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An Essay on Euteleostean Classification

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ABSTRACT

The anatomy of the occipital region and rostral cartilage in euteleostean fishes is reviewed in some detail. These data, in combination with other anatomical features taken from the literature, have led to a reassessment of interrelationships within the Euteleostei. This review supports the notions that the Salmoniformes, Aulopiformes, Myctophiformes, and Beryciformes are nonmonophy-

letic and raises questions about the monophyly of the fishes formerly grouped in the Osmeroidei. Evidence is presented on how the occipital region might be used in acanthomorph systematics, and includes reasons for rejecting the concept of the Paracanthopterygii, as this group was formerly constituted.

INTRODUCTION

The earliest general classification of fishes in which it is possible to pick out many of the main components of the Euteleostei is that of Johannes Müller (1844), in which the teleosts as a whole were presented as a vertebrate subclass, and their components as orders. These orders of Müller's bore names that may seem strange and unfamiliar to today's student, but the etymological characteristics of many of them were preserved for some time, a few even to the present.

Some of these names and their cross-equivalents in different classifications were reviewed and explained in detail by Myers (1958) and now it remains only to emphasize that these many different classifications [Müller (1844), Agassiz (1858), Günther (1859-1870), Gill (1872), Boulenger (1904), Regan (1909, 1929), Goodrich (1909), Jor-

dan (1923), A. Smith-Woodward (1932), Norman (1934), Berg (1940) and its various translations, reprinted editions and slightly modified versions, and lastly Greenwood et al. (1966), McAllister (1968), and J. Nelson (1984)] went through an evolution from the early nonsubordinated, ordinal classifications of Müller (1844), Agassiz (1858), Gill (1872), Boulenger (1904), and Regan (1909, 1929), to the complex subordinated, hierarchical system of Goodrich (1909). It was Goodrich (1909) who introduced the use of uniform group endings, a practice that was adopted by Berg (1940) and his successors, to ease recognition of the hierarchical position of a group in the general classification.

During all of this history some of the fishes now assigned to the Euteleostei were distributed throughout most of the higher taxa rec-

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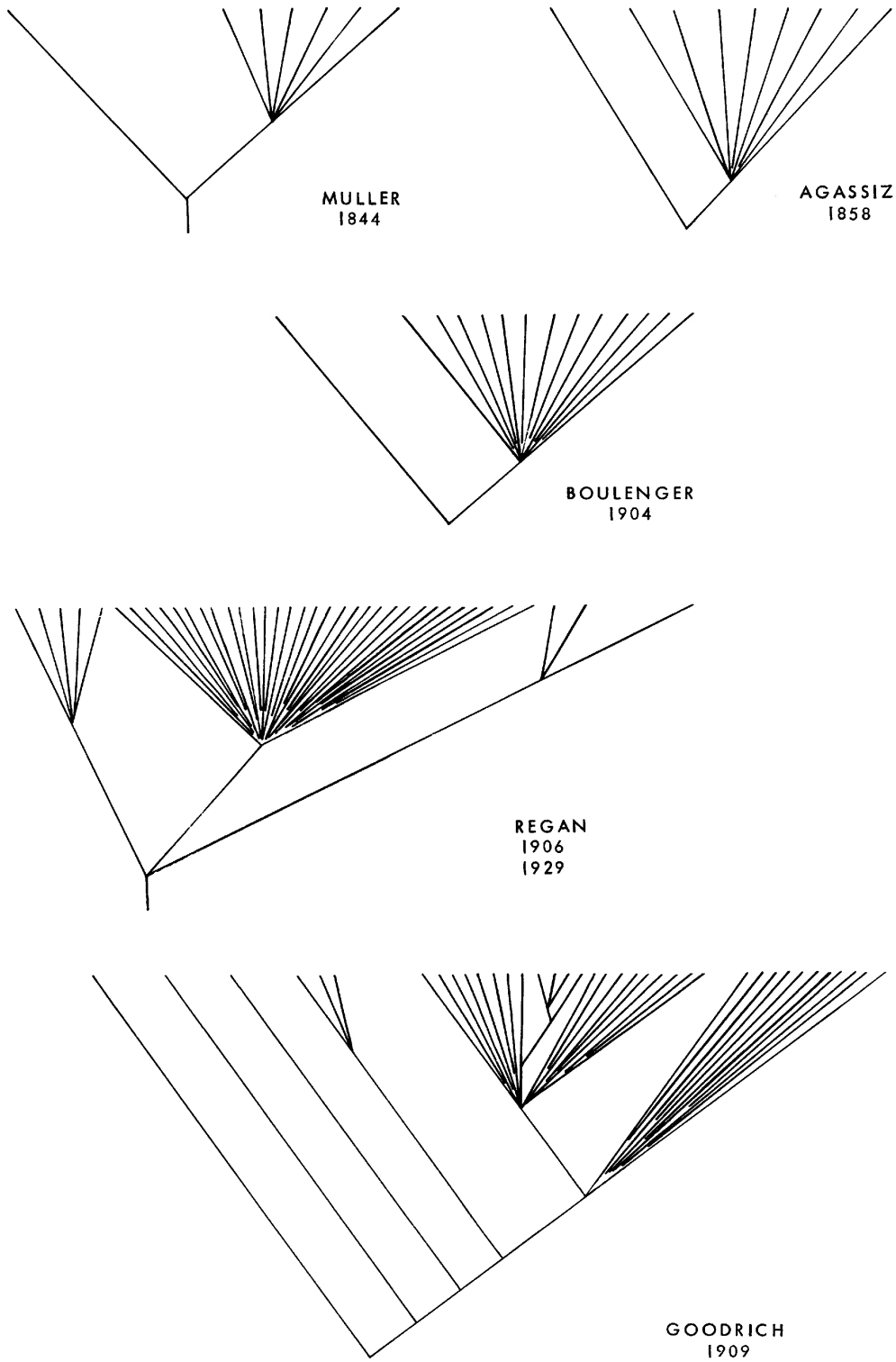


FIG. 1. Branching diagrams representing the degree of resolution of teleostean classifications from 1844 (Müller) to 1909 (Goodrich) and 1929 (Regan).

ognized by earlier authors. For example, in Müller's (1844) classification of fishlike vertebrates, the subclass Teleostei included six orders, each of which included taxa now encompassed by the Euteleostei. Thus, his Acanthopteri included "perciform" fishes; the Anacanthini, the codfishes, cusk eels, and flatfishes; Pharyngognathi, the labrids, and their immediate allies; the Phystomi, the otophysan Ostariophysi, percopsiforms, myctophids, salmonids, galaxiids, synbranchid eels, pikes, and mudminnows; the Plectognathi, members of the modern Tetraodontiformes; and the Lophobranchii, the pipefishes, and seahorses. The Physostomi of Müller also included some osteoglossomorphs and the former is understood to be more or less equivalent to the Malacopterygii, Isospondyli, and Clupeiformes in classifications as recent as Berg's (1940). The three latter "groups" were unnatural assemblages of primitive teleosts, which included numerous taxa later treated by Greenwood et al. (1967) as euteleosteans in another unnatural assemblage that Greenwood et al. (1966) had previously termed the Protacanthopterygii. Progress has been slow, teleost classifications going through a long period when all teleosts were assembled into one of three main kinds: lower, intermediate, or higher even as recently as Gosline (1971).

The first comprehensive modern attempt at detailed hierarchical synthesis since Goodrich (1909) was that of Greenwood et al. (1966), closely followed by that of McAllister (1968). This history is best appreciated by examining a sprinkling of branching diagrams extracted from the main components of each of the systems proposed since 1844 (figs. 1 and 2).

It might be guessed that many major taxonomic problems have remained unsolved once an interest in cladistic methods of analysis and classification was adopted by the ichthyological community and most of these problems might be expected to be within the Euteleostei, as the largest of all recognized teleostean assemblages. I do not regard these problems as close to solution since there exists, still, significant disagreement amongst ichthyologists on the interpretation of character information and the delimitation of natural groups (Fink, 1984). This disagree-

ment is a sign of health and vigor in the field that should serve as an example for other vertebrate systematists, some of whom have abandoned the search for hierarchical order in favor of general ecological research or laboratory studies of the behavior of selected species.

This paper is premised on certain new observations and interpretations of teleostean anatomy and the cladistic notions derived from them. One of these notions, in agreement with Fink and Weitzman (1982) and Fink (1984), is that the Salmoniformes of Rosen (1974) is not monophyletic. The second is that the Aulopiformes of Rosen (1973) is also not monophyletic. A third is that *Polymixia* and the acanthomorph neoteleosteans are defined, in part, by the absence of a residual neural arch between the first vertebra and the occiput that is primitively present in most halecostomes, many primitive euteleosts, and in neoscopelids but not myctophids among the Myctophiformes, as redefined by Rosen (1973) to include the myctophids and neoscopelids.² A fourth is

² This and other characters conflict with four shared, derived features for myctophids and neoscopelids given by Stiassny (MS), but are consistent with the presence of a subocular shelf, and single, medial, rostral cartilage in most polymixiids and acanthomorphs (absent in neoscopelids), and three or fewer predorsal bones in myctophids, polymixiids, and acanthomorphs (four in neoscopelids). One of Stiassny's characters linking the two families is the cone-shaped ventrally directed parapophyses for Baudelot's ligament that will, I believe, prove to be the primitive state of a similar structure in *Polymixia* and other acanthomorphs (fig. 18). Another of Stiassny's reasons for linking myctophids and neoscopelids is described by Lauder (1983). In Lauder's paper, he stated that "all myctophiforms (including neoscopelids; Rosen, 1973) possess a unique attachment of the branchial skeleton to the urohyal." In myctophids, however, the third hypobranchials have long anteroventral tips that clasp the urohyal laterally, whereas in neoscopelids, the anteroventral tips of the third hypobranchials extend forward above the urohyal to the dorsal edge where they are attached by ligament. The latter condition is similar to that for primitive acanthomorphs (e.g., *Polymixia*) except that in the latter, the ligaments from the third hypobranchials extend forward to contact the dorsal edge of the urohyal more anteriorly. In any event, I see no character here that clearly aligns myctophids with neoscopelids. This leaves two ligament characters of Stiassny's to align those taxa, as compared with the eight

that the Neoteleostei is characterized by a tripartite occipital condyle (the basioccipital and two exoccipital condyles), as described and illustrated by Rosen and Patterson (1969), and which unites stomiiforms with them, as elaborated by Fink and Weitzman (1982) and Fink (1984). A fifth is that, in disagreement with Fink and Weitzman (1982), the presence of a well-defined triple joint that incorporates two large exoccipital condyles is not evidence for linking the Salmonidae with the neoteleosts since this type of joint has a limited distribution only in Recent salmonines and is, therefore, probably convergent. A sixth is that neoteleosts primitively show a cervical gap between the occiput and first vertebra. A seventh is that the Acanthomorpha are defined by complete closure of the cervical gap via two prezygapophyseal exoccipital facets and a basioccipital facet from the body of the vertebral centrum. An eighth is that *Polymixia* is the sister group to the Acanthomorpha, thus defined because it possesses exoccipital facets but retains a part of the cervical gap in the basioccipital position. Other "beryciforms" have a more derived "percoid-like" condition.

←

features that relate myctophids, but not neoscopelids, to the acanthomorphs. (1) a large subocular shelf (like that in *Polymixia*), (2) rostral cartilage a simple median structure (with relic pairs of lateral cartilages, or no paired cartilages), (3) an interarcual cartilage between the first and second gill arches (small, when present, and absent in some species including *Polymixia* and some primitive acanthomorphs), (4) only three predorsal bones, (5) partial closure of the cervical gap, (6) absence of an accessory neural arch in cervical region, (7) presence of neural arch prezygapophyses on the first vertebra, (8) direct connection (via ligaments) of the autocentrum of first vertebra with the exoccipital condyles. Character 3 is questionable because several groups of primitive acanthomorphs lack an interarcual cartilage and characters 6 through 8 might be manifestations of only a single developmental shift. Even allowing for the latter two ambiguities, there are four trenchant features suggesting nonmonophyly of the myctophids plus neoscopelids (characters 1, 2, 4, and 5–8) as contrasted with the two remaining ligament features proposed by Stiassny. This state of affairs indicates to me that myctophids are the sister group of acanthomorphs (in a restricted ctenosquamata), but that neoscopelids, for reasons discussed in this paper, are best regarded, at present, as part of major polychotomy immediately preceding the ctenosquamata in the cladogram (fig. 45).

Certain subsidiary notions also emerge as consequences of this work, (1) that the "osmeroids" and the Salmonidae might not be monophyletic groups. Peñáz (1983, p. 370) recently attempted an ontogenetic diagnosis of the Salmonidae, but pointed out that some of the diagnostic features may also be found in other fish groups, (2) that *Aulopus*, and perhaps some closely allied forms excluding *Chlorophthalmus*, might jointly form the sister group to the Ctenosquamata based, in part, on the anatomy of the rostral cartilage, and (3) that within the groups that remain, the old Paracanthopterygii toadfishes and their immediate allies might be more closely linked to cods and their than the cods are to cusk eels and brotulas based on both neurocranial, vertebral, and gill arch evidence.³

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ANATOMICAL ABBREVIATIONS

ACCNA, accessory neural arch
 ABAUDLIG, attachment for Baudelot's ligament
 ANA, ankylosed neural arch
 ARTPR, articular process
 ASCPR, ascending process
 AUTLIG, autocentral ligament
 AUTNA, autogenous neural arch
 BAUDLIG, Baudelot's ligament
 BO, basioccipital
 BOC, basioccipital condyle
 BOF, basioccipital facet
 CG, cervical gap

³ The gill arch evidence will be discussed in a subsequent paper by Patterson and Rosen.

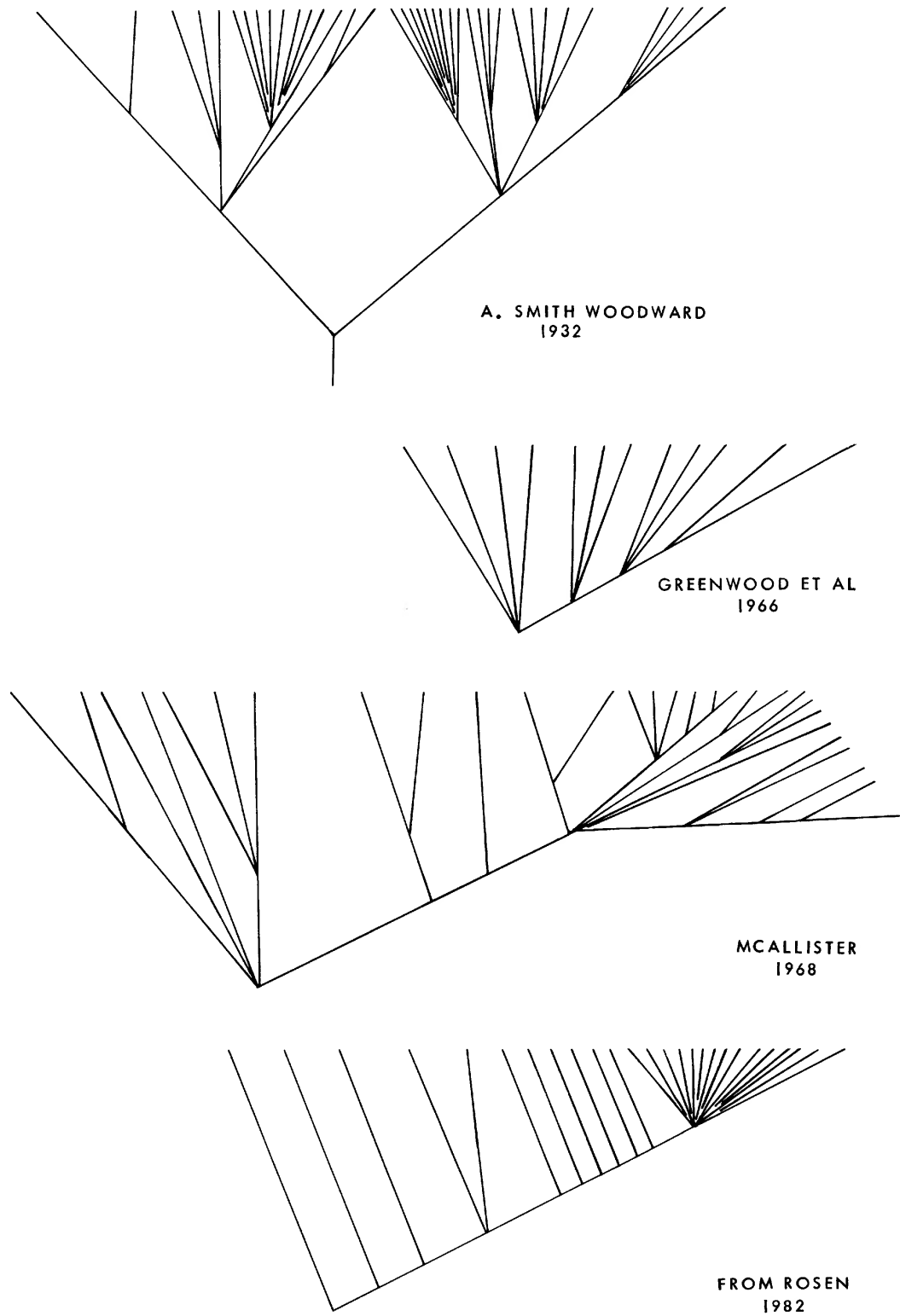


FIG. 2. Branching diagrams representing the degree of resolution of teleostean classifications from 1932 (A. Smith-Woodward) to the present time as summarized by Rosen in 1982.

CTNOT, connective tissue sheath of notochord
 ?CART, questionably cartilaginous
 DNA, depression in autocentrum for neural arch base
 ENR, epineural rib
 EP, epural
 EXO, exoccipital
 EXOC, exoccipital condyle
 EXOF, exoccipital facet
 EXO FRAGMENTS, exoccipital fragments from site of attachment of autocentral ligament
 HYP1-6, hypural 1 to 6
 LEXO, left exoccipital
 MEDCART, medial upper jaw cartilage
 MX, maxilla
 NA, neural arch
 NAPZYG, prezygapophyseal neural arch
 NOT, notochord
 NPU2, 3, neural spines on second and third pleural centrum
 PAL, palatine
 PAR, parapophysis
 ?PAR, questionably a parapophysis
 PARHYP, parhypural
 PD1, first predorsal bone
 PMX, premaxilla
 POPMYO, posterior opening of posterior myodome
 PMXCART, premaxillary cartilage
 PR, pleural rib
 PTMXPR, postmaxillary process of premaxilla
 PU1, 2, first or second preural centrum
 PZYG, prezygapophysis
 RCART, rostral cartilage
 RETDORS TENDON, tendinous origin of retractor dorsalis muscle
 REXO, right exoccipital
 RV1NA, right half of neural arch on first vertebra
 RV1NSP, right half of neural arch and spine on first vertebra
 SACBUL, saccular bulla
 SEXOF, site for development of exoccipital facet
 STEG, stegural
 U1, 2, first or second ural centrum
 UN1, 2, first or second uroneural
 V1, 2, 3, first, second or third vertebra
 VIANA, ankylosed neural arch of first vertebra
 V1NSP, neural arch and spine of first vertebra
 X, foramen for vagus nerve

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History
 MCZ, Museum of Comparative Zoology, Harvard University

ANATOMICAL EVIDENCE

THE NEUROCRANIAL JOINT WITH THE FIRST VERTEBRA: It has been proposed (Patterson,

1964; Rosen and Patterson, 1969; and Fink and Weitzman, 1982) that advanced euteleosts can be characterized by the presence in the posterior neurocranium of an inverted Y-shaped junction between the basioccipital and the exoccipitals. This configuration can be seen in primitive myctophids, stomiiforms, †*Ctenothrissa radians*, and *Polymixia* (Patterson, 1964). This condition appears to differ from that of primitive teleosts in which the basioccipital occupies the entire area of these three bones for contact with the centrum of the first vertebra. When that basioccipital contact is reduced, the exoccipitals enter the posterior neurocranial surface to form a tripartite condylar surface for contact with the first vertebra.

Fink and Weitzman (1982), citing the earlier paper by Rosen and Patterson (1969), called attention to the tripartite occipital condyle as a synapomorphy of neoteleosts. Finding a similar occipital joint in the gonostomatid stomiiform, *Diplophos*, they proposed that this is one of two features that unites stomiiforms with neoteleosts. The other feature, a rostral premaxillary cartilage, is discussed below. Fink and Weitzman also used the tripartite condyle and rostral cartilage to propose a sister-group relationship of the Salmonidae with the neoteleosts plus stomiiforms.

The nature of the occipital joint with the first vertebra has attracted the attention of several investigators. Ridewood (1904, 1905) held the view that a tripartite joint is primitive for teleosts, but is masked by the fusion of the first vertebral centrum (V1) to the occiput so as to exclude the exoccipitals from the joint surface. In that view, what is identified in most teleosts as the basioccipital is actually a vertebra fused to the braincase. Removal of this vertebra should, therefore, reveal the primitive tripartite arrangement. Patterson (1975, p. 318) proposed that the basioccipital condyle, rather than being a vertebra, is made up of a plug of osteoid tissue representing the ossification of the small anterior part of the notochord that penetrates the basioccipital bone, and that it is the growth of this osteoid plug that excludes the exoccipitals from the posterior face of the occiput.

Cavender and Miller (1972) also reviewed the origin of the salmonid occipital joint and

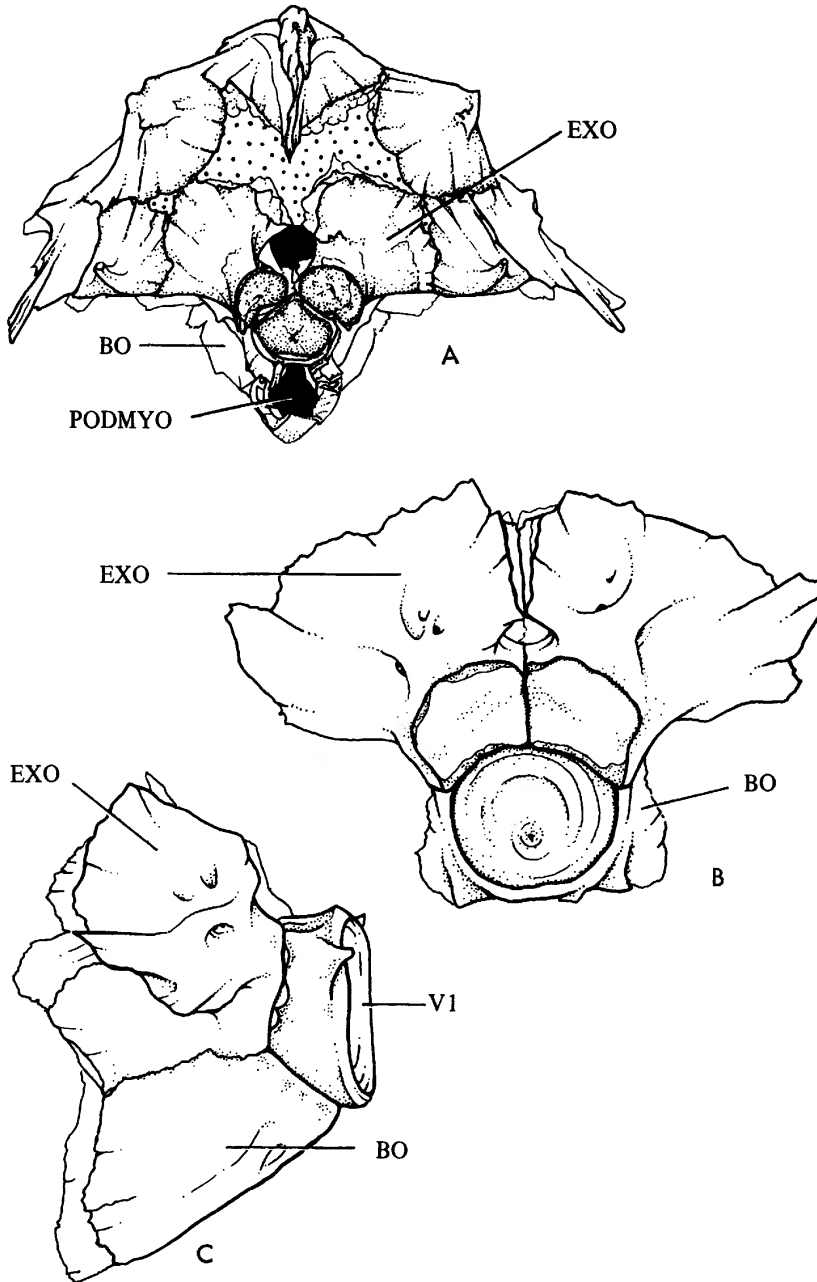


FIG. 3. Salmonine occipital regions show character and disposition of the condyles that articulate with the first vertebra. A. *Salmo salar* Linnaeus, AMNH 39098, posterior view of skull of adult specimen. B and C. *Oncorhynchus tshawytscha* (Walbaum), AMNH 21719. B. Posterior view of exoccipital and basioccipital bones. C. As in B, but in lateral view with first vertebra in place (see fig. 4).

concluded, correctly in my view, that the tripartite condition of salmonids is present or not as a consequence of whether a vertebra fuses or does not fuse with the braincase.

