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Notes on the Structure and Relationships of the Alepocephaloid Fishes

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ABSTRACT

The alepocephaloid fishes, which have had a long, uncertain taxonomic history, are compared with members of the Argentinoidei. The two groups share a distinctive pharyngobranchial structure not known to occur in any other major group of fishes. Study of the caudal skeleton of alepocephaloids and argentinoids reveals additional trenchant similarities between these two groups. Other anatomical information is consistent with the hypothesis that alepocephaloids and argentinoids form a monophyletic assemblage. The two groups are included as two superfamilies, the Alepocephaloidea and Argentinoidea, of the suborder Argentinoidei. Suggested rearrangements of members of the Argentinoidea also are proposed.

INTRODUCTION

Until recently the alepocephaloid fishes were uncertainly classified either with the clupeoid or salmonoid fishes. Gosline (1969) reviewed the group and implied a relationship of the alepocephaloids with the osmeroid fishes and concluded that the alepocephaloids are “. . . least unlike the osmeroids among modern fishes.” The alepocephaloids are thus left as much *incertae sedis* as they were before. Gosline's review did not

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include any comparisons of alepocephaloids with the argentinoid fishes. The investigation reported here is an attempt to fill that gap. The following account compares a variety of argentinid, bathylagid, opisthoproctid, alepocephalid, bathyprionid, searsiid, and bathylaconid species. From these comparisons we have arrived at a new hypothesis regarding the relationships of the alepocephaloids, which we reflect in a taxonomic proposal.

The classification of argentinoids of Cohen (1964) is used as a basis of analysis and discussion (see list of material examined).

ACKNOWLEDGMENTS

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MATERIALS AND METHODS

Dissections, or cleared and stained alizarin and methylene blue specimens, or both, were prepared from the following materials:

ALEPOCEPHALIDAE

- Alepocephalus agassizi* Goode and Bean, MCZ 35105-35107
- Alepocephalus rostratus* Risso, MCZ 27237
- Alepocephalus tenebrosus* Gilbert, AMNH 12826, 12827
- Bajacalifornia burragei* Townsend and Nichols, LACM 9714-19
- Binghamichthys* sp., USNM uncatalogued
- Leptochilichthys agassizi* Garman, USNM 200518
- Leptoderma springeri* Mead and Böhlke, USNM uncatalogued
- Leptoderma* sp., USNM uncatalogued
- Rouleina squamilateratus* (Alcock), USNM 137752
- Talismania poregoni* Parr, USNM uncatalogued
- Xenodermichthys copei* (Gill), USNM 187670

ARGENTINIDAE

- Argentina aliciae* Cohen and Atsoides, USNM 202459
Argentina brucei Cohen and Atsoides, USNM 200429
Argentina georgei Cohen and Atsoides, USNM 187834
Argentina stewarti Cohen and Atsoides, USNM 202999
Argentina striata Goode and Bean, AMNH 29681
Glossanodon polli Cohen, USNM 203236
Glossanodon pygmaeus Cohen, AMNH 29682
Glossanodon struhsakeri Cohen, AMNH 29683
Microstoma microstoma (Risso), AMNH 29684
Nansenia oblita (Facciola), AMNH 29685

BATHYLACONIDAE

- Bathylaco nigricans* Goode and Bean, AMNH 29686

BATHYLAGIDAE

- Bathylagus longirostris* Maul, USNM uncatalogued
Bathylagus stilbius (Gilbert), AMNH 29687

BATHYPRIONIDAE

- Bathyprion danae* Marshall, USNM 150189

GONOSTOMATIDAE

- Gonostoma denudatum* Rafinesque, AMNH 29690

OSMERIDAE

- Hypomesus olidus* (Pallas), AMNH 27417
Osmerus eperlanus (Linnaeus), AMNH 292

OPISTHOPROCTIDAE

- Opisthoproctus soleatus* Vaillant, AMNH 29688
Rhynchohyalus natalensis (Gilchrist and von Bonde), AMNH 29689

SEARSIIDAE

- Barbantus curvifrons* (Roule and Angel), USNM 201158
Mentodus rostratus (Günther), USNM 137754-137759
Platyroctes apus Günther, USNM 201651, 201652
Searsia koefoedi Parr, USNM uncatalogued, BMNH 1957.11.4.5

INSTITUTIONAL ABBREVIATIONS

AMNH, the American Museum of Natural History

ANSP, the Academy of Natural Sciences, Philadelphia
BMNH, British Museum (Natural History)
LACM, Los Angeles County Museum of Natural History
MCZ, Museum of Comparative Zoology, Cambridge
USNM, United States National Museum, Smithsonian Institution

ANATOMICAL ABBREVIATIONS

acc-cb₅, accessory cartilage of the fifth ceratobranchial
acc-cb₅ + cb₅cart, accessory cartilage fused with cartilaginous head of fifth ceratobranchial
am, adductor mandibulae muscle
ao, antorbital
bh, basihyal
cart, cartilage
cb₄₋₅, fourth and fifth ceratobranchials
cor, coronoid process of lower jaw
cr, cruminal organ
dcb, dermal ceratobranchial toothplate
deb, dermal epibranchial toothplate
deth, dermethmoid
dpch, dorsal pouch
dspho, dermosphenotic
eb₁₋₅, epibranchials
ep, epural
epo, epiotic
exo, exoccipital
fc, supraorbital canal
fr, frontal
gr, gill raker
hsp, hsp₂, hemal spine; hemal spine on second preural centrum
hyp₁₋₆, hypurals
io₂, second infraorbital
io₅, fifth infraorbital
iop, interopercular
lac, lacrimal
leth, lateral ethmoid
lig, ligament
meth, mesethmoid
mx, maxilla
na, nasal
not, notochord
nsp₂₋₃, neural spines
op, opercular
pa, parietal
pal, palatine
phyp, parhypural
phyp¹⁻², anterior and posterior parhypurals
pmx, premaxilla

pop, preopercular
pto, pterotic
pu₁₋₂, preural centra
puf, preural flange
rna, rudimentary neural arch
snl, supraneural lamina
so, supraorbital
soc, supraoccipital
sop, subopercular
spho, sphenotic
stc, supratemporal canal
stg, stegural
tcm, supratemporal commissure
t.mx, maxillary tendon from adductor mandibulae
u₁₋₂, ural centra
ud, urodermal
un₁₋₄, uroneurals
unc, uncinat process of the fourth epibranchial for articulation with third epibranchial
vo, vomer

COMPARATIVE ANALYSIS

GILL ARCH STRUCTURE

One of the outstanding specializations of the alepocephaloid fishes is a complex posterior branchial structure that has usually been referred to as an epibranchial organ (Gegenbaur, 1878; Weitzman, 1967; Svetovidov and Skvortzova, 1968; Gosline, 1969; Bertmar, Kapoor, and Miller, 1969). Nelson (1967) believed the identification of an epibranchial organ in alepocephaloids to be erroneous, but he did note and figure the presence in *Alepocephalus macropterus* of an accessory cartilaginous element on the fifth ceratobranchial that was not then known in any other group of teleosts. Although we concur that an epibranchial organ, as usually understood, does not occur in alepocephaloids, there is nevertheless a complex bilaterally paired structure that takes the form of a pair of flattened, somewhat angular pouches, or purses, and that involves the last two gill arches and the anterior limits of the esophagus.

To emphasize the distinctness of the alepocephaloid structure we refer to it herein as a crumenal¹ organ. As indicated above, the main distinguishing detail in the crumenal organ is an accessory cartilage that, according to Nelson (1967), may have arisen by segmentation from the posterior cartilaginous articular surface of the fifth ceratobranchial. That the accessory cartilage is not a fifth epibranchial or a part thereof, as its

¹ From the Latin *crumena*, meaning a pouch or purse.

