divergent, specializations. But Ebeling (1962, p. 11) quoted the opinion of Rofen that *Rondeletia* is closely related to *Gibberichthys*, and *Rondeletia* was transferred to the Xenoberyces (= Stephanoberycoidei) by Parr (1929: "a typical representative of the Xenoberyces") because it agrees with those fishes in the structure of the upper jaw, the toothless palate, 19 principal caudal rays, and the absence of a subocular shelf and orbitosphenoid. None of these characters is decisive, but Parr was impressed by the over-all similarity of *Rondeletia* not only to the stephanoberycoids but to the "true Berycomorphi" (= Berycoidei) and believed that separation of the two groups was hardly justified, a conclusion expressed by Marshall's (1960, p. 56) inclusion of the Xenoberyces as a suborder of Beryciformes. *Rondeletia* has abdominal pelvics without a spine and no dorsal or anal fin spines (as in Stephanoberycidae), but has procurrent caudal spines, a typical beryciform feature. Parr (1929, fig. 18) illustrated a caudal skeleton of *Rondeletia* that has a full neural spine on the second pre-ural centrum (a difference from all known beryciforms except the individual of *Monocentris* figured by Patterson, 1968b, fig. 14). We have examined the caudal skeleton of the holotype of *Rondeletia bicolor* and find it to be of normal berycoid type, with a low neural crest on the second pre-ural centrum, three epurals, six hypurals, and a free second ural centrum. There is no swim bladder (as in *Scopelogadus beani*, Ebeling, 1962, table 3), but Marshall (1960, p. 43) found a "curiously regressed" swim bladder in the cetomimid *Ditropichthys*, and concluded that the larva of this fish must have a well-formed swim bladder. In comparison with the gibberichthyid-like *Rondeletia*, *Barbourisia* and, in particular, the cetomimids seem to present a sequence of "regressive" developments, associated with life in the deep bathypelagic environment, similar to those discussed by Marshall (1960, pp. 99–113, figs. 42, 44) in stomiatoids. We feel confident that the correct position of the cetomimoids is within the Beryciformes.

From the above information we feel justified in concluding that the myctophoids, paracanthopterygians, and acanthopterygians represent three independent, parallel, and more or less equally advanced radiations into what could conveniently be termed an advanced neoteleostean grade. Our interpretation of the myctophoids as a radiation advancing in parallel with the paracanthopterygians and acanthopterygians carries with it the clear implication that the myctophoids are not at all a primitive group, as they have consistently been treated in the past. So

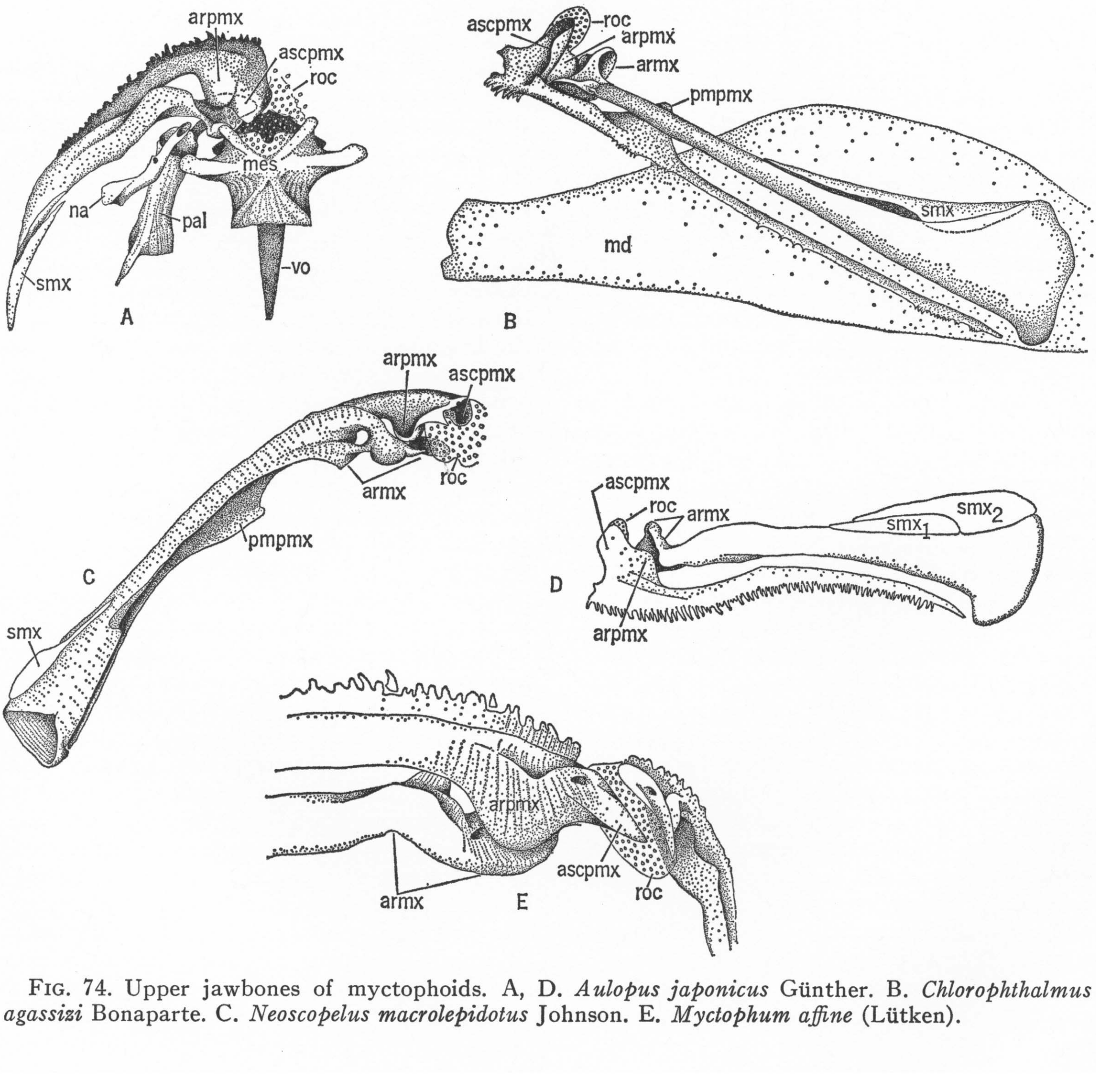

FIG. 74. Upper jawbones of myctophoids. A, D. *Aulopus japonicus* Günther. B. *Chlorophthalmus agassizi* Bonaparte. C. *Neoscopelus macrolepidotus* Johnson. E. *Myctophum affine* (Lütken).

prevalent has been the notion of their primitive qualities that statements of their characteristics in formal classifications have generally been introduced with the phrase: "As Isospondyli (or Clupeiformes), but upper jaw bordered by premaxillaries only." Emphasizing the length of the premaxillary alveolar arm is, however, grossly misleading. Partial exclusion of the maxilla from the gape is not necessarily more or less significant than total exclusion by the premaxilla (cf. text figs. 67, 74). More important, at the myctophoid level of organization the premaxilla has the very specializations (ascending, articular, and postmaxillary processes, and corresponding maxillary modifications) that characterize the protrusile upper-jaw mechanism of the "higher" teleosts (text figs. 67, 74).

The atherinomorph fishes, which have so far not been mentioned, evidently represent still another major radiation into the advanced neoteleostean grade. One of their chief points of interest concerns the special features of their feeding mechanism. A discussion of this mechanism should be prefaced, however, with some new observations and new thoughts on the origin of the protrusile upper-jaw mechanism of the higher fishes.

From the moment in time when the maxilla was freed from the bones of the cheek in the holostean fishes, all the successive actinopterygian types of jaw were characterized by some form of kineticism. In these later actinopterygians, the maxilla responded to depression of the mandible by rotating forward to a degree determined by the downward movement of the lower jaw, its point of ligamentous attachment to the coronoid process of the mandible, and by its length in relation to the rotational fulcrum. The rotational fulcrum in the holosteans and early teleosts was at the proximal end of the short premaxilla to which it was joined serially. When the alveolar process of the premaxilla began to lengthen, and the maxilla and premaxilla came to lie in tandem rather than in series, the forward rotation of the maxilla required a corresponding rotation of the premaxilla. The overlapping alveolar premaxillary arm obviously would have impeded maxillary movement unless it too were capable of movement. The net effect of the development of premaxillary mobility was to shift the rotational fulcrum for the upper jaw upward to the rostrum above and behind the premaxillary symphysis (see Schaeffer and Rosen, 1961, for a more detailed account).

The evolution of premaxillary mobility brought into prominence another structure, the rostral cartilage, which initially probably did double service as the new rotational fulcrum and as a cushion between the now mobile premaxilla and the ethmoid. Eventually, as the connective tissues of the rostrum became increasingly flexible to allow for premaxillary movement, the premaxilla was able to slide forward slightly away from the rostrum, carrying with it the rostral cartilage and the associated investing connective tissues. It was presumably out of these connective tissues that the complex upper-jaw ligaments condensed in relation to the lines of stress set up by the sliding and rotational movements (Schaeffer and Rosen, *ibid.*, p. 201).

The development of a sliding motion at the premaxillary symphysis obviously was the critical development that made possible the later evolution of the protrusile jaw. It is also clear, however, that the ascending processes of the premaxilla, which have had attributed to them the principal mechanical role in making protrusion possible, cannot have had any importance whatever in the early development of the mechanism. If protrusibility is defined as the forward displacement of the premaxilla away from the rostrum by means of a sliding or slipping motion, then it is evident that the chief role in forward translation must have been played by the rostral cartilage and connective tissues. The ascending premaxillary processes, in their original development, served the necessary but passive role of anchoring the upper jaw to the rostral cartilage, as may be seen in myctophoids (text fig. 74) and the more primitive paracanthopterygians. In these fishes an ascending process of the advanced acanthopterygian type does not exist. The process is low and hollow so that it may fit snugly around the oval cartilage. Its size and shape may be seen to be closely related to the size and shape of this cartilage.

Nevertheless, a sliding motion is a principal feature of all the generalized myctophoid and paracanthopterygian jaws, slight though it may be. The initial advantage of this type of jaw was probably to permit an increase in the degree of abduction of the mandible and hence greatly to increase the size of the gape in generalized predatory fishes. It is certainly not the only way in which the mouth may be made more effective for fishes of predatory habits, but it must have represented a vast improvement as a trap over the small and relatively akinetic mouths of ctenothrissoids. The ultimate advantage of the system was to provide the raw materials for the evolution of highly protrusile and specialized mouths by an elaboration of the various complex maxillary and premaxillary processes that were built into the mechanism (see Schaeffer and Rosen, *ibid.*, pp. 199–203). An increase in the degree of protrusion was dependent, however, on the appropriate muscular control of the upper jaw. As pointed out above, a notable increase in the forward translation of the upper jaw in paracanthopterygians was impeded by the insertion of a large inner division of the adductor mandibulae (lms) onto the dorsal part of the upper jaw in a manner that restricted the mobility of the upper maxilla and, hence, the premaxilla to which it is joined via the articular process. Paracanthopterygians, except for the gobiesocids, seem to have developed only further refinements of the basic predatory mechanism. No such impediment to sliding motion developed in acanthopterygians, however, in which maxillary control is achieved by a more ventral superficial division of the adductor mandibulae (A_1). Atherinomorph fishes clearly have followed the general line of specialization of acanthopterygians both with respect to the source of the muscle used in maxillary control and in its point of insertion on the maxilla. It is probable that in atherinomorphs the whole mechanism underwent an early specialization in protrusility involving the independence of the rostral cartilage from the premaxillary symphysis. Typically the atherinomorph cartilage is bound to an internal hook on the head of the maxilla and to the spongy investing connective tissues that serve also to bind together the two premaxillae (see Alexander, 1967b). Also typically the left and right premaxillae of atherinomorphs are capable of, and normally undergo, independent movement during jaw protrusion. The independence of these two upper jawbones is clearly indicated in atherinoid fishes in which the ascending processes are crossed or converge at their tips when the jaw is retracted (Rosen, 1964, fig. 5A) and are well separated and more or less parallel when protruded. It seems very likely to us from the lateral displacement of their bases in many forms and from their invariable functional association with the articular head of the maxilla, that the atherinomorph ascending processes may, in fact, be highly modified articular processes and that true ascending processes never did develop in this group. In cyprinodontoids small symphyseal structures rather like the more primitive ascending processes of myctophoids often are present, although the larger, somewhat pointed, subterminal process that interlocks with the maxillary head also is developed. The principal difference between cyprinodontoids and atherinoids is in the extent to which the processes associated with the head of the maxilla have enlarged, to mimic in some instances the acanthopterygian ascending processes. Whether or not atherinomorphs have true ascending processes, which in our view evolved as a means of joining the premaxillary symphysis to the rostral cartilage, it is clear that the atherinomorphs and acanthopterygian systems show many differences and may have evolved independently (Alexander, 1967a, 1967b).

The other early, and presumably limiting, specialization of the atherinomorph jaw is the very great elongation and expansion of the alveolar arm of the premaxilla. The alveolar arm has been interpolated between the maxilla and the mandible and has become directly associated by a ligament with the coronoid expansion of the lower jaw. The maxilla now is carried and controlled by the premaxilla during the initial phases of mouth protrusion (Schaeffer and Rosen, 1961, pp. 199–201; Rosen, 1964, pp. 222–223; Alexander, 1967b).

In a host of features the atherinomorphs can be, and have been, shown to parallel the acanthopterygians (Rosen, 1964, and Greenwood, Rosen, Weitzman, and Myers, 1966). Gosline (1963) has shown acanthopterygian similarities to be especially characteristic of the atherinoid fishes, although he disagrees with the basic concept of the atherinomorphs as a monophyletic group. If their phylogenetic integrity is accepted, however, it is probable that the atherinomorphs are most nearly related to the acanthopterygians. The earliest definite evidence of fossil atherinomorphs is in the Middle Eocene. Detailed work on these fossils is needed, but they seem to differ very slightly from living forms, indicating only that the three atheriniform suborders were already well established. The group presumably arose before the Eocene, and in the fresh waters of the Old World tropics (Rosen, 1964).

In summary, we find that three main lineages can be defined among the various groups now under consideration, the first including only the myctophoid fishes; the second, the polymixioids and paracanthopterygians; and the third, the atherinomorphs and the acanthopterygians. We envision a ctenothrissoid radiation as being at the base of these lineages, even though the known ctenothrissoids seem to be most closely allied with the acanthopterygians. We further believe these several groups of fishes to represent an evolutionary development that is separate and distinct from all other groups of euteleosteans (see Greenwood, Myers, Rosen, and Weitzman, 1967), and it is clear to us that they must all somehow be brought together as a recognizable assemblage in the hierarchy of current classification. In the recent arrangement proposed by Greenwood, Rosen, Weitzman, and Myers (1966), our studies have the profoundest effects on the superorder Protacanthopterygii, in which the ctenothrissoids are included as an order and in which the myctophoids are treated as a suborder of the order Salmoniformes. The studies of Weitzman (1967; and in preparation) also have important consequences for the arrangement of salmoniform groups, and continuing investigations of the gonorynchiforms by Pfeiffer (1967a, 1967b) suggest a close alignment of these protacanthopterygian fishes with the ostariophysans. Just as our present work has dictated to us the necessity of removing the myctophoids to a new alignment near the paracanthopterygians and acanthopterygians, so future studies may ultimately necessitate the transfer of the gonorynchiforms to the Ostariophysi. The few opportunities we have had to examine cetomimiform protacanthopterygians indicate that at least some of them also may be most closely related to groups treated in this work (and see also Robins, 1966). Our objective in pointing to the possibility of imminent change in the alignment of protacanthopterygian groups is not an attempt to prejudge the results and implications of future studies. Our purpose is rather to show that the hierarchical system proposed by Greenwood, Rosen, Weitzman, and Myers (1966) is not fully equipped to cope with some of the possible changes in group allocation. If, for example, the strongest evidence warranted the inclusion of the Gonorynchiformes in the superorder Ostariophysi, there would be no way, in the present hierarchical scheme, of distinguishing the gonorynchiforms from the obviously more closely related cypriniforms and siluriforms. The difficulty lies in the absence of, and in the above example, the obvious need for, a collecting category of some sort between the order and superorder. A difficulty, and a need, of exactly that nature has arisen in the present work. The polymixioids, for instance, appear to be most closely allied to the paracanthopterygians and should be included in that category. Yet the polymixioids must also stand apart from the other paracanthopterygians as a distinct, though kindred, line. The alignment of the atheriniforms within the Acanthopterygii, which is in our view of their relationships very desirable, presents similar problems. The solution to the dilemma seems to us to lie in the establishment of a descriptive, intermediate category without formal rank, and we have elected to use for this purpose the neutral term "series." The three main groupings, representing parallel radiations into a "neoteleostean" grade, may be arranged as follows, with the equivalents given in Greenwood, Rosen, Weitzman, and Myers (1966) in brackets and parentheses:

Superorder Scopelomorpha, new name
    Order Myctophiformes (= Myctophoidei)
Superorder Paracanthopterygii
  Series Polymixiomorpha, new
    Order Polymixiiformes, new (= Polymixioidei)

- Series Salmopercomorpha, new
  - Order Percopsiformes
  - Order Gadiformes
  - Order Batrachoidiformes
  - Order Lophiiformes
  - Order Gobiesociformes
- Superorder Acanthopterygii
  - Series Atherinomorpha
    - Order Atheriniformes
  - Series Percomorpha
    - Order Lampridiformes [=Lampridiformes + Ateleopodoidei + Mirapinnatoidei, in part (Mirapinnidae + Eutaeniophoridae) + Megalomycteroidei (Myers and Freihofer, 1966)]
    - Order Beryciformes [=Stephanoberycoidei + Berycoidei + Cetomimoidei + Mirapinnatoidei, in part (Kasidoroidae)]
    - Order Perciformes and related groups

The sequence of superorders within Division III of Greenwood, Rosen, Weitzman, and Myers (1966) or the equivalent cohort, Euteleostei, of Greenwood, Myers, Rosen, and Weitzman (1967) would then be: Protacanthopterygii, Ostariophysi, Scopelomorpha, Paracanthopterygii, Acanthopterygii. Within this scheme, we are treating the ctenothrissoid fishes as an order of the Protacanthopterygii, although we recognize their seeming relevance to the history of the Acanthopterygii. As discussed above, in our opinion there is not yet decisive evidence on the nearest relatives of the Lampridiformes. Rather than erect yet another higher category to contain them, we leave them in the Acanthopterygii.