Cavender and Miller took an interest in this matter after finding and describing a large middle Pliocene salmonid from western North America (*†Smilodonichthys rastro-*

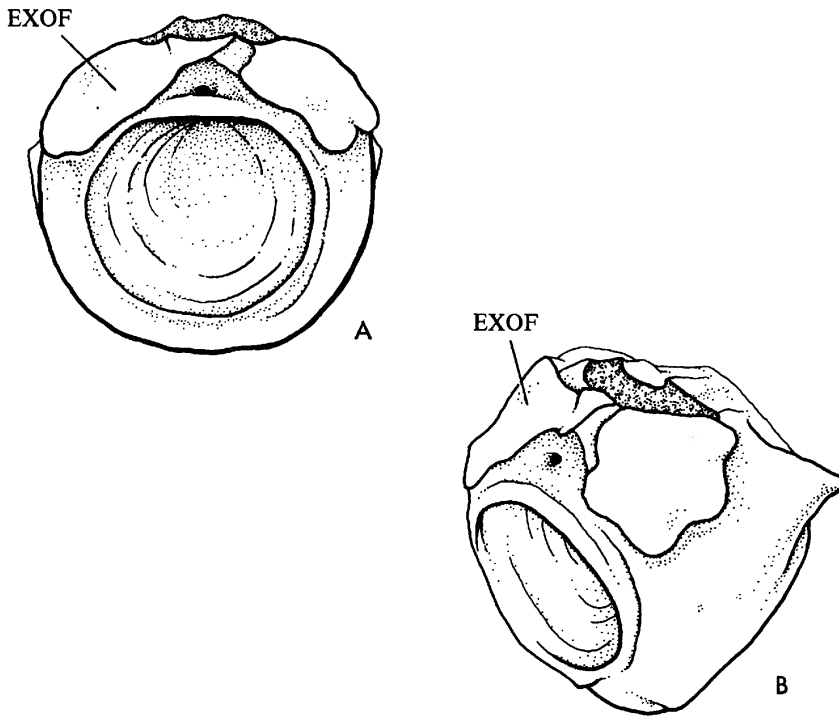


FIG. 4. The first vertebra of *Oncorhynchus tshawytscha* (Walbaum), AMNH 21719, in posterior (A) and three-quarter posterodorsal (B) views. This vertebra contains a pair of wells on its dorsal surface underlying a poorly developed (accessory) neural arch that does not bear a neural spine.

sus); they proposed that it has a close relationship to the species of *Oncorhynchus*. After noting that *Oncorhynchus* has a tripartite joint (figs. 3B, C, 4, 5) and †*Smilodonichthys* but a simple basioccipital condyle, they reviewed the distribution of these different kinds of articulations in a variety of teleosts. Cavender and Miller concluded that there is evidence of a vertebra fusing with the braincase in the Pliocene fossil and that such fusion is by no means unusual or restricted to just a few taxa. In fact, they report that “in *Coregonus* two centra may be fused with the basioccipital” and that the “condition in *Prosopium williamsoni* and [*Thymallus*, Norden (1961)] is somewhat intermediate” between the tripartite condyle and the single one in *Coregonus*.⁴ They also write that “close in-

⁴ Fink (1984) argued that because *Prosopium* has the exoccipitals participating in the occipital condyle along with *Thymallus* and the Salmoninae that the tripartite condition is primitive for the Salmonidae in general, and

← can therefore be used as evidence to link the salmonids with the neoteleosts. But in my material, exoccipital participation is not true of *Prosopium williamsoni*, *P. cylindraceum*, or any other coregonine examined (figs. 7, 8, 13) and the condition in *Thymallus* is hardly different from that of *Albula* (fig. 9) and *Pterothrissus*, among other teleosts, in which only a small extension of the exoccipital is visible posteriorly without noticeably affecting the shape of the basioccipital. The tripartite occipital condyle of salmonines is more derived than the simple, inverted Y-shaped morphology in primitive ctenosquamates (except during early ontogeny, fig. 12A), resembling in the adult state that of an advanced percomorph (e.g., *Lutjanus*, cf. figs. 3B and 24, 25). Thus the resemblance is probably secondary. This conclusion predicts a different ontogeny for the salmonine and ctenosquamate conditions which, if found, would indicate their nonhomology (see below, p. 54). Perhaps the problem is, as stated by Fink (1984), that the monophyly of the Salmonidae “is based primarily on a single character, apparent polyploidy of the karyotype . . .” and that, as enunciated by him, many of the salmoniform taxa are unnatural (e.g., “salmonids,” “osmeroids,” and “esocoids”).

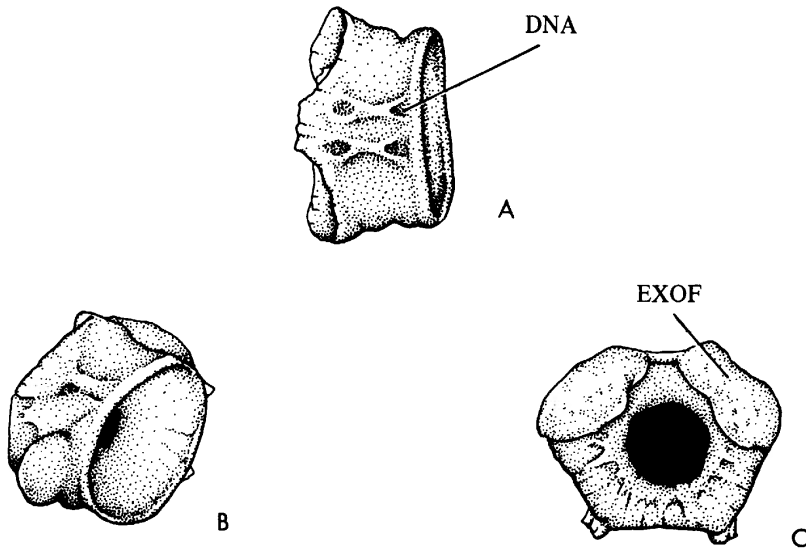


FIG. 5. First vertebra of *Salmo gairdneri* Richardson, AMNH 40268, parr stage (ca. 10 cm total length). A. Dorsal view to show wells for accessory neural arch. B. Three-quarter posterior view. C. Anterior view to show extent of development of facets that articulate with exoccipital condyle. Note large notochordal canal in centrum.

spection of the condyle [in †*Smilodonichthys*] shows that it is . . . a fused centrum that supported a neural arch [in] a pair of indentations . . . on its dorsal surface" (cf. figs. 3–8). And further, that this "basicranial-vertebral joint is similar to that found in *Tarpon* [sic] *atlanticus*, *Megalops cyprinoides* (Greenwood, 1970), [and] *Albula vulpes* . . ." Their claim is problematical because ontogenetic data illustrating the course of vertebral fusion are lacking for most cited examples. Such data are available for *Megalops atlanticus*, however (fig. 9A, B). Strong circumstantial support for the idea can be found in other elopomorphs, as illustrated by Forey (1973), where the part claimed to be a fused centrum not only bears a neural arch but parapophyses as well (Forey, 1973, figs. 3, 5, 21–23, 31).

In *Elops*, which appears to have a vertebra that is ontogenetically a part of the basioccipital (fig. 10 and illustrations in Forey, 1973), Baudelot's ligament is attached to the ventrolateral aspect of the first free vertebra. Whitehead and Teugels (in press) describe a situation much like that of *Elops* in a freshwater herring, *Sierrathrissa*. They state that "the posterior half of a first vertebral centrum

[appears to have] become trapped by flanges from the exoccipital and basioccipital . . .," thus agreeing with Ridewood's (1904) interpretation of the clupeid occipital region (and see Greenwood, 1968, on *Denticeps*). Additional circumstantial support for the primitive ontogenetic incorporation of vertebrae with the braincase in modern halecostomes comes from the correlation of the occurrence of accessory, free-floating neural arches with fusion of vertebrae to the occiput [e.g., in *Amia* (Jollie, 1984a, p. 431)].

The clupeocephalan first neural arch is reduced and incomplete (figs. 11A, 12B) as compared with the neural arch associated with the basioccipital in some elopomorphs (fig. 10), and might, therefore, be another synapomorphy of the Clupeocephali. This line of argument depends on an assumption that the position of Baudelot's ligament is a reliable landmark for the identification of a given vertebra. In osteoglossomorphs there is no evidence, direct or circumstantial, that a centrum is primitively fused with the braincase (e.g., in *Hiodon* or *Scleropages*), but in a more derived condition several vertebrae either are closed adherent to the basioccipital (*Osteoglossum*) or are included in a complex an-

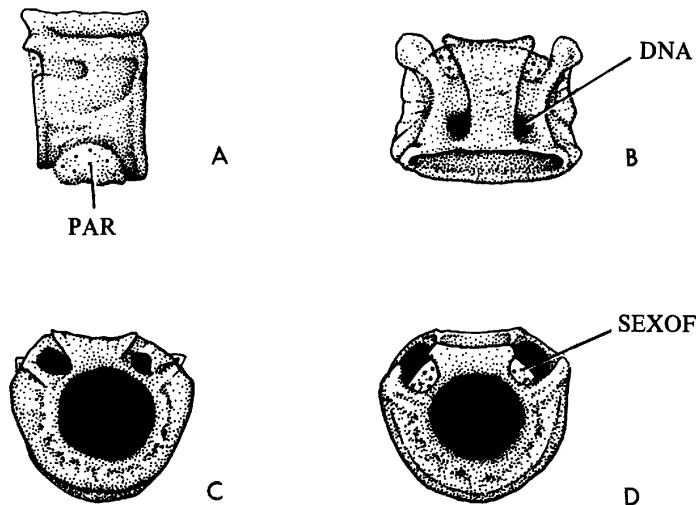


FIG. 6. First vertebra of juvenile lake trout, *Cristivomer namaycush* (Walbaum), AMNH 39269 (ca. 6 cm total length). A. Lateral view (anterior to left). B. Dorsal view (anterior up) to show position of wells for accessory neural arch. C. Posterior view. D. Anterior view to show areas where exoccipital facets develop in larger specimens. Note large notochordal canal in centrum.

kylosed structure (*Arapaima*, *Notopterus*). In *Hiodon*, *Scleropages*, and *Osteoglossum*, Baudelot's ligament arises on V1 as opposed to its attachment to the basicranium in taxa with fused centra. That correlation is not true of ostariophysans, however, where there is no evidence of a centrum fused to the braincase; yet, as pointed out by Fink and Fink (1981), the ligament attaches to V1 in cyprinoids, and to the basicranium in the other otophysans.⁵ All one can say about this sit-

⁵ All one can say for the Otophysi is that the ontogenetic mechanism for transferring the ligament from V1 to the basioccipital is unknown but the character appears to be consistent and therefore usable taxonomically. The alternative is that there is no such implied character transformation because the two kinds of ligaments in the Otophysi are not homologous. In fact, if one envisions a whole series of ligaments arising primitively on the basioccipital and V1, and inserting on the shoulder girdle—and the disappearance of one or more of these in the ontogeny of different taxa—the ligament that is left becomes a retained primitive character and the absence of ligaments from certain areas, the derived condition. Under such circumstances, comprehensive survey of shoulder girdle support ligaments would have to be made before one could use the character in a cladistic sense. Nevertheless, I am inclined to treat the ligaments as homologous when the insertion on the shoulder girdle is as precisely similar as illustrated by Fink and Fink (1981).

uation in the osteoglossomorphs and elopoccephalans is that the ontogenetic mechanism for moving the ligament between V1 and the basicranium is unknown. But if the position of Baudelot's ligament in elopoccephalans is correctly judged to be primitively V1 and is stable, then two possible explanations for its variable attachment are: (1) the nonhomology of the vertebral and basicranial ligaments,⁴ and (2) the presence or absence of a centrum fused to the braincase, as in †*Smi-lodonichthys* and some coregonines (according to Cavender and Miller, 1972).

In a recent account of the development of the syncranium of salmonines, Jollie (1984b) states that there is no vertebra fused with the braincase, but he did not comment on Cavender and Miller's (1972) paper, nor did he illustrate the presence of an accessory neural arch between the braincase and the first cervical vertebra (bearing Baudelot's ligament), which appears to be a general feature of my material. I cannot resolve these inconsistencies.

An accessory neural arch is present in primitive neoteleosts (figs. 14B, 15), and most primitive neoteleosts exhibit a gap between the braincase and the first vertebra. This cervical gap is progressively smaller in more derived neoteleosts (figs. 14–17), being taken up by ligament or bony facets from the au-

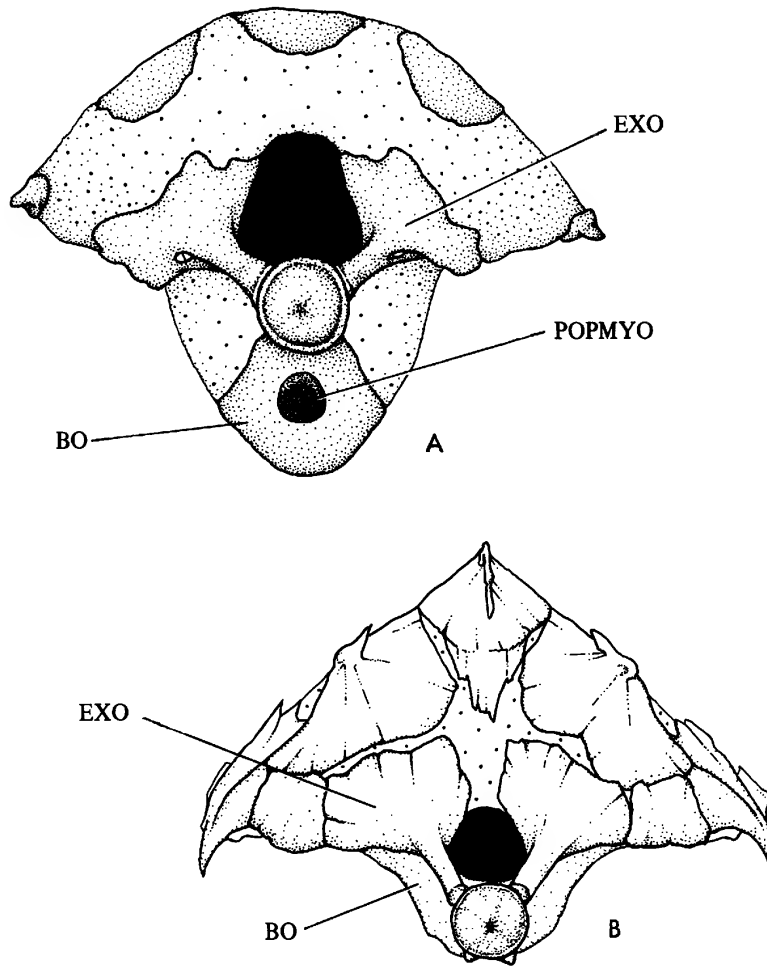


FIG. 7. Occipital views of neurocranium. A. *Coregonus artedi* Lesueur, AMNH 20096 (ca. 7 cm total length). B. *Thymallus arcticus* (Pallas), after Norden (1961). Note posterior opening of posterior myodome in A and compare with fig. 3A and apparent absence of same in B. Note also that the exoccipitals are masked posteriorly by basioccipital condyle in A and are almost excluded from the condylar surface in B. Compare with figures 3 and 8.

tocentrum in ctenosquamates (myctophoids plus acanthomorphs). The complete closure of this gap is correlated with (1) the absence of the accessory neural arch (figs. 16, 17), (2) the formation of vertebral facets for the exoccipitals, and (3) the presence of prezygapophyses on the neural arches. These three features are synapomorphies of the Acanthomorpha (cf. figs. 14–20).

Patterson (1975, p. 318) argued that the appearance of a small centrum (or part of a centrum) fused to the braincase is merely a false impression produced by the centrumlike ossification of the notochord in the basioc-

cipital and the growth dorsally of this centrumlike disc to exclude the exoccipitals. His argument carries with it the implication that the tripartite arrangement of bones on the posterior face of the braincase is a primitive feature that has been restored in neoteleosts and some primitive euteleosts by a means so far unknown.

The question of which is the first and which the second centrum in elopoccephalans is, as Whitehead and Teugels (in press) remarked, "left open." Detailed histological investigations of early ontogeny might "close" the question.

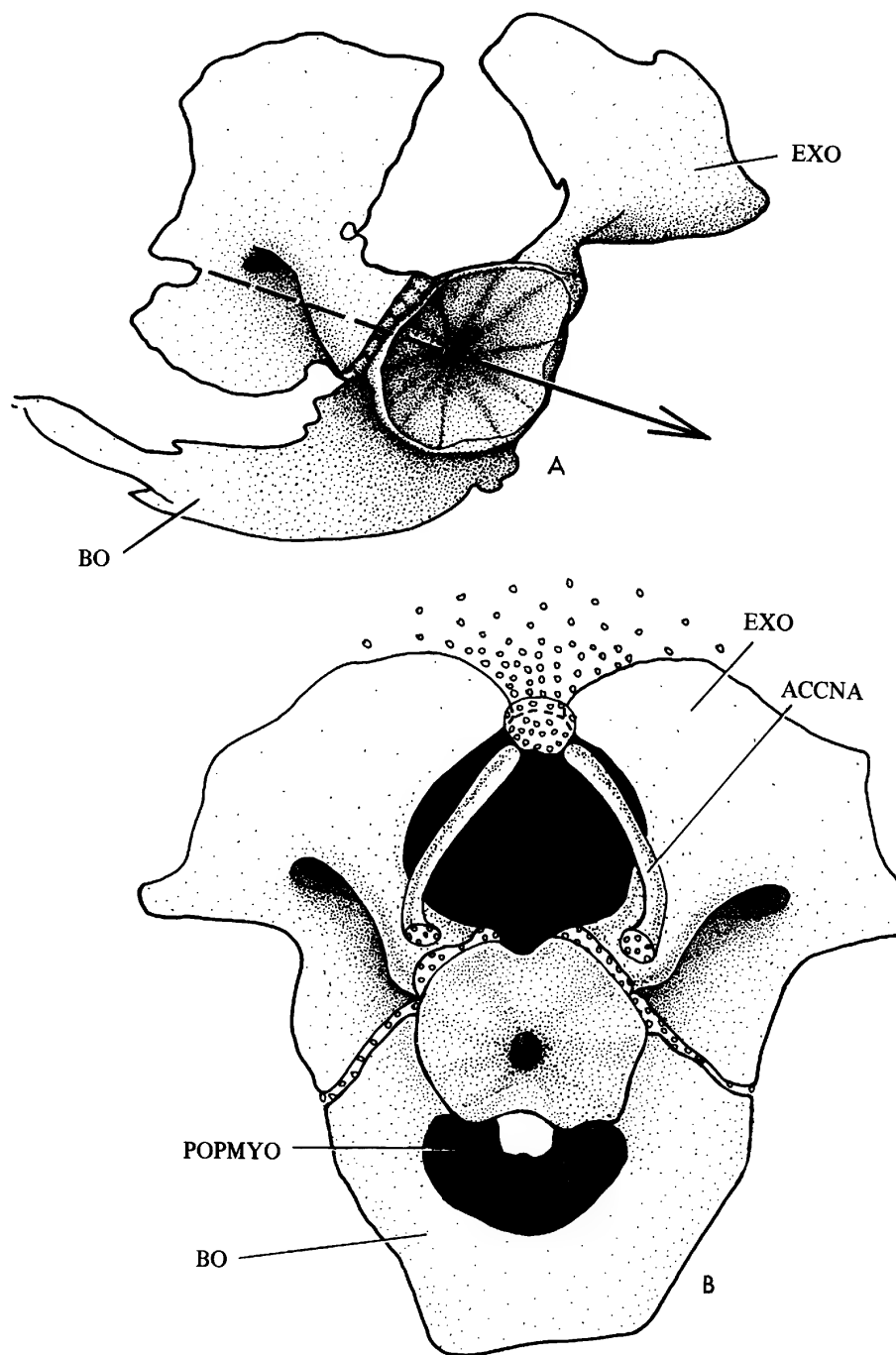


FIG. 8. Occipital region. A. *Prosopium cylindraceum* (Pallas), AMNH 31044 (ca. 10 cm total length), shown in three-quarter view with the arrow representing the anteroposterior axis. B. *Prosopium williamsoni* (Girard), AMNH 37967 (ca. 27 cm total length), in posterior view, showing position of accessory neural arch above basioccipital condyle. Note that, in both, the exoccipitals are masked posteriorly by basioccipital condyle. Compare with figures 3, 7, and 13B.

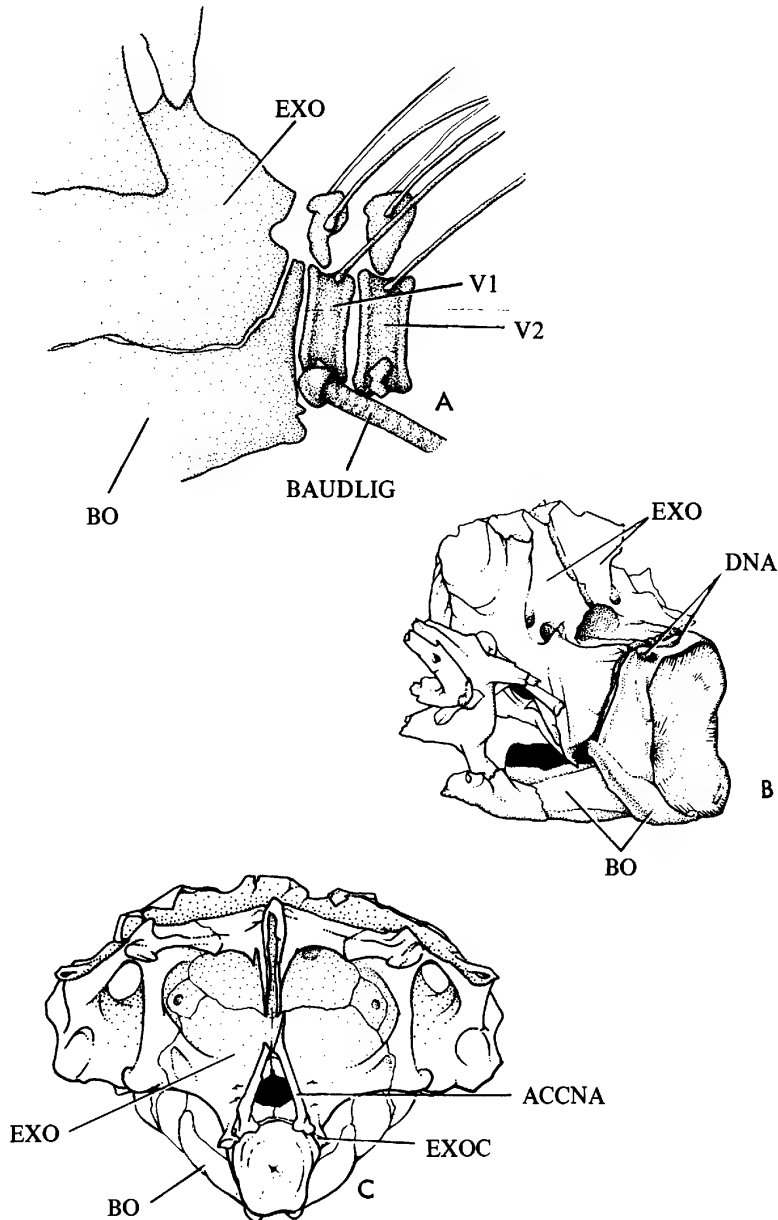


FIG. 9. Occipital regions in the elopomorphs, *Megalops atlanticus* Valenciennes (A, B) and *Albula vulpes* (Linnaeus) (C). A. A 10 cm total length juvenile (AMNH uncataloged). B. An 80 cm subadult, AMNH 55321. C. Subadult specimen, AMNH 21516. Note in B the ankylosis of the first vertebra with the basioccipital and the presence of wells on its dorsal margin for the small neural arch shown in A. In C, note especially the presence of an accessory neural arch articulating between the exposed tips of the exoccipitals which resemble those of *Thymallus* (fig. 7B). Compare also with figure 10.

Neoscopelids, chlorophthalmids, and aulopids have a large notochordal gap and an

accessory neural arch (Rosen and Patterson, 1969, figs. 61–63). (Rosen and Patterson mis-

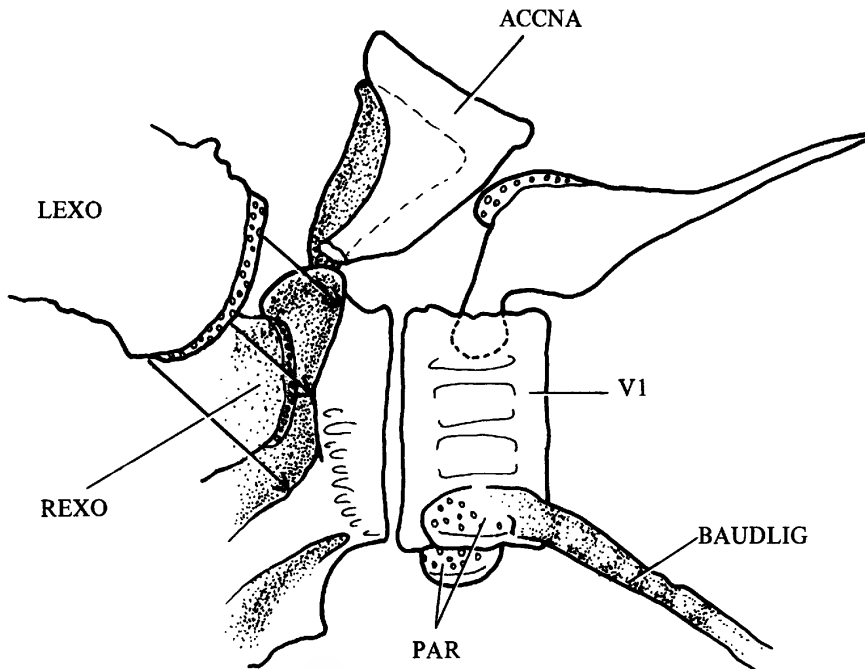


FIG. 10. Occipital region and first vertebra of a 6 cm *Elops saurus* Linnaeus, AMNH 51485. The left exoccipital is separated from the basioccipital to illustrate the latter's resemblance to a foreshortened cervical vertebra (demarcated by the sculpturing around the ventral half). The accessory neural arch corresponds with a pair of dorsal indentations or wells as in *Megalops*, figure 9B.

takenly labeled the first of four predorsal bones in their fig. 61A as a neural arch in *Neoscopelus*, however.) Myctophids have a remnant of the gap which is being closed by ligaments and bone from the autocentrum (figs. 16–17) in the position of acanthomorph prezygapophyses (figs. 18–20) and they and acanthomorphs lack an accessory neural arch. These shared derived states of myctophids and acanthomorphs, and the absence of same in *Neoscopelus* suggest that the Ctenosquamata should be restricted (as noted above) to the Myctophidae and the Acanthomorpha.² The primitive position of Baudelot's ligament on the first cervical (fig. 17) is retained in some primitive acanthomorphs such as amblyopsids (Woods and Inger, 1957), but Baudelot's ligament has made its way onto the basicranium of many acanthomorphs, including atherinomorphs (Woods and Inger, 1957). A survey needs to be conducted to discover the anatomical position and possible ontogenetic correlatives of this ligament

within the immense acanthomorph assemblage.