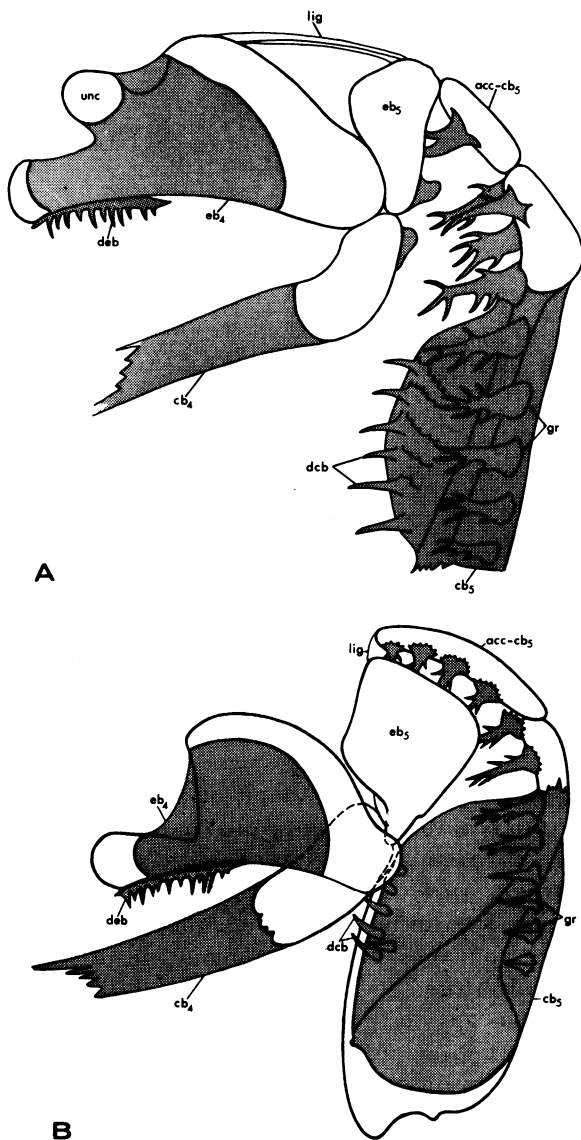


FIG. 1. Crumena organ skeleton: A, *Searsia koefoedi*; B, *Alepocephalus tenebrosus*.

position would seem to indicate, is suggested by the presence of a well-developed fifth epibranchial in its normal teleostean position just behind, and articulated with, the fourth gill arch (figs. 1-3). The ontogeny of the

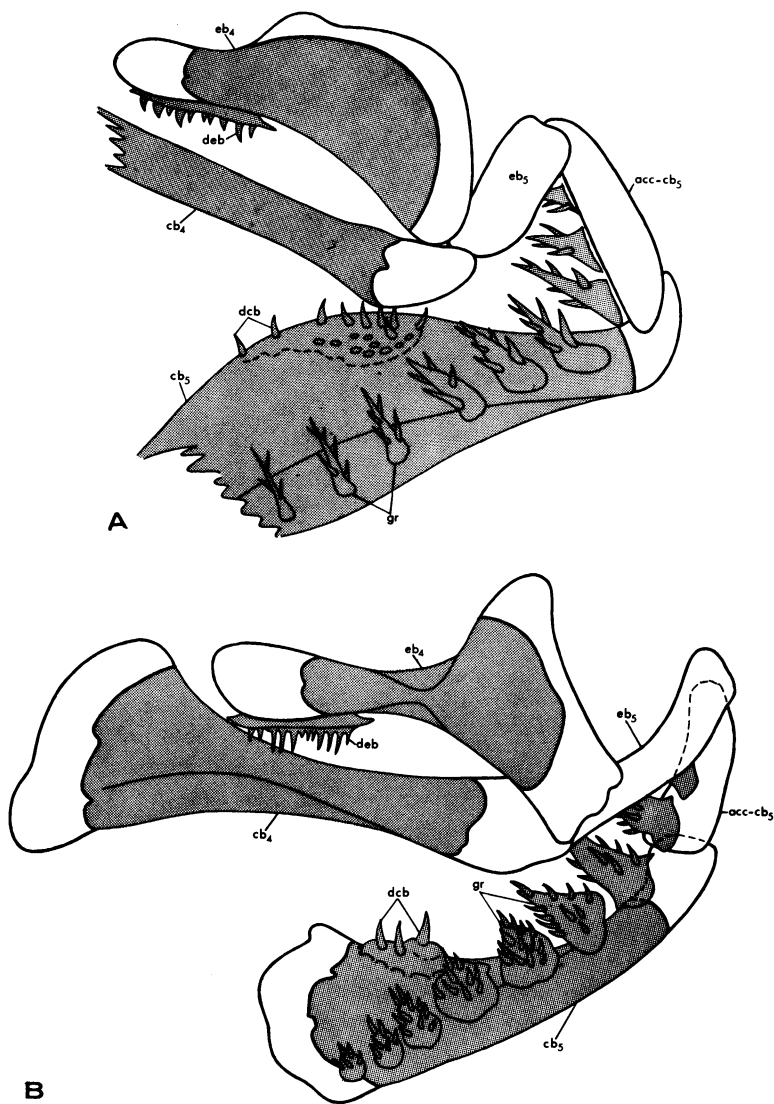


FIG. 2. Crumena organ skeleton: A, *Xenodermichthys copei*; B, *Leptoderma* sp.

fifth epibranchial was studied by Bertmar (1959), and its identity commented on by Nelson (1967, p. 82; 1969, p. 520). The accessory cartilage joins the often enlarged fifth ceratobranchial to the posterodorsal tip of the fifth epibranchial, and together these three elements support the

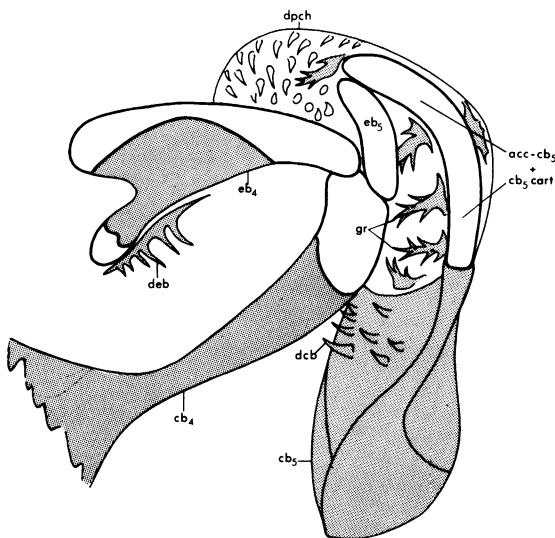


FIG. 3. Cruminal organ skeleton: *Leptochilichthys agassizi*.

narrow posterior margin of the pouch.

Anterior to the cruminal organ, the orobranchial chamber is divided longitudinally either by tissue from the floor of the mouth or by a direct upgrowth of the dermal bone over the basibranchial chain. Each pouch of the cruminal organ thus receives food particles that are channeled to it from its own side. The food particles are trapped in the pouches dorsally by large, interlocking dentate gill rakers.