SUMMARY

1. The aim of this work has been to discover whether the superorder Paracanthopterygii is a monophyletic group, and, if so, to find its limits and relationships. The supposed members of this superorder are the Percopsiformes, Gadiformes, Batrachoidiformes, Lophiiformes, and Gobiesociformes. The paper contains illustrated anatomical accounts of the living and fossil members of these groups, and detailed descriptions of the fossil percopsiforms *Trichophanes* (Oligocene, Aphredoderidae), *Amphiplaga*, *Erismatopterus* (both Eocene, Percopsidae), and *Sphenocephalus* (Upper Cretaceous, Sphenocephalidae), and the possibly related *Asineops* (Eocene).

2. Although no single character or combination of characters can be found which occurs in all paracanthopterygians and in no other fish, the conjunction of a distinctive type of jaw musculature and caudal skeleton in all living percopsiforms (percopsids, aphredoderids, amblyopsids), most gadiform suborders (gadoids, muraenolepoids, ophidioids), and batrachoidiforms (batrachoidids) justifies the hypothesis that these three orders are members of a monophyletic group distinct from the acanthopterygians.

3. The most distinctive feature of the paracanthopterygian jaw is the presence of a levator maxillae superioris muscle, which seems to be derived in phylogeny from the upper part of the outer division of the adductor mandibulae. The levator maxillae superioris originates on the palatoquadrate and inserts near the head of the maxilla, serving as a tensor which positions and restrains the maxilla during opening of the mouth. The presence of this muscle limits the degree of jaw protrusion; rather than a truly protrusile mouth paracanthopterygians tend to develop a large, circular gape by pivoting the maxilla and premaxilla.

4. Correlated with the presence of the levator maxillae superioris are a number of features of the skull and jaws, especially the tendency to develop a broad, shallow head, with consequent modifications of the skull roof, occipital condyle, and operculum.

5. A levator maxillae superioris muscle and jaws of paracanthopterygian type also occur in macrouroids and zoarcoids (the remaining gadiform suborders) and in antennarioid and some ceratioid lophiiforms. The remaining lophiiforms and the gobiesocids are without a levator maxillae superioris. Outside the Paracanthopterygii, a levator maxillae superioris is known to occur only in myctophid myctophoids and in some cyclopterid scorpaeniforms.

6. The paracanthopterygian caudal skeleton is characterized by the presence of a second ural centrum which is fused with the upper hypurals, two or fewer epurals, and a full neural spine on the second pre-ural centrum. This neural spine appears to be a primary structure, not the result of fusion between an epural and a neural arch. In addition to the percopsiforms, gadoids, muraenolepoids, ophidioids, and batrachoidids, a caudal skeleton of this type also occurs in at least one zoarcoid, although most zoarcoids and the macrouroids have the caudal skeleton reduced beyond recognition. It does not occur in lophiiforms or gobiesociforms, in which the caudal supports are fused in such a way that they resemble those of some advanced acanthopterygians. In Eocene and Cretaceous percopsiforms and in a few living gadoids the caudal skeleton is more primitive, having the upper hypurals autogenous (four upper hypurals in percopsiforms, three in gadoids).

7. Lophiids and gobiesocids, which lack the paracanthopterygian pattern both in the jaw musculature and the caudal skeleton, are linked with batrachoidids and more generalized lophiiforms by a large number of specializations, especially in the skull and shoulder girdle.

8. Apart from the primary specializations of the jaw musculature and caudal skeleton, other paracanthopterygian group trends include: reduction in the bony cover of the cephalic sensory canals, the development of large, well-separated, exoccipital condyles, crowding of the anterior vertebrae, loss of supramaxillae, development of a deep notch behind the postmaxillary process of the premaxilla, shortening of the basibranchials so

that the gill arches converge ventrally, development of projections on the heads of the posterior branchiostegals, increase in the number of pectoral radials, extension of the median fins, and reduction of the squamation.

9. Primitive features of paracanthopterygians that distinguish the group from the acanthopterygians include the presence of an adipose fin, pelvic splint (both in percopsiforms only), basibranchial teeth and second ural centrum, and the absence of a subocular shelf, predorsal bones, and a pelvic spine (a spinelet, questionably homologous with the acanthopterygian spine, present in some ophidioids, batrachoidids, lophiiforms, and gobiesocids).

10. Morphological and paleontological analysis of the paracanthopterygians indicates that the Percopsiformes, which existed in Cretaceous seas, stand near the origin of the group, occupying much the same position as do the Beryciformes among acanthopterygians. The closest relatives of the percopsiforms are the gadiforms, especially the merlucciid gadoids, with which they share many specializations. Within the Gadiformes, two main lineages are recognizable, the gadoid lineage and the ophidioid-zoarcoid lineage. These two lines must have separated in the Cretaceous. The position of the macrouroids and muraenolepoids in relation to these two lineages is still obscure: the Macrouroidei may contain convergently modified gadoid and ophidioid derivatives. The batrachoidiforms, lophiiforms, and gobiesociforms, the precise interrelationships of which remain to be discovered, form a separate lineage which must have diverged from the percopsiform-gadiform line during the Cretaceous or Paleocene.

11. The fossil record of the percopsiforms shows that some trends followed during the evolution of this group (and probably also in the gadiform and batrachoidiform-lophiiform-gobiesociform lineages) are the reverse of those typical of acanthopterygian evolution, notably reduction in the depth of head and trunk and reduction in fin spines and in spination of the skull bones and scales. A corollary of these trends is that the paracanthopterygians must have shared a closer common ancestry with the acanthopterygians than with the myctophoids.

12. The higher euteleosteans are envisaged as comprising three main radiations, the myctophoid radiation, stemming from aulopid-like ancestors, the paracanthopterygians stemming from percopsiform-like ancestors, and the acanthopterygians from berycoid-like ancestors. The distinctions between these are blurred by parallelism and convergence among the three (e.g., development of a subocular shelf, levator maxillae superioris, and fin spines in myctophid myctophoids; convergent resemblance between ophidioids and blennies and between batrachoidids and some scorpaeniforms) and by the existence of groups that appear to be equally ancient but do not fit easily into any of the three radiations, being in many ways intermediate between them (ctenothrissoids intermediate between myctophoids and acanthopterygians; polymixioids, lampridiforms, and *Asineops* intermediate between paracanthopterygians and acanthopterygians; atherinomorphs resembling but clearly distinct from acanthopterygians).

13. Some groups, previously placed in the protacanthopterygian order Cetomimiformes, seem to belong with these higher euteleosteans; the kasidoroids and cetomimoids are beryciforms, the ateleopoids, mirapinnids, and eutaeniophorids may be lampridiforms.

14. These conclusions are expressed in a new classification (p. 460) which incorporates a new category, "series," between order and superorder.

15. New taxa proposed are as follows: *Sphenocephalus brachypterygius*, new species; suborder Sphenocephaloidei (Percopsiformes); order Polymixiiformes (=Polymixioidei); series Polymixiomorpha, Salmopercomorpha, Atherinomorpha, Percomorpha; superorder Scopelomorpha (=Myctophiformes).

16. *Erismatopterus endlichi* Cope and *E. rickseckeri* Cope are synonyms of *Amphiplaga brachyptera* Cope and *E. levatus* (Cope), respectively. The family Trichophanidae Cockerell is synonymous with the Aphredoderidae; the family Erismatopteridae Jordan is synonymous with the Percopsidae; the family Kasidoroidae Robins and De Sylva is synonymous with the Gibberichthyidae. The suborder Amblyopsoidei is merged with the Aphredoderoidei; the members of the Cretaceous beryciform suborder Dinopterygoidei are distributed between the Lampridiformes and the Polymixiiformes.

APPENDIX: RECENT COMPARATIVE MATERIALS EXAMINED

- Amblyopsidae
  - *Amblyopsis spelaea* DeKay, B.M.N.H. No. 1847.10.18.7; A.M.N.H. No. 2000
- Anomalopidae
  - *Photoblepharon palpebratus* (Boddaert), A.M.N.H. No. 15361
- Anoplogasteridae
  - *Anoplogaster cornutus* (Valenciennes), U.S.N.M., uncatalogued
- Antennariidae
  - *Antennarius scaber* (Cuvier), A.M.N.H. No. 20256
  - *Histrio histrio* (Linnaeus), A.M.N.H. No. 17950
- Aphredoderidae
  - *Aphredoderus sayanus* (Gilliams), U.F. No. 8362; B.M.N.H. No. 1898.12.29.141, 150
- Argentinidae
  - *Argentina striata* Goode and Bean, U.S.N.M. No. 188224
- Aulopidae
  - *Aulopus filamentosus* Cloquet, M.C.Z. No. 40523
  - *Aulopus japonicus* Günther, A.M.N.H. No. 13024
  - *Aulopus nanae* Mead, M.C.Z. No. 40516
  - *Aulopus purpurissatus* Richardson, M.C.Z. No. 25688
- Barbourisiidae
  - *Barbourisia rufa* Parr, U.S.N.M. No. 197858
- Bathymasteridae
  - *Ronquilus jordani* (Gilbert), U.M.M.Z. No. 93896
- Batrachoididae
  - *Batrachoides pacifici* (Günther), B.M.N.H. No. 1860.4.1.2
  - *Daector dowi* (Jordan and Gilbert), A.M.N.H. No. 16084
  - *Halophryne diemensis* (Lesueur), B.M.N.H. No. 1867.5.6.13
  - *Opsanus beta* (Goode and Bean), U.F. No. 4231; B.M.N.H., skeleton
  - *Opsanus tau* (Linnaeus), A.M.N.H., uncatalogued
  - *Porichthys margaritatus* (Richardson), B.M.N.H. No. 1948.8.6.1401
  - *Porichthys notatus* Girard, A.M.N.H., uncatalogued
  - *Porichthys porosissimus* (Cuvier), A.M.N.H. No. 19563; B.M.N.H. No. 1890.11.15.150
  - *Thalassophryne maculosa* Günther, A.M.N.H., uncatalogued
  - *Thalassophryne megalops* Bean and Weed, U.S.N.M. No. 187946
- Berycidae
  - *Beryx splendens* Lowe, U.S.N.M. No. 158873
- Blenniidae
  - *Blennius cristatus* Linnaeus, A.M.N.H. No. 20295
  - *Blennius pavo* Risso, A.M.N.H. No. 14832
  - *Entomacrodus textilis* (Quoy and Gaimard), A.M.N.H. No. 20294
  - *Halmablennius lineatus* (Valenciennes), A.M.N.H. No. 16386
  - *Hypleurochilus geminatus* (Wood), A.M.N.H. No. 4551
  - *Hypsoblennius hentz* (Lesueur), A.M.N.H. No. 4321
  - *Hypsoblennius ionthas* (Jordan and Gilbert), A.M.N.H. No. 16373
  - *Istiblennius periophthalmus* (Valenciennes), A.M.N.H. No. 17886
  - *Ophioblennius atlanticus* (Valenciennes), A.M.N.H. No. 23016
  - *Salarius fasciatus* (Bloch), A.M.N.H. No. 17521
  - *Scartichthys gigas* (Steindachner), A.M.N.H. No. 17914
- Bregmacerotidae
  - *Bregmaceros macclellandi* Thompson, A.N.S.P. Nos. 51314–51316
- Brotulidae
  - *Bidenichthys capensis* Barnard, B.M.N.H. No. 1933.10.31.6.
  - *Brotula barbata* (Bloch and Schneider), B.M.N.H. No. 1933.10.12.98
  - *Brotula multibarbata* Schlegel, B.M.N.H. No. 1891.2.9.30
  - *Dicrolene longimana* Garman, B.M.N.H. Nos. 1939.5.24.1445, 1939.5.24.1446
  - *Dinematichthys* sp., A.M.N.H. No. 16597
  - *Genypterus blacodes* (Forster), B.M.N.H. Nos. 1845.11.12.52, 1896.6.17.73
  - *Lucifuga subterranea* Poey, A.M.N.H. No. 3284
  - *Neobythites steatiticus* Alcock, B.M.N.H. No. 1910.1.31.11
  - *Ogilbia* sp., A.M.N.H. No. 23160; U.F. No. 1390
  - *Oligopus claudei* (Huerta de la Torre), A.M.N.H., uncatalogued
  - *Petrotyx sanguineus* (Meek and Hildebrand), A.M.N.H. No. 23346
  - *Porogadus brevipes* Garman, A.M.N.H. No. 8456
  - *Porogadus promelas* (Gilbert), A.M.N.H. No. 12809
  - *Pycnocraspedum squamipinne* Alcock, B.M.N.H. Nos. 1939.5.24.1497, 1939.5.24.1498

Sirembo imberbis (Temminck and Schlegel), B.M.N.H. Nos. 1905.2.4.450–1905.2.4.454
Stygicola dentatus (Poey), A.M.N.H. No. 1537

Caproidae
Capros aper Lacépède, A.M.N.H. No. 482

Carangidae
Caranx oblongus (Cuvier), A.M.N.H. No. 15216
Caranx ruber (Bloch), A.M.N.H. No. 3396
Decapterus macrosoma Bleeker, A.M.N.H. No. 15921

Carapidae
Carapus bermudensis (Jones), A.M.N.H., uncatalogued
Carapus dentatus (Cuvier), vexillifers, B.M.N.H. No. 1912.12.30.59–1912.12.30.64
Pyramodon ventralis Smith and Radcliffe, U.S.N.M. No. 74155, type
Snyderidia canina Gilbert, U.S.N.M. No. 51646, type

Centropomidae
Lates microlepis Boulenger, B.M.N.H. Nos. 1936.6.15.1672–1936.6.15.1686

Ceratiidae
Cryptopsaras couesii Gill, B.M.N.H. No. 1932.5.3.31

Cetomimidae
Cetomimus gilli Goode and Bean, U.S.M.N. No. 35529
Gyrinomimus parri Bigelow, U.S.N.M. No. 196180

Chaunacidae
Chaunax pictus Lowe, A.M.N.H. No. 1921

Chlorophthalmidae
Chlorophthalmus agassizi Bonaparte, U.S.N.M. Nos. 159377, 159397
Parasudis truculentus (Goode and Bean), M.C.Z. Nos. 17678, 37875, 41821

Clinidae
Gibbonsia elegans (Cooper), A.M.N.H. No. 17910
Hemiemblemaria simulus Longley and Hildebrand, A.M.N.H. No. 23537
Labrisomus bucciferus Poey, A.M.N.H. No. 23018
Labrisomus gobio (Valenciennes), A.M.N.H. No. 23406
Labrisomus guppyi (Norman), A.M.N.H. No. 23491
Labrisomus haitensis Beebe and Tee-Van, A.M.N.H. No. 23625
Labrisomus nigricinctus Howell Rivero, A.M.N.H. No. 23234
Labrisomus nuchipinnis (Quoy and Gaimard), A.M.N.H. No. 3809
Labrisomus xanti (Gill), A.M.N.H. No. 5388
Malacoctenus aurolineatus Smith, A.M.N.H. No. 23022
Malacoctenus gilli (Steindachner), A.M.N.H. No. 1677
Malacoctenus triangulatus Springer, A.M.N.H. No. 23048
Malacoctenus zonifer (Jordan and Gilbert), A.M.N.H. No. 17158
Mnierpes macrocephalus (Günther), A.M.N.H. No. 8324
Paraclinus nigripinnis (Steindachner), A.M.N.H. No. 23025
Starksia atlantica Longley, A.M.N.H. No. 23318

Congrogadidae
Congrogadus subducens (Richardson), U.M.M.Z. No. 100250

Cyclopteridae
Cyclopterus lumpus Linnaeus, B.M.N.H. No. 1968.12.31.2
Liparis liparis (Linnaeus), B.M.N.H. Nos. 1966.11.21.60–1966.11.21.63
Paraliparis sp., B.M.N.H. Nos. 1939.6.20.41–1939.6.20.43

Eutaeniphoridae
Eutaeniophorus festivus Bertelsen and Marshall, U.S.N.M., uncatalogued

Gadidae
Boreogadus saida (Lepechin), A.M.N.H. No. 17050
Enchelyopus sp., U.S.N.M., uncatalogued
Gadus morhua Linnaeus, A.M.N.H., uncatalogued
Gaidropsarus sp., B.M.N.H. Nos. 1960.1.8.2–1960.1.8.5
Melanogrammus aeglefinus (Linnaeus), A.M.N.H., uncatalogued
Microgadus tomcod (Walbaum), A.M.N.H., uncatalogued
Physiculus argyropastus Alcock, B.M.N.H. No. 1901.1.30.22
Pollachius virens (Linnaeus), A.M.N.H. No. 2262
Theragra chalcogramma (Pallas), A.M.N.H. No. 8975
Trisopterus minutus (Müller), B.M.N.H. No. 1888.4.3.55
Urophycis floridanus (Bean and Drexel), U.F. No. 2680

Gadopsidae
Gadopsis marmoratus Richardson, B.M.N.H. Nos. 1914.8.20.228–1914.8.20.233

Gibberichthyidae
Gibberichthys pumilus Parr, U.S.N.M. No. 187665

Giganturidae
Bathyleptus lisae Walters, U.S.N.M., uncatalogued
Gigantura vorax Regan, U.S.N.M., uncatalogued