Thus, the tripartite joint of neoteleosts is a very old feature and the primitive and widespread presence of an accessory neural arch is inferred to be the remains of an ontogeny that had incorporated vertebral fusion with the occiput. In the fossil salmonine described by Cavender and Miller (1972), V1 is fused to the occiput to produce a *Coregonus*-like single condylar articulation. A situation like that in some species of *Salmo* and *Oncorhynchus* was previously described by Gosline (1969, fig. 7) in a species of the argentinoid genus *Alepocephalus*, but I know of none of the above described conditions in esocoids or ostariophysans, except to note that in *Esox* the back end of the basioccipital forms a disclike ossification resembling the articular surface of a centrum (rings of acellular bone that constrict the notochord), which grows rapidly, occluding the exoccipitals from the joint. This disc resembles that of *Osmerus*

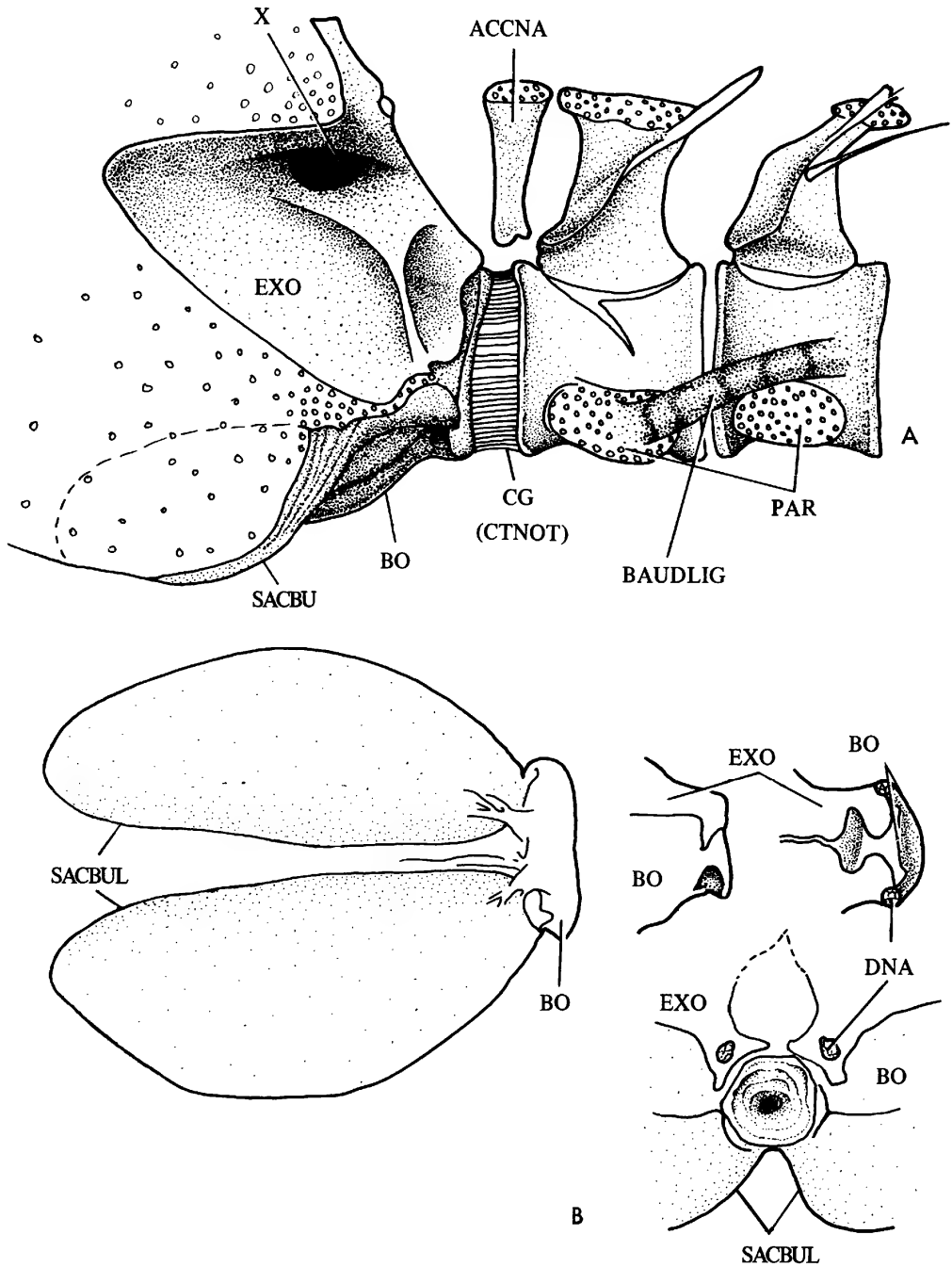


FIG. 11. Osmeroid occipital regions. A. *Spirinchus thaleichthys* (Ayres), ca. 8 cm, AMNH 51363, showing the extent of the cervical gap just below an accessory neural arch. B. *Osmerus mordax* (Mitchill), AMNH 21727; occipital region in specimens ranging in size from 1 to 3 cm in length. In B, the dimensions of the saccular bullae and their relation to the basioccipital condyle in a 2 cm individual in ventral view are shown at left; in the upper row, the middle figure shows the conjunction of the exoccipital and basioccipital; the same area appears at right in dorsal view in which articulation points for an accessory neural arch are also shown; the same area is again shown at lower right to illustrate where the basioccipital condyle is deformed by the neural arch bearing exoccipitals. Compare with figure 12B of a 3 cm individual.

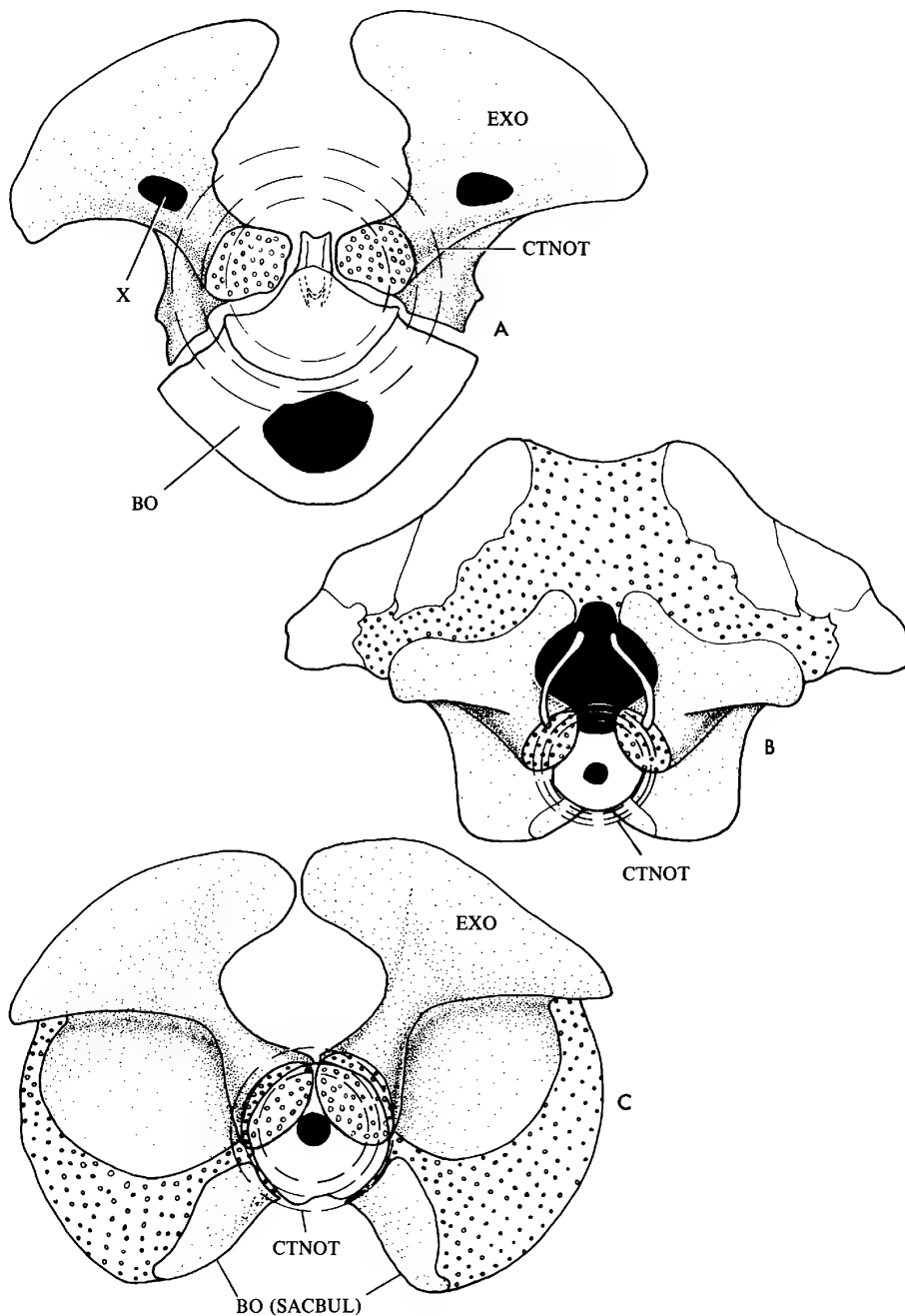


FIG. 12. Occipital region in a salmonine and two osmeroids. A. *Salmo gairdneri* Richardson, AMNH 40308 (ca. 6 cm). B. *Osmerus mordax* (Mitchill), AMNH 108093 (ca. 3 cm). C. *Spirinchus thaleichthys* (Ayres), AMNH 51363 (ca. 7 cm). An accessory neural arch is shown in B. In A, B, and C, there is a cervical gap between the occiput and first vertebra occupied by unconstricted notochord and its connective tissue sheath, as indicated. The basioccipital part of the vertebral joint is incompletely developed in each. In B and C, the posterior cartilage cores of the exoccipitals are visible through the still poorly ossified, rounded basioccipital condyle; bits of the exoccipitals are visible above it and remain so to produce an effect like that in some coregonines.

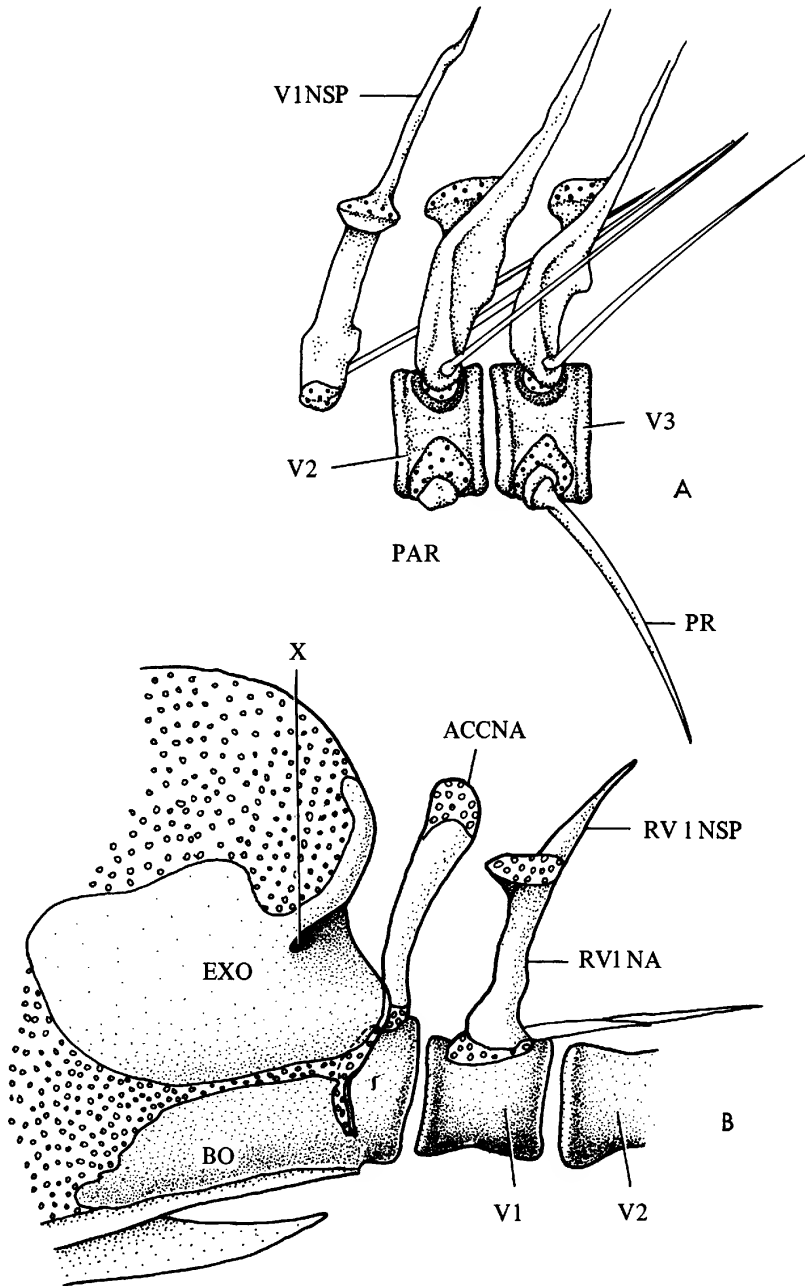


FIG. 13. A. Neural arches and spines of first three vertebrae of *Salmo gairdneri* Richardson, AMNH 40508, to illustrate the absence of neural arch prezygapophyses and the extent of the ventral cartilage base seated in dorsal vertebral wells; vertebral body of first vertebra and left half of its arch and spine omitted. B. Occipital region and cervical vertebral elements in *Prosopium williamsoni* (Girard), AMNH 37967 (ca. 7 cm) to show a vertebral-like basioccipital condyle and its association with a differentiated neural arch without a spine. This neural arch resembles the accessory arch in other primitive euteleosts. Compare with figure 8 and figure 10 of *Elops*.

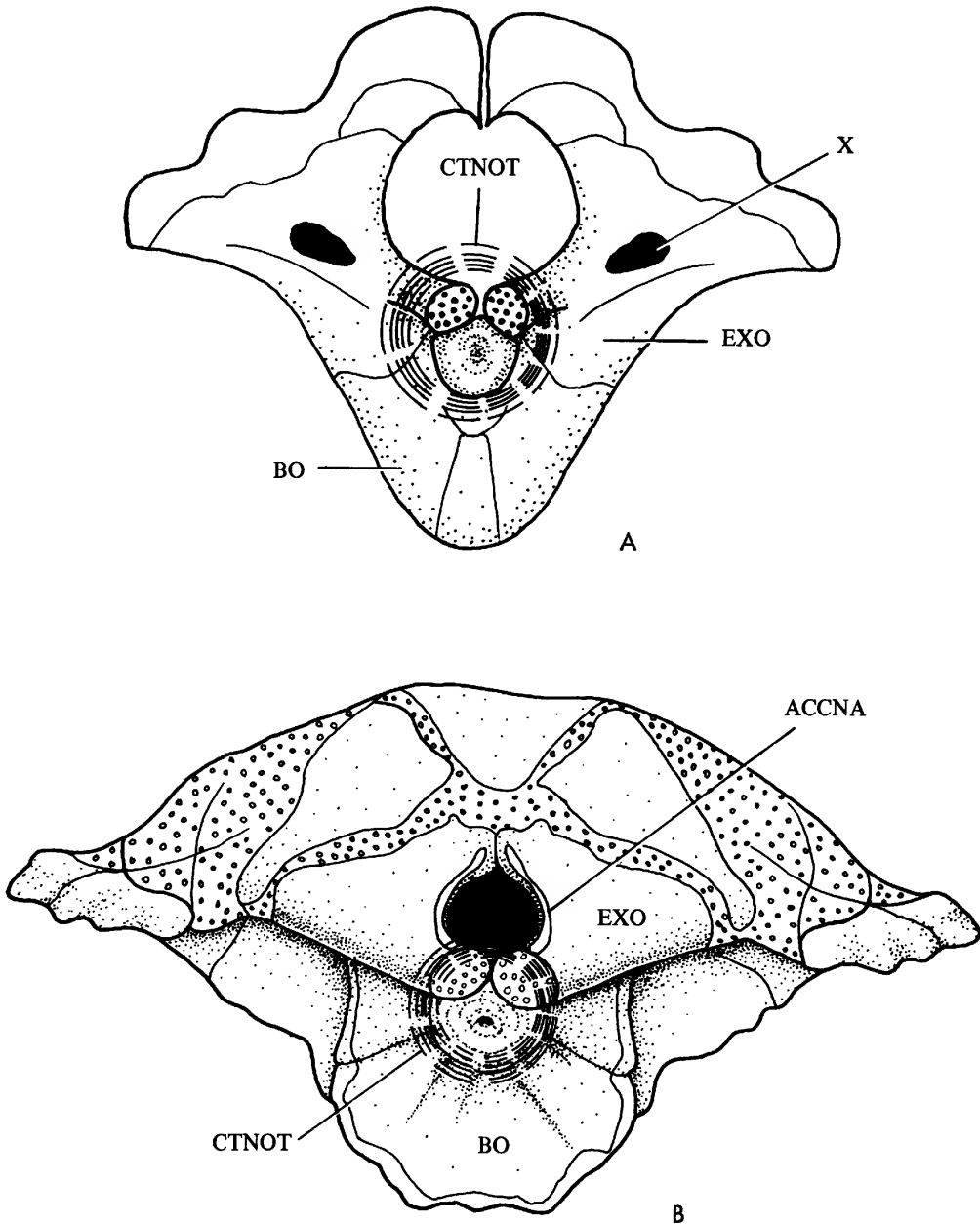


FIG. 14. Occipital regions. A. *Chlorophthalmus agassizi* Bonaparte, AMNH 27402. B. *Aulopus japonicus* Günther, AMNH 28635. The cervical gap between the occiput and the first vertebra is occupied by an unconstricted notochord and its connective tissue sheath, as indicated. In both species, the exoccipitals are exposed posteriorly above the basioccipital.

mordax, described below. Its removal in either *Osmerus* or *Esox* would expose, not a tripartite joint, but the empty interior of the basioccipital and the formerly occluded ends

of the exoccipitals (i.e., a dual, rather than tripartite, articular surface).

Study of the occipital region of *Osmerus mordax* at different sizes (figs. 11B, 12B) (1-

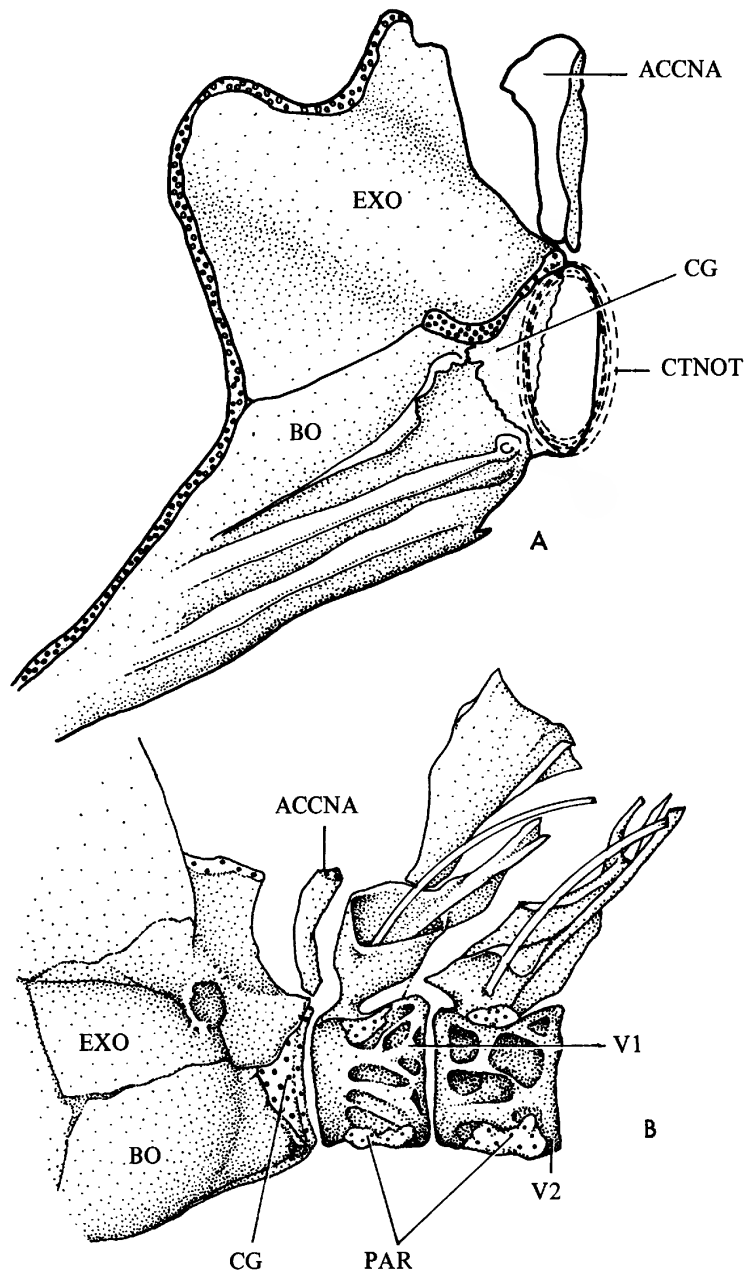


FIG. 15. The occipital region of *Aulopus japonicus* Günther, AMNH 28635, to show the extent of the cervical gap between the occiput and the first vertebra and its relation to the accessory neural arch. A. Posterior quartering view. B. Lateral view. The connective tissue in the region of the gap shows a slight degree of staining with alizarine dye, indicating the presence of some calcification or ossification. This slightly stained, transparent connective tissue gap is hypothesized here to be what remains of a single basioccipital facet that would normally occlude the exoccipitals from the posterior face of the occiput as in *Elops* and *Prosopium* (figs. 8, 10, and 13).

5 cm in standard length) suggests how the neoteleostean condition might have arisen.

At 2 cm, neural arches are well developed along the vertebral axis and a small less well-

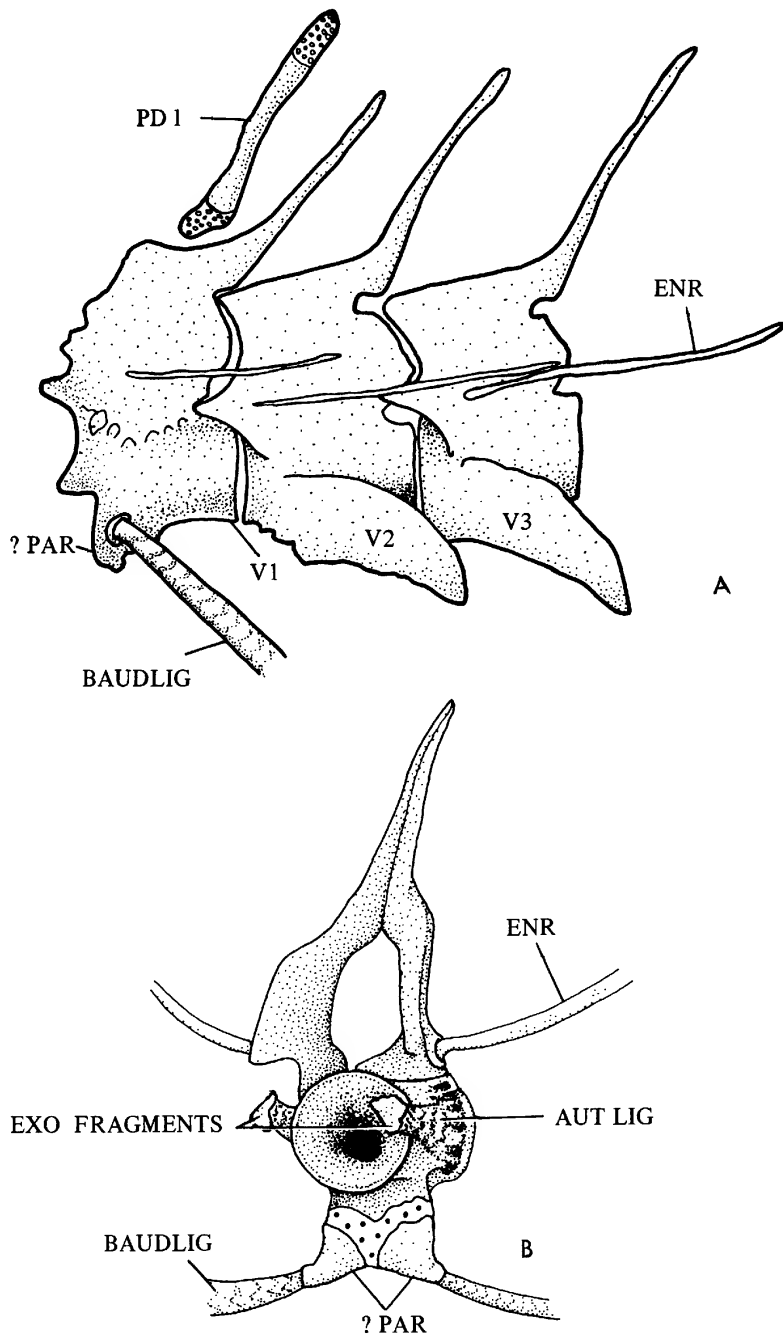


FIG. 16. Anterior vertebrae in myctophids. A. *Rhinoscopelus tenuiculus* (Garman), AMNH 1915. B. *Myctophum nitidulum* Garman, AMNH 25022. In B, separation of V1 from the occiput caused the dense autocentral ligaments to break away with fragments from the exoccipitals. In A, a bit of neural arch base of V1 has grown forward into such ligaments (not shown here, but see fig. 17).

formed arch is present between the occiput and V1. At 5 cm, the accessory neural arch is ossified except at its dorsal and ventral tips

and it articulates ventrally with a notochordal-connective tissue plug in a distinct gap between the occiput and the first cervical ver-

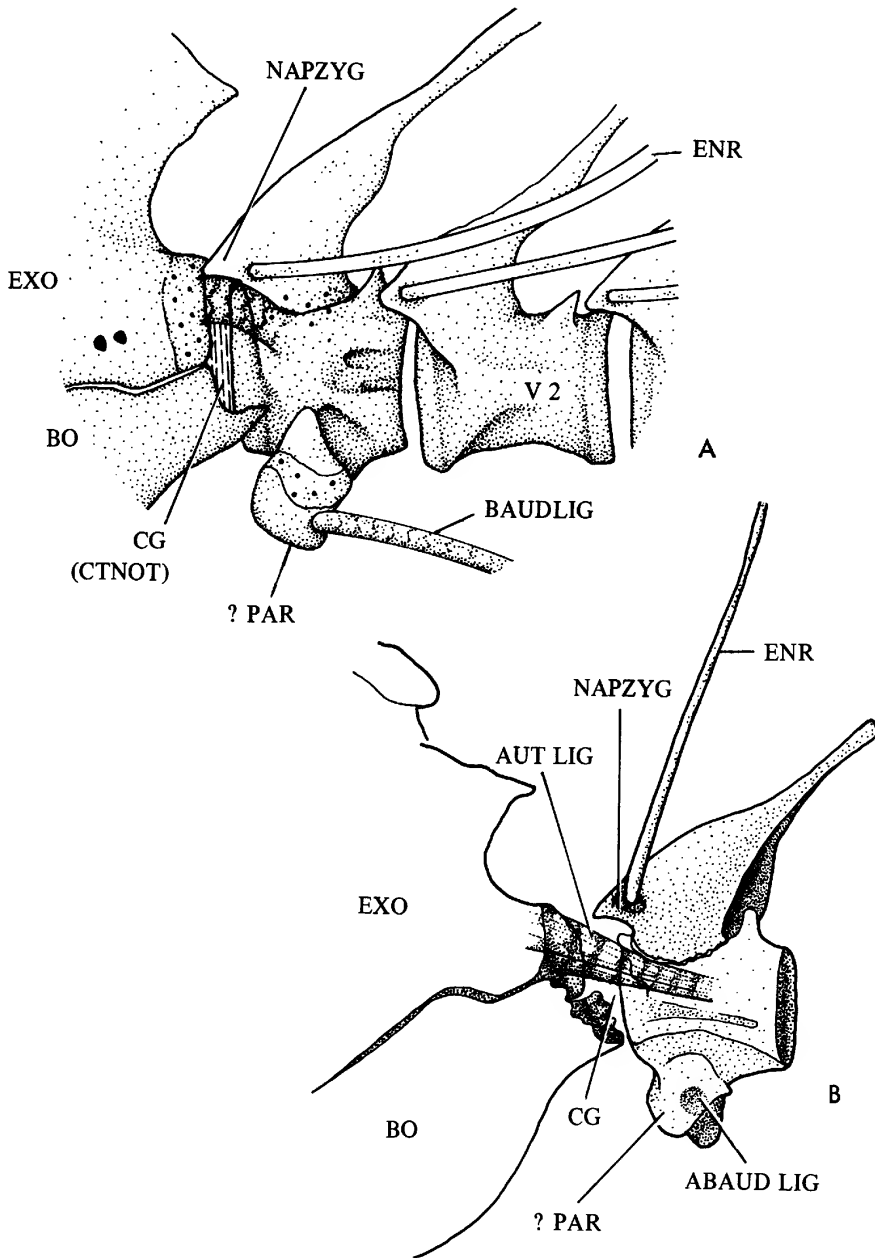


FIG. 17. Myctophid occipital regions to show the extent of the cervical gap and the autocentral ligaments to the exoccipitals just below prezygapophyses on the neural arches. These ligaments are hypothesized to be the primitive state of exoccipital facets (as prezygapophyses) in more derived ctenosquamate conditions. A. *Myctophum obtusirostre* Tåning, AMNH 25022. B. *M. aurolaternatum* Garman, AMNH 15975.

tebra (fig. 11, 12B). At 2 cm, the small arch articulates ventrally with a flat disc that is adherent to the basioccipital and is somewhat indented dorsolaterally by the exoccipitals.