The largest single element in the cruminal organ is always the fifth ceratobranchial and its accessory cartilage. The ossified part of the fifth ceratobranchial is sometimes greatly expanded medially, but regardless of the degree of expansion, the median edge of this bone rises upward to meet the edge of its companion bone in the midline. A ridge is formed that is continuous with the longitudinal basibranchial ridge dividing the orobranchial chamber in two. In general, the cruminal organ is posterolateral in position, and has its main bony structural components formed from the ceratobranchial elements. It differs in anatomy and topography from the suprabranchial or epibranchial organs of other fishes.

A cruminal organ has been found well developed in all alepocephaloid species examined. Gosline (1969) reported not finding one in the searsiid, *Searsia koefoedi*, but in our examples it is clearly evident (fig. 1A). Gosline's (1969) illustration of the pharyngobranchials of *Alepocephalus rostratus*

does not show the separation of the accessory cartilage (misabeled as the fifth epibranchial) from the cartilaginous articular surface of the fifth ceratobranchial, nor does it show the actual fifth epibranchial. Our specimen of *A. rostratus* has the arrangement typical of other alepocephaloids.

The alepocephaloid crumenal organs studied here may be grouped into two main types¹: 1) that of *Searsia* in which there is a short uncinat process on the fourth epibranchial for articulation with the third epibranchial; 2) those without an uncinat process (all alepocephalids). The alepocephalids may be subdivided into species with a distinct accessory cartilage on the fifth ceratobranchial (*Leptoderma*, *Alepocephalus*, *Xenodermichthys*, *Binghamichthys*), and those in which the accessory cartilage apparently has secondarily fused with the articular cartilage of the fifth ceratobranchial (*Leptochilichthys*, *Rouleina*). *Leptochilichthys* and *Rouleina* (see fig. 3) also have developed a dorsal pocket on the posterodorsal edge of the main pouch and this pocket is lined with small teeth similar to those on the shaft of the gill rakers more ventrally. The dorsal pocket is the only feature in which the alepocephaloid crumenal organ resembles the suprabranchial or epibranchial organ of other fishes.

An examination of the pharyngobranchial apparatus of argentinid, bathylagid, opisthoproctid, and bathylaconid fishes reveals that a crumenal organ is present and well developed in all species studied. The organ in *Bathylaco nigricans* is indistinguishable from that of *Alepocephalus* (fig. 1B) in the details that we can observe in our single specimen. That the crumenal organ of *Bathylaco* is alepocephaloid in character is further attested by the nature of the gill rakers of that organ which, as in all alepocephaloids, consist of a broad-based raker shaft around which emerge slender, pointed conical teeth at an oblique angle to the raker base. Crumenal gill rakers in all examined members of the argentinoid families (Argentinidae, Bathylagidae, Opisthoproctidae) are longer and more slender, and do not bear teeth.

The crumenal organs in argentinoids (figs. 4–6) are readily separated into three distinct types. The argentinid type (*Argentina*, *Glossanodon*), is characterized by the presence of an uncinat process on the fourth epibranchial and of two separate posterior articular processes; a small round patch of five to 10 moderately large teeth on the fourth epibranchial;

¹ In *Bathyprius*, unlike other alepocephaloids, the accessory cartilage appears to be only a small cap on the tip of the fifth ceratobranchial and the gill rakers appear to be toothless. If these details are confirmed, the crumenal organ of *Bathyprius* would constitute a third type among alepocephaloids. The gill rakers are short and broad-based as in other alepocephaloids, however.

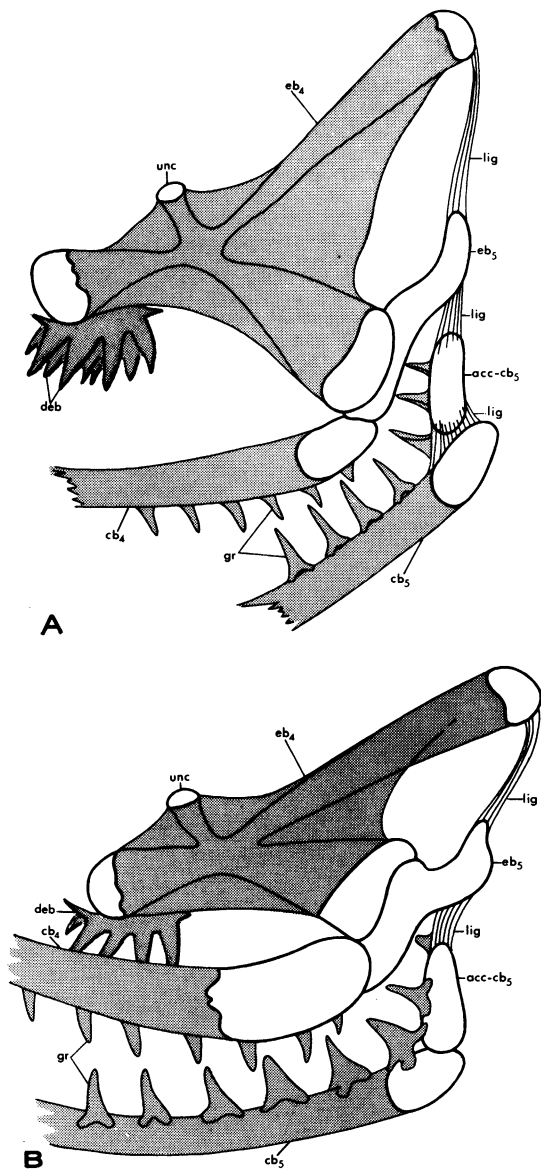


FIG. 4. Crumena organ skeleton: A, *Argentina brucei*; B, *Glossanodon pygmaeus*.

a sinuous fifth epibranchial in the form of an open S; and a small accessory cartilage that articulates at a right angle with the posterior tip of

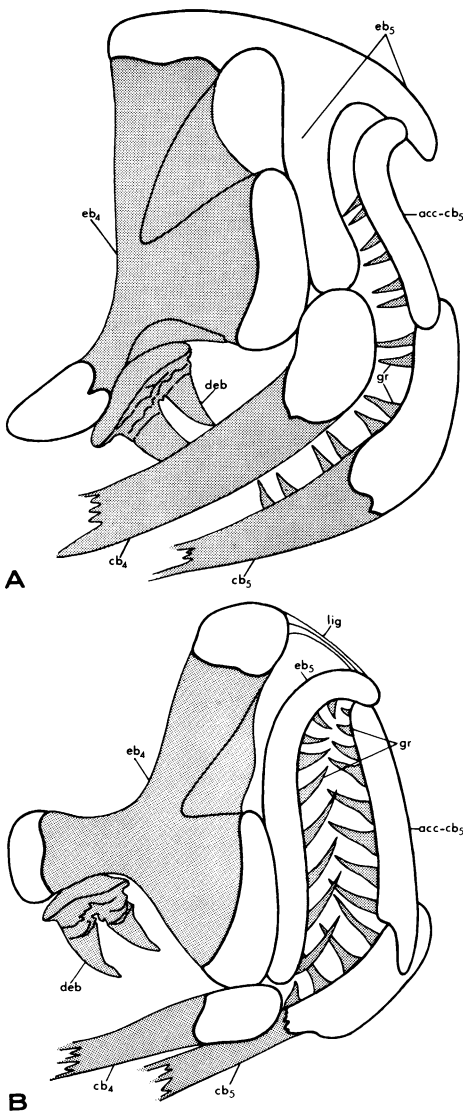


FIG. 5. Crumena organ skeleton: A, *Microstoma microstoma*; B, *Nansenia oblita*.

the fifth ceratobranchial, and with the tip of the fifth epibranchial¹ by means of a narrow, well-defined ligament (fig. 4). The second type, seen

¹ The accessory cartilage and fifth epibranchial were omitted from Nelson's (1970) figure 2A, B of *Argentina striata*.