- Gobiesocidae
  - *Acyrtus rubiginosus* (Poey). A.M.N.H. No. 23998
  - *Crepidogaster* sp., A.M.N.H. No. 15367
  - *Gobiesox adustus* Jordan and Gilbert, A.M.N.H. No. 9085
  - *Gobiesox funebris* Gilbert, A.M.N.H. No. 5557
  - *Gobiesox maeandricus* (Girard), A.M.N.H. No. 2667
  - *Gobiesox strumosus* Cope, A.M.N.H. No. 18762
  - *Lepadogaster lepadogaster* (Bonnaterre), A.M.-N.H. No. 16875
  - *Rimicola eigenmanni* (Gilbert), A.M.N.H. No. 18705
  - *Sicyases sanguineus* Müller and Troschel, A.M.N.H. No. 19556
  - *Tomicodon chilensis* Brisout de Barneville, A.M.N.H. No. 7908
  - *Tomicodon eos* (Jordan and Gilbert), A.M.N.H. No. 5611
  - *Tomicodon humeralis* (Gilbert), A.M.N.H. No. 5559
- Harpadontidae
  - *Harpadon nehereus* (Hamilton-Buchanan), A.M.N.H. No. 17563
- Holocentridae
  - *Holocentrus ascensionis* (Osbeck), A.M.N.H., uncatalogued
  - *Holotrachys lima* (Cuvier), U.M.M.Z. No. 185693
  - *Myripristis jacobus* Cuvier, A.M.N.H. No. 23421
  - *Plectrypops retrospinus* (Guichenot), U.M.M.Z. No. 176518
- Lamprididae
  - *Lampris regius* (Bonnaterre), A.M.N.H., uncatalogued
- Lophiidae
  - *Lophius americanus* Valenciennes, A.M.N.H., uncatalogued
  - *Lophius piscatorius* Linnaeus, B.M.N.H. Nos. 1935.5.2.190, 1956.7.12.12
- Macrouridae
  - *Chalinura occidentalis* (Goode and Bean), U.M.M.L. No. 7316
  - *Coelorhynchus atlanticus* (Lowe), B.M.N.H. No. 1905.2.2.18
  - *Hymenocephalus antraeus* Gilbert and Cramer, A.M.N.H. No. 3551
  - *Hymenocephalus cavernosus* (Goode and Bean), U.F. No. 3901
  - *Lionurus liolepsis* (Gilbert), A.M.N.H. No. 12865
  - *Malacocephalus laevis* (Lowe), B.M.N.H. No. 1904.11.30.33
  - *Trachyrincus trachyrincus* (Risso), B.M.N.H. No. 1888.6.15.7
- Melamphaeidae
  - *Melamphaes bispinosus* Gilbert, U.M.M.Z. No. 176340
- Melanocetidae
  - *Melanocetus johnsonii* Günther, B.M.N.H. No. 1914.6.23.1
- Melanonidae
  - *Melanonus gracilis* Günther, N.I.O.
  - *Melanonus zugmayeri* Norman, N.I.O.
- Merlucciidae
  - *Macrouronus novaezealandicae* Günther, B.M.-N.H., skeleton
  - *Macrouronus* sp., U.S.N.M., uncatalogued
  - *Merluccius bilinearis* (Mitchill), A.M.N.H. No. 3375
  - *Merluccius capensis* Castlenau, B.M.N.H. Nos. 1898.12.17.17, 1898.12.17.18
  - *Merluccius merluccius* (Linnaeus), B.M.N.H. Nos. 1898.12.17.17, 1898.12.17.18
  - *Merluccius productus* (Ayres), A.M.N.H. No. 2699; B.M.N.H. No. 1896.9.25.6
  - *Steindachneria argentea* Goode and Bean, U.M.M.L. No. 7127
- Monocentridae
  - *Monocentris japonicus* (Houttuyn), A.M.N.H., uncatalogued
- Moridae
  - *Antimora viola* (Goode and Bean), B.M.N.H. No. 1903.9.29.7
  - *Eretmophorus kleinenbergi* Giglioli, B.N.M.H. No. 1902.2.11.5
  - *Mora mora* (Risso), B.M.N.H. No. 1892.2.27.27
  - *Salilota australis* (Günther), B.M.N.H. Nos. 1936.8.28.392, 1936.8.28.393
- Mugiloididae
  - *Parapercis sexfasciata* (Temminck and Schlegel), U.M.M.Z. No. 176691
- Muraenolepidae
  - *Muraenolepis marmoratus* Günther, B.M.N.H. No. 1890.2.26.138
  - *Muraenolepis microps* Lönnberg, B.M.N.H. No. 1937.7.12.11–17
  - *Muraenolepis orangiensis* Vaillant, B.M.N.H. No. 1936.8.26
- Myctophidae
  - *Diaphus dumerili* (Bleeker), A.M.N.H. No. 23098
  - *Diaphus theta* Eigenmann and Eigenmann, U.S.N.M. No. 199852
  - *Lampanyctus lacerta* Goode and Bean, A.M.N.H. No. 15076
  - *Lampanyctus leucopsarus* (Eigenmann and Eigenmann), U.M.M.Z. No. 129010
  - *Lampanyctus mexicanus* (Gilbert), A.M.N.H. No. 17229
  - *Lampanyctus regalis* (Gilbert), A.M.N.H. No. 12840

Myctophum affine (Lütken), A.M.N.H. No. 18149
Myctophum aurolaternatum Garman, A.M.N.H. No. 15985
Myctophum evermanni Gilbert, A.M.N.H. No. 15976
Myctophum pristolepis (Gilbert and Cramer), A.M.N.H. No. 18153
Myctophum spinosum (Steindachner), A.M.N.H. No. 18150
Rhinoscopelus tenuiculus (Garman), A.M.N.H. No. 1915
Symbolophorus californiense (Eigenmann and Eigenmann), U.S.N.M. No. 201235

Neoscopelidae
Neoscopelus macrolepidotus Johnson, U.S.N.M. No. 188293; M.C.Z. No. 35596; A.M.N.H. No. 20545
Scopelengys tristis Alcock, U.S.N.M. No. 132459
Solivomer arenidens Miller, U.S.N.M. No. 135928

Ogcocephalidae
Halieutichthys aculeatus (Mitchill), A.M.N.H. No. 16324
Ogcocephalus vespertilio (Linnaeus), A.M.N.H. No. 146

Ophidiidae
Barathronus sp., U.S.N.M., uncatalogued
Brosmophycis marginata (Ayres), U.S.N.M., uncatalogued
Lepophidium graellsi (Poey), U.M.M.L. No. 6743
Luciobrotula corethromycter Cohen, U.S.N.M., uncatalogued
Petrotyx hopkinsi Heller and Snodgrass, U.S.N.M., uncatalogued
Rissola marginata (DeKay), U.M.M.L. No. 8541

Paralepididae
Lestidium speciosum (Bellotti), A.M.N.H. No. 17232
Macroparalepis sp., U.S.N.M. No. 201186
Paralepis elongata (Brauer), M.C.Z. No. 43125

Percidae
Perca flavescens (Mitchill), B.M.N.H. Nos. 1893.2.7.27–1893.2.7.36

Percopsidae
Percopsis omiscomaycus (Walbaum), A.M.N.H. No. 21019; U.F. No. 8718; B.M.N.H. Nos. 1892.12.30.371–373, 1898.12.29.183
Percopsis transmontana (Eigenmann and Eigenmann), U.S.N.M. No. 104650; B.M.N.H. No. 1892.12.30.421

Pholidae
Apodichthys flavidus Girard, A.M.N.H. No. 462
Enedrias nebulosus (Temminck and Schlegel), A.M.N.H. No. 470
Pholis ornatus (Girard), A.M.N.H. No. 309
Ulvicola sanctaerosae Gilbert and Starks, U.M.M.Z. No. 141287
Xererpes fucorum (Jordan and Gilbert), A.M.N.H. No. 17913

Polymixiidae
Polymixia japonica Steindachner, U.M.M.Z. No. 180102; B.M.N.H. No. 1890.2.26.24
Polymixia lowei Günther, U.S.N.M. Nos. No. 157751, 157754
Polymixia nobilis Lowe, B.M.N.H. No. 1895.5.28.1

Regalecidae
Regalecus glesne (Ascanius), U.S.N.M. No. 164226

Rondeletiidae
Rondeletia bicolor Goode and Bean, U.S.N.M. No. 38202; B.M.N.H. No. 1929.5.3.1

Rosauridae
Rosaura sp., U.S.N.M., uncatalogued

Scopelarchidae
Scopelarchoides nicholsi Parr, U.S.N.M. No. 201154

Scorpaenidae
Scorpaena isthmensis Meek and Hildebrand, B.M.N.H. No. 1923.7.30.320–323

Scytalinidae
Scytalina cerdale Jordan and Gilbert, A.M.N.H. No. 3253

Serranidae
Epinephelus sp., B.M.N.H. No. 1956.9.6.95

Siganidae
Siganus sp., A.M.N.H., uncatalogued

Stephanoberycidae
Acanthochaenus lutkenii Gill, U.S.N.M. No. 35464
Stephanoberyx monae Gill, U.S.N.M. No. 46122

Stichaeidae
Anoplarchus purpurescens Gill, A.M.N.H. No. 19659
Epigeichthys atropurpureus (Kittlitz), A.M.N.H. No. 17911
Lumpenus lumpretaeformis (Walbaum), A.M.N.H. No. 20129
Lumpenus maculatus (Fries), A.M.N.H. No. 20122
Phytichthys chirus (Jordan and Gilbert), A.M.N.H. No. 2677
Stichaeus punctatus (Fabricius), A.M.N.H. No. 17859
Xiphister mucosus (Girard), A.M.N.H. No. 17268

Synodontidae
Saurida brasiliensis Norman, U.S.N.M. No. 185852
Saurida gracilis (Quoy and Gaimard), A.M.N.H. No. 7741

Saurida tumbil (Bloch), A.M.N.H. No. 17265
Synodus foetens (Linnaeus), A.M.N.H. No. 18161
Synodus synodus (Linnaeus), A.M.N.H. No. 23108
Trachinocephalus myops (Forster), A.M.N.H. No. 13226
Trachichthyidae
Gephyroberyx sp., U.M.M.Z. No. 180097
Hoplostethus mediterraneus Valenciennes, U.M.M.Z. No. 142821; B.M.N.H. No. 1878.4.5.8
Trachipteridae
Trachipterus rexsalmonorum Jordan and Gilbert, A.M.N.H., uncatalogued
Desmodema sp., U.S.N.M. No. 164327
Tripterygiidae
Enneanectes altivelis Rosenblatt, A.M.N.H. No. 23064
Tripterygion atriceps Jenkins, A.M.N.H. No. 12117
Veliferidae
Velifer hypselopterus Bleeker, B.M.N.H. No. 1849.10.9.16
Zeidae
Zeus japonicus Cuvier, A.M.N.H. No. 894
Zoarcidae
Lycodapus dermatinus Gilbert, A.M.N.H. No. 12837
Lycodes frigidus Collett, B.M.N.H., No. 1887.12.9.5
Lycodes reticulatus Reinhardt, A.M.N.H. No. 20127
Lycodopsis pacifica (Collett), A.M.N.H. No. 2715
Macrozoarces americanus (Bloch and Schneider), A.M.N.H., uncatalogued
Rhigophila sp., U.M.M.Z. No. 179558
Zoarces viviparus (Linnaeus), B.M.N.H. No. 1938.2.21.2–4

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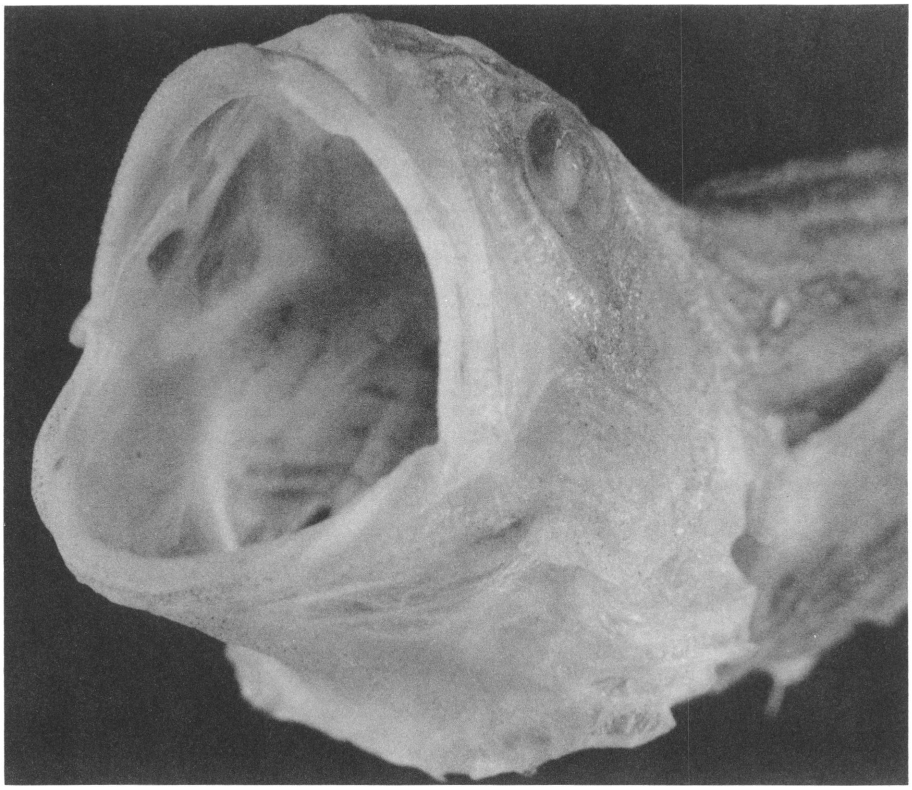

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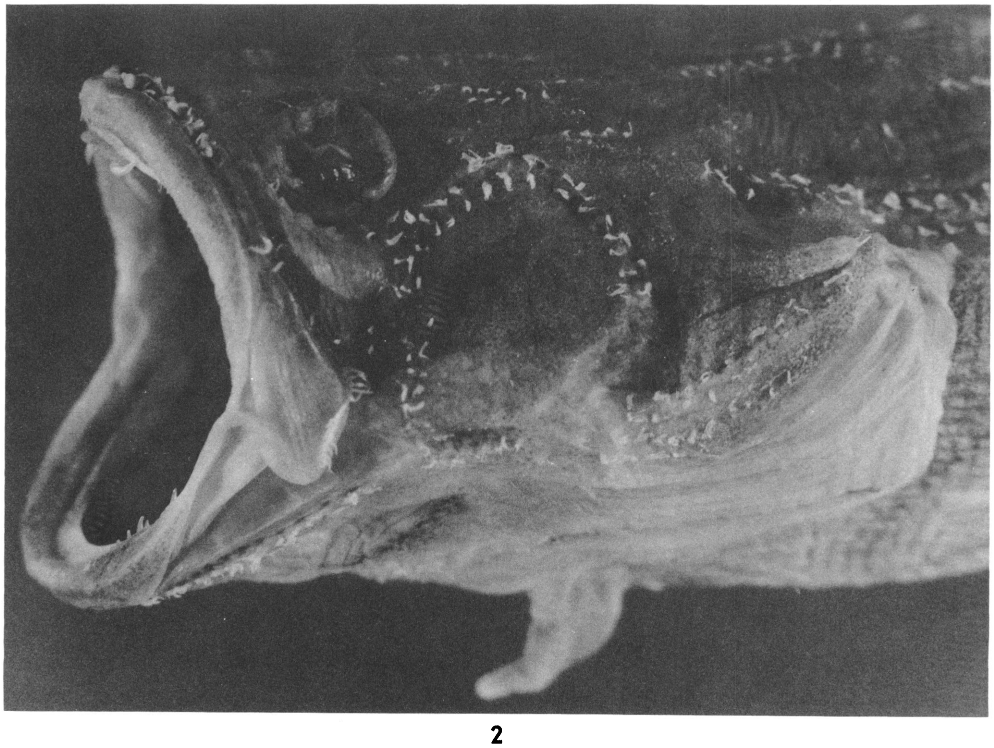
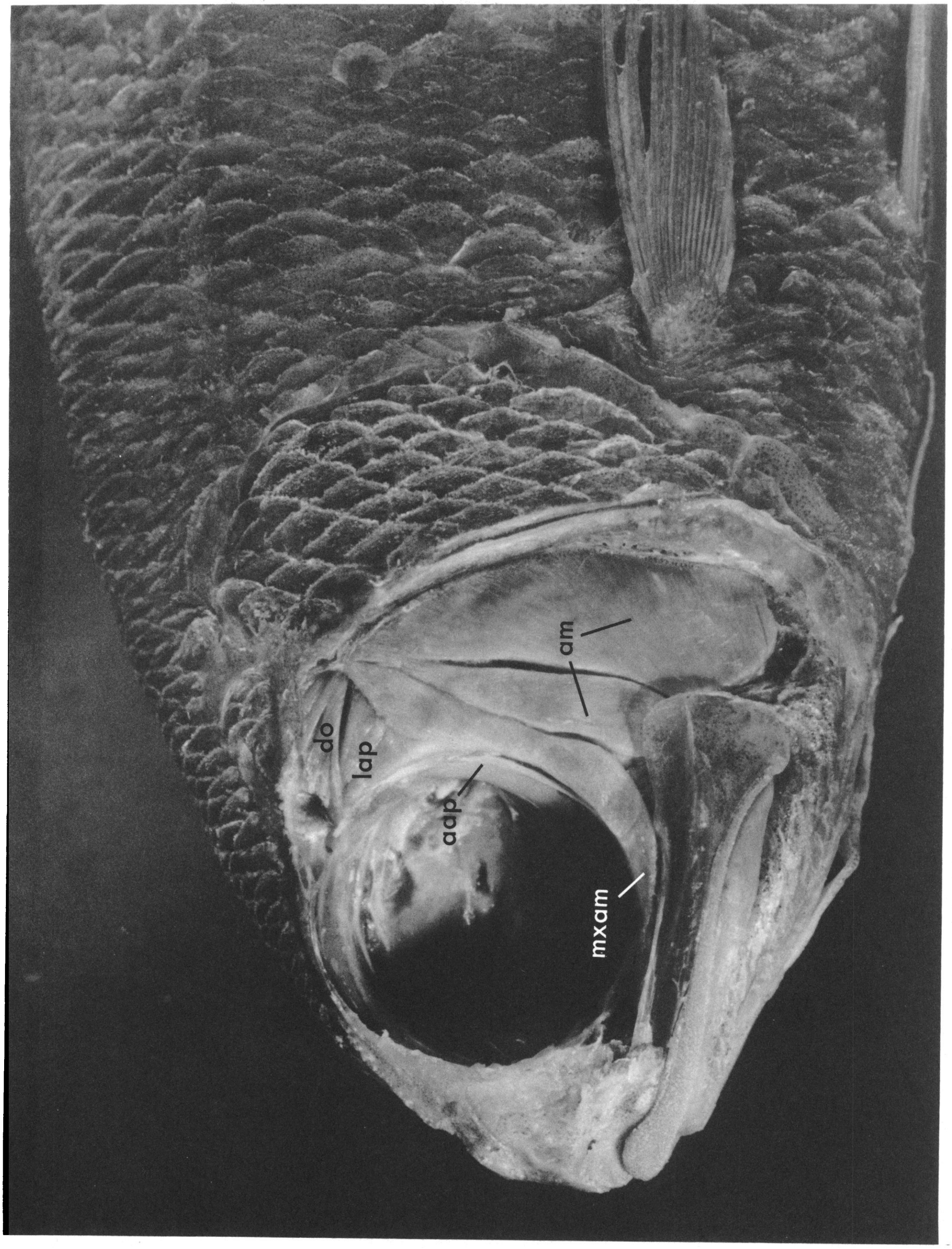