The anteroposterior dimension of this disc is very small (fig. 11B), indicating that if it is a centrum, that centrum has formed only around a narrow anterior part of the noto-

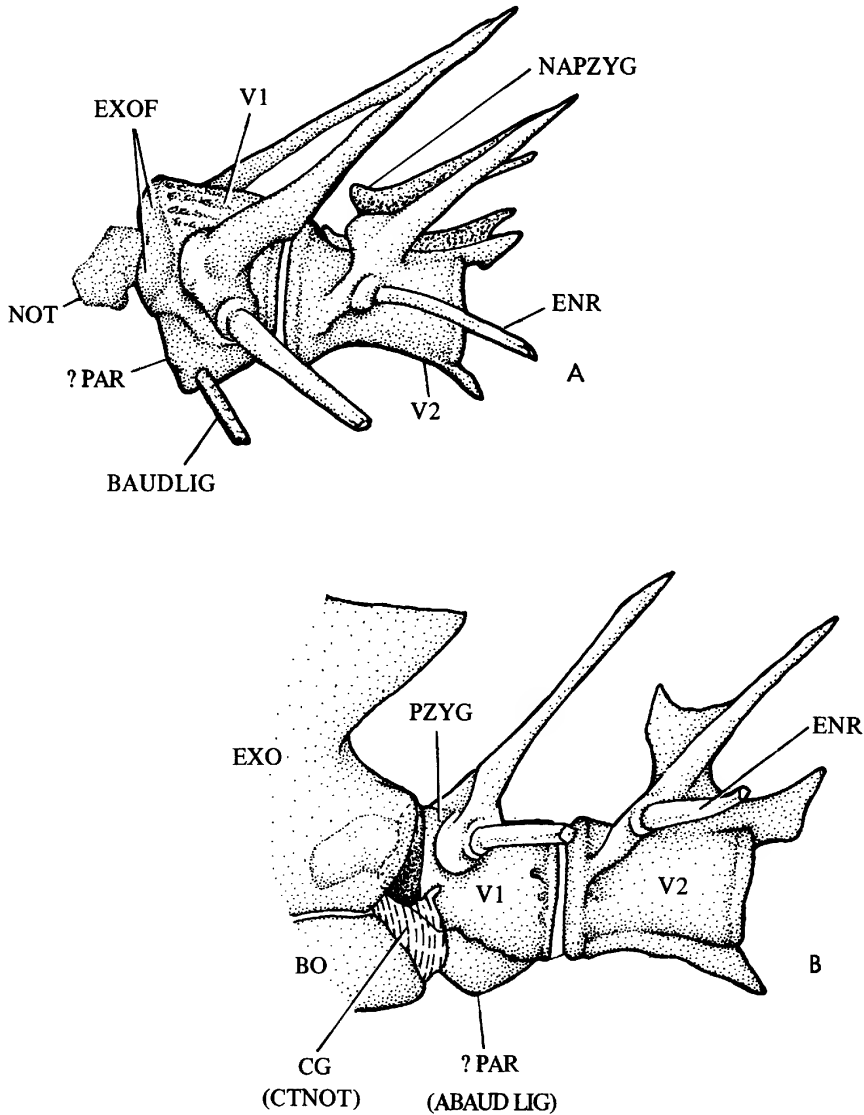


FIG. 18. The cervical region of *Polymixia lowei* Günther, AMNH 37335. A. First two vertebrae showing the exoccipital facets and a persisting notochordal plug on V1. B. The vertebrae in A in their articulated position. Note that the cervical gap is closed dorsally by autocentral prezygapophyses to the exoccipitals, but still open ventrally.

chordal sheath which is easily deformed by the exoccipitals.

As hypothesized above, the presence of an accessory neural arch, in the absence of an underlying centrum, is inferred to represent a retention of the neural arch component of a vertebral segment that either is incomplete or had been incorporated indistinguishably into the braincase.

The origin of the ctenosquamate triple joint appears to follow a direct course involving the following steps: (1) formation of a gap between the occiput and V1 and exposure of the basi- and exoccipitals as attachment or articular surfaces (figs. 14, 15); (2) loss of the accessory neural arch in all myctophids and acanthomorphs (figs. 16–20); (3) attachment of the dorsolateral part of V1 with the ex-

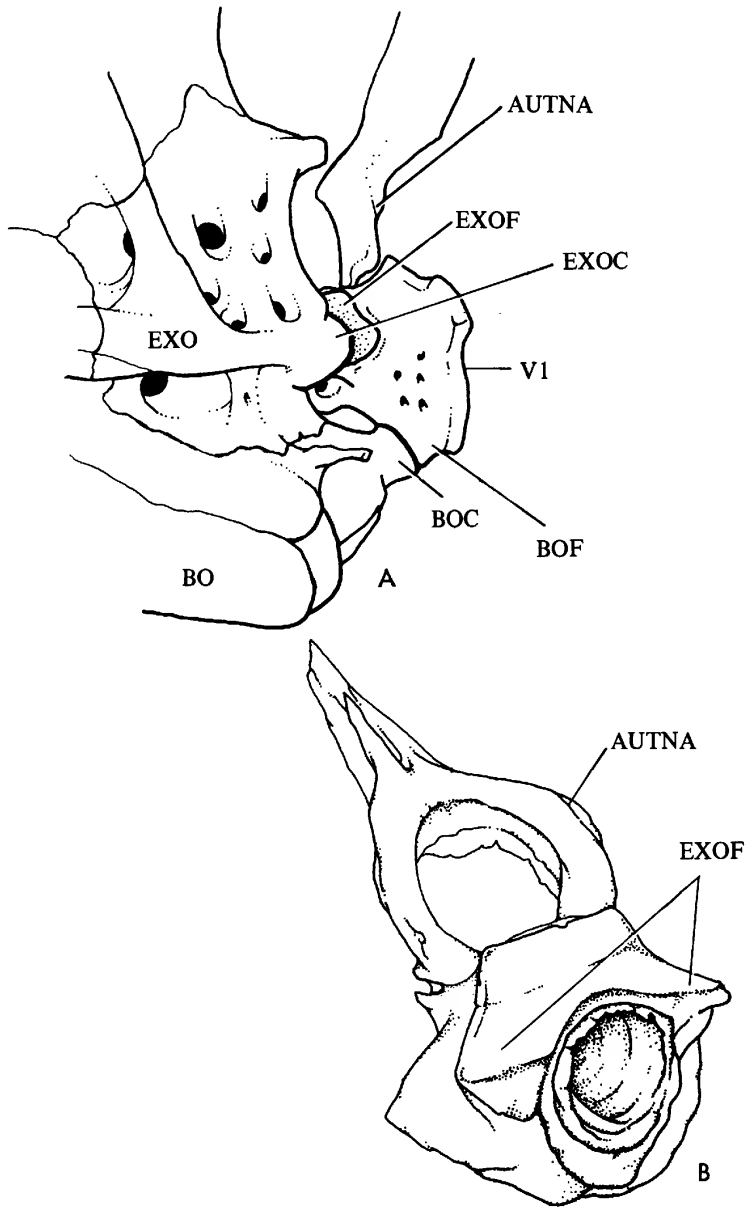


FIG. 19. Holocentrid cervical anatomy. A. Occiput and first vertebra of *Holocentrus rufus* (Walbaum), AMNH 35497. B. Anterior quartering view of the first vertebra of *H. ascensionis* (Osbeck), AMNH 22006, showing the single, continuous exoccipital facet and autogenous neural arch and spine.

occipital, initially by ligament (figs. 16, 17); (4) the growth posteriorly of the exoccipital into this ligamentous network as in *Chlorophthalmus* and at least one myctophid (fig. 16) accompanied by the growth of autocentral prezygapophyses toward the exoccipitals (fig. 18) and the closure of the gap by the basioccipital and the body of the centrum

(figs. 19, 20); and (5) finally the full development of bone-to-bone condylar articulations between the occipital region and facets on V1.

Primitively, V1 in ctenosquamates has a neural arch with a ventral cartilage tip seated in dorsal depressions in the centrum (figs. 4–6), or is at least sutured, rather than anky-

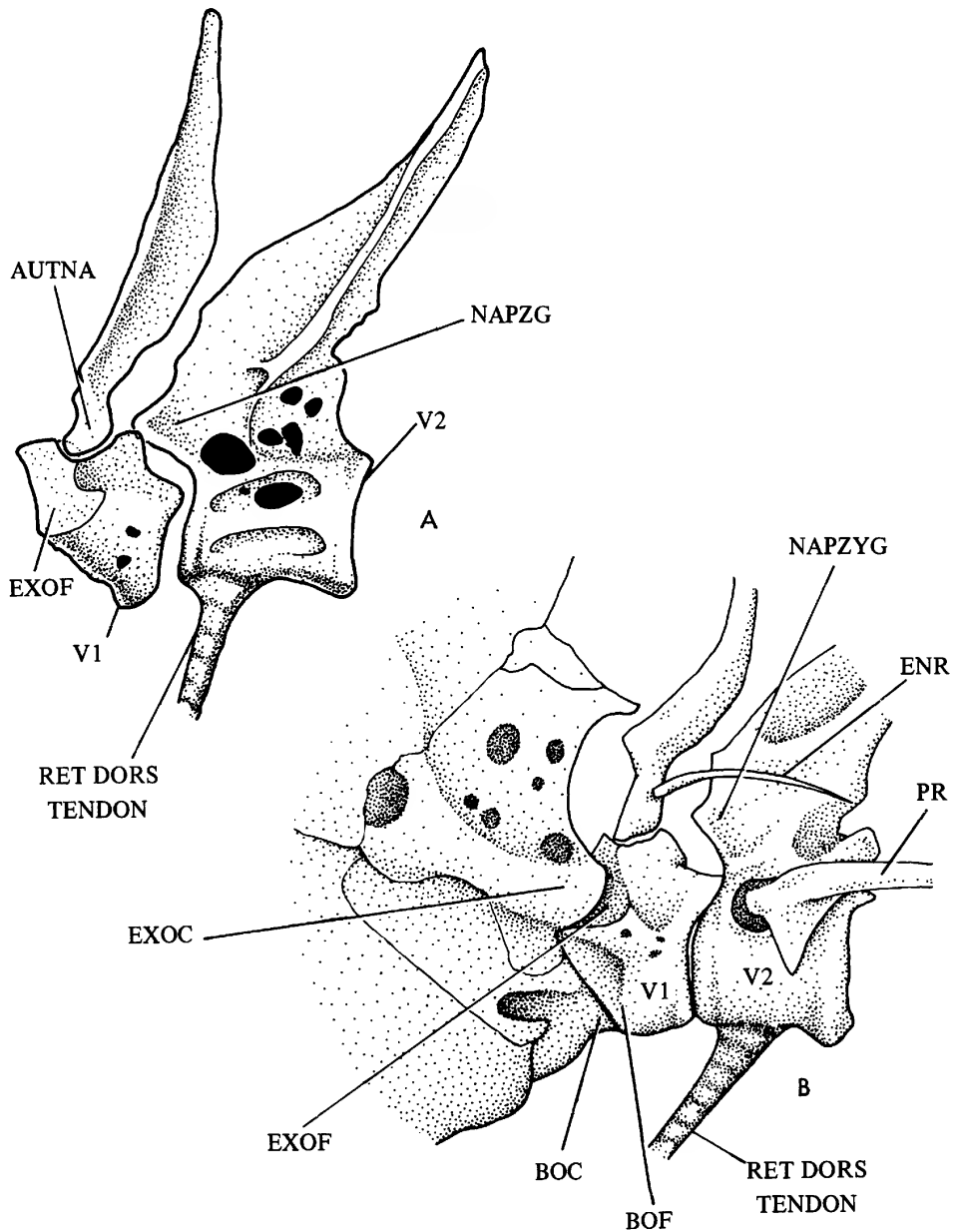


FIG. 20. Holocentrid cervical anatomy. A. *Holocentrus rufus* (Walbaum), AMNH 35456, first two vertebrae, showing, in lateral view, the exoccipital facet and autogenous neural arch and spine on V1. B. *H. rufus*, AMNH 35477, showing the first two vertebrae in normal articulation with the occiput. The tendon for the retractor dorsalis muscle is shown on V2 in A and B.

losed with the autocentrum. There is some question about the generality of that last statement, since my specimen of adult *Myctophum aurolaternatum* (fig. 17B) shows the suture line clearly, whereas Jollie's (1954) figure 22 of the first vertebra of *Lampanyctus*

leucopsarus shows the arch to be completely ankylosed with the centrum. Yet another myctophid, *Rhinoscopelus*, is consistent with Jollie's figure of *Lampanyctus* (fig. 16A). The neural arch of V1 is unfused in holocentrids (figs. 19, 20) and primitive "percoids" such

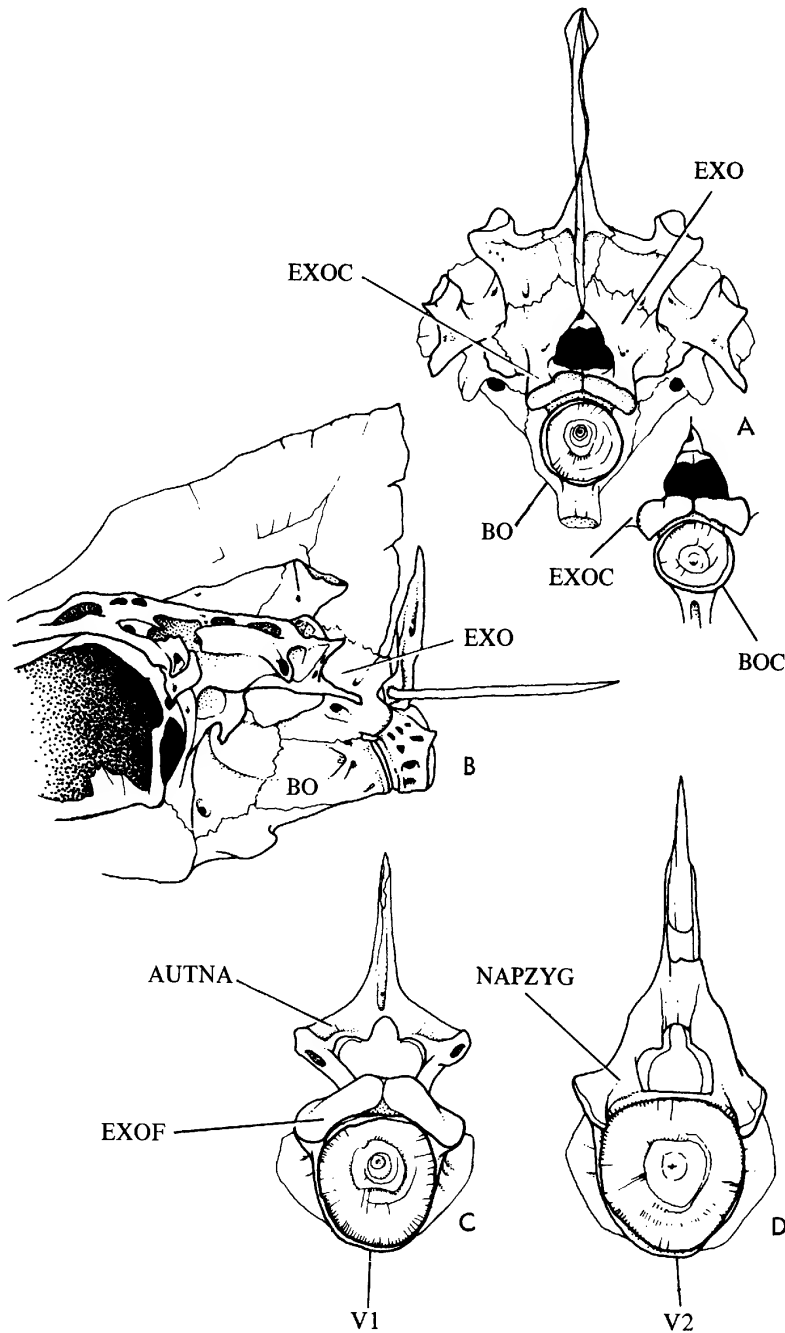


FIG. 21. Occipital region and first two vertebrae of *Haemulon album* Cuvier, AMNH 30827. In A, the occipital condyle is shown from a slightly ventral orientation (inset) to clarify condyle shape. Vertebrae (C and D) in anterior view. Neural arch on V1 autogenous.

as haemulids, gerreids, lutjanids, and lethrinids (figs. 21–28), whereas it is ankylosed in stephanoberycoids and many apomorph groups of “perciforms,” recalling Patterson’s

(1964) earlier supposition that the acanthopterygians might not represent a monophyletic group.

The taxonomic implications of occipital

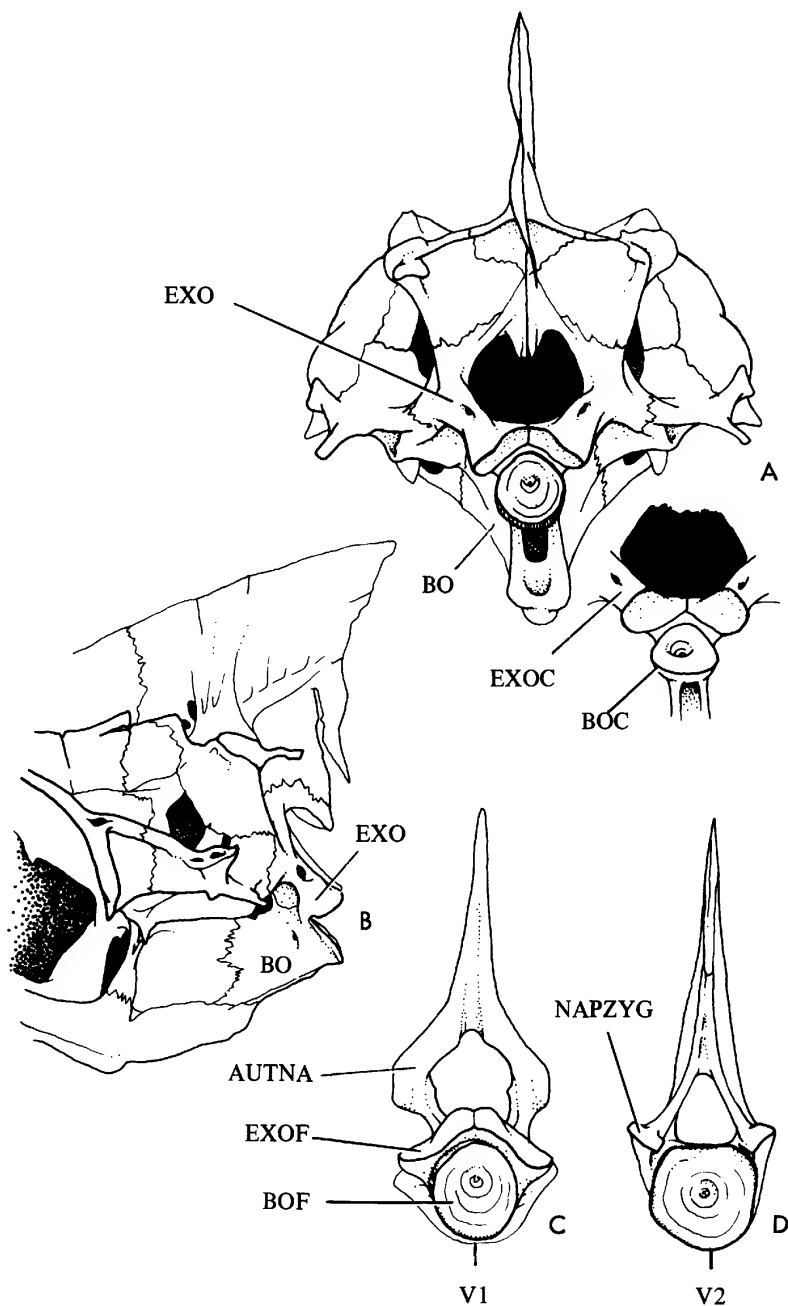


FIG. 22. Occipital region and first two vertebrae of *Gerres cinereus* (Walbaum), AMNH 21732. In A, the occipital condyle (inset) is shown from a slightly ventral orientation to clarify condyle shape. B. Lateral view as in A. Vertebrae (C and D) in anterior view. Neural arch on V1 autogenous.

anatomy do not stop there, however. Primatively, the exoccipital condyles meet in the midline just above the notochordal canal. In holocentrids (fig. 29A), they are united by a

delicately interdigitating suture (fig. 29A). A similar arrangement has also been found in trachichthyids and berycids. Reference to Patterson's (1964) account of the acanthop-

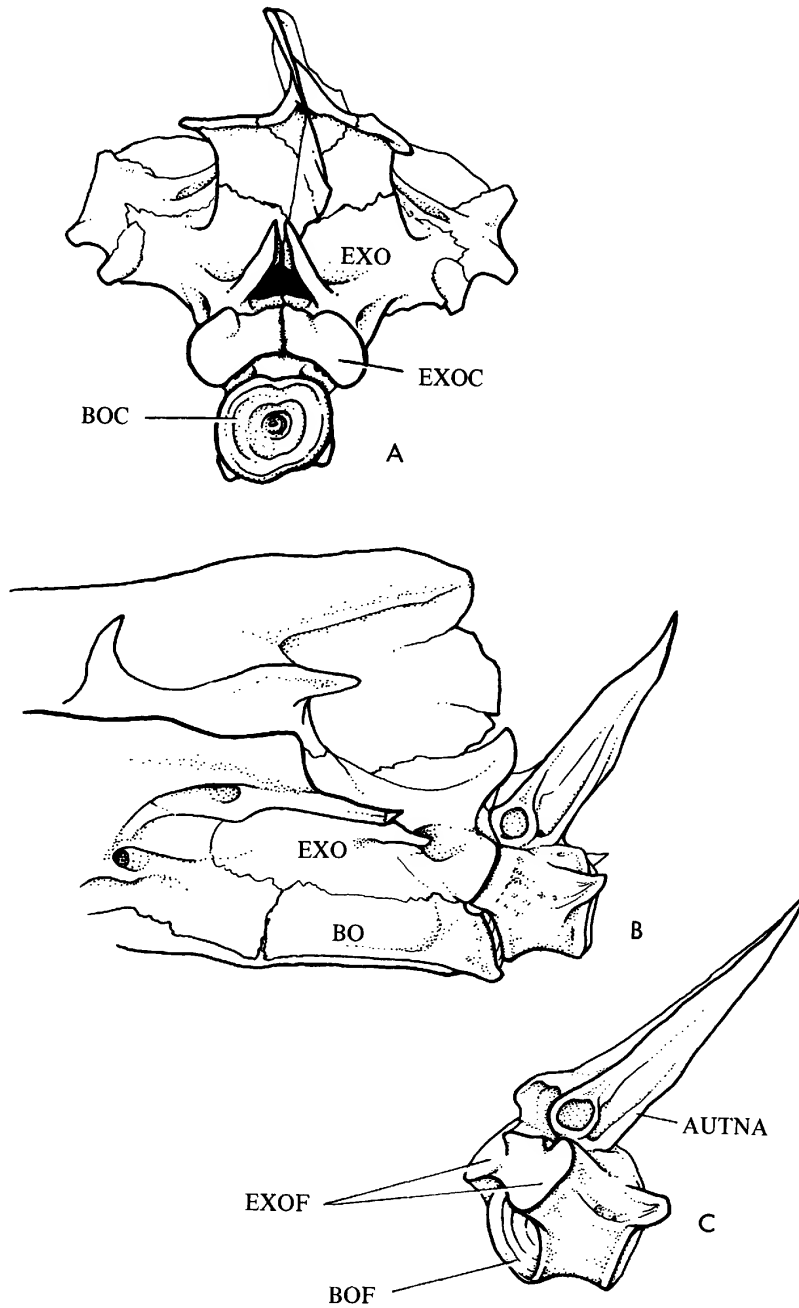


FIG. 23. Occipital region (A, B) and first vertebra (C) of *Pomatomus saltatrix* (Linnaeus). Neural arch on V1 autogenous.

terygian fishes of the English Chalk shows that the pattern formed by these two condyles is very old and occurs in such primitive creatures as †*Aulolepus typus*. The arrangement produced by these condyles is best described

as an elongate rectangle that forms a concave arc posteriorly. A single convex facet on the first cervical vertebra of similar shape articulates with these medially united condyles. The exoccipital condyles retain this basic form