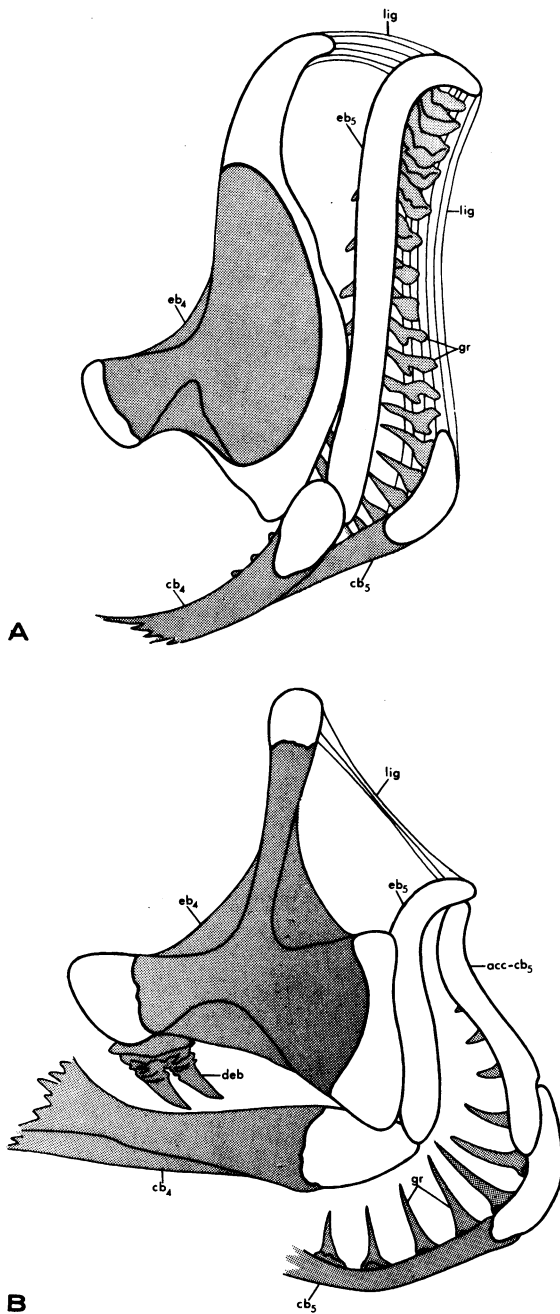


FIG. 6. Cruminal organ skeleton: A, *Opisthoproctus soleatus* (that of *Rhynchohyalus natalensis* is identical); B, *Bathylagus stilbius*.

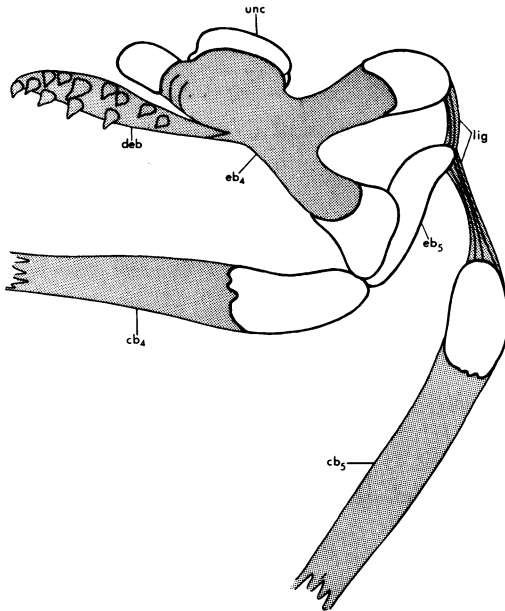


FIG. 7. Posterior epibranchial and ceratobranchial skeleton: *Osmerus eperlanus*. Note absence of accessory cartilage in lower ligament above fifth ceratobranchial.

in *Microstoma*, *Nansenia*, and *Bathylagus* (figs. 5, 6B), lacks an uncinus process, has two separate posterior articular processes, and one to three much enlarged teeth on a small, rounded toothplate on the fourth epibranchial, a rather long, fifth epibranchial in the form of an inverted J, and a similarly enlarged accessory cartilage that makes direct contact with the tips of the fifth ceratobranchial and epibranchial. In *Microstoma* the ligament that occupies the space between the posterodorsal articular process of the fourth epibranchial and the dorsal tip of the fifth epibranchial is replaced by a narrow bridge of cartilage. The opisthoproctid type (*Opisthoproctus*, *Rhynchohyalus*) generally resembles the microstomatine type (see fig. 6A) except that teeth are lacking on the fourth epibranchial, the posterior articular surfaces of this bone have run together as a single, long expanse of cartilage (although the form of the cartilage closely resembles the bifid condition), and that the accessory cartilage is replaced by a cylindrical muscle.

In summary, the crumenal organs of argentinoids differ from those of alepocephaloids in only two main features. In argentinoids the fourth

epibranchial is bifid posteriorly (or has a modification of the bifid condition as in opisthoproctids), and has simple, acuminate gill rakers. In alepocephaloids the fourth epibranchial has a single, broad posterior articular surface, and the gill rakers are broad-based and bear numerous teeth.

Neither a crumena organ nor an accessory cartilage on the fifth ceratobranchial is yet known to occur among elopomorphs, osteoglossomorphs, clupeomorphs, salmonoids, characoids, gonorynchiforms (Nelson, 1967), osmerids (fig. 7), or in any of the more advanced fishes, in which the fifth epibranchial also may not be present as a separate element or is wanting (Nelson, 1969).

CAUDAL FIN SKELETON

The caudal fin skeleton of alepocephaloids (figs. 8–11) is characterized by the presence of three (rarely four) uroneurals, the first not fused to any underlying centra, and extending to the second preural centrum; the first full neural arch and spine on PU_2 (rarely on PU_3 , as in one specimen of *Xenodermichthys copei*); no stegural¹ but a variously expanded supraneural lamina on the arch of U_1 , PU_1 , or both; generally two epurals (rarely one or three), and, in some genera, small flanges on the anterior face of the posterior preural hemal spines.

We have reviewed the different types of caudal fin skeleton in lower teleostean fishes as a basis for comparison of the alepocephaloid skeleton (table 1). Patterson (1968), using the leptolepidid pattern as a primitive teleostean type, has made some observations on elopoid and alepocephaloid caudals with particular reference to the fate and spatial distribution of uroneurals, and his observations are incorporated into our tabular analysis.

There are a number of distinct patterns involving, especially, uroneural length, number and relationship to the vertebrae, and the fate of neural arch and spine material associated with PU_1 and U_1 centra. Furthermore, it is clear that all the various conditions (including that of the elopoids)

¹ We restrict the term "stegural" to a bony extension developed from the upper margin of the first uroneural (as typified in salmonid fishes). Monod (1968) would identify the supraneural lamina of argentinoids as a stegural. But, as this bone is invariably attached to the underlying centrum by one or two neural arch rudiments (and is rarely fused with the uroneural) it is necessary to employ a different terminology for it, viz., supraneural lamina.

Without ontogenetic evidence it is impossible to tell whether the stegurals of lower euteleosts and of neoteleosts are homologous structures [see Cavender (1970) for notes on the development of a stegural in *Salmo clarki*].