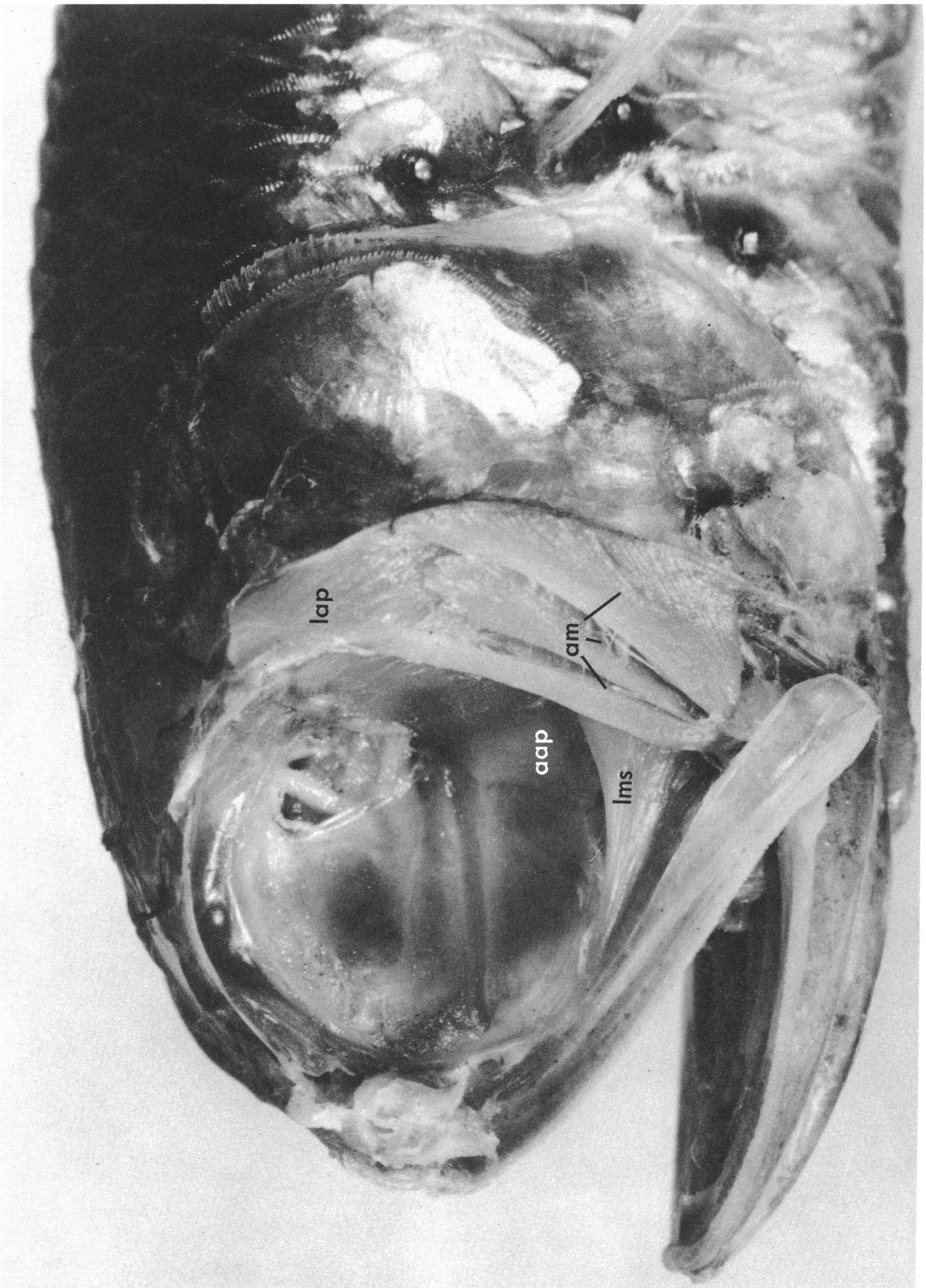
2

1. *Pycnocraspedum squamipinne* Alcock, with mouth widely opened. 2. *Porichthys margaritatus* (Richardson), with mouth widely opened

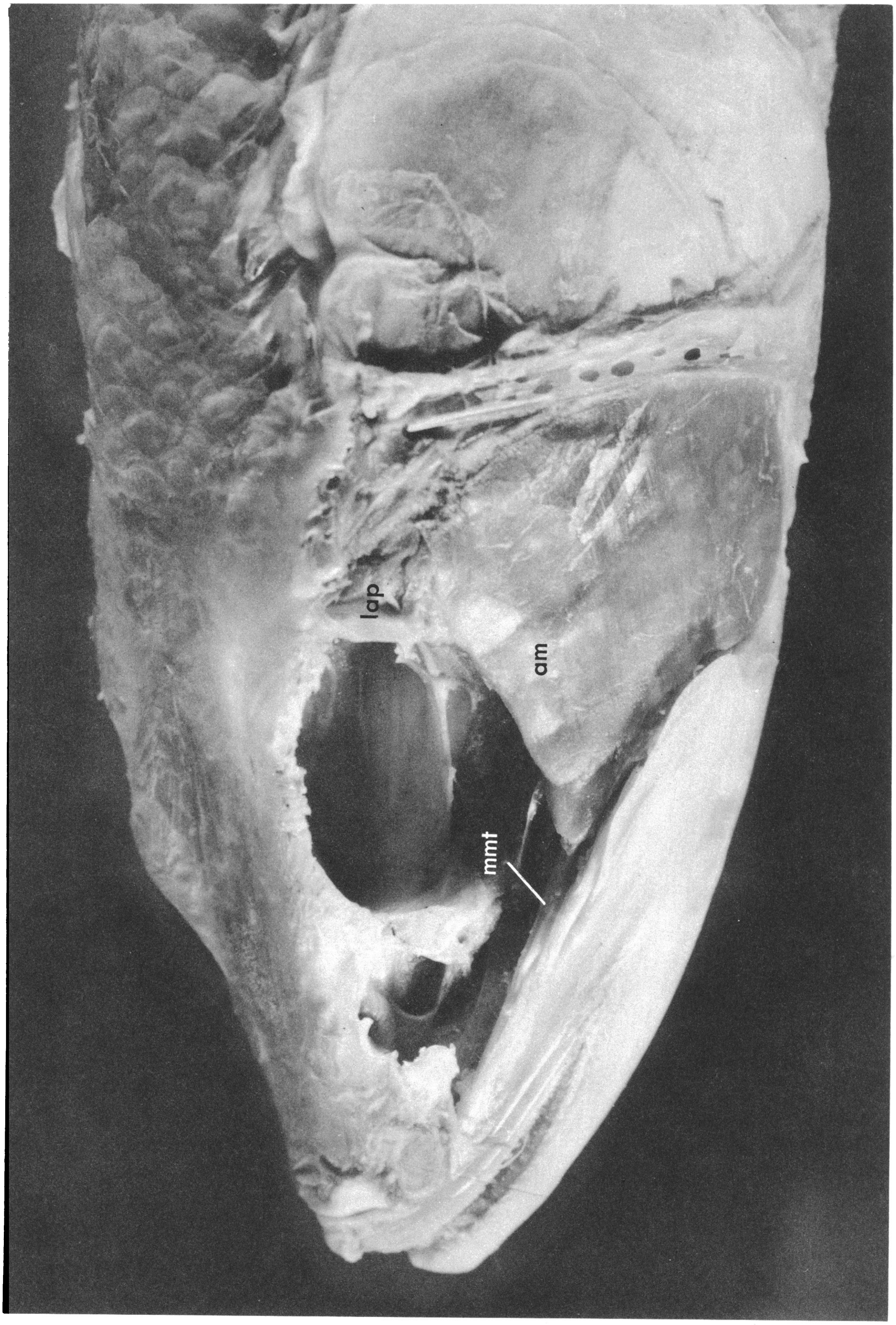


Superficial cheek dissection of *Polymixia lowei* Günther

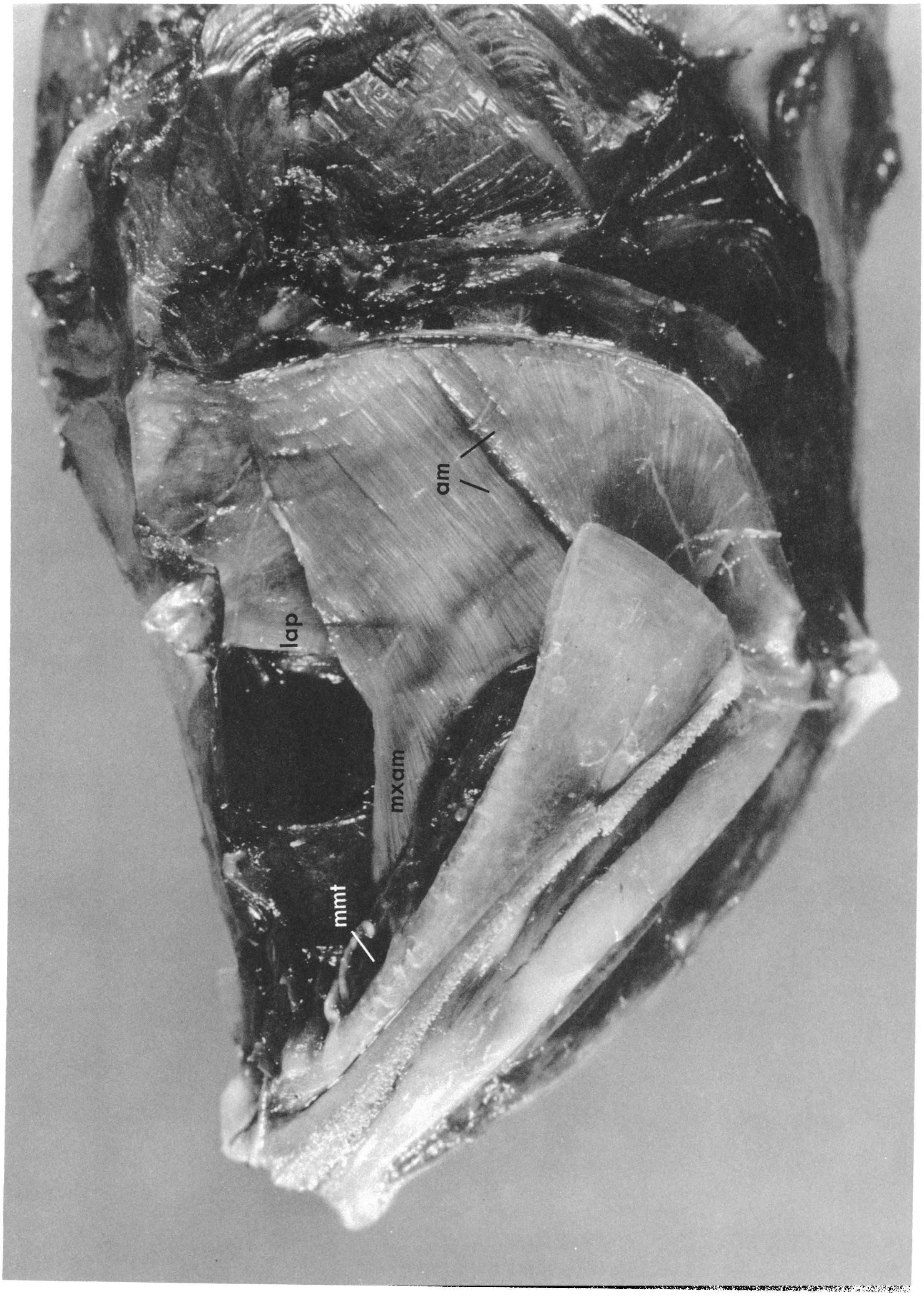
Superficial cheek dissection of *Gadopsis marmoratus* Richardson



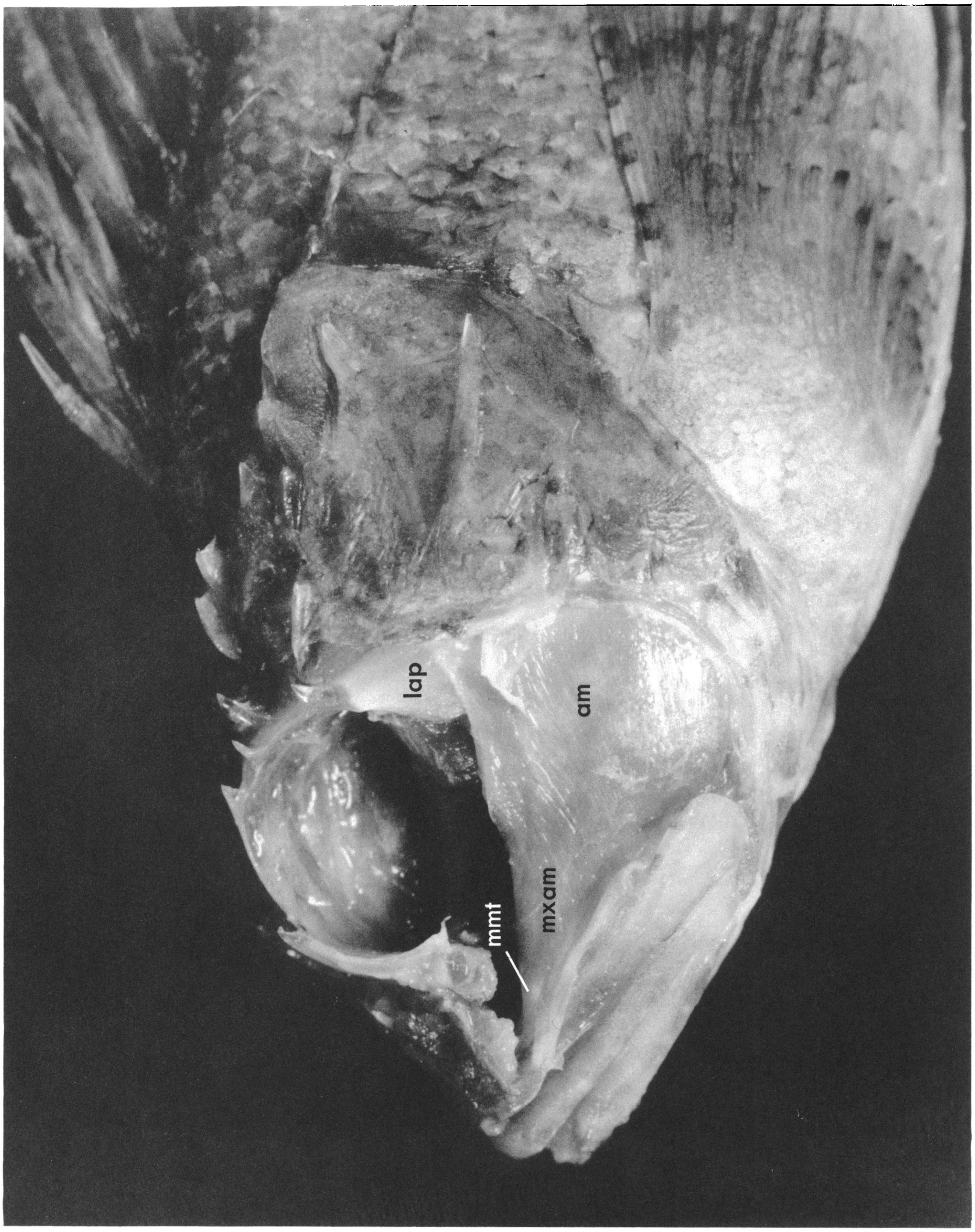
Superfical cheek dissection of *Myctophum spinosum* (Steindachner)



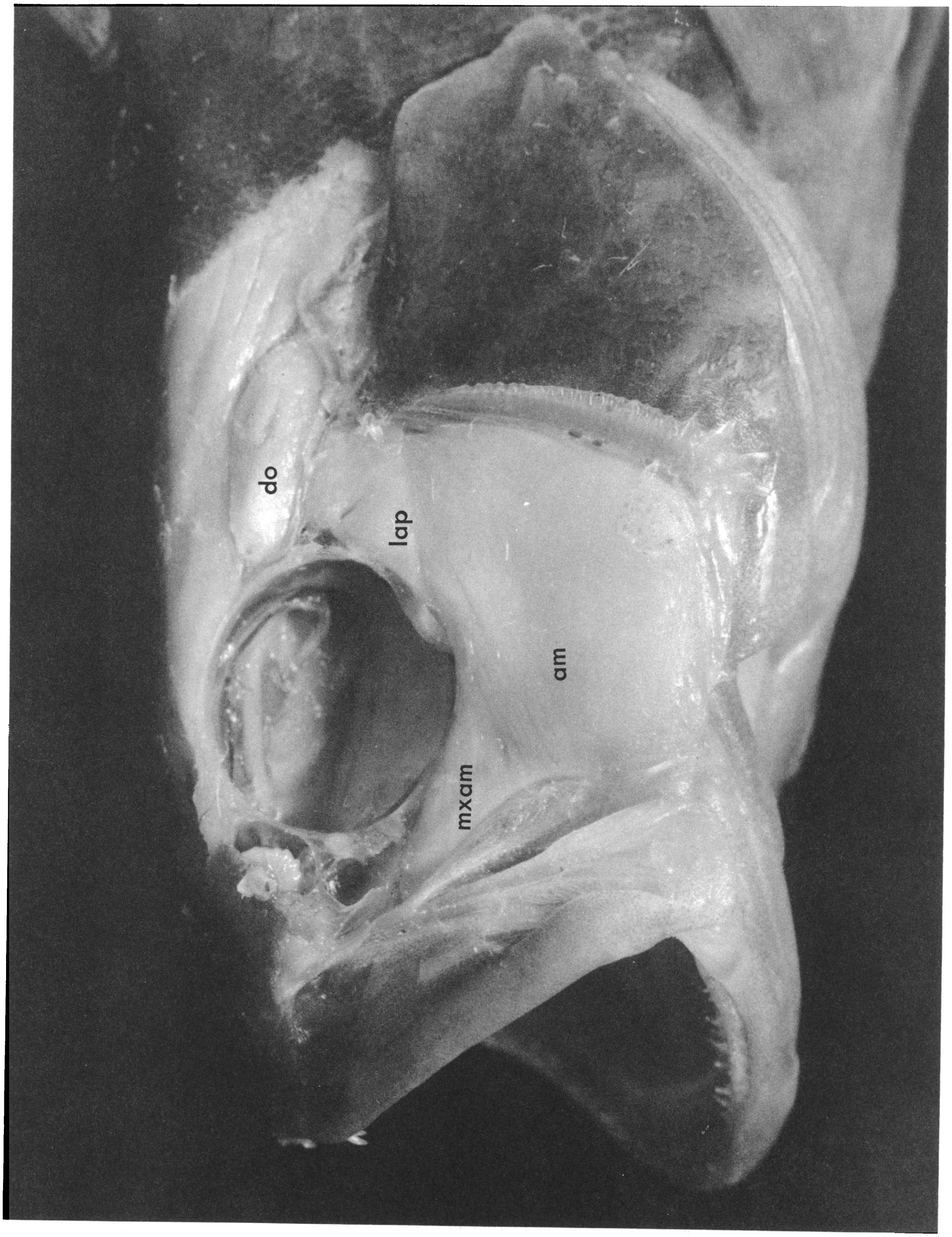
Superficial cheek dissection of *Aulopus purpurissatus* Richardson