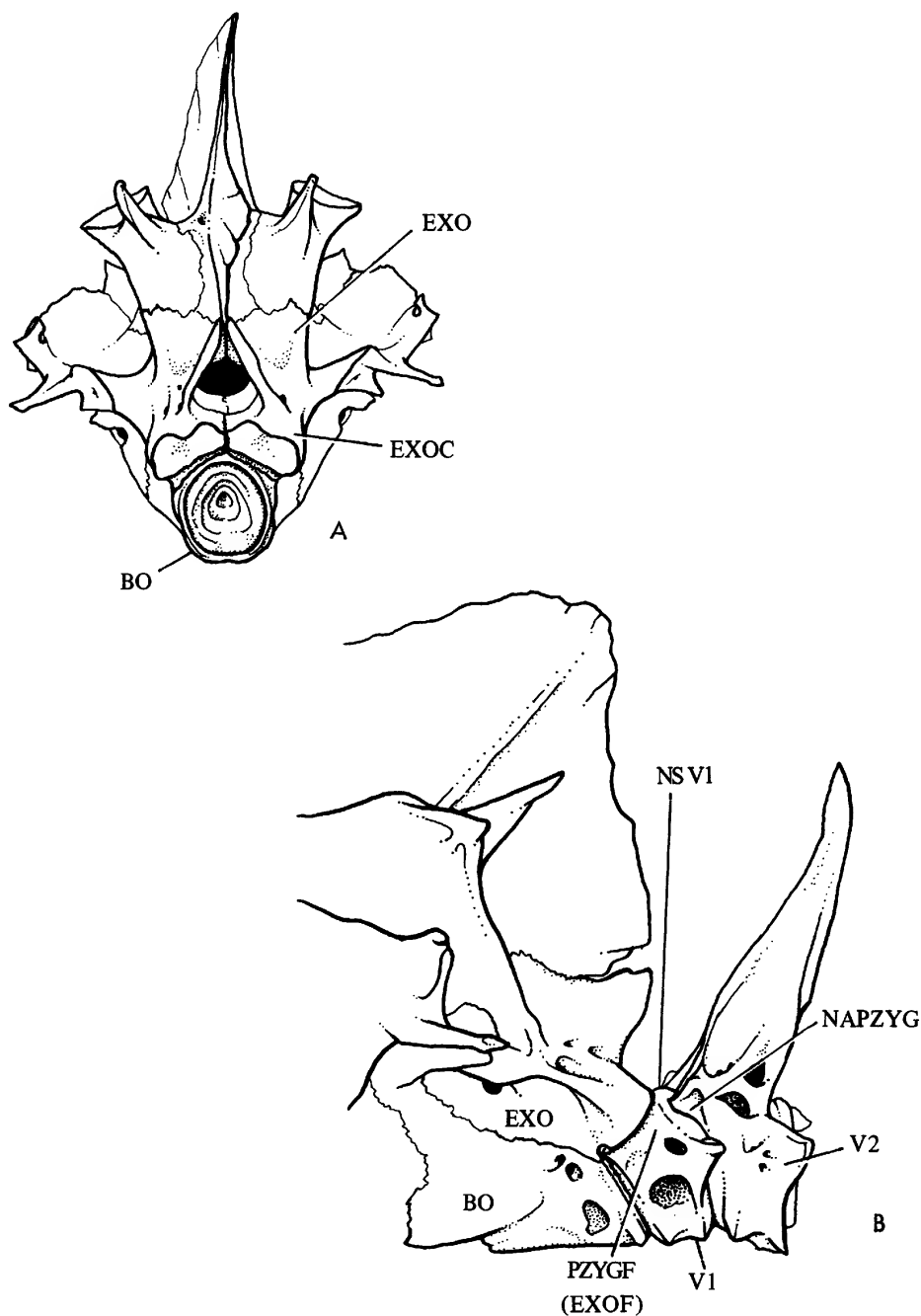


FIG. 24. Occipital region and first two vertebrae of *Lutjanus campechanus* (Poey). A. AMNH 21632. B. AMNH 21688. In B, the autogenous neural arch of V1 had fallen off and was lost during preparation.

and remain medially united in a variety of fishes that have been regarded as “basal percoids” (see figs. 21–28, 29B, C). Thus, the “percoid” condition includes two primitive

features that are shared with at least some “berycoids” (e.g., holocentrids): the medially united condyles forming a long concave rectangle and an autogenous neural arch on the

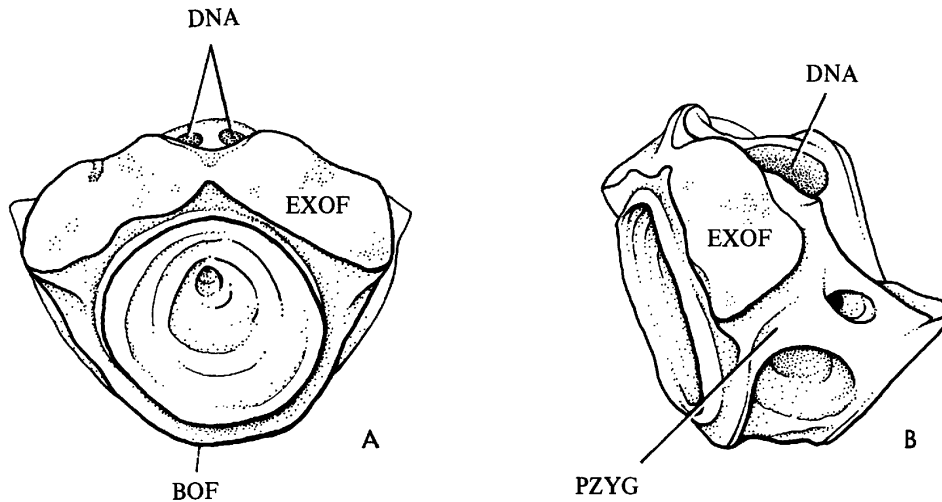


FIG. 25. Anterior (A) and lateral (B) views of the first vertebra of *Lutjanus campechanus* (Poey), AMNH 21632. The autogenous neural arch was removed to show the articular wells on the dorsal surface.

first cervical. Derived transformations of these conditions involve lateral displacement of the condyles accompanied by an alteration of their rectangular shape and the shape and position of the articular facets on the first cervical vertebra (figs. 29D, 30–32), and ankylosis of the neural arch with the centrum of this vertebra (figs. 33, 34). A comprehensive survey needs to be made before the taxonomic usefulness of this area can be judged fully, but, in at least two cases, modifications of the occiput and first vertebra suggest affinities between major fish groups that were major components of the Paracanthopterygii (figs. 35–39). In each of the batrachoid-lophiiform and ophidiiform-gadiform groups, the exoccipital condyles primitively receded from the posterior occipital margin and consist of widely separated, cartilage-filled tubes to which prezygapophyses from the first cervical articulate. In all of these fishes the neural arch and spine of the first cervical vertebra is ankylosed to the centrum and both are firmly joined to the back end of the skull.

THE ROSTRAL CARTILAGE: The rostral cartilage is another feature that has been given prominent attention as a neoteleostean synapomorphy. Here again, Fink and Weitzman (1982) have found paired elements in some salmonines and one coregonine that are small discs of cartilage affixed to the inner face of

the premaxillae (fig. 40A), and hypothesized that the elements are a synapomorphy of salmonids and neoteleosts. But not all salmonids, or even salmonines, have such cartilages (I have not found one in any species of *Salvelinus*) and at least one osmeroid, *Osmerus mordax*, does have them (fig. 41A). Among neoteleosts, however, *Chlorophthalmus* has them well developed in connection with a series of premaxillary processes (figs. 40C, 41B) almost certainly synapomorphic for a group defined previously as the Eurypterygii (Rosen, 1973). One stomioid also has a *Chlorophthalmus*-like upper jaw with a similar, though slight, indication of cartilage development. By this, I mean that it stains prominently for mucopolysaccharides with alcian blue, as does cartilage, and the stained area appears to contain a few cells as well as connective tissue fibers (fig. 40B). This stomioid is *Maurolicus muelleri*, but Fink and Weitzman (1982) treat this as homoplasious on the grounds that *Maurolicus* is a derived member of an apomorph group of stomioids (the sternoptychids)—ruling out the possibility of a retained primitive feature.

They claimed, however, that in *Diplophos* there is a rostral cartilage which, in their view, corroborates the placement of stomioids with neoteleosts. What they illustrated in this instance, though, is a flat, median domino-

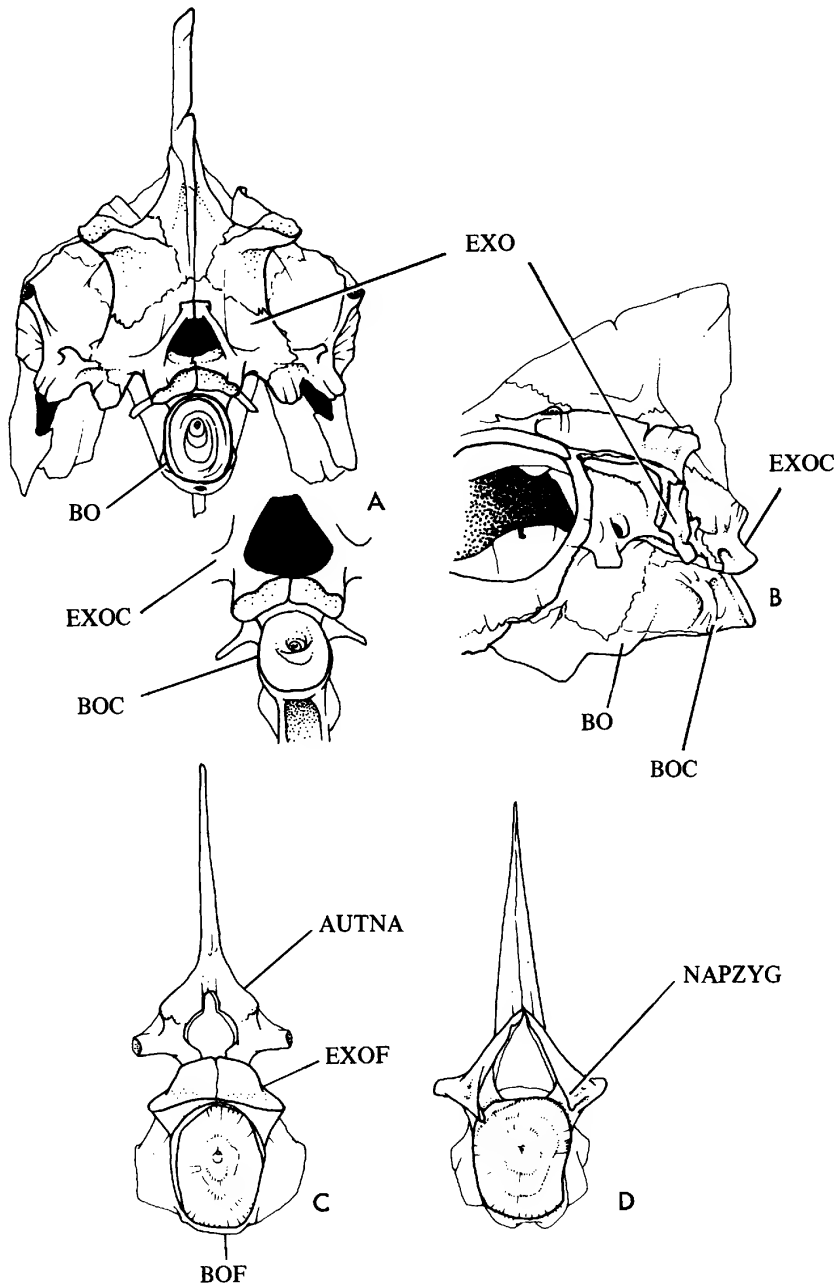


FIG. 26. Occipital region and anterior two vertebrae of *Lethrinus* sp., AMNH 30872. In A the condyles are shown from a slightly ventral orientation (inset) to clarify condyle shape. Neural arch of V1 autogenous.

shaped element not firmly bound to the premaxillaries or oriented like the median element in neoteleosts. But S. Weitzman informs me (*in litt.*) that the cartilage is actually

a long cylinder surrounded by connective tissue, so that as redescribed it still does not fit the anatomical requirements of a neoteleostean rostral cartilage.

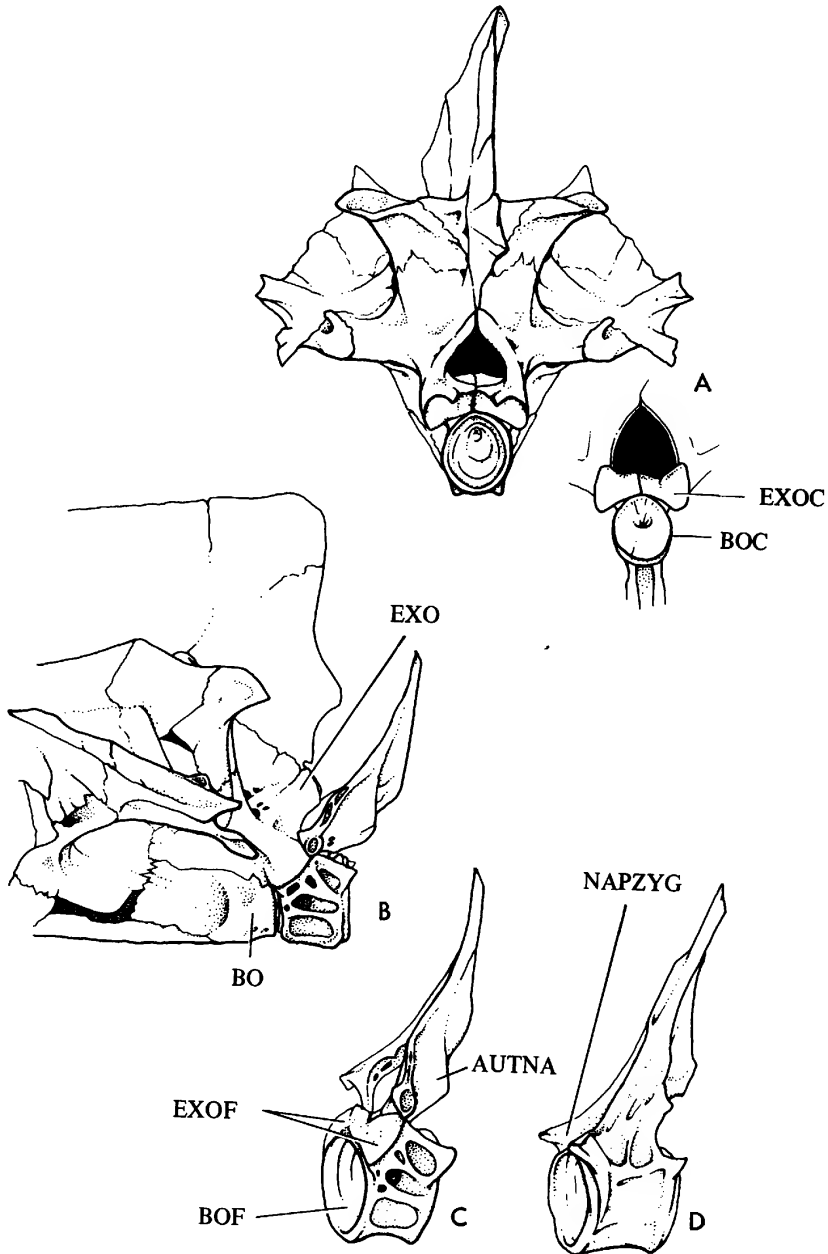


FIG. 27. Occipital region and anterior two vertebrae of *Seriola* sp., AMNH 30856. In A, the condyles are shown from a slightly ventral orientation (inset) to clarify condyle shape. Neural arch of V1 autogenous.

Nevertheless, Fink and Weitzman (1982) deserve much credit for making these initial observations of the cartilaginous skeleton and thereby opening up new avenues for profitable research.

The manner in which paired premaxillary

cartilages transform into the median element of neoteleosts is suggested by a series of structures found amongst neoscoelids and some ctenosquamates (figs. 24–25). (K. Sulak, personal commun., informs me that paired cartilages occur also in *Ateleopus*, a fish that has

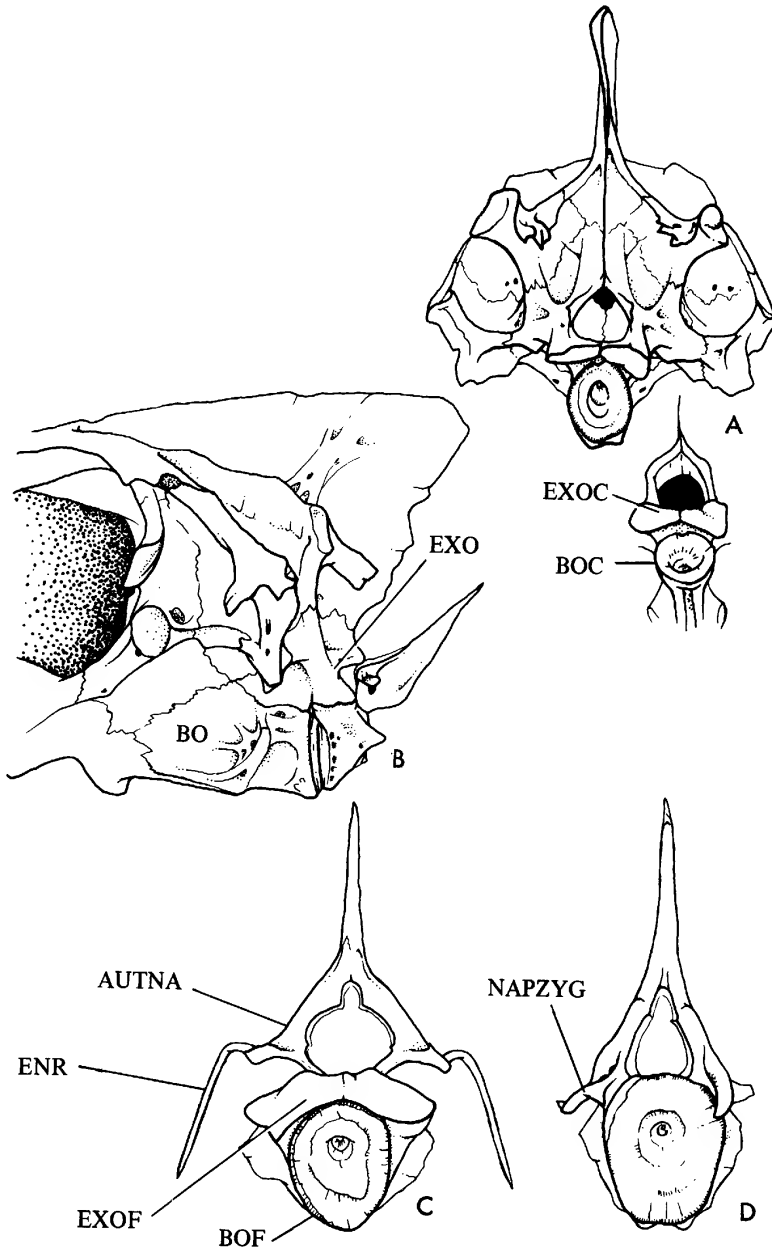


FIG. 28. Occipital region and anterior two vertebrae of *Archosargus probatocephalus* (Walbaum), AMNH 21663. In A, the condyles are shown from a slightly ventral orientation (inset) to clarify condyle shape. Neural arch of V1 autogenous.

defined placement so far—see comments in Rosen, 1973.) But within neoscopelids (figs. 42, 43A), the paired elements retain their firm association with the premaxillary ascending processes and a median element with which they become fused in *Neoscopelus* (fig. 42B)

appears to form as an extension of chondrification into the interpremaxillary ligament, or perhaps is best described as a sesamoid cartilage that develops in response to the stresses on that ligament. In all events, in *Neoscopelus*, what appear to be three distinct

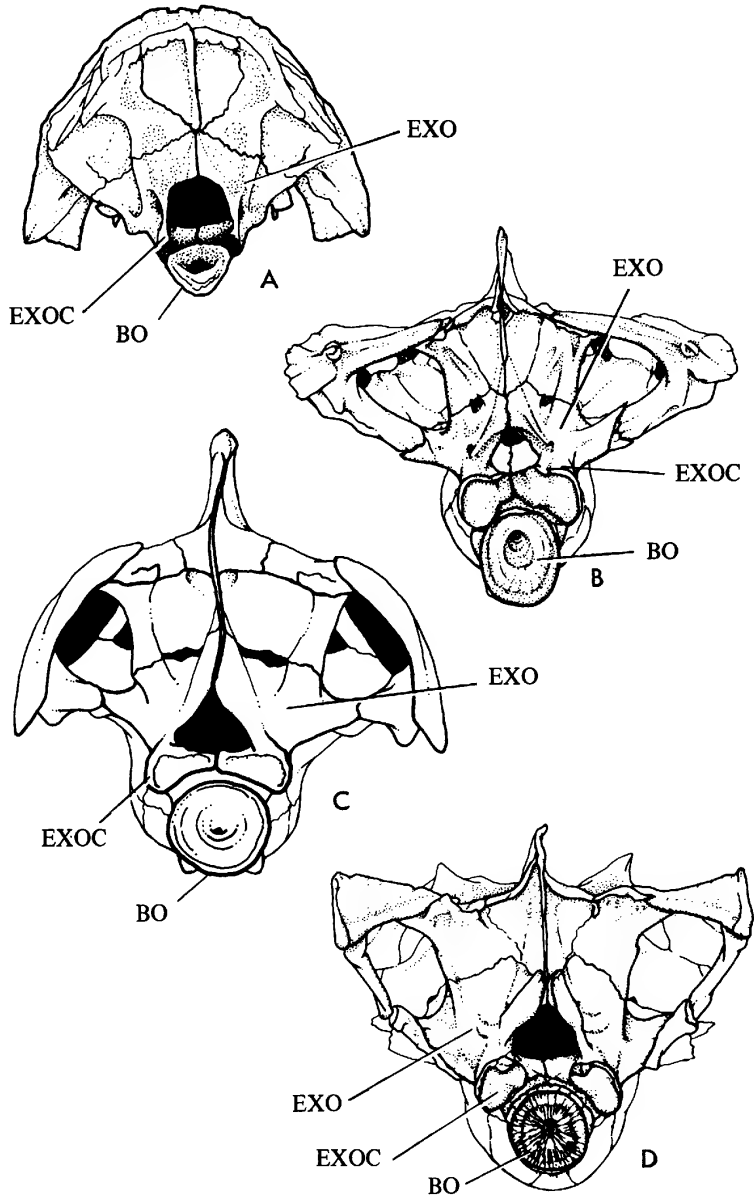


FIG. 29. Comparison of primitive and derived acanthopterygian occipital regions. A. *Holocentrus ascensionis* (Osbeck), AMNH 22086, showing the planar exoccipital condyles suturally united medially. B. *Centropomus undecimalis* (Bloch), AMNH 28058, showing the laterally expanded exoccipital condyles retaining the medial suture. C. *Morone chrysops* (Rafinesque), AMNH 22528, showing condition as in B. D. *Sebastes* sp., AMNH 36935, showing a more derived condition in which the exoccipital condyles are displaced laterally.

cartilages become one, and apparent evidence of a tripartite history may still be detected in the structure of some other ctenosquamates (figs. 43B–D). *Aulopus* (fig. 41C) appears to have a rostral cartilage that in pos-

terior view resembles a somewhat reduced version of the *Neoscopelus* structure (fig. 43A).

If the foregoing analysis is correct, a new cladogram for the Euteleostei is needed. Fink and Weitzman wished to extend the resolved

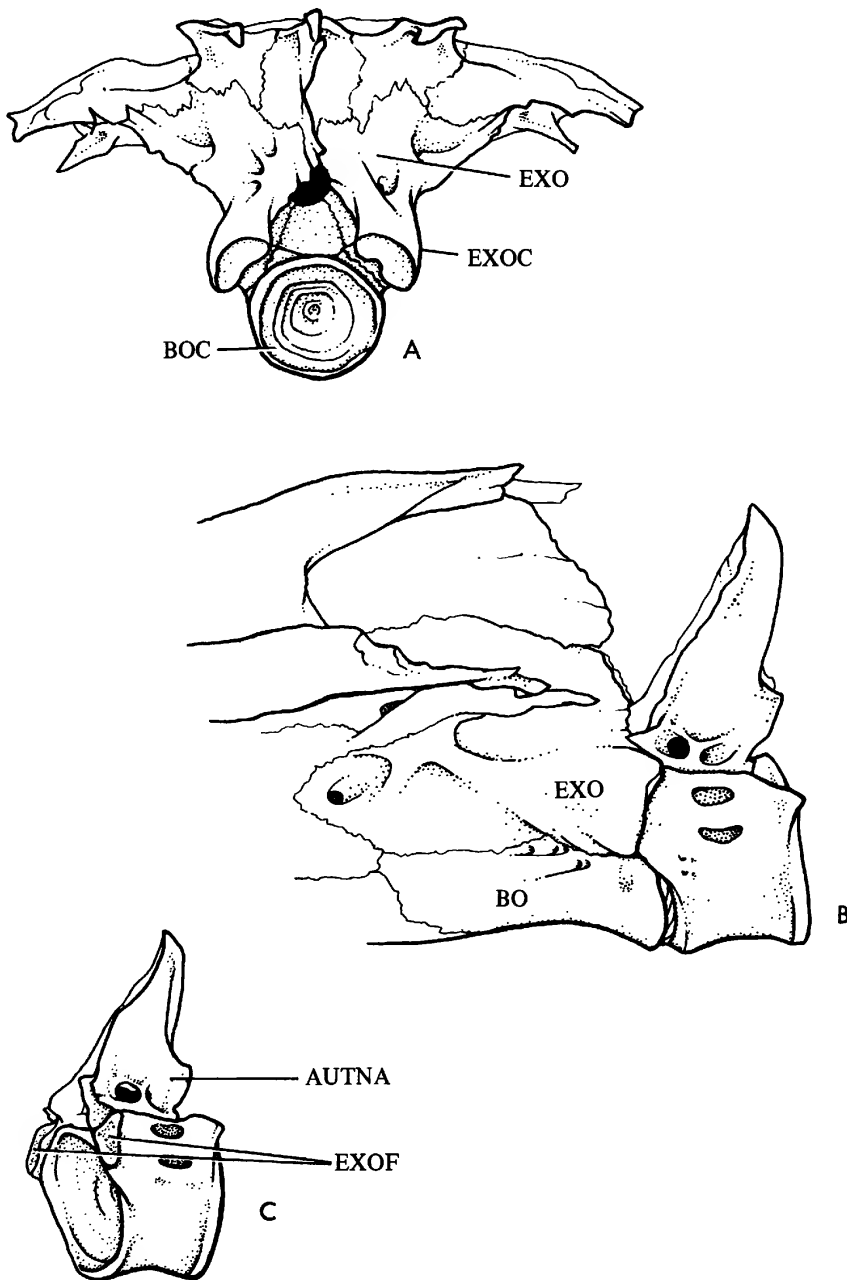


FIG. 30. Occipital region and first vertebra of *Rachycentron canadum* (Linnaeus), AMNH 22135, showing laterally displaced exoccipital condyles. Neural arch on V1 is still autogenous, however.

part of this character-state tree to include the sister group of the Neoteleostei, which they identify as the Salmonidae. But they base this conclusion on features not diagnostic of all salmonids. The difficulty is that an equally

good case can be made for the Osmeridae, which incidentally show the same spottiness of character distribution. For example, *Spirinchus* shows the primitive neoteleostean cervical gap between the occiput and the first