TABLE 1
COMPARISON OF SOME ASPECTS OF LOWER TELEOSTEAN CAUDAL SKELETONS^a

	Uroneurals		First Uroneural Extending to:	First Full Neural Arch and Spine on Vertebra	Number Ossified Epurals	Supraneural Laminae Arising from Arch Rudiments on U ₁ and/or PU ₁	Stegural ^b
	Long	Medium Short					
Leptolepididae	3-4	0-1	2-3	PU ₂ -PU ₃	3	—	—
Elopoidei	2	0	1	PU ₂	3	—	—
Albuloidi	1	1	0	PU ₁ -PU ₂	2-3	+	—
Hiodontoidi	3-4	0	0	PU ₂	1	—	—
Salmonoidi	1	1	0-1	PU ₁ -PU ₂	2-4	—	+
Argentinoidi	1	1	1	PU ₁	0-2 ^d	+	—
Alepocephaloidei	1	1	1-2	PU ₂	1-3 ^e	+	—

^a The clupeoids are omitted because of their peculiarly specialized caudal skeleton (see Greenwood, 1968).

^b See text for definition.

^c Including osmeroids and galaxioids except for the Galaxiidae.

^d Usually two, rarely one or none.

^e Usually two, rarely one or three.

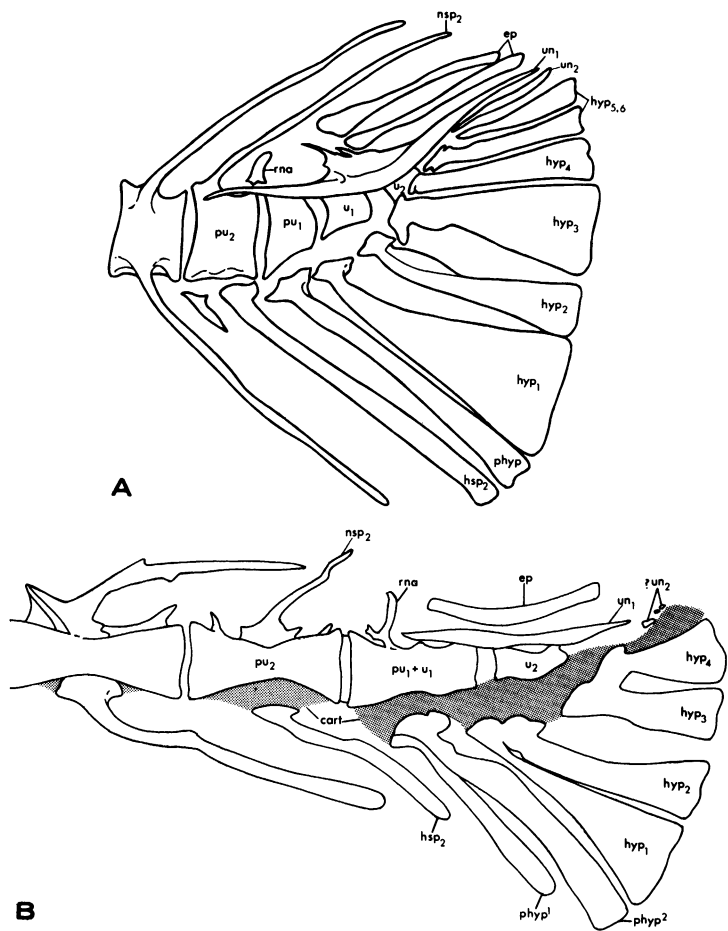


FIG. 9. Caudal fin skeleton: A, *Xenodermichthys copei*; B, *Leptoderma* sp. Note reduction in number of hypurals, uroneurals, and epurals.

exemplified by *Searsia koefoedi*. In this species the juvenile condition is typically alepocephaloid (cf. figs. 11A and 8–10), but the adult has a largely argentinoid configuration (cf. figs. 11B and 9–15; and see below).

A generalization that may be made about primitive euteleostean caudal skeletons is that laminar bone tends to be laid down in association with a wide variety of structures posteriorly from the third or fourth preural centra to the hypurals. Among these fishes, however, there are two fundamental patterns in the way in which this laminar bone is incorporated into the region posterior to the last full neural spine below the epurals

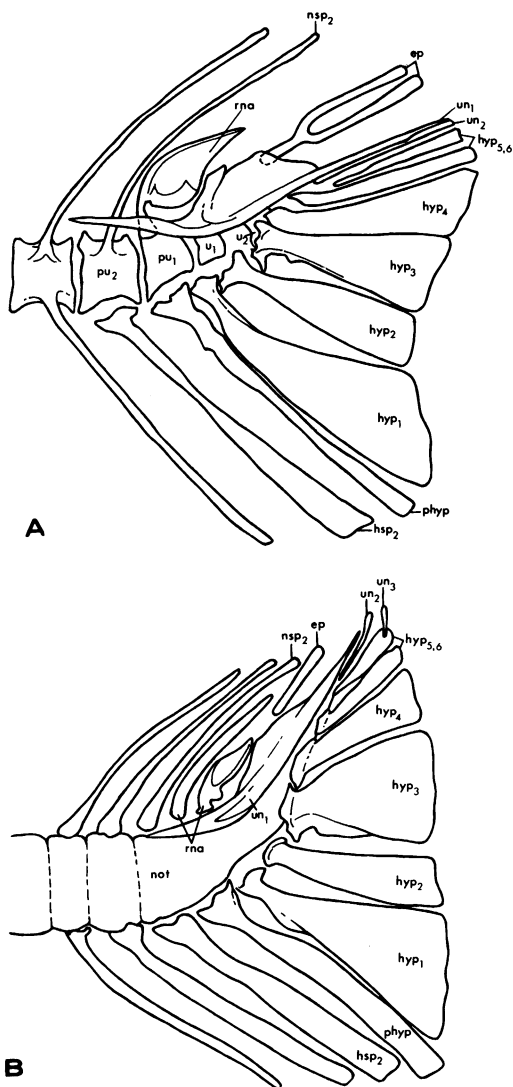


FIG. 10. Caudal fin skeleton: A, *Rouleina squamilateratus*; B, *Leptochilichthys agassizi*. Note lack of central ossification.

and above the first preural and first ural centra. In argentinoids (figs. 12-15) bony laminae seem to be built up in relation to the presence of one or two rudimentary neural arches that always are present above PU_1 and U_1 , for these laminae in every case are fully integrated into the neural arch superstructure. In salmonoids, osmeroids (fig. 16), and galaxioids much laminar bone also is present in essentially the same area,

the upper edge of the first pair of uroneurals, to form what we refer to as a stegural. Some of the more advanced argentinoid caudal skeletons approach the salmonoid condition by secondarily fusing these supraneural laminae to platelike bony extensions from each of the first uroneurals. For example, in *Argentina stewarti* the posterior supraneural lamina extends between the platelike extensions from the first pair of uroneurals, but is also firmly ankylosed to the uroneurals. Regardless of such similarities the two kinds of caudal skeleton remain fundamentally different in appearance depending on whether the laminar bone develops in relation to neural arch rudiments. As a consequence of this basic difference in architecture, the supraneural superstructure in argentinoids invariably is seated on the first preural and first ural centra, whereas in salmonoids and related fishes the region directly ventral to this superstructure appears as a deep excavation entirely devoid of bone as far posteriorly as the lower leading edge of the first uroneurals. Finally, because neural arch rudiments are a common feature of other teleostean groups—elopoids, hiodontoids, clupeoids—we interpret the argentinoid condition to be based on a more primitive structural plan than that of the salmonoids in which these neural arch rudiments appear to have been lost.