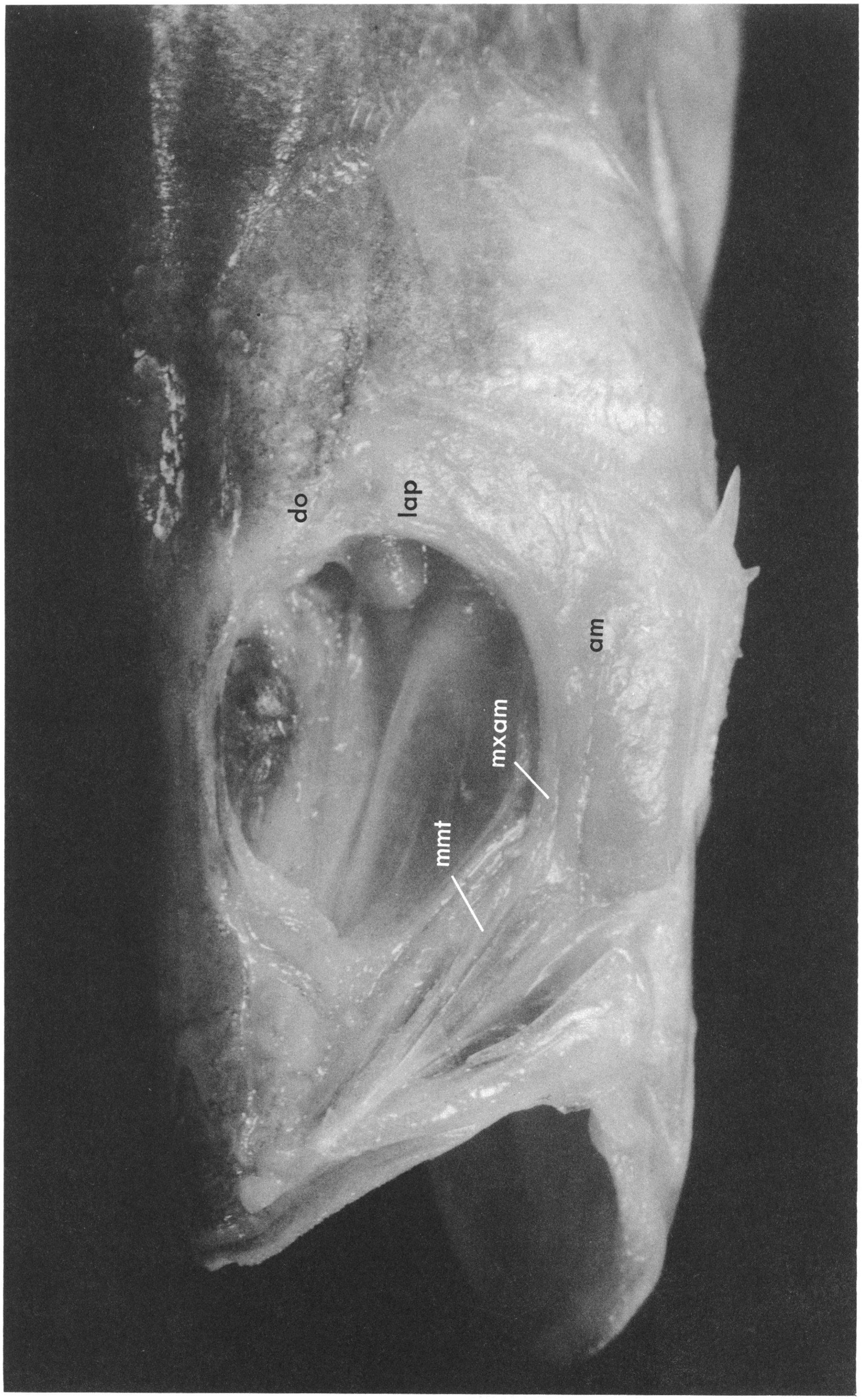
Superficial cheek dissection of *Scopelengys tristis* Alcock



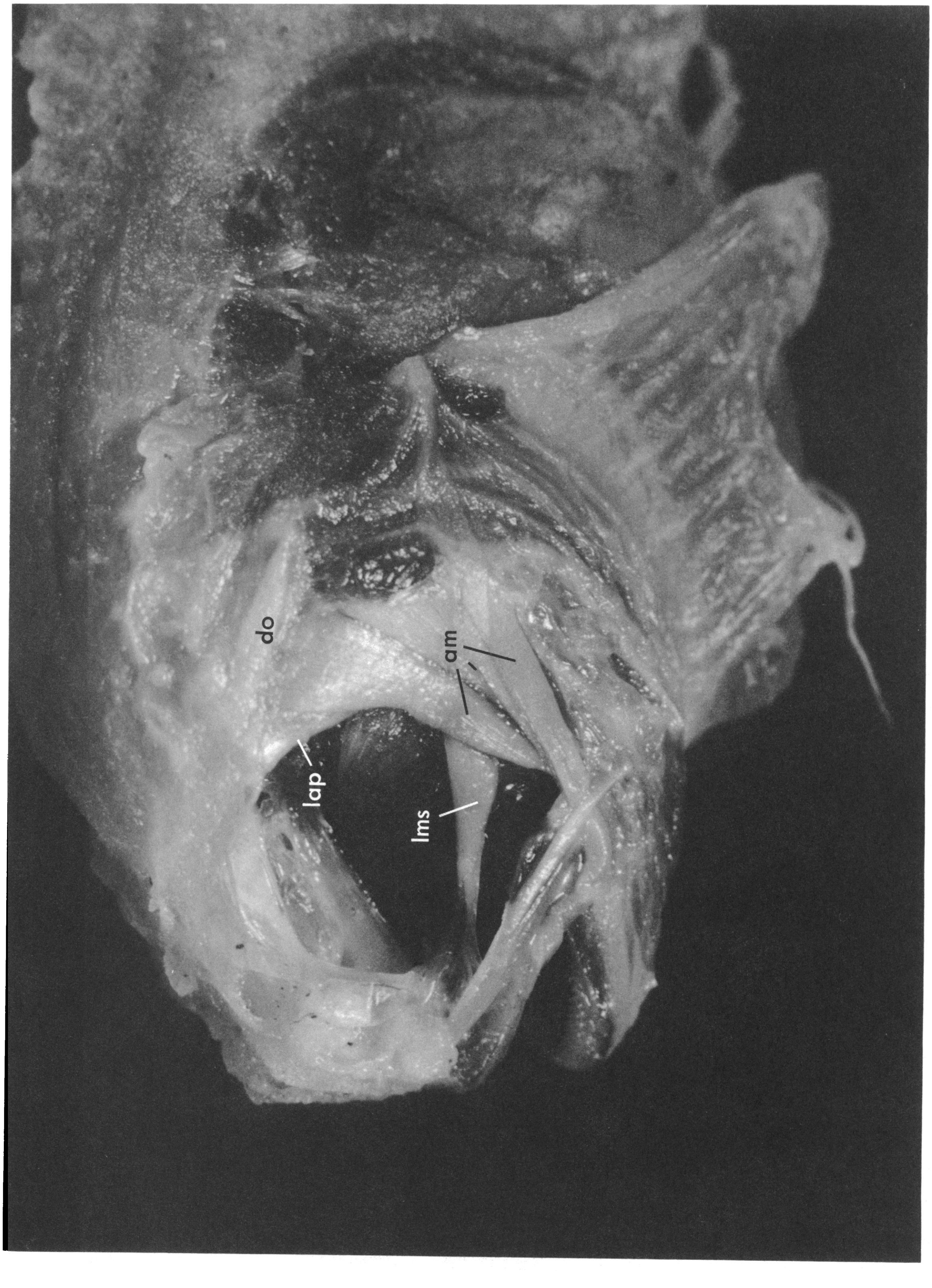
Superficial cheek dissection of *Scorpaena isthmensis* Meek and Hildebrand



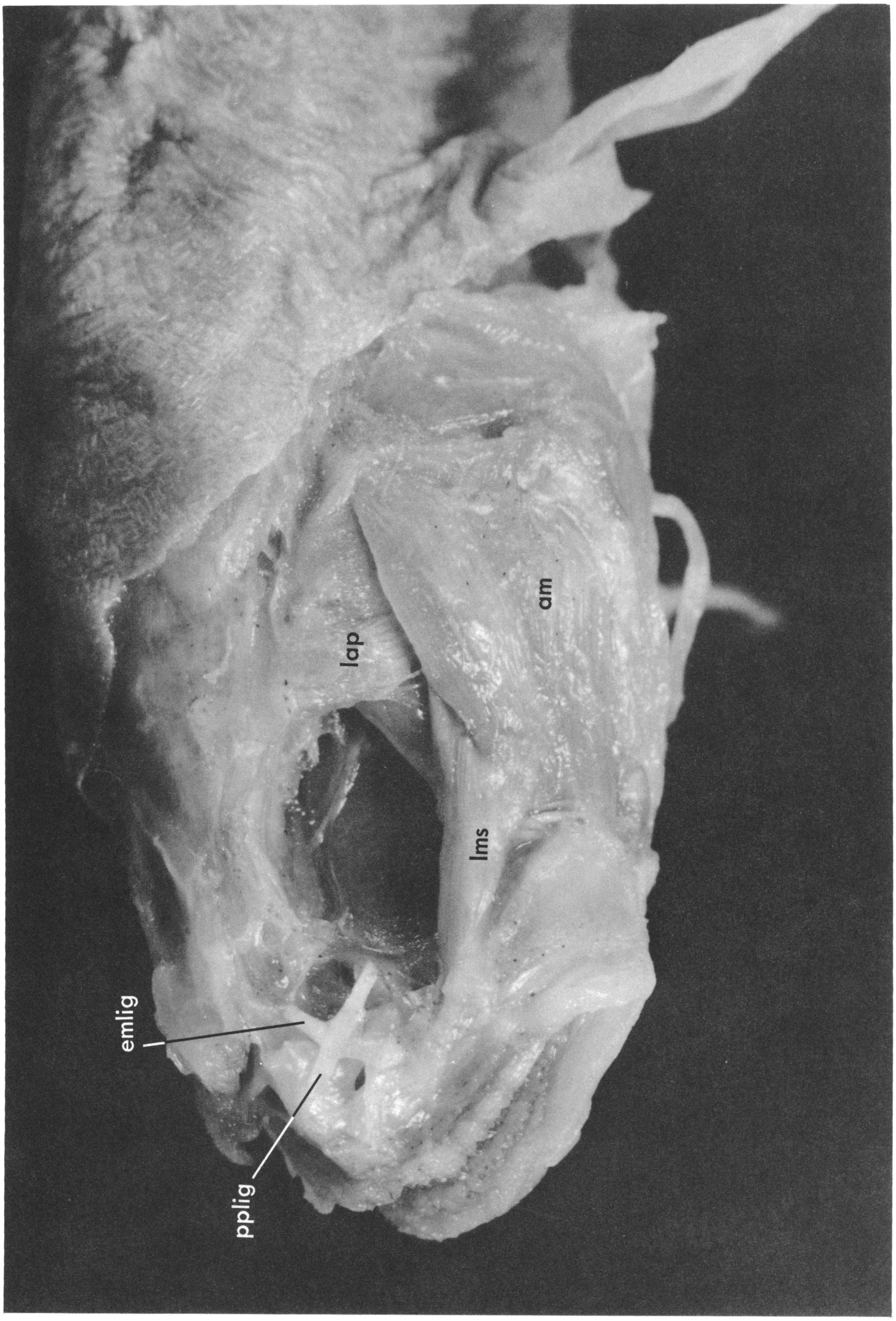
Superficial cheek dissection of *Epinephelus* sp.



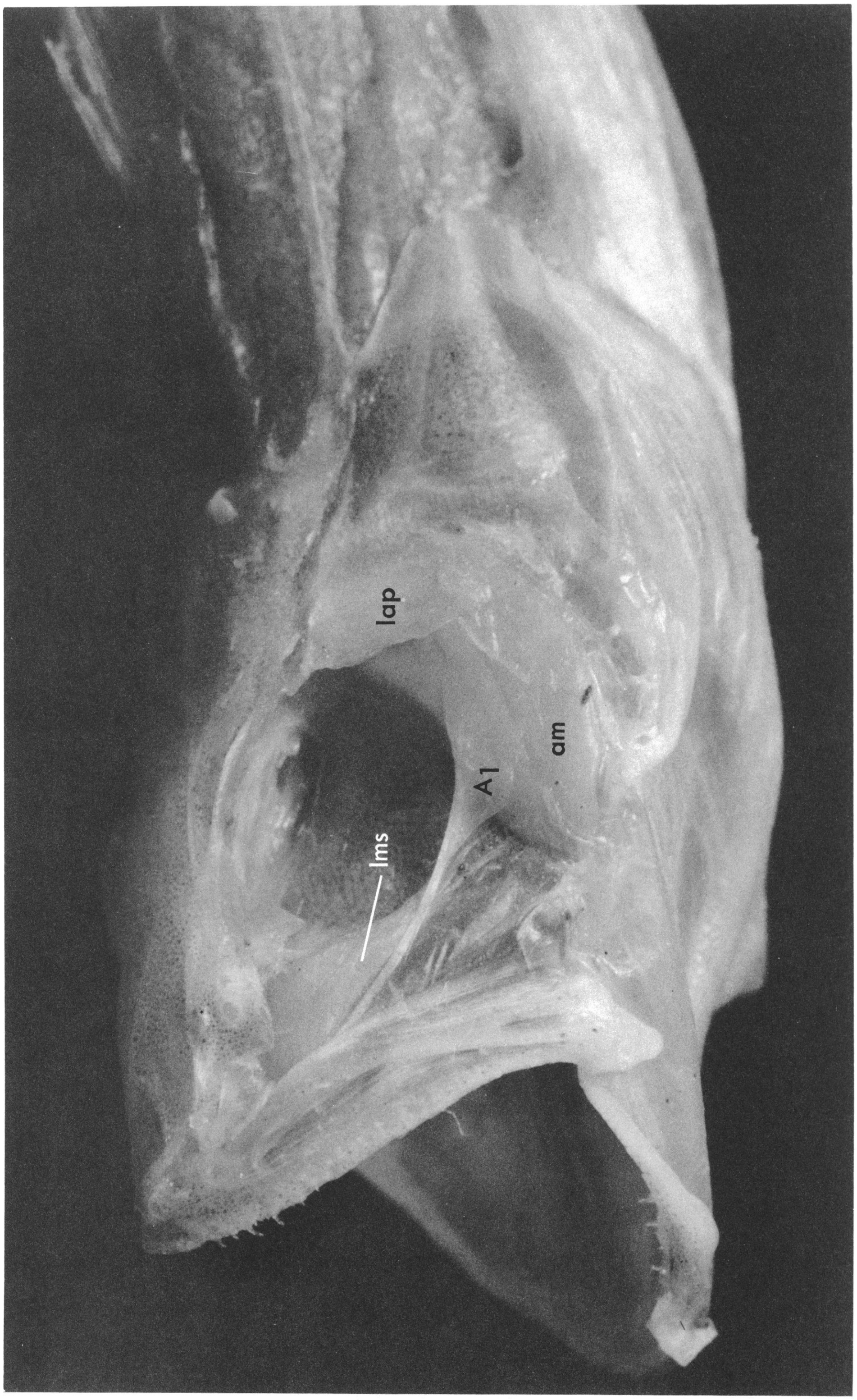
Superficial cheek dissection of *Lates microlepis* Boulenger



Superficial cheek dissection of *Paraliparis* sp.