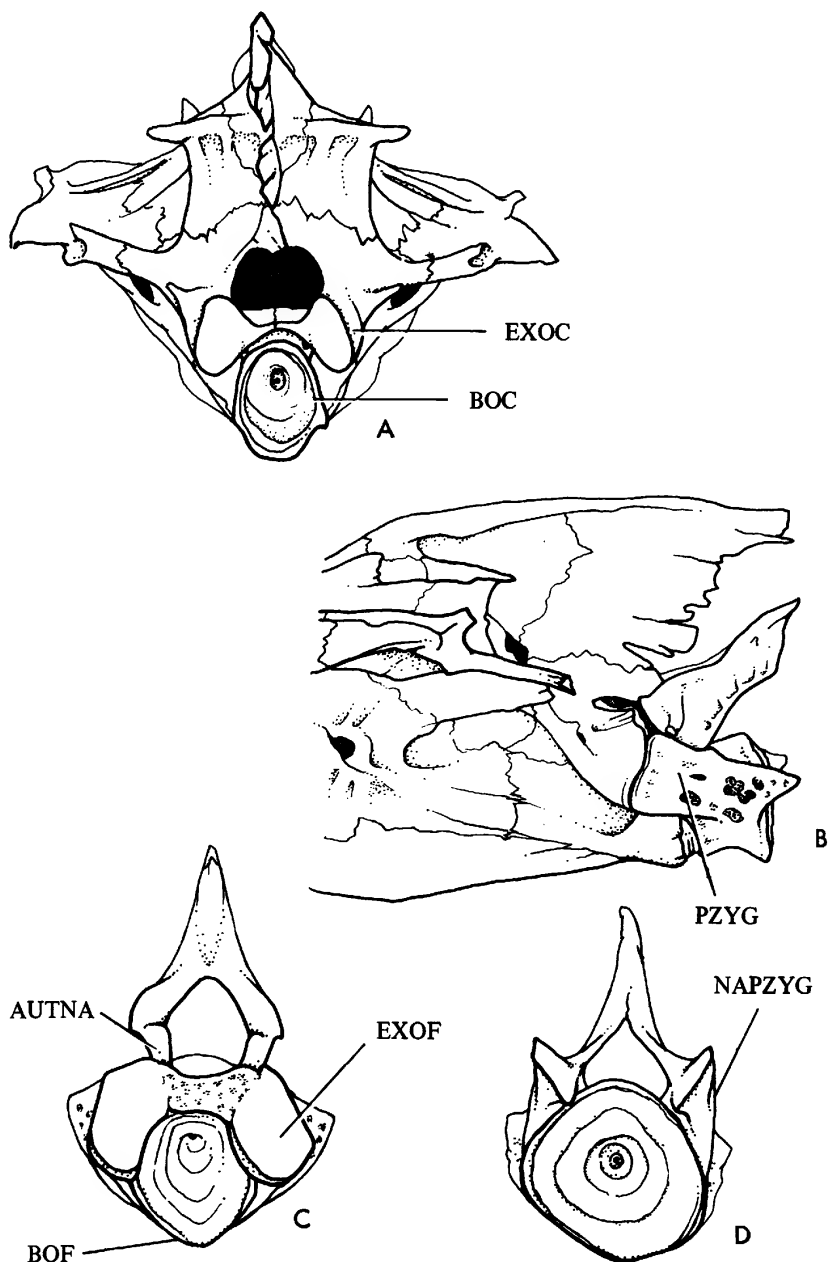


FIG. 31. Occipital region and first two vertebrae in *Arripis trutta* (Bloch and Schneider), AMNH 21632, showing laterally expanded exoccipital condyles just barely in contact in midline. Neural arch on V1 autogenous.

vertebra (figs. 11A, 12C) and has, as a consequence, exoccipitals that have exposed posterior condyle-like faces, and *Osmerus mordax* has the paired premaxillary cartilages (fig. 41A) developed to the same extent as they are in *Prosopium williamsoni* (the only cor-

regonine I have seen that shows the condition). But if we must make a choice from amongst the old "salmoniforms" for a neoteleostean sister group, then the Osmeroidei, or at least *Spirinchus*, is a better choice than salmonids on three counts:

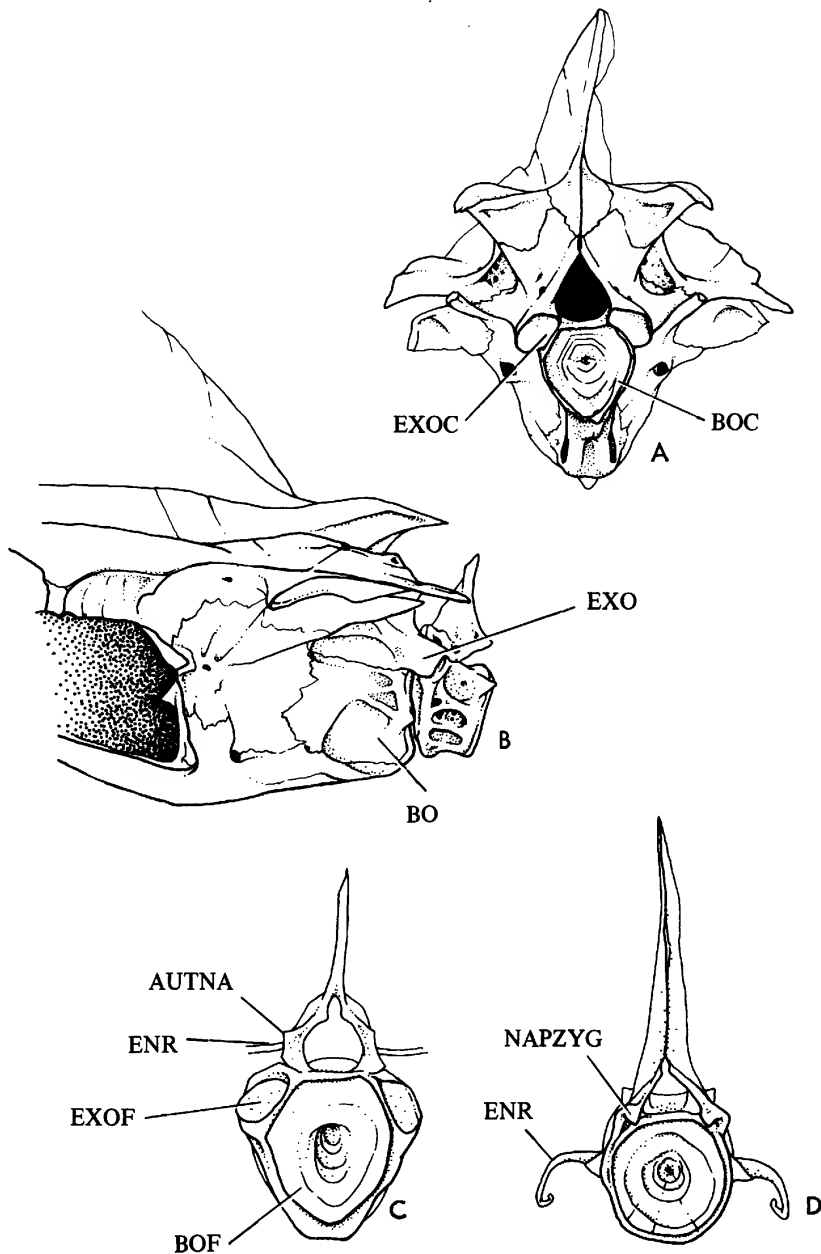


FIG. 32. Occipital region and first two vertebrae in *Coryphaena hippurus* Linnaeus, AMNH 21750, showing laterally displaced exoccipital condyles and a still autogenous neural arch on V1.

1. All osmeroids have a modified neural spine definitely associated with the second preural centrum which is reduced in height in virtually all cases and fitted with laminar bone fore and aft, resembling this spine in aulopids. Salmonines, in contrast, have a full, strong spine on the second preural centrum

(see Vladykov, 1962, figs. 1–3) when the association of spine and centrum is of a definite sort [although the spine is short in coregonines (fig. 44) and might be primitive for the Salmonidae if that group is monophyletic]. If Fink and Weitzman (1982) and Fink (1984) are correct in aligning galaxioids with os-

meroids, then a similar problem arises in the osmeroid complex since galaxioids, but not osmeroids, have a full spine on PU2. Which state is primitive for such an osmeroid complex?⁶

2. The premaxillary has an alveolar process of sorts (fig. 41A) under which there are no maxillary teeth (in other words, they show a simple tandem arrangement of these bones as opposed to their more primitive serial alignment in salmonids (fig. 40A).

3. The osmeroids (as defined by Fink and Weitzman) so far studied (a species of *Osmerus* and *Galaxias*) have acellular bone in common with neoteleosts (Parenti, MS), whereas the salmonids studied have a mixture of primitive cellular and some acellular bone. Thus, the relatively smaller, usually definitely shortened spine in osmeroids, a simple form of tandem upper jaw bone alignment and acellular bone, are synapomorphies that osmeroids, but not salmonines, share with the Neoteleostei.

CHARACTER CONFLICTS

The evidence gathered so far for overall euteleostean classification involves a number

⁶ Fink and Weitzman (1982) and Fink (1984) argued for a linkage between "osmeroids" and galaxiids mainly on the grounds that both possess a distinct row of teeth dorsomedially on the mesopterygoid. Pterygoid teeth are primitive for teleosts, and when the mesopterygoid patch is reduced, it usually leaves such a row in the dorso-medial position (e.g., in *Pterothrissus gisu* and the Eocene †*Diplomystus dentatus*). Such teeth also are present in some primitive neoteleosts such as synodontids (K. Sulak, personal commun.). Galaxiids show other plesiomorphic features not occurring in "osmeroids." These include three, and in some cases, four small, accessory rays in advance of the dorsal fin. And, in the caudal skeleton, neural arches, and often spines, are associated with the first ural and first preural centra (cf. Rosen, 1974, figs. 18, 19, and illustrations in Patterson and Rosen, 1977). Small, but well-ossified, posteriorly cocked, neural arches also occur in some "salmonid" species, especially coregonines, directly over or adjacent to the first preural centrum and on both the first ural and first preural in a variety of primitive teleosts. These are part of a derived caudal feature of tailed elopomorphs (Patterson and Rosen, 1977, cf. figs. 23, 27, 35, 36). Fink's (1984) summary of the problems of "lower" euteleostean classification is an exemplary statement illustrating the need for comprehensive character surveys.

of inconsistencies, some more obvious than others, involving the rostral cartilage, the occipital region of the skull, the caudal skeleton, and the muscle that retracts the dorsal gill arch elements (discussed below).

ROSTRAL CARTILAGE: Among primitive ctenosquamates there is a conflict arising from the fact that myctophids, but not neoscolepids, always have a single median cartilage and a subocular shelf, as in *Acanthomorpha*. This conflict is resolved by simply admitting that the group *Myctophidae* + *Neoscolepidae* = *Myctophiformes*, is unnatural, and should be so represented in the cladogram (fig. 45). Stiassny (MS) treats the group as natural based on several synapomorphies, however.²

OCCIPITAL REGION: The capricious manner in which the tripartite occipital joint is present or not (except within the Neoteleostei where it is diagnostic) has already been alluded to, and has several possible taxonomic implications: (1) the Salmonidae is non-monophyletic; (2) the Osmeridae is non-monophyletic; (3) the Clupeiformes and/or Clupeomorpha are non-monophyletic, although the significance of a triple joint in *Denticeps* is overridden by the congruence of many other characters (Grande, MS); (4) the presence of a tripartite joint in *Lepidogalaxias* (Fink, 1984) might be one more example of character capriciousness if Rosen (1974) was correct in linking that genus with the pikes and mudminnows.⁷

THE RETRACTORES ARCUUM BRANCHIALIUM MUSCLE: It has been known for some

⁷ Fink (1984) supports his argument that *Lepidogalaxias* is allied to neoteleosts by his discovery of a dorsal retractor muscle in this fish. And Fink and Weitzman (1982) disagree with my earlier (1974) alignment of it with esocoids, partly, and I think correctly, on the grounds that my comparison of anterodorsal outgrowths of its first uroneural with those of esocoids leaves a great deal to the imagination. An alternative placement of *Lepidogalaxias* is suggested by the resemblance of its cephalic sensory pit-lines with those of *Dallia* (Nelson, 1972, p. 38). A case might also be made for its original placement as a galaxiine (see Rosen, 1974) based on dorsal and caudal fin anatomy and position, or even with its alignment to a *Novumbra-Dallia* esocoid subgroup defined by having but a single epural and uroneural in the caudal skeleton. Fink's (1984) statement that the "position of *Lepidogalaxias* is controversial" is unarguable.

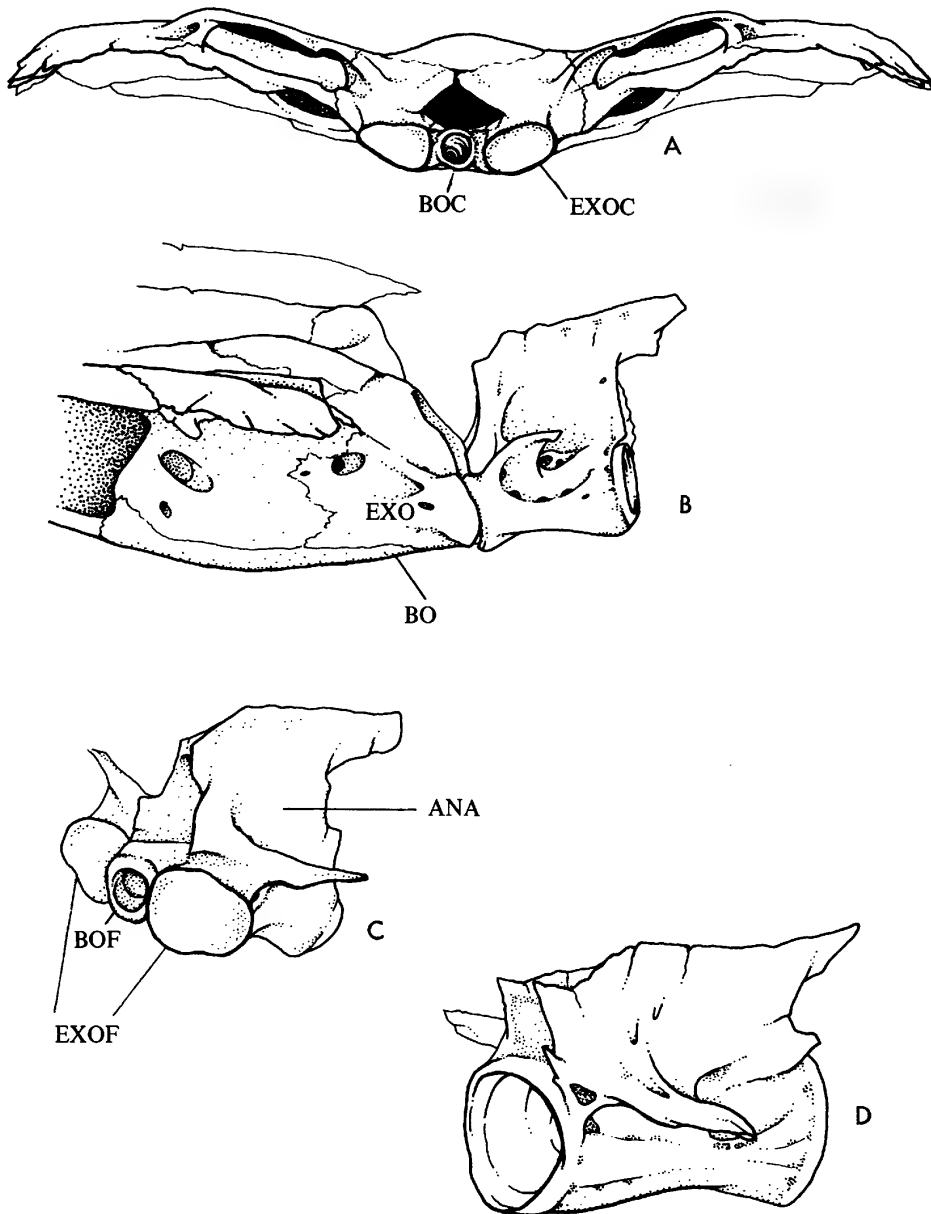


FIG. 33. Occipital region and first two vertebrae in *Echeneis naucrates* Linnaeus, AMNH 21844, showing enlarged lateral exoccipital condyles and the neural arch on V1 ankylosed.

time that the retractor dorsalis, as this muscle has been called, has a sporadic occurrence among halecomorph fishes, which Rosen (1973) commented upon earlier. Most recently, Fink (1984) has identified one in *Lepidogalaxias salamandroides*. The problem of the homology of these different retractor

muscles has been investigated in some detail in relation to the monophyly at the Aulopiformes by Stiassny (work in progress), whose conclusions are consistent with my own present and prior observations. A difficulty in character interpretation arises when this feature is used if one considers that *Aulopus*,

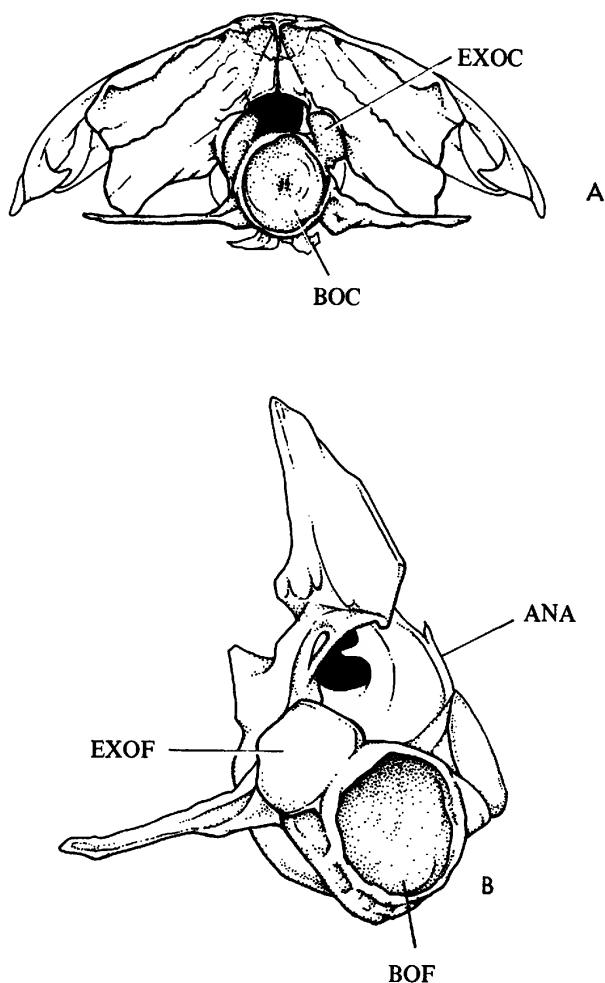


FIG. 34. Occipital region and first vertebra of *Strongylura marina* (Walbaum), AMNH 27805, showing laterally displaced exoccipital condyles and the neural arch on V1 ankylosed.

Chlorophthalmus, and neoteleosts, in general, are characterized by a very short retractor that inserts on the inner faces of the third and fourth pharyngobranchials, as opposed to the more posterior insertion in some stomiiforms and alepisauroids on the fourth pharyngobranchial, which often bears a single large toothplate with recurved, fanglike teeth. Stomiiforms have a variety of specialized retractor origins, including the shoulder girdle and ribs as in sternoptychids but the condition in *Aulopus*, *Chlorophthalmus*, and mycophids with the anterior origin and double pharyngeal insertion appears to be an advanced neoteleostean synapomorphy. Here I simply defer to Stiassny's work in progress which will deal with the analysis of this char-

acter in more detail. It appears possible that stomiiforms and alepisauroids are linked by a peculiar type of dorsal retractor, although each of these groups are individually diagnosable, the stomiiforms by the peculiar type of photophores (Fink and Weitzman, 1982) and at least some alepisauroids by the extremely attenuated second pharyngobranchial described by Rosen (1973).

THE POSITION OF AULOPUS AND IMMEDIATELY ALLIED FORMS: The title of this subsection is phrased somewhat ambiguously for a good reason—no one knows with any degree of certainty what those immediately allied forms might be, but perhaps they are bathysaurids, bathypteroids, and ipnopids. But whoever they are, later collectively termed

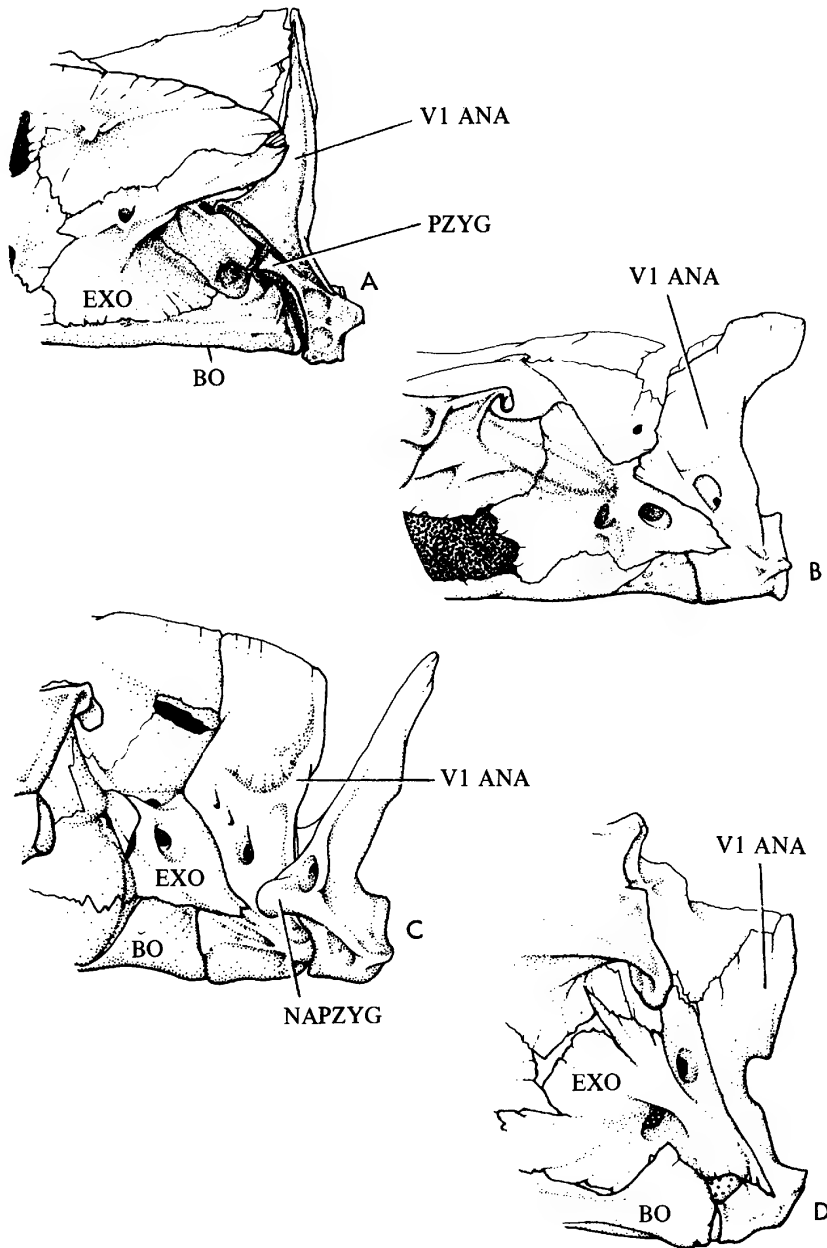


FIG. 35. Comparison of the occipital region and anterior vertebrae in a gadiform and some members of the batrachoid-lophoid clade. A. *Gadus morhua* Linnaeus, AMNH 21680. B. *Porichthys notatus* Girard, AMNH 22432. C. *Opsanus tau* (Linnaeus), AMNH 21564. D. *Lophius americanus* Valenciennes, AMNH 22129. Note integration of neural arch on V1 with the occipital bones, the sharply angled autocentral prezygapophyses, and their integration with a complex exoccipital condyle. Both the V1 prezygapophysis (exoccipital facet) and the exoccipital condyle are formed around cores of cartilage so that the condyle-facet contact is cartilage-to-cartilage. Compare with figures 36 to 38.

“aulopoids,” at least *Aulopus* may be treated as a sister group to the Ctenosquamata on the

basis of its (1) high-set pectorals, (2) subthoracic pelvics, (3) ctenoid scales, (4) three pre-

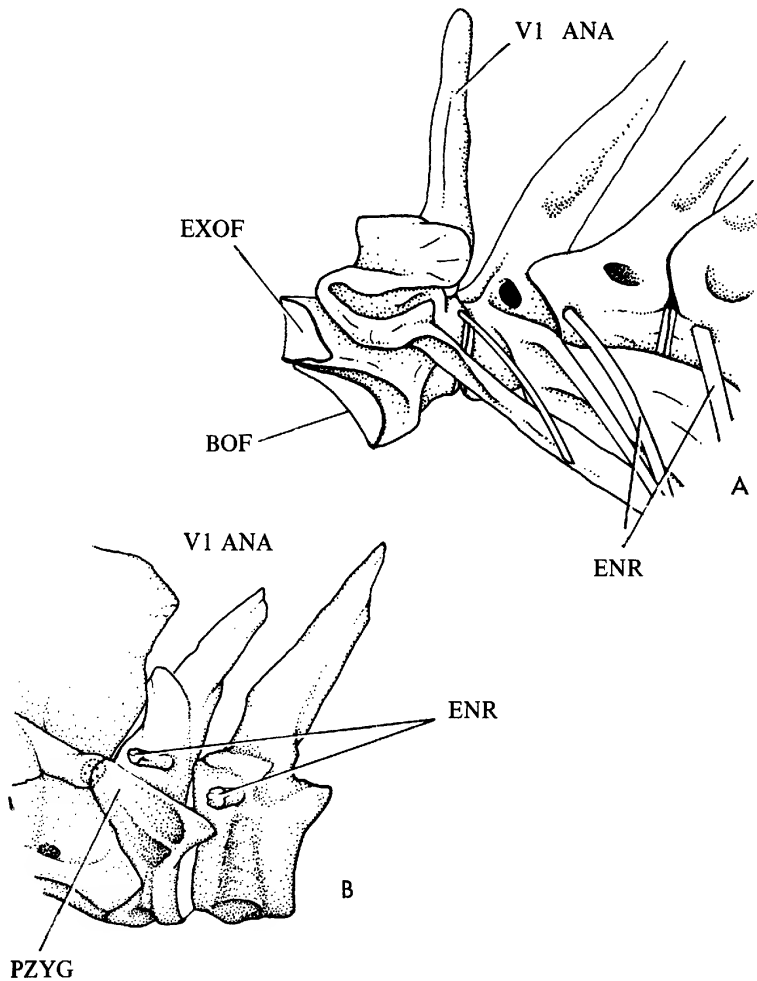


FIG. 36. Occipital region and anterior vertebra in "ophidiiforms." A. *Ophidion holbrookii* (Putnam), after Rose (1961). B. *Ogilbia cayorum* Evermann and Kendall, AMNH 26098. A, an ophidioid has a relatively primitive, planar exoccipital facet whereas B, a bithytoid, has paired, codlike facets. Both show the more posterior position of the basioccipital facet.

dorsal (or supraneural) bones, (5) a reduced spine on NPU2, (6) derived premaxillary morphology (see Rosen and Patterson, 1969), (7) type of dorsal retractor muscle, (8) a toothplate fused to the third epibranchial (Rosen, 1973), and (9) median rostral cartilage.