The argentinoid caudal skeleton (figs. 12–15) is characterized by having a full arch and spine on PU_2 ; an expanded plate or plates (the supraneural laminae) formed on the neural arch of U_1 and PU_1 and attached through one or both of these arches to the underlying compound centrum, or to PU_1 if a separate U_1 is present, or to the first uroneural; the first uroneural extended anteriorly as far as PU_1 (sutured or ankylosed to that centrum), its dorsal margin with a large anteriorly directed expansion which contacts, or envelops part of, the supraneural lamina; two epurals (except in opisthoproctids and in *Bathylagus* where there are one or two cartilaginous plates); a basal expansion (the preural flange) on the anterior face of the posterior two or three neural and hemal spines; a urodermal (except in *Bathylagus*); PU_1 and U_1 fused (except in opisthoproctids), and a distinct U_2 centrum.

Alepocephaloids (figs. 8–11), relative to argentinoids, have little plate-like bone on spines or arches, or on the neural arch rudiments on U_1 and PU_1 . A small platelike supraneural process is associated with the neural arch of U_1 in bathylaconids, juvenile *Searsia*, and in *Bajacalifornia* among the alepocephalids where it is incorporated with the arch rudiment of PU_1 . The adult and juvenile *Searsia koefoedi* differ with respect to the development of a supraneural lamina on the rudimentary neural arches. In the juvenile, the small laminae are closely similar to those of some adult alepocephalids, but in the adult the plates are much expanded and

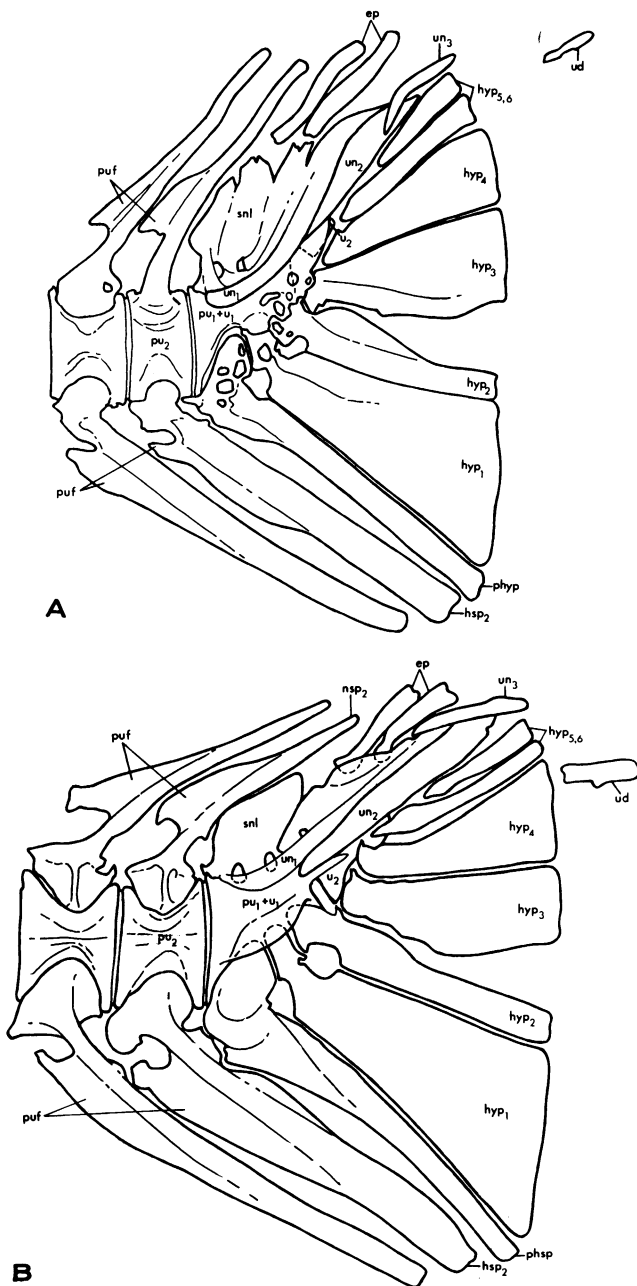


FIG. 12. Caudal fin skeleton: A, *Argentina brucei*. Note that UN₁ is fused with supraneural lamina; B, *Glossanodon pygmaeus*. Note that UN₁ and supraneural lamina are in contact but barely fused.

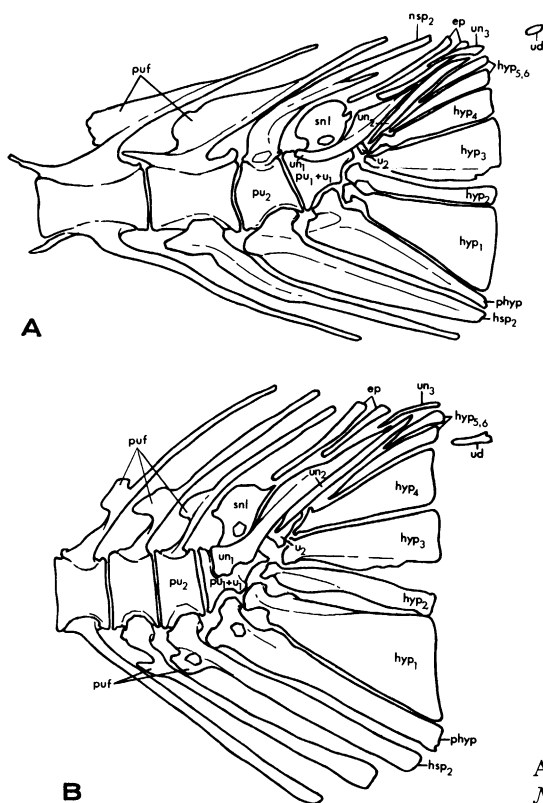


FIG. 13. Caudal fin skeleton:
A, *Microstoma microstoma*; B,
Nansenia oblita.

come to resemble those of the argentinoids. In most alepocephalids the processes are variously developed, as a slender spinelike projection on the arches of both PU₁ and U₁, or PU₁ alone when there is no process on U₁, as a leaflike plate on PU₁, or as a spine and a low ridge on PU₁ and U₁ respectively. Except in *Leptoderma* (fig. 9B), PU₁ and U₁ are separate and there is invariably a distinct U₂. However, some individual variability may occur, as a large (55 cm. standard length) *Alepocephalus agassizi* has PU₁ and U₁ fused, whereas these centra are separate in two smaller individuals.

The first uroneural in all alepocephaloids extends farther anteriorly than in argentinoids, reaching to PU₂ or the posterior part of PU₃; in no alepocephaloid is this bone sutured or ankylosed to any centrum. The dorsal expansion of the first uroneural is well developed in some genera (*Xenodermichthys*, *Searsia*, *Rouleina*) but absent in others (*Alepocephalus*, *Talismania*, *Leptoderma*, *Bajacalifornia*). The long, free first uroneural