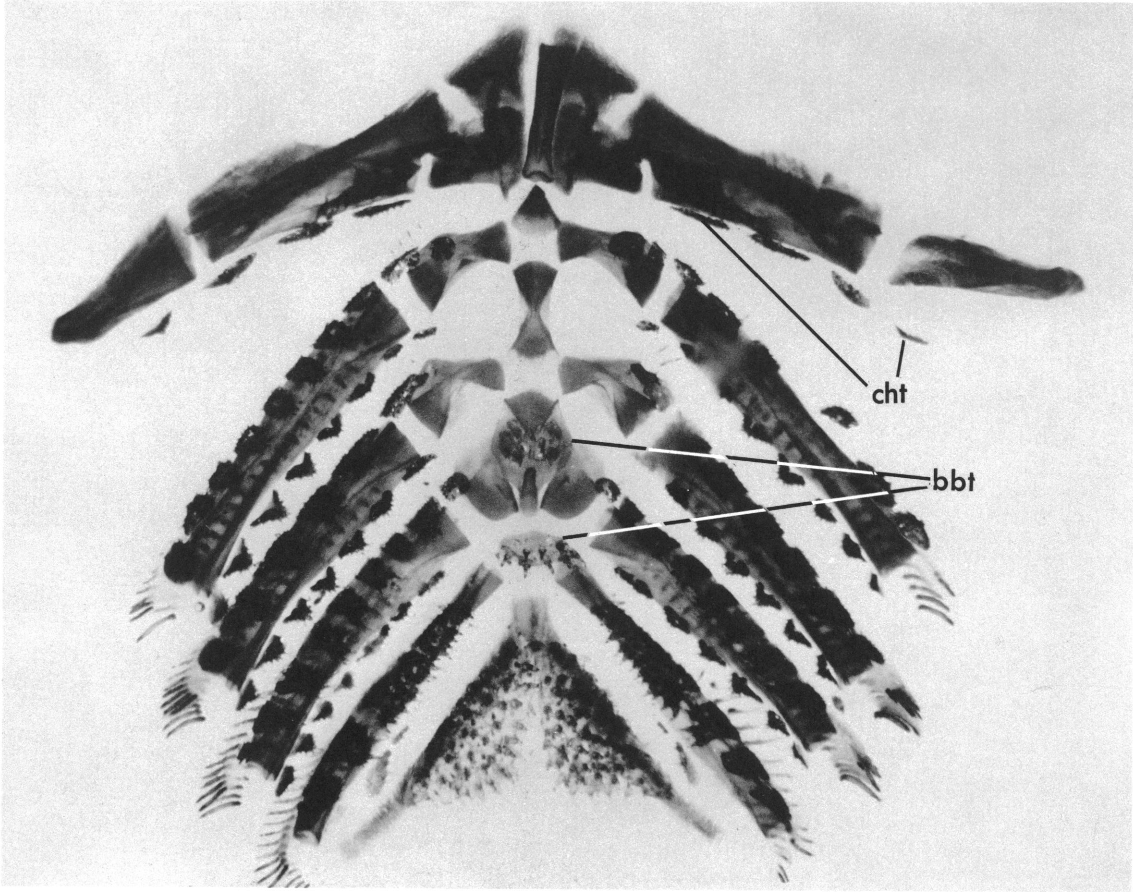


Superficial cheek dissection of *Muraenolepis microps* Lönnberg



Superficial cheek dissection of *Merluccius capensis* Castlenau

Photomicrograph of a cleared and stained caudal skeleton of *Percopsis omiscomaycus* (Walbaum), showing doubling of the neural spine and the base of the haemal spine on the second pre-ural centrum



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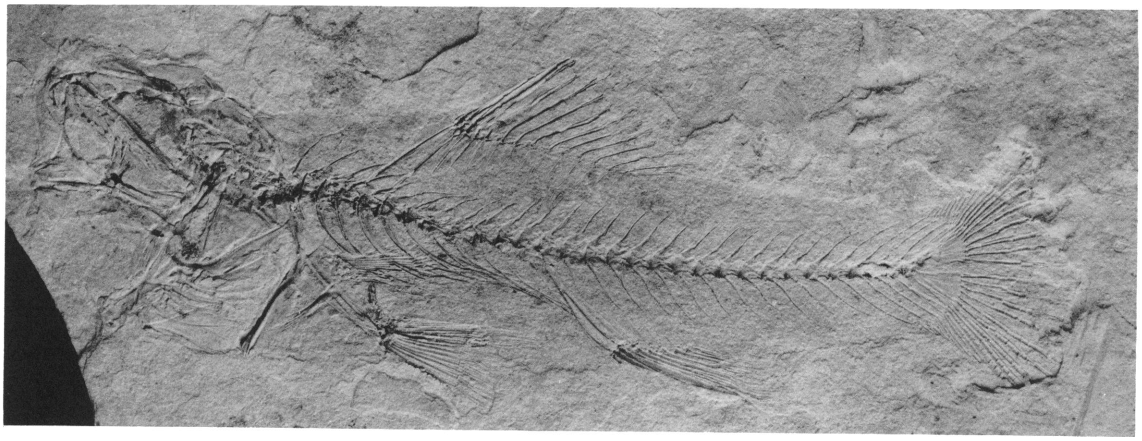
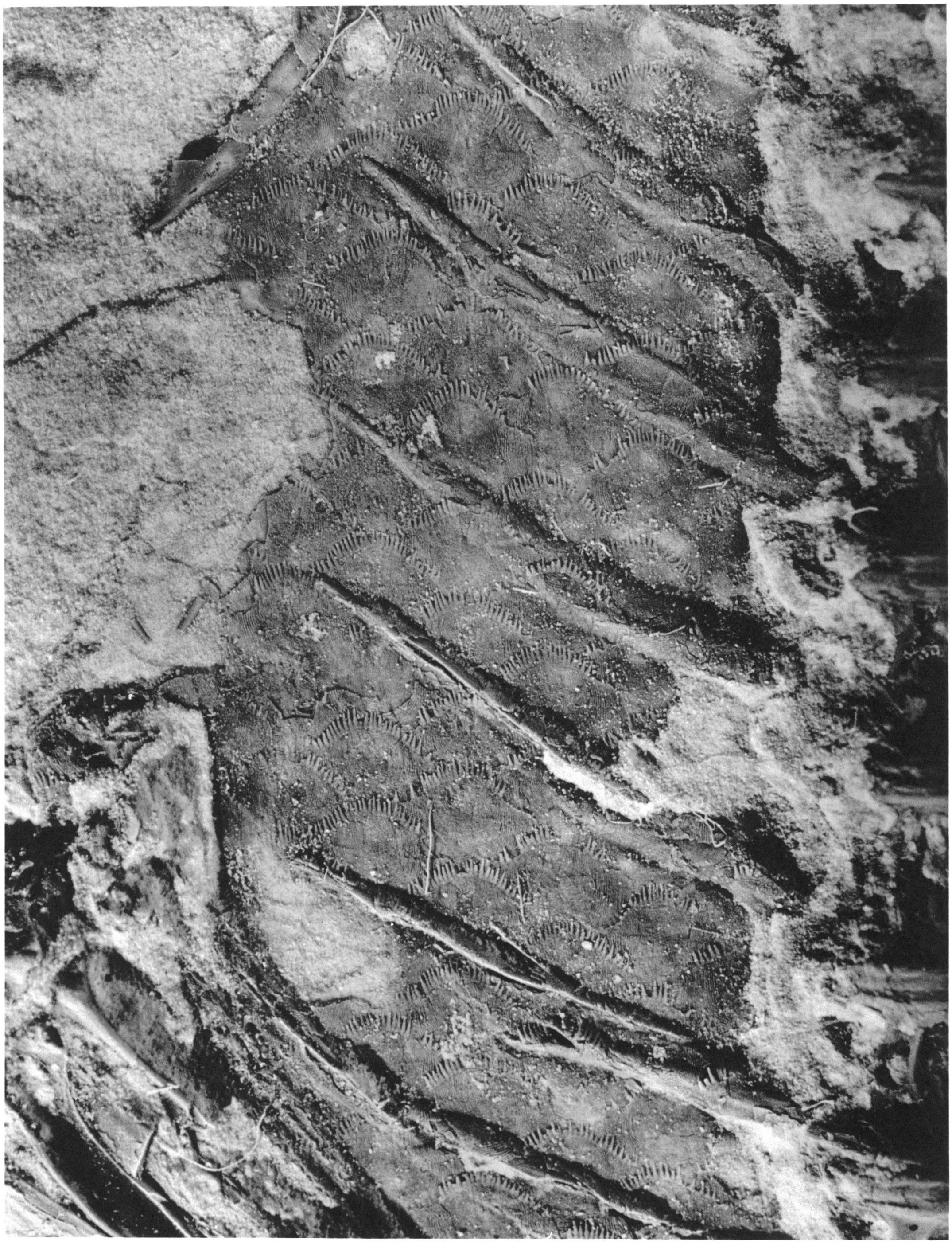


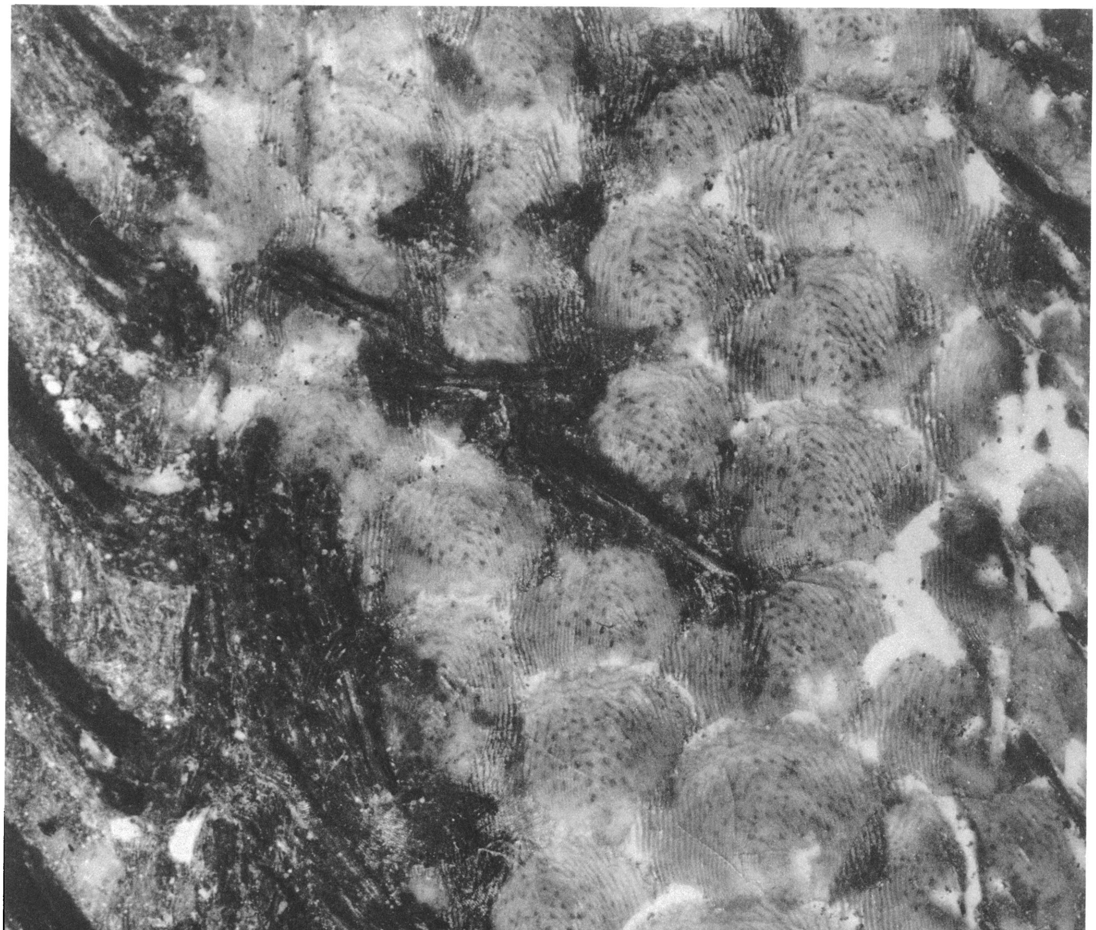
2

1. Photomicrograph of the hyoid bar and ventral half of the pharyngobranchial apparatus of *Percopsis transmontana* (Eigenmann and Eigenmann), showing the distribution of dermal tooth-bearing plates

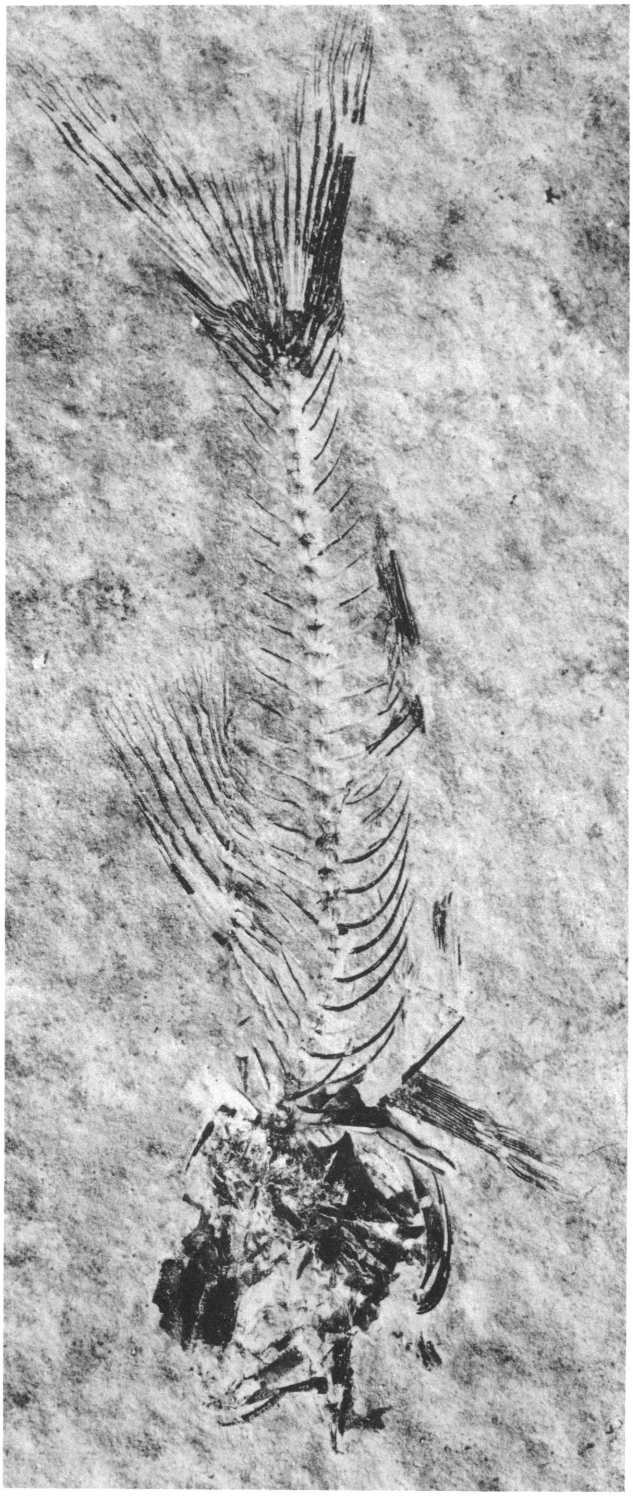
2. *Trichophanes foliarum* Cope, Oligocene, Florissant lake beds, Florissant, Colorado; B.M.N.H. No. P.12506



Amphiplaga brachyptera Cope, Middle Eocene, Green River Shales, Wyoming. Enlarged sections of caudal peduncle below and behind dorsal fin to show ctenoid scales; U.S.N.M. No. 4011



Asineops squamifrons Cope, Middle Eocene, Green River Shales, Wyoming. Enlarged section of trunk below dorsal fin spines to show large cycloid scales; U.S.N.M. No. 19873



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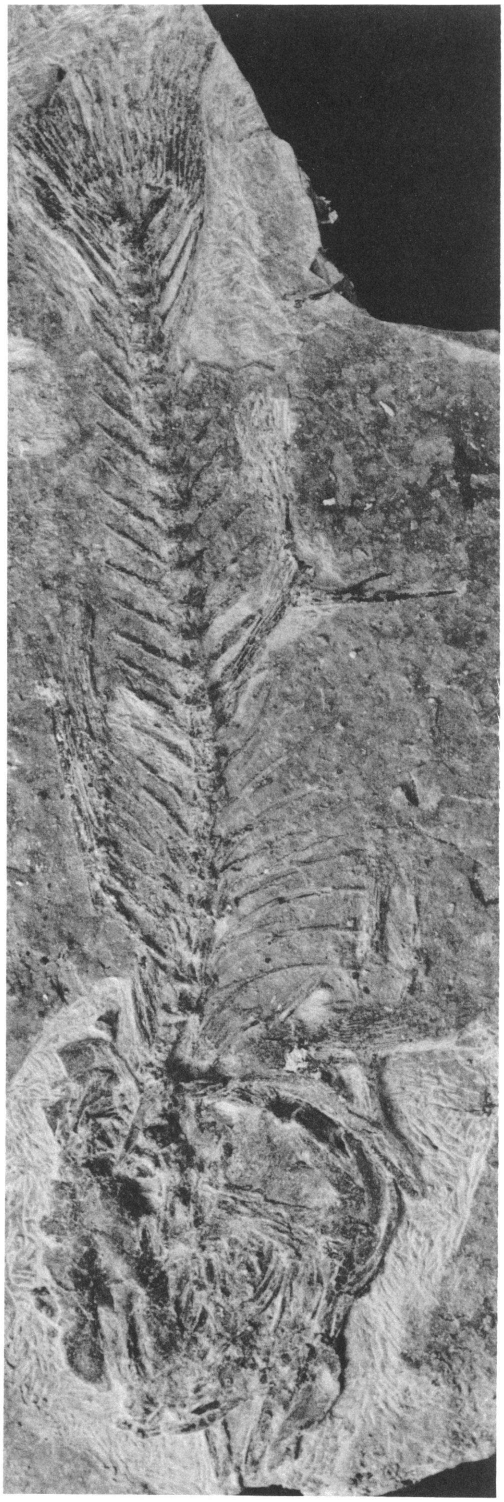

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1. *Amphiplaga brachyptera* Cope, Middle Eocene, Green River Shales, Wyoming; U.S.N.M. No. 18133
2. *Erismatopterus levatus* Cope, Middle Eocene, Green River Shales, Wyoming; uncatalogued A.M.N.H. specimen

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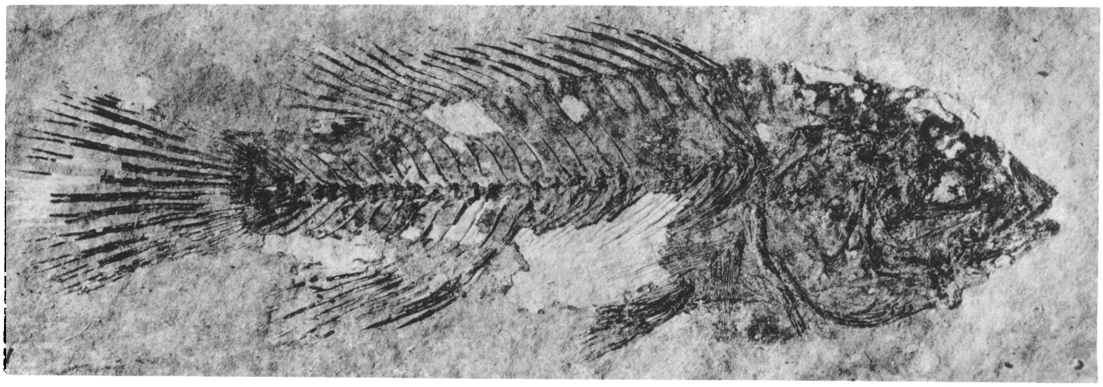
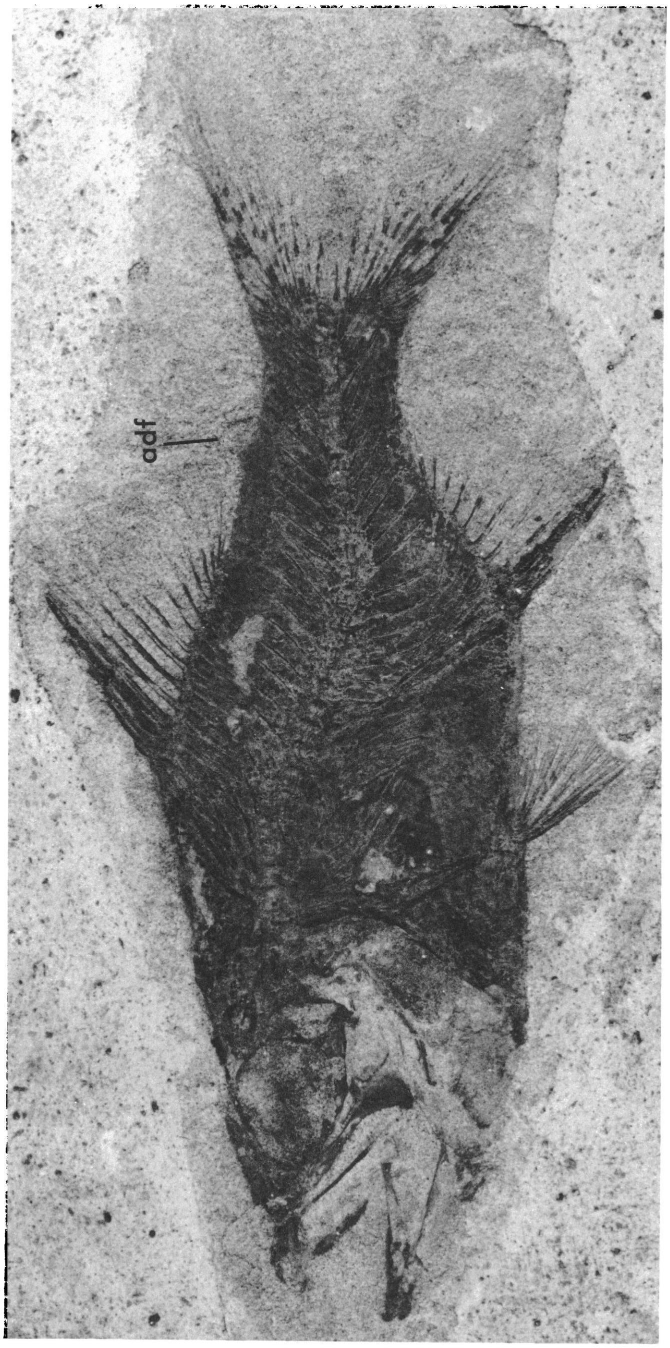