STATUS OF THE PARACANTHOPTERYGII: Of all the proposals for subdividing the old Acanthopterygii or Percomorpha, none has been more controversial, or, in my present view, ill-fated, than the Paracanthopterygii. The taxon was proposed partly in an effort to narrow the enormous scope of the taxonomic problem posed by 6000 or so species

of spiny-finned euteleosts, and of advancing a specific proposal that could be addressed, or even openly attacked. There was not long to wait after the initial publication of the 1966 general classification of modern teleosts. In fact, its first reviewer, Carl Hubbs, referred to it as a bizarre collection of odd bedfellows.

Rosen and Patterson (1969) rooted the problem firmly by producing a monograph whose sole, and now seemingly unfortunate purpose, was to entrench the problem by collecting "confirmatory" evidence of paracanthopterygian substance. Now, the spirit of the times has changed, and neither Patterson nor I would consider that a worthy purpose. In

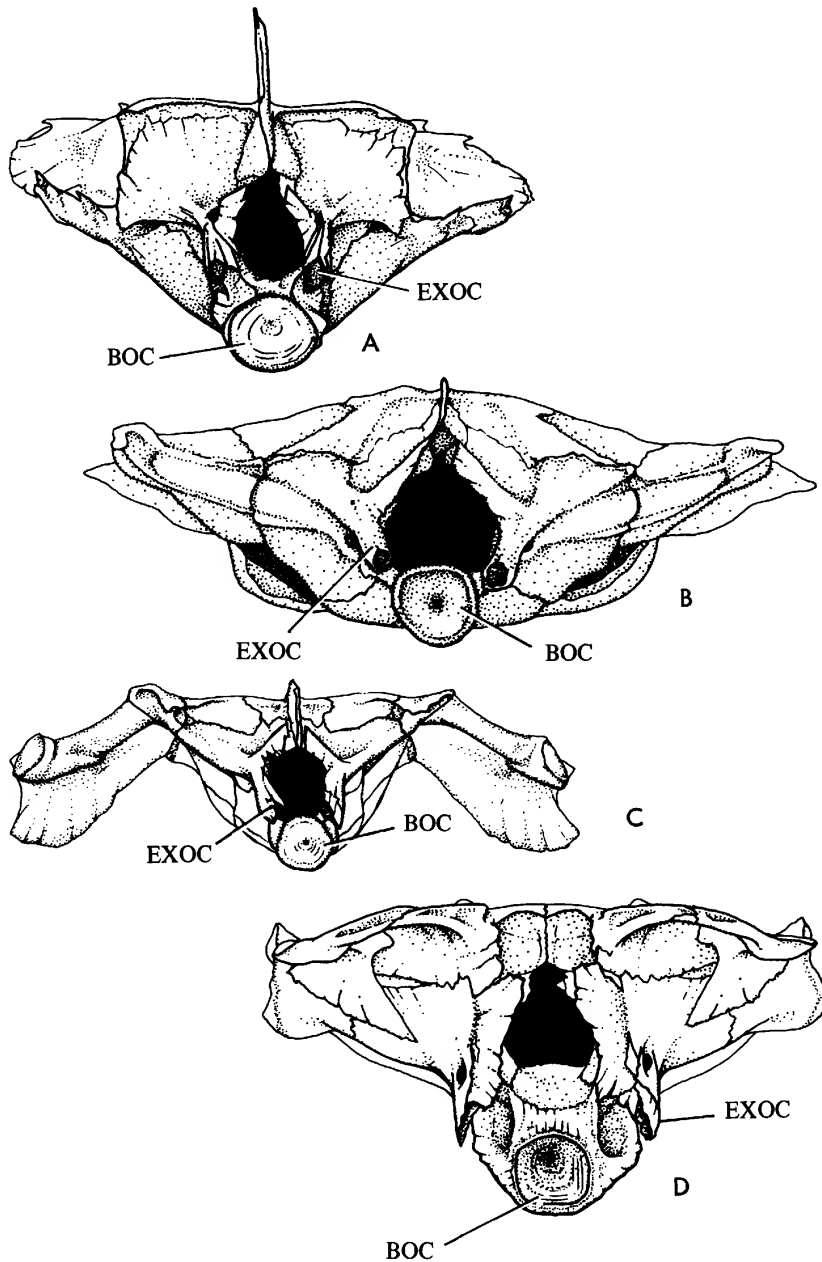


FIG. 37. Occipital regions of a gadiform and members of the batrachoid-lophiiform clade. A. *Gadus morhua* Linnaeus, AMNH 21680. B. *Porichthys notatus* Girard, AMNH 22432. C. *Opsanus tau* (Linnaeus), AMNH 21564. D. *Lophius americanus* Valenciennes, AMNH 22129. Note the small, laterally displaced, cartilage-filled, tubelike exoccipital condyles. In D, the cartilage core is hidden by lateral wings of bone.

fact, my object now is to show that Hubbs' criticism was well taken, and not only that the paracanthopterygians no longer can be accepted as a natural group, but to point out

that some of its constituents can no longer be accepted as natural. I refer particularly to the percopsiforms that have never had as defining traits anything but shared primitive

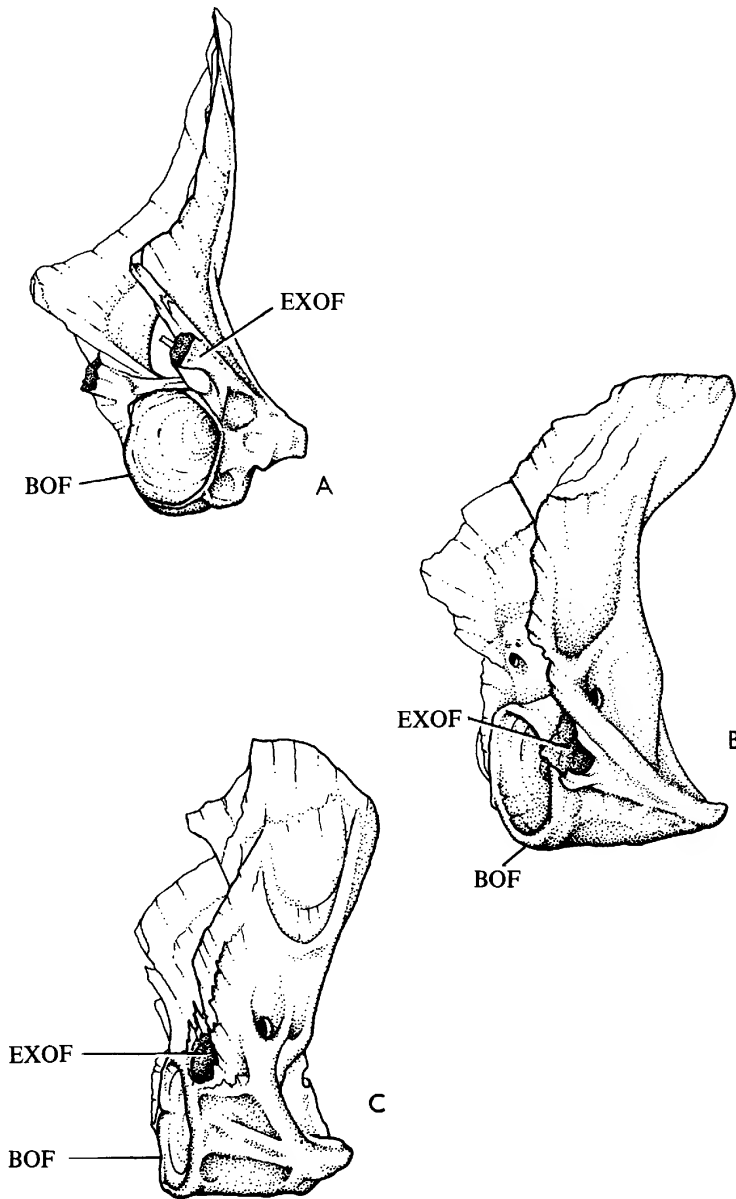


FIG. 38. The first vertebra in a gadiform and two batrachoids to illustrate the very derived autocal prezygapophyses. A. *Gadus morhua* Linnaeus, AMNH 21680. B. *Porichthys notatus* Girard, AMNH 22432. C. *Opsanus tau* (Linnaeus), AMNH 21564.

features. Aphredoderids do align themselves with amblyopsids on the basis of the thoracic anus and segmented premaxilla, but nothing of which I am aware properly unites them with percopsids. In fact, I find it difficult even to state features which link the living and few fossil percopsids—apart from the broadly arched alveolar premaxillary process.

Percopsids are, of course, euteleosts because they possess that group's single defining trait, the adipose fin. And they are, presumably, some form of primitive ctenosquamate because of their premaxillary processes, rostral cartilage, pectoral fin position, and fin spines. At least one of them, *Percopsis omiscomaycus*, is known to have a complex series

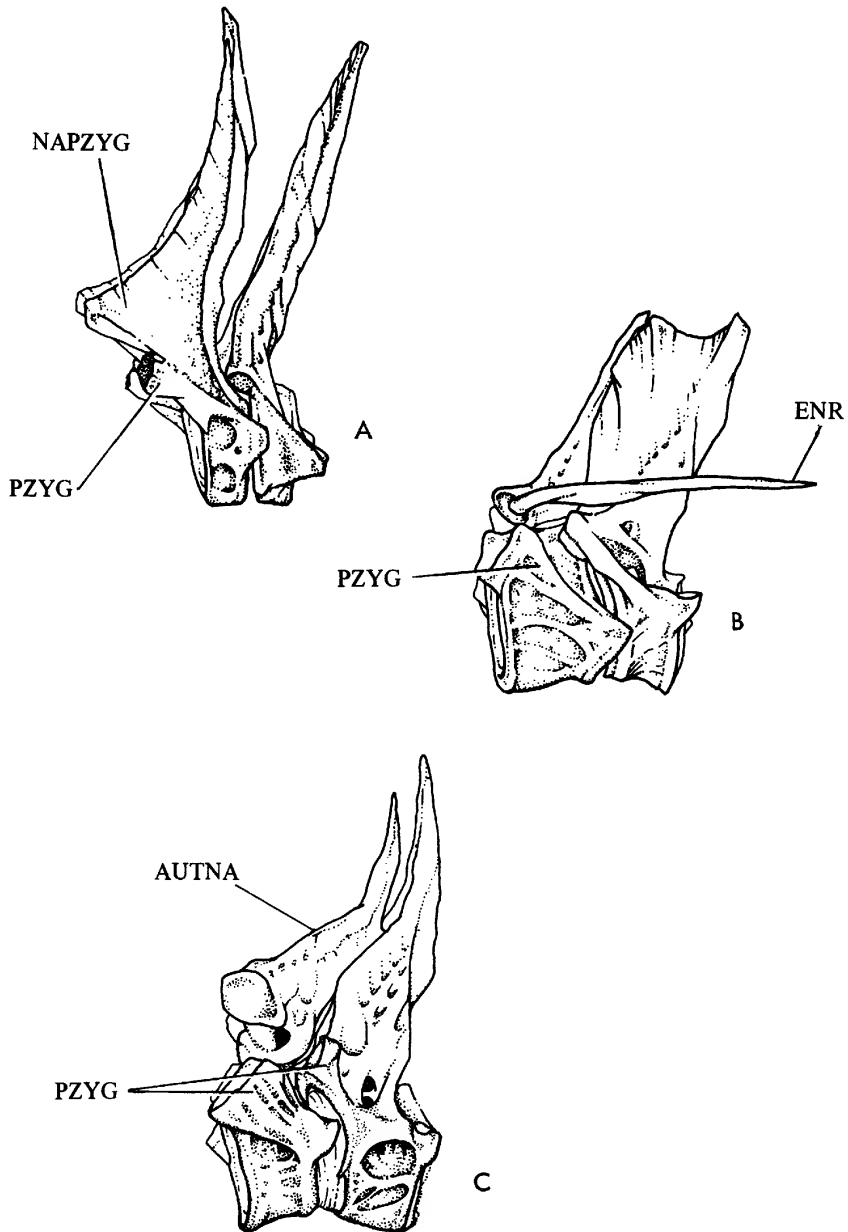


FIG. 39. Comparison of first two vertebrae in a gadiform and two acanthopterygians. A. *Gadus morhua* Linnaeus, AMNH 21680. B. *Centropomus undecimalis* (Bloch), AMNH 28058. C. *Sebastes* sp., AMNH 36935. Note that exoccipital facets are of autocentral origin, following the angle of a neural arch prezygapophysis on either V1 or V2.

of jaw muscles found also in some gadoids, but as Dietz (1914) pointed out, so do some liparids. The one thing they share that is derived in relation to current character interpretation is a full spine on PU2, but that character seems to come and go with such

frequency that investigators would be foolhardy to base major taxonomic judgments upon it unless we could formulate an argument involving a unique ontogeny that documents the redevelopment of a full NPU2. No such empirical ontogenetic data yet exist.

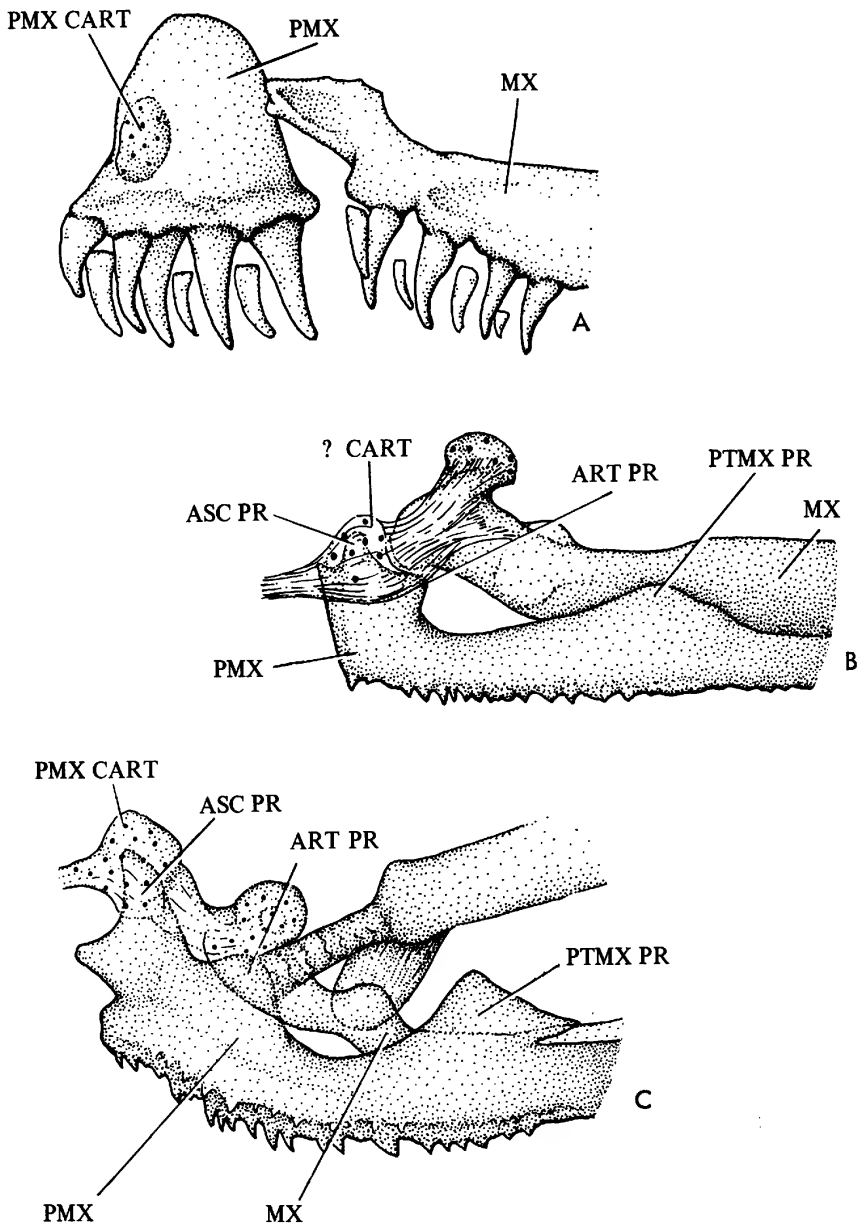


FIG. 40. Euteleostean upper jaw bones in medial view. A. *Salmo gairdneri* Richardson, AMNH 40268, to show small, adherent, premaxillary cartilage. B. *Maurolicus muelleri* (Gmelin), AMNH 37329. C. *Chlorophthalmus agassizi* Bonaparte, AMNH 40812. Note the serial (end-to-end) alignment of the two bones in A and their tandem (overlapping) alignment in B and C. Note also the distribution and shape of premaxillary processes in B and C. Cartilage, shown by the presence of black dots, is inferred in B because of specific alcian blue staining for mucopolysaccharides and the presence of some cellularity within the fibrous tissues engulfing the ascending process. Compare C with figure 41B.

All "percopsiforms" are primitive with respect to the presence of an unconsolidated second ural centrum, an adipose fin, and more than 15 branched caudal rays. They are de-

rived in having enlarged infraorbital canal bones not supporting a subocular shelf, but the latter might also be primitive or simply homoplasious since similar infraorbitals oc-

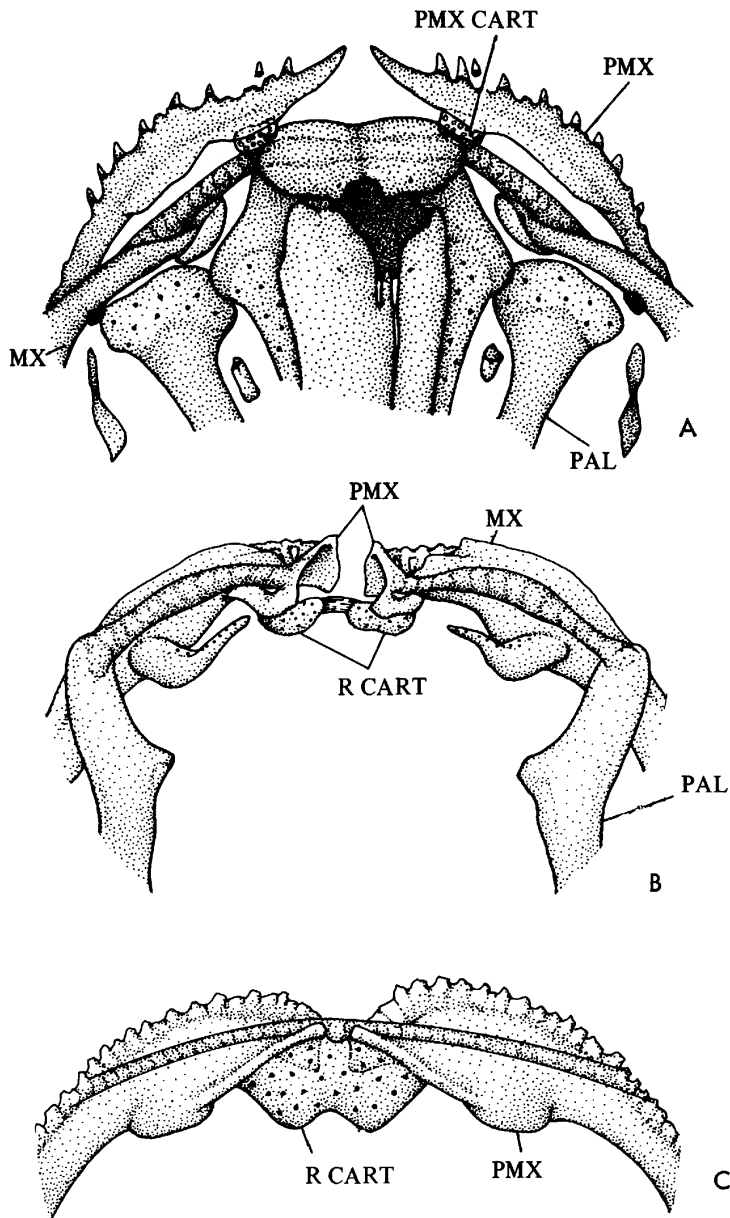


FIG. 41. Euteleostean upper jaw bones in dorsal view. A. *Osmerus mordax* (Mitchill), AMNH 40726. B. *Chlorophthalmus agassizi* Bonaparte, AMNH 40892. C. *Aulopus japonicus* Günther, AMNH 28635. Note paired premaxillary cartilages in A and B; those in A are similar to ones observed in *Prosopium williamsoni* and *P. cylindraceum*, except that in the latter two taxa the cartilages are only loosely associated with the premaxillae rather than firmly adherent to them as in *S. gairdneri* (fig. 40A) or *O. mordax* (A). The cartilage depicted in C is similar to that shown in figure 43A.

cur in stephanoberycoids. In their dorsal gill arches they lack an interarcual cartilage, originally shown sometime ago to be present in other primitive ctenosquamates such as myctophids by Malcolm Jollie (1954) in a sadly

underused thesis of considerable breadth and insight. The interarcual cartilage has since been found to be absent in other myctophids, however (Stiassny, MS). As for the polymixiids, the most interesting thing I can think of

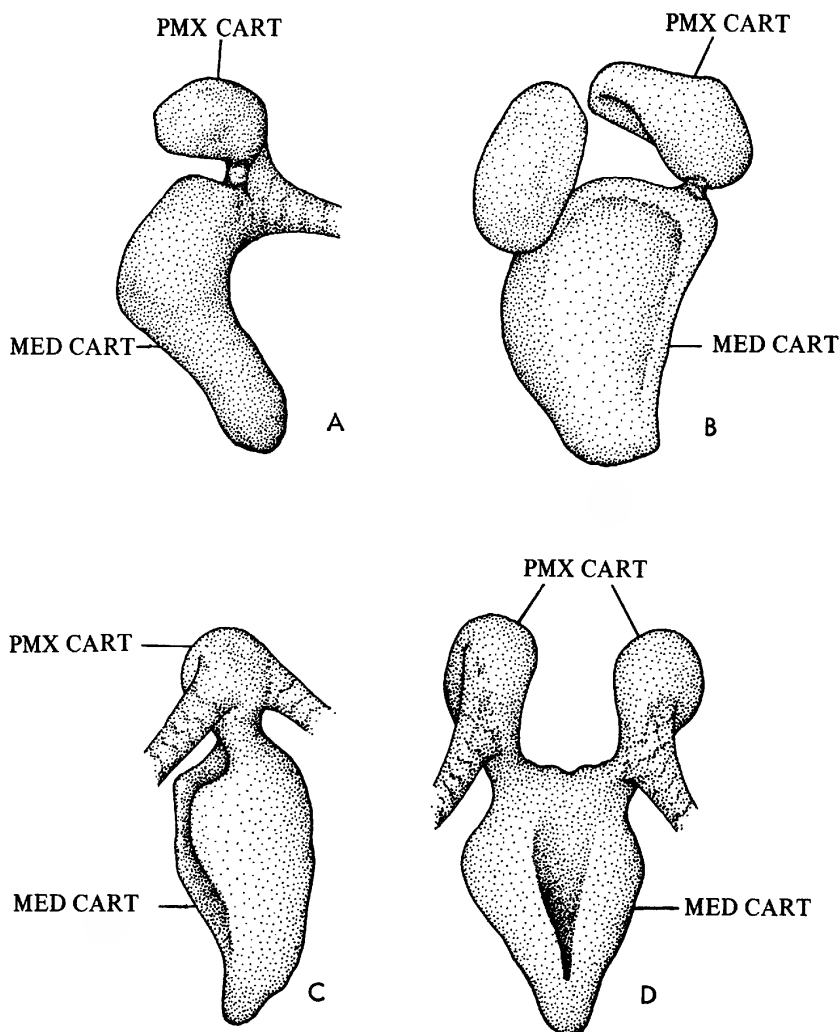


FIG. 42. Rostral cartilages of neoscopelids. Anterior to left in A, right in C; B, three-quarters posterior view; D, posterior view. A and B. *Scopelengys dispar* Garman, AMNH 12841. C and D. *Neoscopelus macrolepidotus* Johnson, MCZ (uncat.). B and D are posterior views, B turned slightly to the right. In A and B the paired and median elements are joined by connective tissues with only the slightest amount of chondric invasion. In C and D the necks that join the three elements are fully chondrified. C and D based, in part, on information from M. Stiassny.

saying about them is that they look like huge spiny myctophids but are closer to the original percomorph assemblage because the anterior vertebra has developed ossified auto-central prezygapophyses that articulate directly with the exoccipital condyles. They also are primitive in retaining a free second ural centrum, a first abdominal vertebral centrum that does not contact the basioccipital, many branched pelvic rays, more than 15 branched caudal rays, and an undifferentiat-

ed subocular shelf like that of myctophids. They are autapomorphic (i.e., diagnosable) in possessing numerous dorsal fin spines, a full spine on PU2, and a pair of long mental cirri that give them their name of beardfishes.