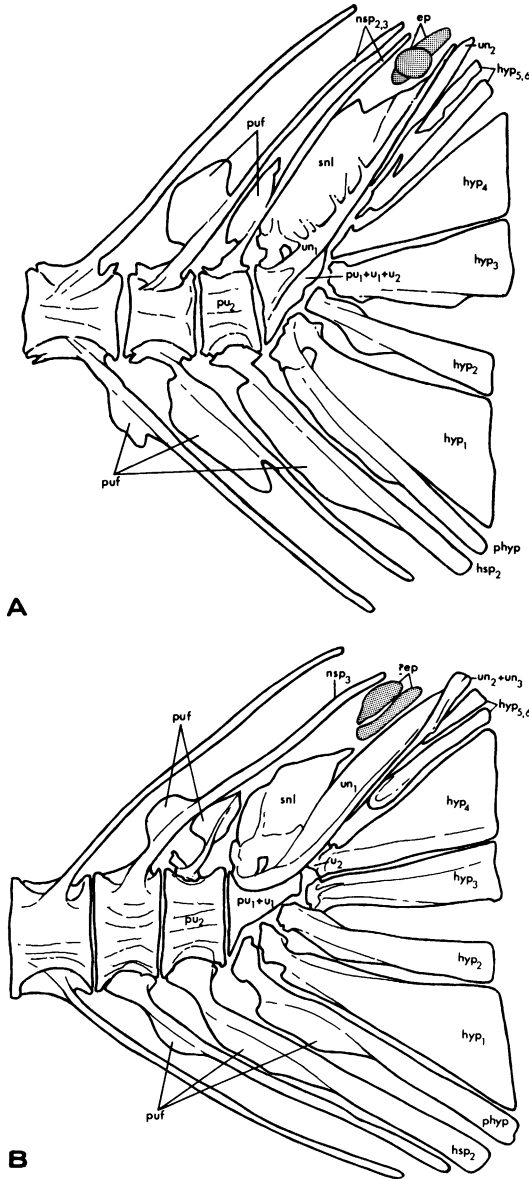


FIG. 14. Caudal fin skeleton: *Bathylagus stilbius*. A, small specimen (41 mm.); B, larger fish (93 mm.). Note constancy of preural flange on neural spine of PU_2 despite variation in spine length; also greater degree of fusion between supraneural lamina and UN_1 in larger fish and presence of a third uroneural (partly fused with UN_2) in this individual. No urodermal present in either specimen. In *Bathylagus longirostris* there are two fully ossified epurals and only distal half of supraneural lamina is fused with UN_1 .

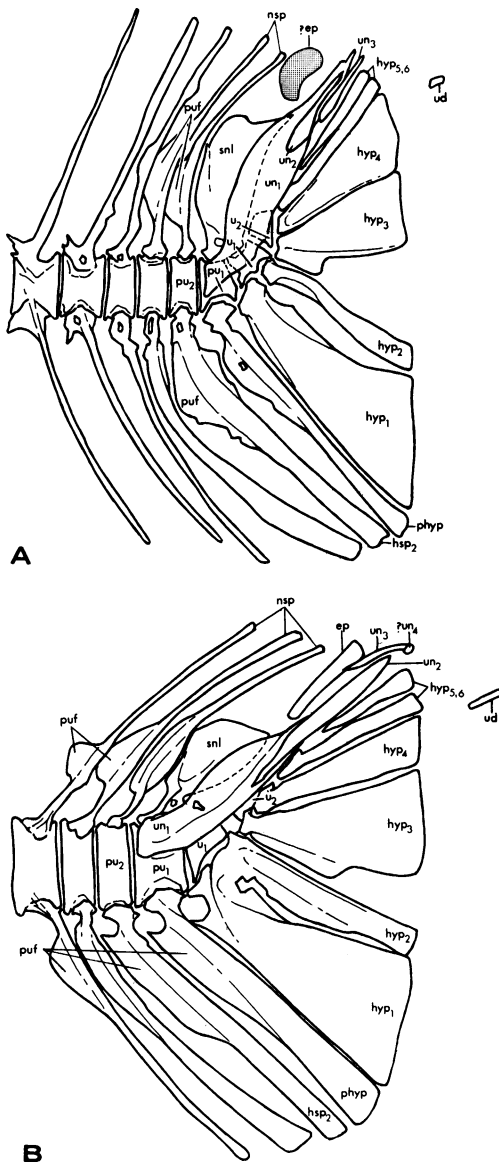


FIG. 15. Caudal fin skeleton: A, *Opisthoproctus soleatus*. Note extensive overlap of first uroneural on supraneural lamina. B, *Rhynchohyalus natalensis*. Note small, globular UN₄ fused to tip of UN₃.

of alepocephaloids seems to represent a more primitive condition than the shorter, sutured or ankylosed bone of argentinoids. Some alepocephaloids have as many as four pairs of uroneurals (e.g. *Alepocephalus*) but in the majority there are three (one elongate, one of medium length.

and one short); the second (a medium length bone) has about the same relative proportions and is situated as in argentinoids (that is, it lies below the upper margin of the first uroneural and not above or lateral to it as in osmeroids and salmonids).

Two epurals are present in most species but three are developed in bathylaconids, and only one in *Leptoderma*, *Leptochilichthys*, and in *Alepocephalus agassizi*.

Preural flanges do not develop in most alepocephaloids, but are present and well developed in adult *Searsia koefoedi* (fig. 11B). In the juvenile, however, the flanges are present in a reduced condition only on the hemal spines.

No urodermal is present in any of the genera examined.

In brief, we would consider the caudal fin skeleton of alepocephaloids to represent, in certain respects, a reduction of that found in argentinoids. This is suggested by the argentinoid character of the caudal fin skeleton in adult *Searsia koefoedi* in which laminar bone is well developed on the posterior neural and hemal spines and on the rudimentary neural arches, and in which the first uroneural does not extend anterior to the first preural centrum. Unless these similarities between *Searsia* and the argentinoids are assumed to have arisen independently in the two groups, one may regard the alepocephaloid caudal skeleton as having become specialized by the loss of laminar bone and the forward extension of the first uroneural over the second preural centrum. This inference about the origin of the alepocephaloid caudal skeleton is in direct opposition to inferences previously drawn by other authors that the absence of laminar bone and the elongate uroneurals of alepocephaloids represent the retention of primitive teleostean features. Reductional trends are clearly manifest in the absence of preural flanges on the hemal and neural spines, and of the urodermal—features that are widespread among primitive euteleosteans, including argentinoids. The retention of separate PU_1 and U_1 centra in most alepocephaloids is a persistent primitive feature.

Patterson (1968) is one of the authors who has expressed the view that the alepocephalid caudal skeleton is one of the most primitive known among living teleosts. He noted that “. . . *Alepocephalus* seems to exhibit the most complete set of uroneurals among living teleosts, with traces of eight neural arches . . .” This conclusion was based on his observation of three or four shallow indentations on the anterior and ventral margin of the first uroneural in a specimen of *Alepocephalus rostratus*. These indentations were interpreted by Patterson as indications of a compound uroneural, composed of four fused elements. Our largest specimen of *A. rostratus* (28 cm. standard length) has seven such indentations and our

small specimen of *A. tenebrosus* (19.4 cm. standard length) has none. We conclude, therefore, that the anteroventral indentations and related surface markings on the first uroneural are not signs of the compound origin of that bone but rather an indication that supporting struts develop as *de novo* outgrowths of the uroneural with increase in the size of the fish.

Since a relationship between the alepocephaloids and the osmeroids has been implied (Gosline, 1969), the caudal fin skeleton of osmerids must be considered briefly in comparison with those of both argentinoids and alepocephaloids.

There are several noticeable differences. For example, and perhaps most significantly, osmerids (fig. 16) have a prominent true stegural occupying most of the space between the neural spine of PU_2 and the first uroneural, whereas in argentinoids and alepocephaloids supraneural laminae are developed (see p. 18); the anterior tip of this uroneural is indistinguishably ankylosed with the compound PU_1 and U_1 centrum, and no neural arches or other neural superstructures are associated with the compound centrum (a correlate of stegural formation). In general, the osmeroid caudal skeleton can be said to have much the same relationship to that of the salmonoids as does the skeleton of argentinoids to that of the alepocephaloids.