2

1. *Spenocephalus fissicaudus* Agassiz, Campanian, Baumberg, Westphalia. Caudal region of B.M.N.H. No. P.9059, showing adipose fin

2. *Asineops squamifrons* Cope, Middle Eocene, Green River shales, Wyoming; M.C.Z. No. 2837



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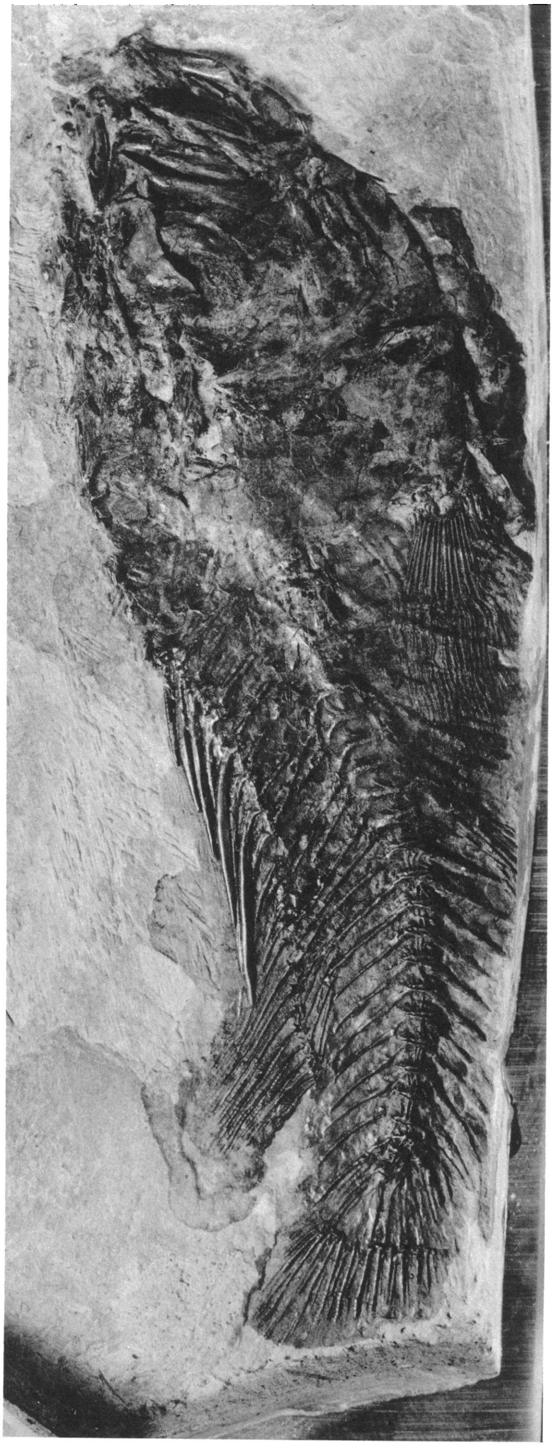

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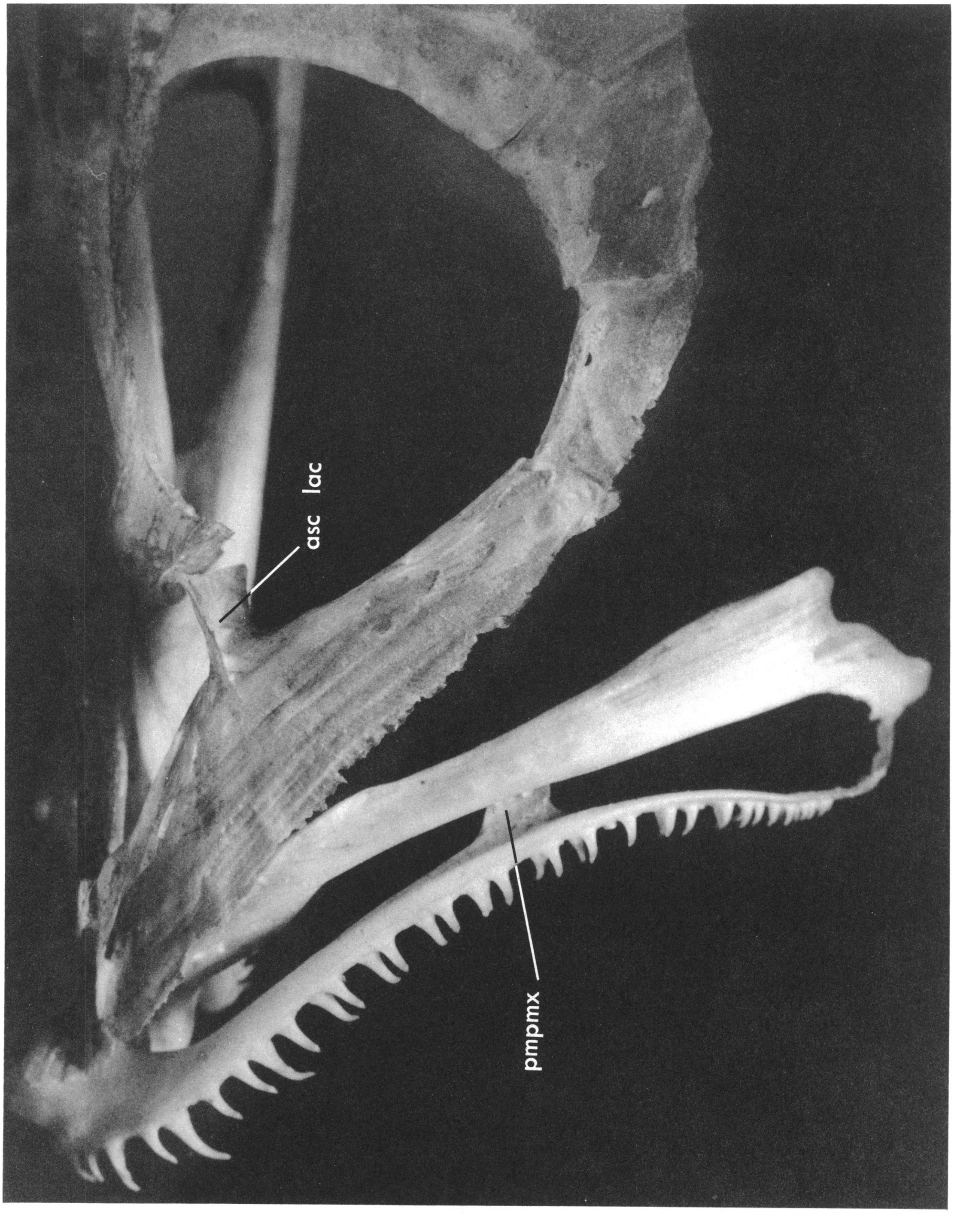
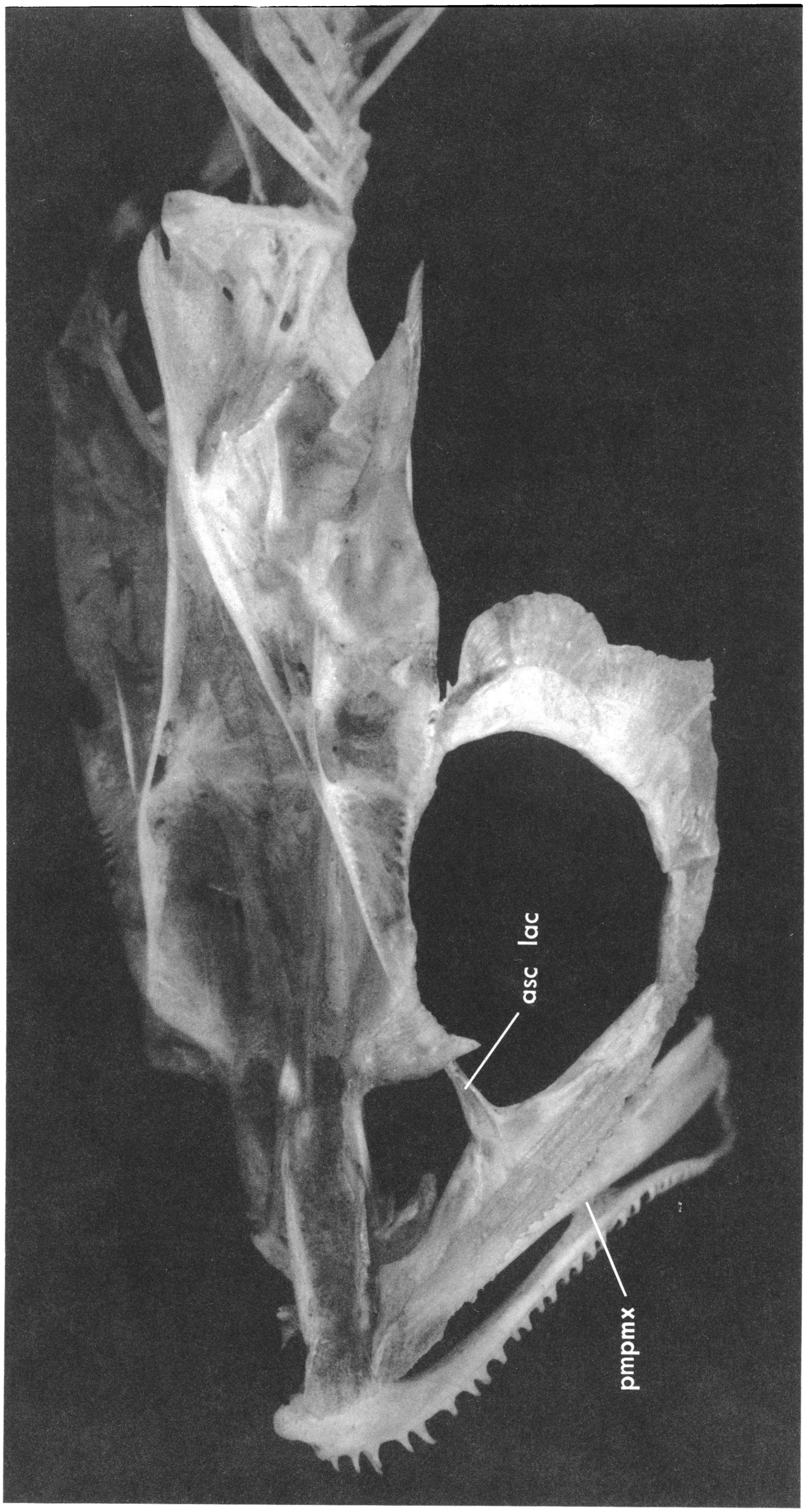
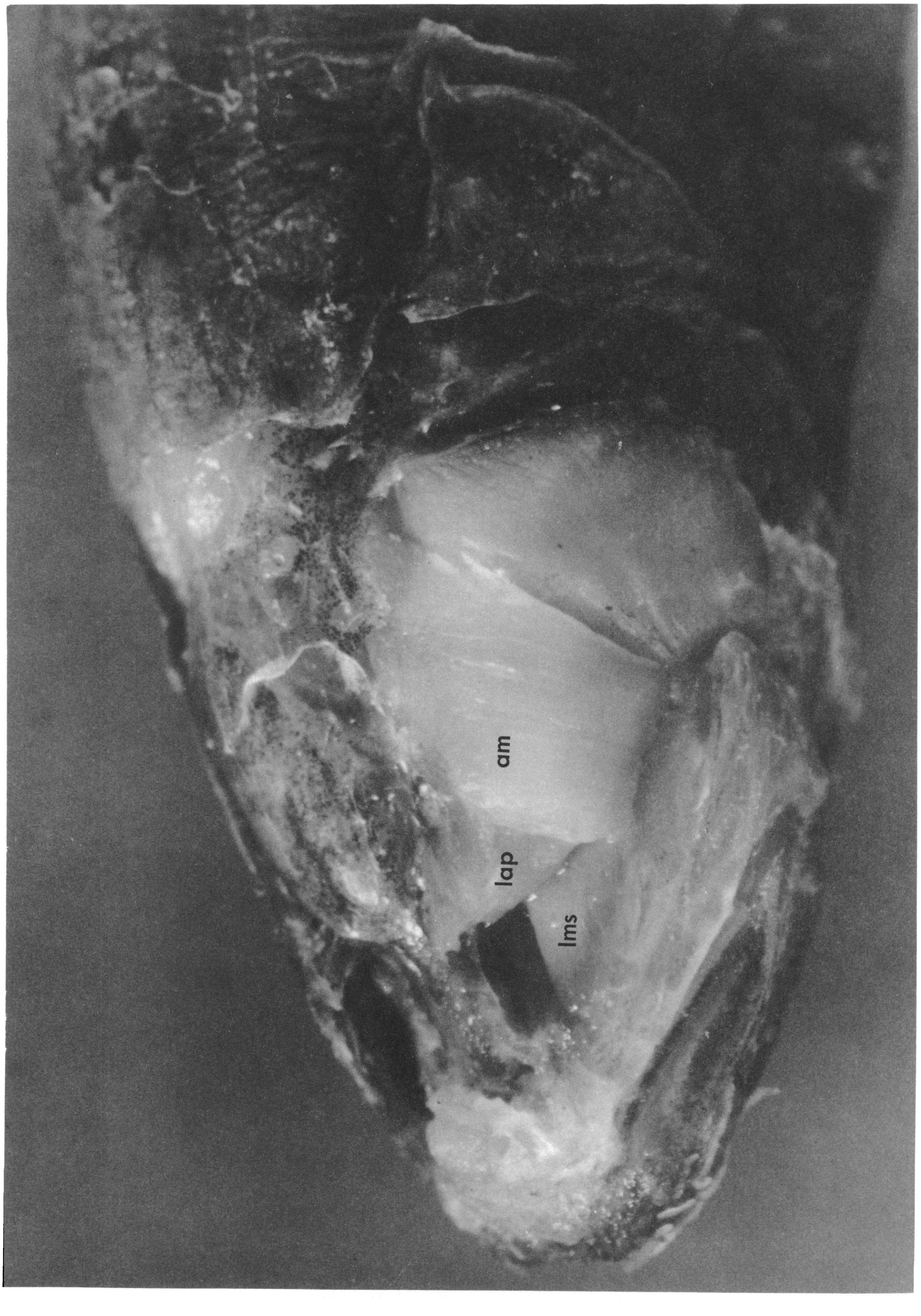
1. *Sphenocephalus fissicaudus* Agassiz, Campanian, Baumberg, Westphalia; G.P.I.M. No. 934
2. *Asineops squamifrons* Cope, Middle Eocene, Green River Shales, Wyoming; U.S.N.M. No. 1111