Clingfishes are clearly autapomorphic in many traits and appear to have dorsal gill arches (fig. 58B in Rosen and Patterson, 1969) like those of tropical blennies. This latter feature is difficult to use decisively because it involves the loss and reduction of so many

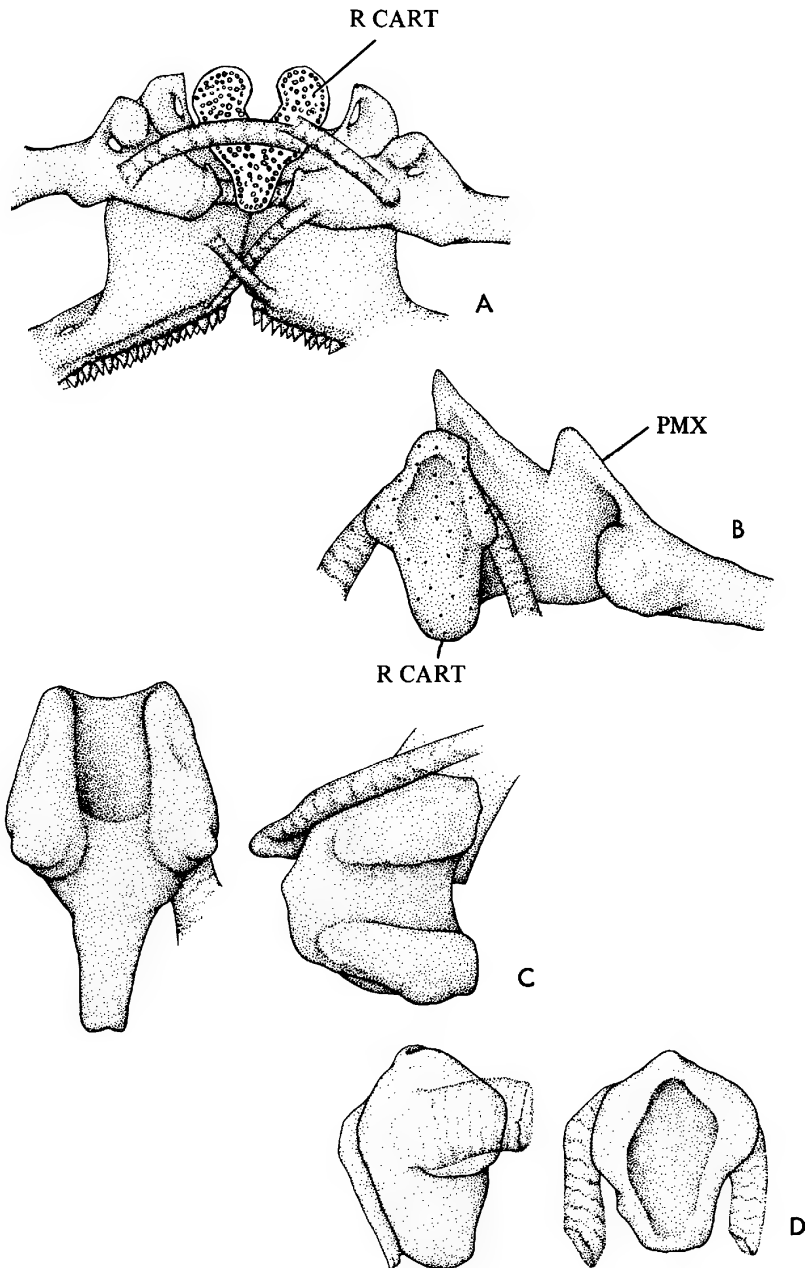


FIG. 43. Ctenosquamate rostral cartilages. A. *Neoscopelus macrolepidotus* Johnson, MCZ (uncat.) (from a sketch by M. Stiassny). B. *Notoscopelus resplendens* Richardson, AMNH 29528. C. *Polymixia lowei* Günther, AMNH 49674. D. *Scopeloberyx* sp., AMNH 40268. Note that indications of a tripartite origin (as per fig. 42) are present in all. A, B, C (left), and D (right) are posterior views. C (right), a dorsal view, anterior to left. D (left), a lateral view, anterior to left. Fink (1984) has reported that in a cichlid species (*Acanthopterygii*), the rostral cartilage has only a dual origin ontogenetically from paired premaxillary cartilages.

gill arch elements; their relationship to dracomettids and callionymids has been sug-

gested by Gosline (1971). The latter (i.e., callionymids) have similar dorsal gill arches. The

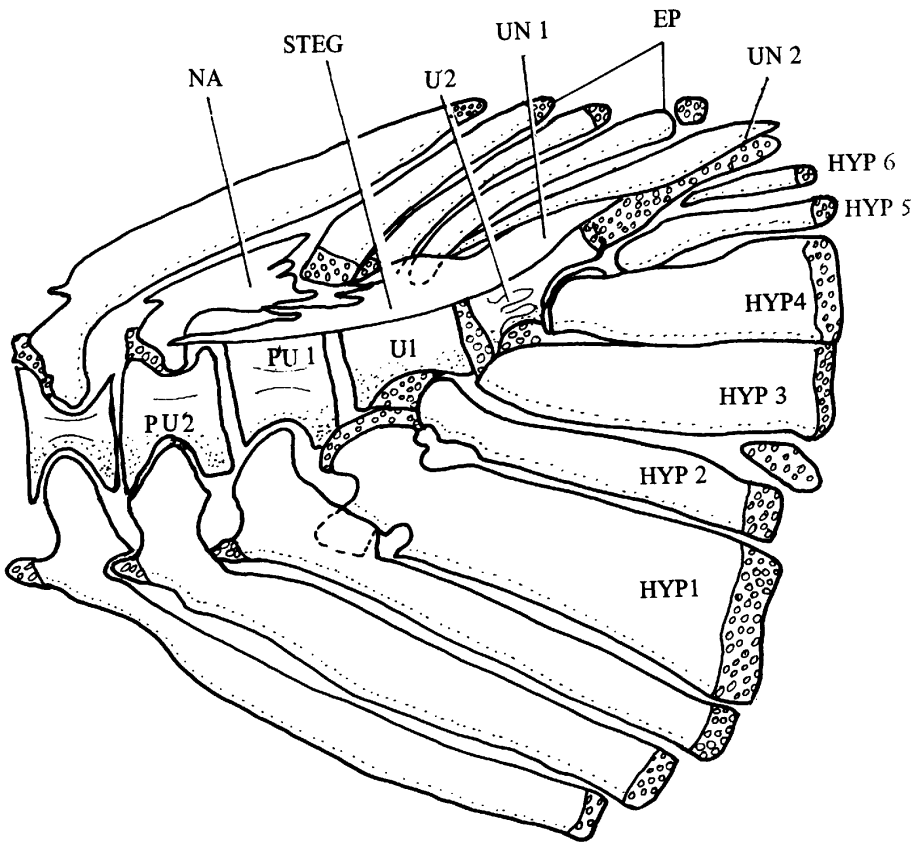


FIG. 44. Caudal skeleton of *Prosopium williamsoni* (Girard), AMNH 37967. The small, recurved, neural arch and spine element on PU2 appears to be a derived feature that occurs in coregonines, and some salmonines and is variably associated with the first or second preural centrum (PU1 or PU2). Within the Salmoninae a usual condition is to have a full spine associated with PU2, whether or not a reduced, recurved element joins it on that centrum. The primitive eurypterygian neoteleost condition, however, is to have a spatulate or broadly lance-shaped, somewhat or greatly reduced spine on PU2 (Rosen, 1973, figs. 46 to 48) and this is true also of osmeroids (excluding salangids) (e.g., Rosen, 1974, figs. 25, 26C, 27 and Greenwood and Rosen, 1971, fig. 16). More primitive neoteleosts such as stomiiforms have usually either a full spine on PU2 (based on a random survey of eight gonostomatids and sternoptychids) or, if somewhat shorter than that on PU3 (e.g., *Diplophos*, as figured by Fink and Weitzman, 1982), it is a narrow spine without platelike expansions. Spines like that of *Diplophos* occur also in some of the more derived paralepidids and evermanellids and full spines on PU2 occur in a variety of acanthomorphs (e.g., in the "paracanthopterygii" and some acanthopterygians). The condition shown here for *Prosopium* might, therefore, serve as a synapomorphy for salmonids.

similarity does not, however, include the closely united third and fourth epibranchials, the converging ventral gill arches, and unossified copula that clingfishes share with lophiiforms or, at least, lophiids and antennariids (fig. 58C in Rosen and Patterson, 1969), but not with callionymids.

What appear to unite the batrachoid clade with the gadiforms are derived features of the

occipital region discussed above, and some features of the dorsal gill arches to be presented in a forthcoming paper.

Features that appear to unite batrachoids, lophiiformes, gadiforms, and bythitoids are the relation between the occipital region and the first vertebra. The contact between the exoccipital facets and the prezygapophyses of the first vertebra is between the cartilage cores

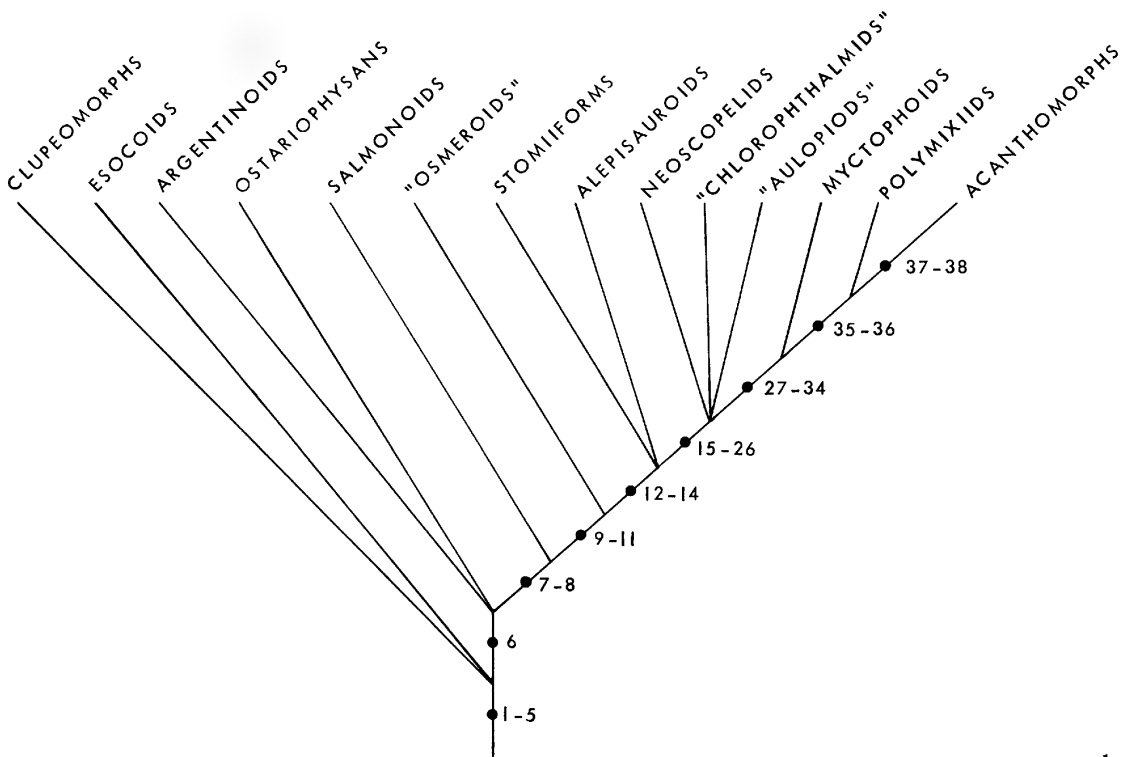


FIG. 45. Proposed interrelationships of the main groups of clupeocephalans, based on the synapomorphies as numbered in the text. Uncertainties about the placement of a number of groups are represented by unresolved polychotomies. This scheme differs from that proposed by Fink and Weitzman (1982) and Fink (1984) mainly in the position of salmonids and "osmeroids" and in excluding *Lepidogalaxias*.

or tips of these elements (figs. 35, 36B, 37, 38, 39A), as compared with the bone-to-bone contacts in acanthopterygians and the berycoid-like arrangement in ophidioids (cf. figs. 19, 20, and 29A with 36A). The other character which also includes ophidioids as well as bythitoids, is the articulation of pleural ribs with ventrolateral cavities in the vertebrae normally occupied by parapophyses.

The feature that might be synapomorphic for gadiforms and at least some ophidiiform subgroups is the position of the exoccipital facets anterior to the basioccipital and the corresponding anterior extension of the first vertebral prezygapophyses onto the back of the occiput to meet the exoccipitals. Neural arches are carried forward along with the prezygapophyses, in some cases firmly incorporated into the exoccipitals and the supraoccipital (figs. 47-49A). These vertebral features, alone, exclude zoarcids and gobie-

socids from the assemblage since they have no derived chondrification associated with the exoccipitals and vertebral prezygapophyses.

As mentioned earlier, it is primitive for neoteleosts to lack a direct vertebral contact with the occiput, and it is this spatial separation that seems most closely correlated with the presence of the exoccipitals in the occipital joint region. What characterizes the ctenosquamates is a gradual closing of this space so that acanthomorph fishes, excluding *Polymixia*, have the first vertebra firmly united with the occiput by one of two means (see, e.g., an atherinomorph, fig. 34). One is unique to acanthomorphs and this is the formation of autocentral prezygapophyses that grow forward to contact the exoccipital condyles. The other is typical of several primitive acanthomorphs (holocentrids, berycids, and ophidioids, for example). Here, the articu-

latory surface on the first vertebra for the exoccipitals is a more-or-less continuous, planar surface (figs. 19B, 36A) that fits neatly against an opposing exoccipital surface clearly divided by suture into right and left halves (fig. 29A).

In fishes that have been previously called acanthopterygians or percomorphs, this type of contact has been altered by the lateral displacement of the two exoccipital facets and their growth backward over the basioccipital (as in *Centropomus* and *Sebastes*, fig. 29B, D). What characterizes the batrachoids, gadiforms, and some ophidiiforms is that (1) the exoccipital facets have moved laterally to an exceptional degree, as noted by Rosen and Patterson (1969), and usually have a deep core of cartilage (fig. 37); and (2) the vertebral prezygapophyses extend well forward onto the braincase, in many cases, carrying a neural arch and spine component with them to meet the epioccipitals, supraoccipital, and the displaced exoccipitals (fig. 35).

Even in the ophidiiforms that retain the primitive, continuous, planar surface for exoccipital contact, these prezygapophyses extend well forward over the centrum as clearly illustrated by Rose (1961) in *Ophidion holbrookii* (fig. 36A). Some of the other ophidiiforms (the bythitoids) are much more codlike (see fig. 36B, which shows separate right and left vertebral facets). And, since ophidiiforms fall readily into two classes based on caudal anatomy, gill arches, viviparity and, to some degree, fin structure (Cohen and Nielsen, 1978, and Patterson and Rosen, work in progress), there is an implication that the ophidiiforms might be nonmonophyletic. One group, the more derived in anatomy (bythitoids) might be linked to cods and batrachoids, and the other (ophidioids) could be the sister group to the whole lot.

SUMMARY AND CONCLUSIONS

According to evidence presented here, the significance of the paired cartilages and tripartite occipital condyles found in some salmonids is ambiguous because of the uneven distribution of the characters, the lack of a good theory of relationships among the taxa, the occurrence of both features in some osmeroids, and a parsimony argument that favors osmeroids as a neoteleost sister group.

The significance of this conclusion is that the monophyly of both the Salmonidae and Osmeroidae should be reevaluated, and that much more detailed character surveys are needed—undertakings that lie outside the scope of this study. Paired rostral cartilages in their transformed or untransformed states are present consistently in members of Rosen's (1973) Aulopiformes, even though that taxon must now be abandoned as monophyletic since *Aulopus* appears to have a rostral cartilage synapomorphic with that of ctenosquamates that is lacking in *Chlorophthalmus*. However, I can find no obstacle to making a transformation sequence between the salmonine occipital region and that of "higher" euteleosteans—unless the Osmeroidae is nonmonophyletic and *Spirinchus* is a more appropriate immediate sister group to the neoteleosts. The latter possibility will depend on two kinds of evidence: (1) that the gap between the occiput and the first cervical vertebra is truly diagnostic for primitive neoteleosts, including stomiiforms, and (2) that the postoccipital gap in *Spirinchus* is synapomorphic, rather than homoplasious, with that of neoteleosts.

If the occipital anatomy of *Spirinchus* is primitive for osmeroids, as Fink and Weitzman (1982) claim the anatomy of *Diplophos* is for stomiiforms, then I would be forced to place osmeroids, stomiiforms, and neoteleosts in an unresolved trichotomy and to exclude the salmonids on two grounds (caudal skeleton and premaxillary anatomy), except perhaps as the sister group to those three if the Salmonidae is monophyletic and the salmonine premaxillary cartilages and occipital anatomy are synapomorphies. Meanwhile, however, I conclude that the type of jaw, caudal skeleton, and bone histology earn the Osmeroidae a closer linkage with stomiiforms and eurypterygians than do these same features in salmonines.

Below is a synapomorphy scheme of the Clupeocephali representing the data presented here and by other workers which summarize anatomical findings relevant to the ctenosquamates and the included acanthomorphs.

Clupeomorphs share the following derived features with euteleosts (Patterson and Rosen, 1977):

1. Articular bone in the lower jaw co-ossified with the angular.
2. Retroarticular in lower jaw excluded from the joint surface.
3. A median (in clupeomorphs) or paired (in euteleosts) anteriorly directed membranous outgrowth on the anterodorsal margin of the first uroneural (the stegural).
4. Neural arch over U1, when present, reduced, rudimentary, lying free over U1 or nestled against the posterior face of the neural arch of PU1, or ankylosed with other neural arch or uroneural complexes, or absent.
5. Toothplates, when present, fused with first three pharyngobranchials and fifth ceratobranchial.

Euteleosts, primitively, have but a single, unambiguous, derived feature:

6. An adipose dorsal fin (not present in esocoids). The stegural feature (character 3) of the first uroneural has been used as a euteleost synapomorphy, but this feature seems properly to define only a subgroup of euteleosts. It does not allow decisive inclusion of the esocoids [which, at best, have an outgrowth of the first uroneural of doubtful homology with the stegural of other euteleosts (see illustrations in Rosen, 1974)].

Within the Euteleostei, the Salmonidae (but not argentinoids or ostariophysans) share with all other groups only:

7. Paired stegural outgrowths of the first uroneural.
8. At least some parts of the endoskeleton with acellular bone (Parenti, ms).

Osmeroids share with stomiiforms and primitive neoteleosts:

9. Acellular endoskeletal bone (but this statement is based only on study of *Osmerus mordax*. However, Kölliker (1859) reported acellular bone in a galaxioid, which is consistent with Fink and Weitzman's (1982) realignment of galaxioids with osmeroids (and see Parenti, ms).
10. A toothed alveolar process on the premaxilla which lies under the maxilla,

completely so in galaxioids (see character conflicts above).

11. In the caudal skeleton, NPU2 is shorter than NPU3 and bladeliike. [NPU2 is also shorter than NPU3 in the stomiiform, *Diplophos*, but is not bladeliike according to Fink and Weitzman (1982, fig. 16).]

Stomiiforms and alepisauroids share with other neoteleosts:

12. The exoccipitals and basioccipital exposed posteriorly and joined by an inverted Y-shaped suture. Presence of a cervical gap between the occiput and first vertebra. [When the first vertebra is remote from the occipital region, it is correlated with the exposure of the exoccipital surfaces as parts of the posterior occipital outline—the basioccipital having dorsolateral depressions to accommodate the exoccipitals in juvenile *Osmerus* (prevertebral space being occupied by the notochord and its connective tissue sheath and by a small, spineless neural arch).] The "osmeroid" *Spirinchus* also has the exoccipitals entering the occipital region posteriorly and future study may demonstrate that osmeroids are nonmonophyletic.
13. An interoperculohyoid ligament, present but feebly developed in stomiiforms (see Lauder and Liem, 1983, p. 34).
14. A retractores dorsalis branchialium muscle [in most stomiiforms and alepisauroids originating far back in the abdominal region, with fibers inserting principally or only on the fourth gill arch (Rosen, 1973), and perhaps nonhomologous with that in eurypterygians, according to work in progress by M. Stiassny].²

Neoscopelids share with primitive ctenosquamates (e.g., myctophids):

15. Ctenoid scales and median fin spines (well developed in Cretaceous forms; see Rosen, 1973, pp. 456–459).
16. Premaxilla with ascending, articular, and postmaxillary processes.
17. Pectoral fins arising laterally rather than ventrally.
18. Pelvic fins arising anteriorly in a sub-

abdominal, rather than in the more posterior abdominal, position.

19. A hyoid bar and branchiostegals of acanthomorph type (see McAllister, 1968).
20. Clamshell-shaped saccular otolith with definitive cauda and ostium in sulcus (Nolf, MS).
21. A pair of small, lateral cartilages joined to the premaxillary ascending processes and to a larger median cartilage.
22. Retractores dorsalis muscle short, originating anteriorly on basioccipital or cervical vertebrae and inserting on connective tissues on dorsomedial edges of third and fourth pharyngobranchials. This assumes character 22 to be a more derived (or simply nonhomologous) condition of character 14.

“Aulopoids” share with ctenosquamates:

23. A median rostral cartilage without lateral components (Stiassny, personal commun., informs me that some myctophids retain small, lateral components, so that this character would be stated more accurately as: distinct lateral components greatly reduced or absent.)
24. Pelvic fins more anterior in a subthoracic position. (Fin spines are unknown in modern “aulopoids,” which could be interpreted as an autapomorphic loss in “aulopoids” or gain in neoscopelids.)
25. Three or fewer predorsal bones (four in neoscopelids).

Chlorophthalmids share with ctenosquamates:

26. A subocular shelf (said by Stiassny, personal commun., to be very narrow and thus interpreted here as primitive relative to the much larger, subocular shelves in ctenosquamates).

Chlorophthalmids exhibit an additional conflicting character in this alignment because, in the upper jaw, they lack a median rostral cartilage, but have well-developed paired ones on the premaxillary ascending processes.

Myctophids share with acanthomorphs:

27. A subocular shelf that extends well under the eyeball (Rosen and Patterson, 1969, fig. 11).
28. Rostral cartilage—a single median struc-

ture of apparently tripartite origin in some species (and with a relic pair of lateral cartilages in a few species).

29. An interarcual cartilage present between the first epibranchial and second pharyngobranchial (small, when present, and absent (according to N. Stiassny, personal commun.) in some taxa.
30. No more than three predorsal bones.
31. Partial closure of the cervical gap between the occiput and first vertebra.
32. Absence of an accessory neural arch in the cervical region.
33. Presence of neural arch prezygapophyses on the anterior vertebrae.
34. Direct connection (via ligaments) of the autocentrum of the first vertebra with the exoccipital condyles.

Polymixiids share with other acanthomorphs:

35. Autocentral prezygapophyses between first vertebra and exoccipital condyles.
36. A pelvic fin spine.

Other acanthomorphs share:

37. Complete closure of the notochordal-connective tissue space between the basioccipital and the centrum of the first vertebra.
38. Primitively, a rodlike interarcual cartilage between the first and second gill arches [in some beryciforms (e.g. anomalopids) and in most “percoids”].

Within the above scheme I recognize three main areas of uncertainty involving the alignment of alepisauroids and other members of the Aulopiformes recognized by Rosen (1973). Unexpectedly, the neoscopelids seem to me now of uncertain status, although they and the myctophids are usually closely linked. Lauder (1983) described a character, the urohyal-third hypobranchial ligament, that he thought was present uniquely in members of these two families, but the neoscopelid ligamentous connection is more like that of *Polymixia*.² I have not searched elsewhere, and I reserve judgment on precise realignment of neoscopelids until all relevant groups have been more thoroughly reviewed.

The various character conflicts noted above extend to other components of the Aulopi-

formes, and each of these is represented either by an unresolved tri- or tetrachotomy. Perhaps others (Fink and Weitzman, 1982; Fink, 1984) would prefer an additional unresolved point involving salmonids and osmeroids, or simply to transpose the two. I cannot, however, accept their evidence of the salmonine occipital joint for the principal reason that the salmonine occiput most closely resembles an advanced acanthomorph occiput rather than the basic inverted Y-junction of primitive neoteleosts and thus appears to be an independent specialization of salmonines, which is nonhomologous with the basic neoteleostean arrangement.

Chlorophthalmids and aulopids appear not to form parts of a monophyletic group because the former have two features (characters 21 and 22) linking them with ctenosquamates, and at least one alepisauroid, a synodontid, also lacks character 21, and also character 22 according to McAllister (1968, plate 12). Furthermore, some alepisauroids have ethmoid cartilages resembling those of stomiiforms (Stiassny, MS) and aulopids have a rostral cartilage of acanthomorph, or at least ctenosquamate, type. Such data effectively dissolve the Aulopiformes of Rosen (1973), and Rosen's (1973) more inclusive taxon, the Eurypterygii, will come to include the Ctenosquamata and perhaps the Chlorophthalmidae and some "aulopoid." I have not restudied the alepisauroid fishes, however, and so these are represented as unresolved in the synapomorphy scheme and summary cladogram.

There are numerous derived anatomical features of euteleostean fishes that appear in a confusing array of taxa which suggest the need for much additional study and the redefinition of taxonomic boundaries. Much of the confusion has resulted from the assignment of "groups," such as "osmeroids" and "aulopiforms" that never were defined properly to begin with. Within the Acanthomorpha, improperly defined taxa are probably the rule rather than the exception. At least ten ambiguous features come immediately to mind among fishes that have been associated at some time or another with the Neoteleostei.

1. Interarcual cartilage present in some

myctophids (Travers, 1981), but not others and absent in neoscopelids and polymixiids.

2. Acanthomorph type of hyoid bar and branchiostegals (see McAllister, 1968) in chlorophthalmids but not in aulopids or synodontids.
3. Presence of three occipital condyles in myctophids and neoscopelids, and, among synodontids, in *Synodus*, but not in *Saurida*.
4. A cervical gap in primitive ctenosquamates, but not in synodontids.
5. Acanthomorph type of rostral cartilage (fig. 43) in some myctophids, but not others, and not in neoscopelids (fig. 42).
6. Paired premaxillary components of rostral cartilage present in some salmonines and coregonines, and not others; present in at least one osmerid.
7. Cervical gap present, and exoccipitals entering occipital joint surface in some osmerids.
8. In the caudal skeleton, a full spine on the second preural centrum in salmonines, but not coregonines.
9. Large, marginal basihyal fangs in salmonines and galaxioids, but not in thymallines or coregonines.
10. Row of dorsomedial mesopterygoid teeth in osmeroids, galaxioids, and also in *Pterothrissus*, in the primitive clupeomorph †*Diplomystus*, and in the ctenosquamate, *Synodus*.
11. Neural spine on second preural centrum reduced to a low crest except in *Polymixia* and fishes formerly united as paracanthopterygians and a few subgroups of acanthopterygians.

In this extended essay on the taxonomy of the single largest recognized group of teleosts, the Euteleostei, I have adopted a scheme of relationships of its subgroups differing somewhat from my own and those of other recent workers. My proposal raises the general question of why taxonomists periodically adopt novel taxonomies. Many years ago it was because taxonomists used symplesiomorphies to describe groups, e.g., the Clupeiformes, Malacopterygii, Isospondyli, and Mesichthys. But the recent flux of fish classifications has other causes, since most ichthyologists have abandoned symplesiomorphy in favor

of synapomorphy as a basis for defining groups.

To me, at least, there appear to be three major reasons for this flux. One is that different taxonomists perceive characters differently. Since our experiences do not coincide, neither do our perceptions. This is a phenomenological problem of what each of us is able to see and how we interpret what we perceive. And it is aggravated by a linguistic problem of how we describe those perceptions. A second main reason for the steady flow of new taxonomic proposals has to do with the willingness of some taxonomists to align groups based on a trait peculiar to one or only a few of its members, a trait that must be suspected of being homoplasious unless it can be argued successfully to be primitive for the entire group. The tripartite occipital condyle and paired rostral cartilages of salmonines would fall in this category (vide Fink and Weitzman, 1982, and Fink, 1984) as would the basihyal dentition of salmonines (vide Rosen, 1974). And evaluation of an ambiguous trait, too, is aggravated by a linguistic problem of how the trait is described. A third main reason is a genuinely new discovery of such a major character that it seems obvious and significant to one and all. An example of this type would be the Weberian apparatus of otophysans or the recessus lateralis of clupeiforms. The retractor dorsalis muscle seemed like one of these characters when it was first reported and described in acanthomorphs by Dietz in a series of papers (see Rosen, 1973) and by Holtzvoogd (1965), but the retractor muscle appears widely amongst halecomorph neopterygians and its homoplasious nature made application of the character ambiguous at various hierarchical levels (Nelson, 1967). There appear to be only two ways of dealing with this ambiguity. One is to conduct an empirical study of the feature in different taxa showing that its ontogeny is unique in some of those taxa and that its final expression is, therefore, homoplasious (i.e., irrelevant because of nonhomology). The other is to study many other features that yield congruent hierarchical arrangements—a congruence which the ambiguous feature does not share (i.e., again, because it is an expression of a different ontogeny and is, therefore, nonhomologous with a trait that it

resembles). But ambiguous or inconsistently distributed characters still plague fish systematics and are used again and again to support some proposed relationship. Having been guilty of the crime myself, I am naturally tolerant of others who commit it, allowing that it is a far better thing to have proposed and been rejected on grounds of nonhomology than never to have proposed at all.

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