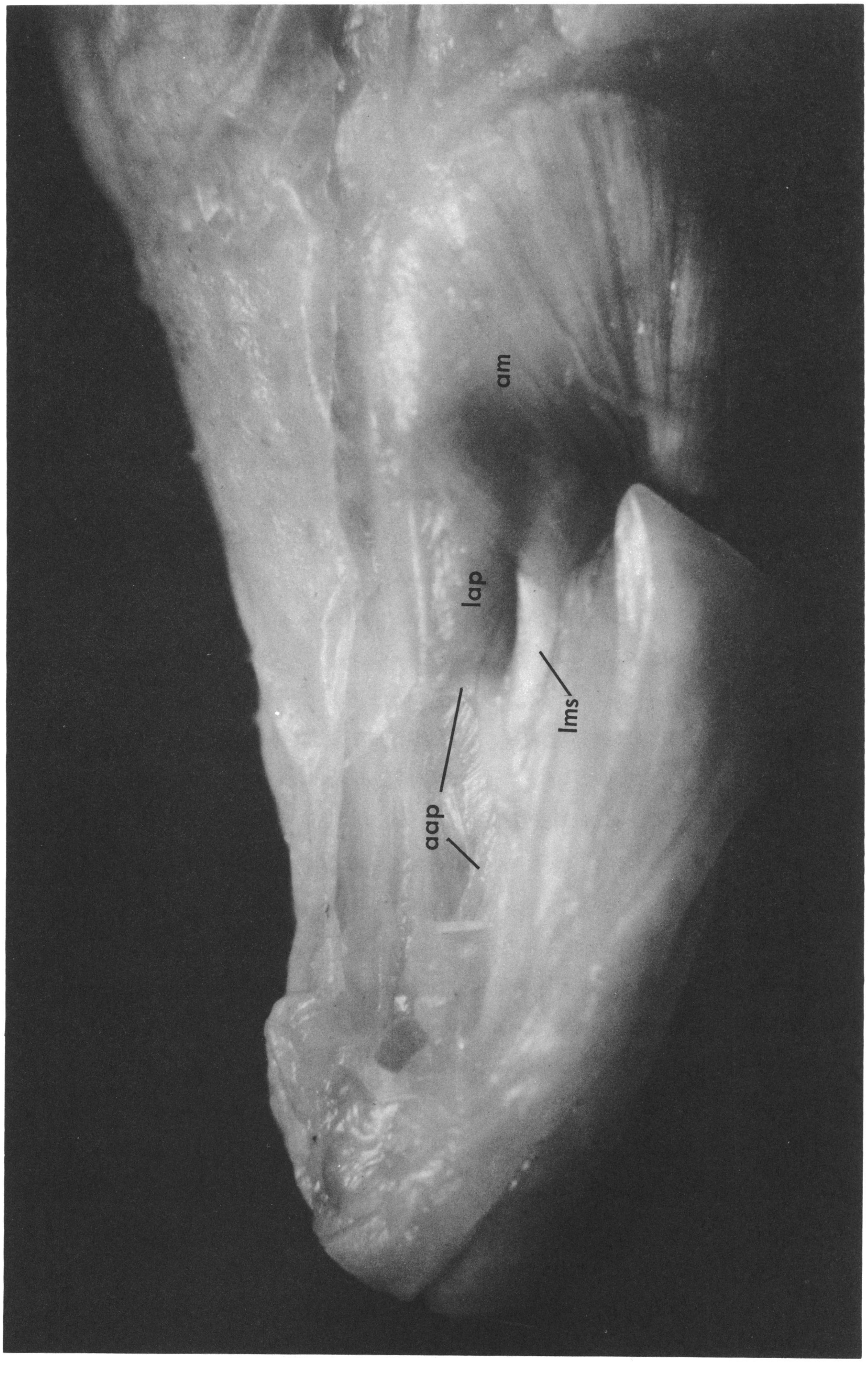
Anterior part of neurocranium and upper jaw of *Merluccius bilinearis* (Mitchill)



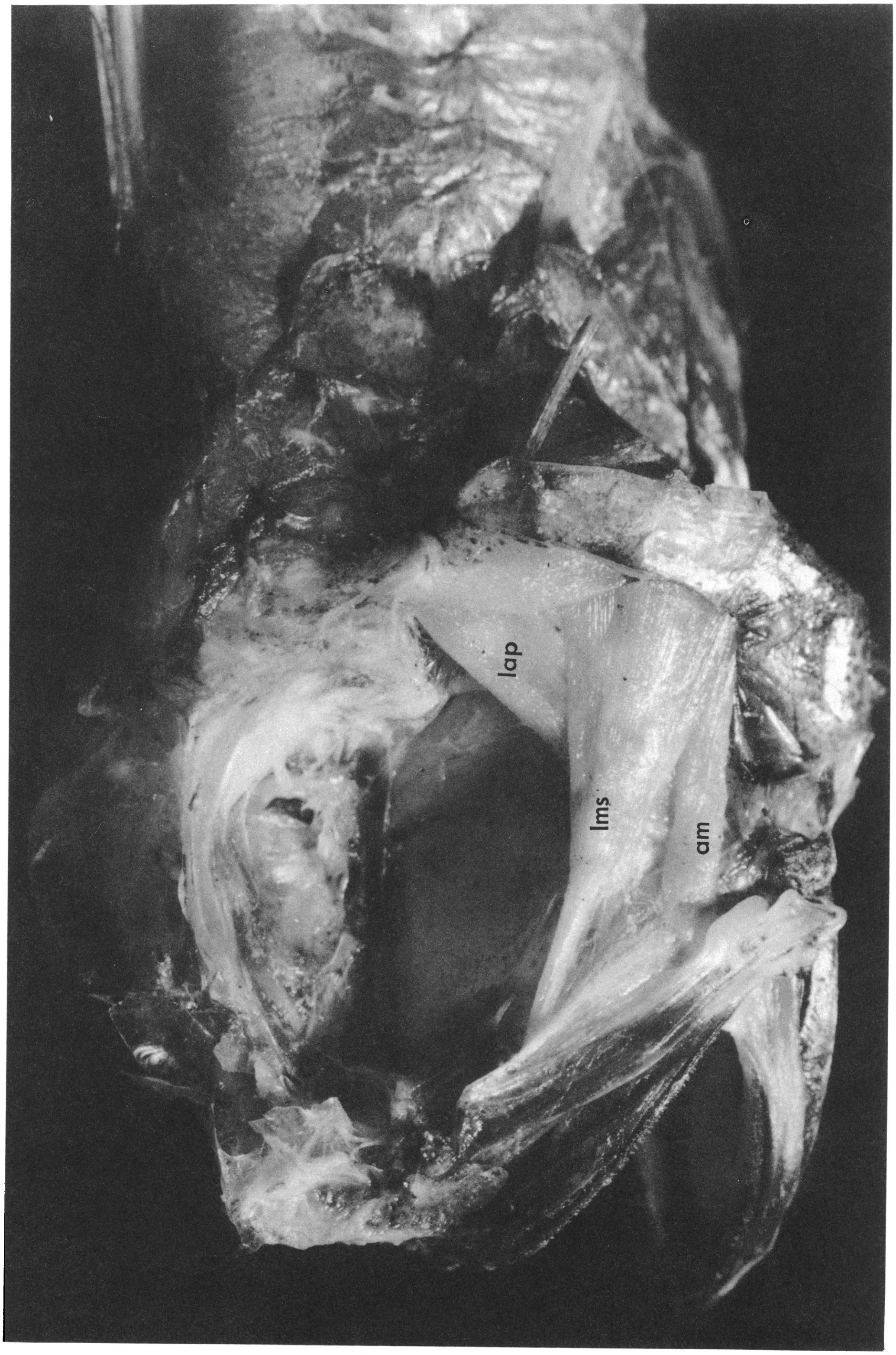
Neurocranium and upper jaw of *Merluccius bilinearis* (Mitchill)



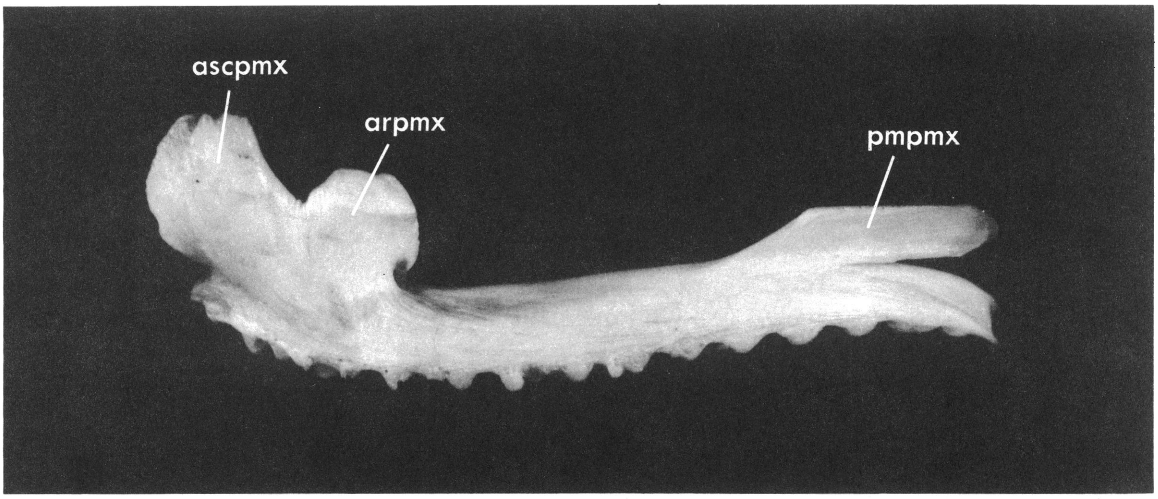
Superficial cheek dissection of *Dinematichthys* sp.



Superficial cheek dissection of *Lucifuga subterraneus* Poey



Superficial cheek dissection of *Hymenocephalus antraeus* Gilbert and Cramer



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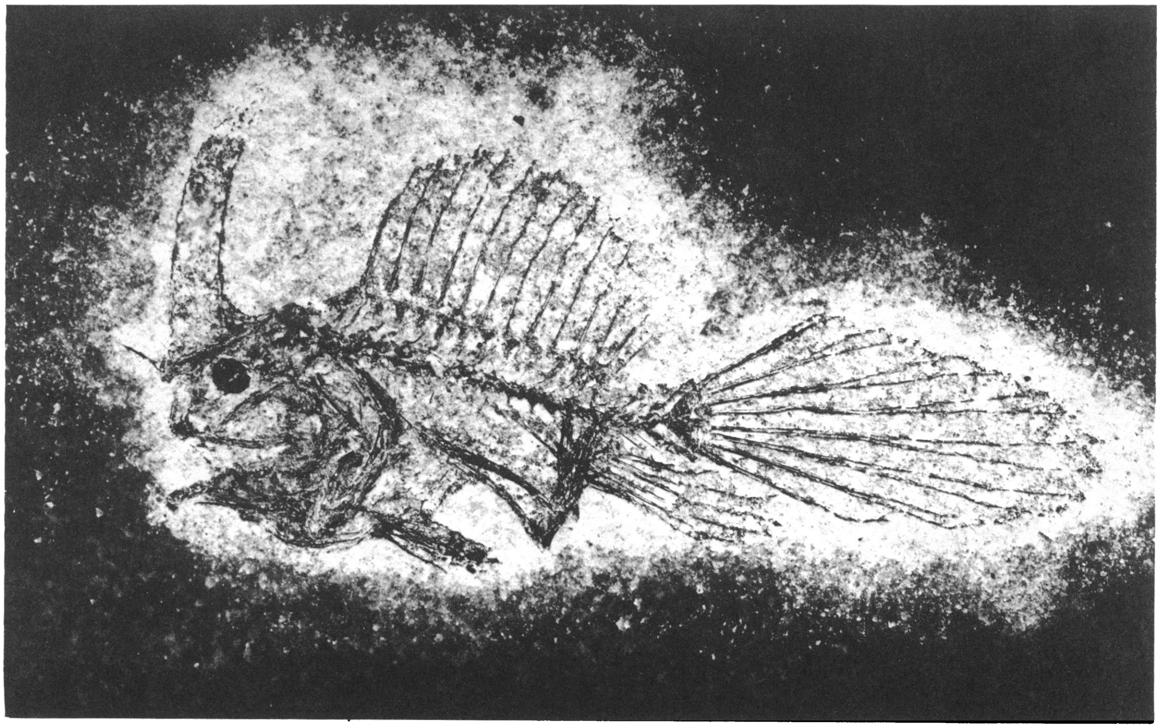
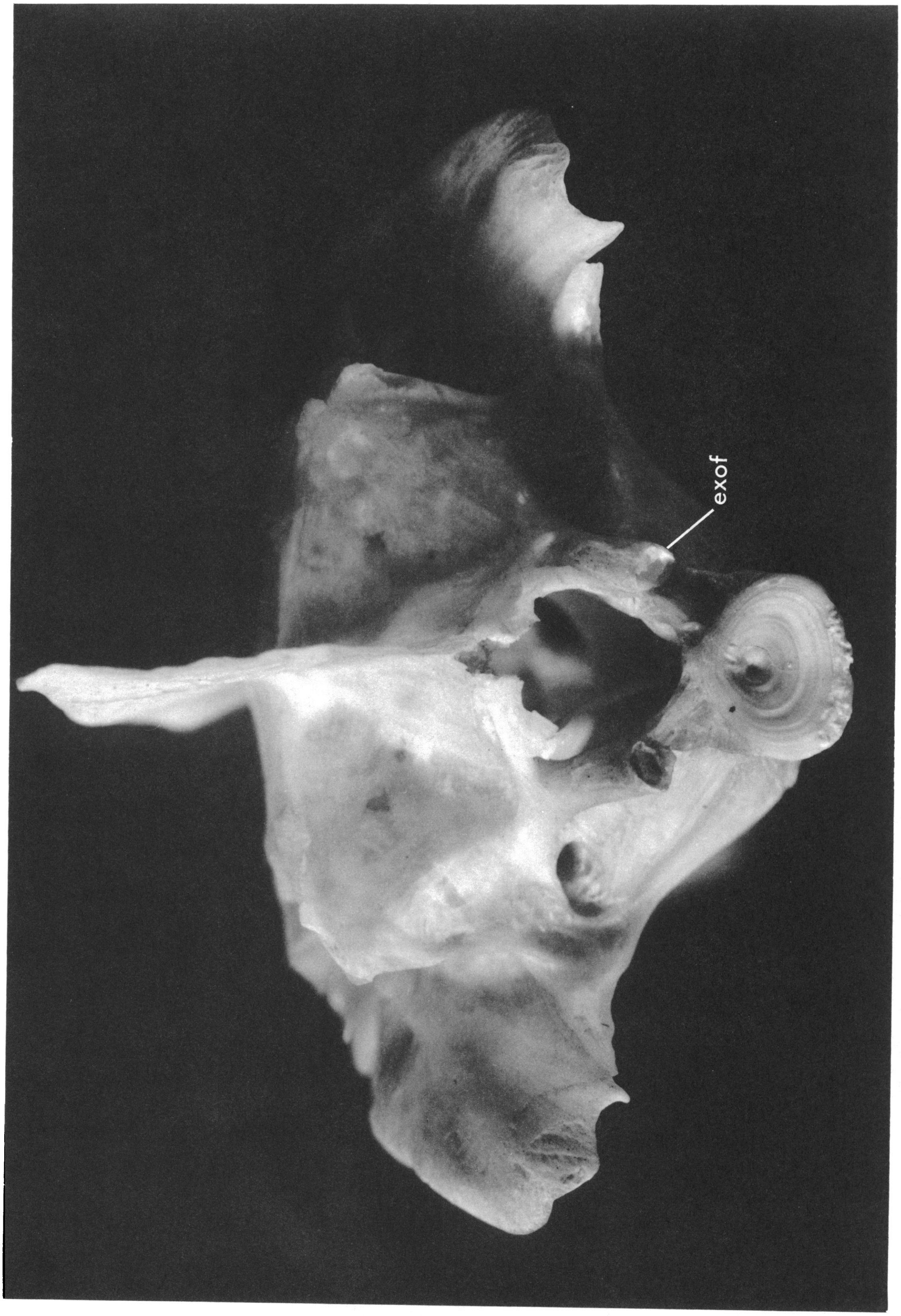
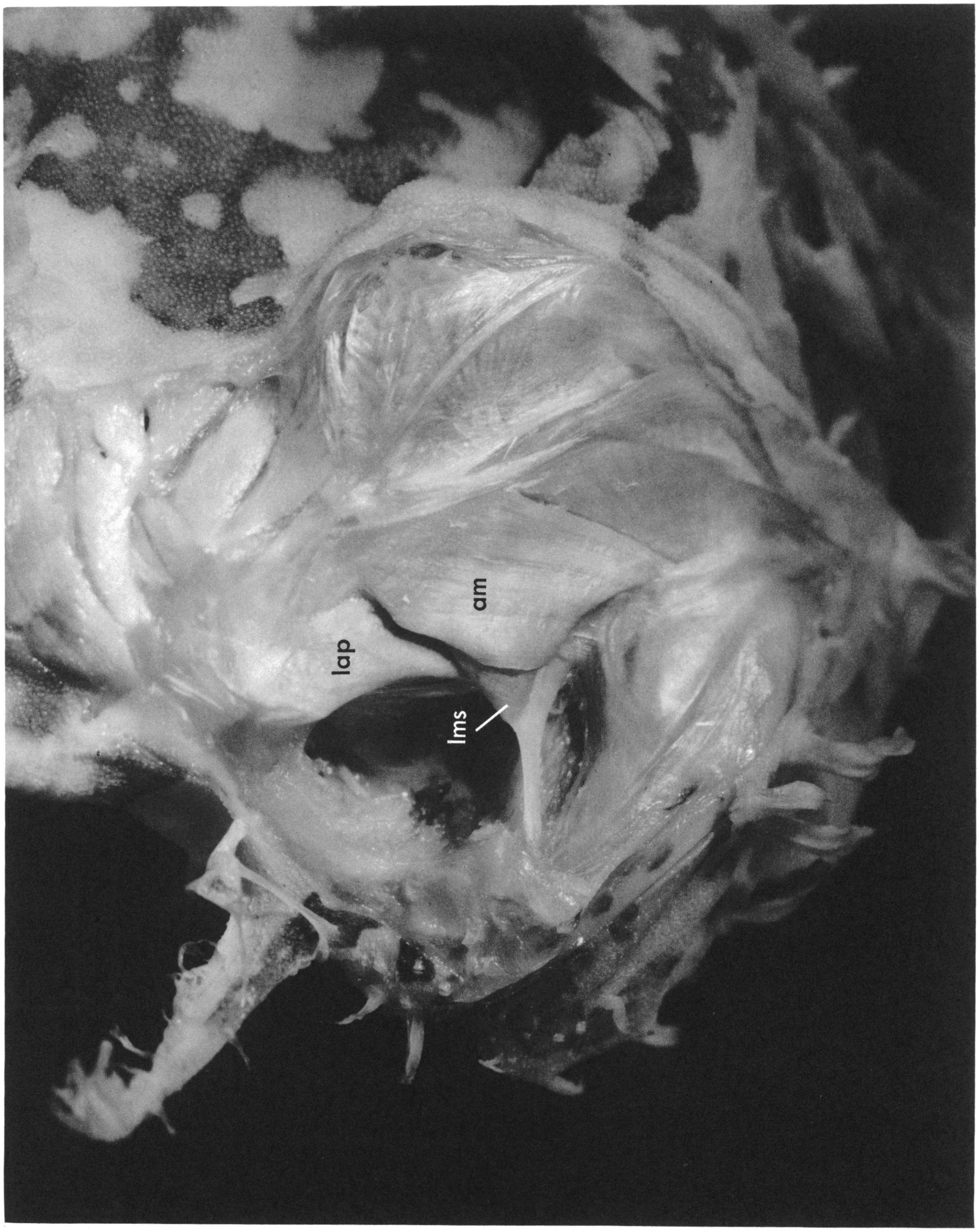


2

1. Premaxilla of adult *Gadus morhua* Linnaeus
2. *Histionotophorus bassanii* (de Zigno), Middle Eocene, Monte Bolca, Italy; B.M.N.H. No. P.19060



Occipital view of neurocranium of *Melanogrammus aeglefinus* (Linnaeus)



Superficial cheek dissection of *Histrio histrio* (Linnaeus)