JAW MUSCULATURE

All alepocephaloids dissected (*Talismania*, *Leptoderma*, and two forms of *Alepocephalus*) have a well-developed, elongate, tendinous insertion of part of the adductor mandibulae muscle onto the anterior part of the maxilla (fig. 17). This tendon arises from the upper part of the adductor muscle, and is presumably the "ligament" which Gosline (1969) noted and figured for *Alepocephalus rostratus*. However, Gosline describes the ligament as linking the maxilla and mandible; we could find no trace of a maxillo-mandibular ligament, presumably because it is taken over by the adductor mandibulae muscle.

The levator arcus palatini, as well as the levator, adductor and dilator operculae muscles are well developed and easily distinguished. The adductor arcus palatini, however, is small and restricted to the upper portion of the posterior orbital wall.

None of the argentinoid genera dissected (*Argentina striata*, *Bathylagus stilbius*, *Opisthoproctus soleatus*) has any part of the adductor mandibulae muscle inserting onto the maxilla (fig. 18), and, in all, the levator arcus palatini and opercular muscles are poorly developed and differentiated. The adductor arcus palatini, in contrast, is somewhat more extensive than in alepocephaloids, and may extend from the posteroventral wall of

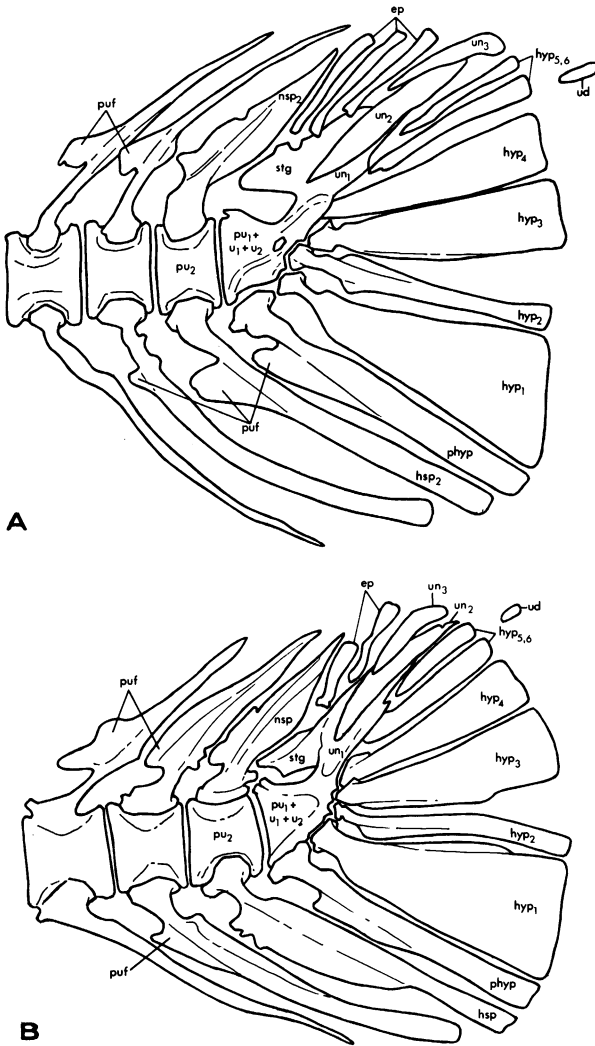


FIG. 16. Caudal skeleton: A, *Osmerus eperlanus*; B, *Hypomesus olidus*. In both, note position of UN₂ relative to UN₁ (i.e., the typical osmeroid-salmonoid relationship of the two bones).

the orbit (as in *Argentina*) almost to below the anterior margin of the eye (*Opisthoproctus*). Although the musculature does not provide indication of relationship between these two groups of fishes, it does enhance precise definition of each group. The differences in musculature presumably are



FIG. 17. Dissection of superficial jaw muscles and levator arcus palatini muscles in *Alepocephalus rostratus*.

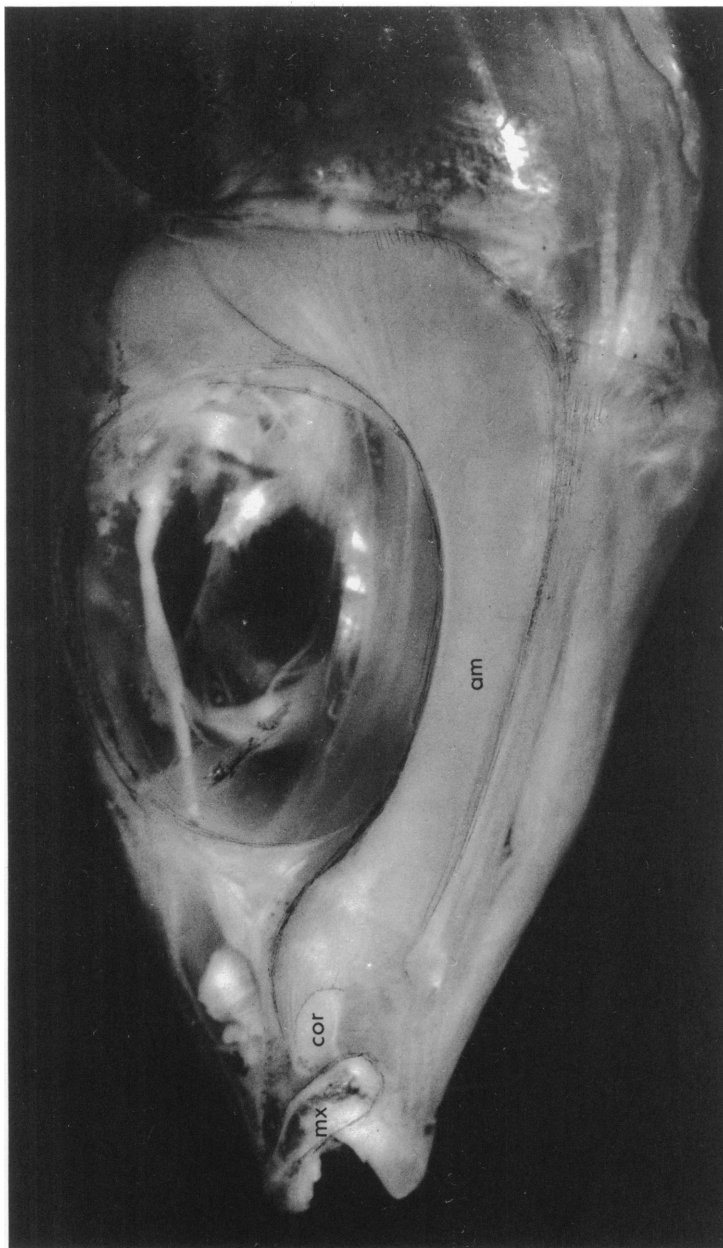


FIG. 18. Dissection of superficial jaw muscles and levator arcus palatini in *Argentina striata*.

related to differences in the size of the gape and the presence or absence of teeth in the jaws.

PREANAL PLATE

A characteristic feature of argentinoids (except the opisthoproctids) is a small but broad plate of bone situated immediately anterior to the first anal pterygiophore; a pair of tendons from the protractor analis muscle insert onto the plate laterally. Its absence in opisthoproctids is undoubtedly associated with the greatly reduced anal fin in these species.

No obvious preanal plate has been found in alepocephaloids, but in *Talismania poregoni* and *Bathylaco nigricans* we have found a condition of the first anal pterygiophore that is suggestive of the way in which the plate has evolved. The first anal pterygiophore in *Talismania* lies at a marked angle to the rest of the series, so that its anterior surface is aligned almost horizontally; its shaft is shorter than that of the second pterygiophore. Relative to the others the head of this pterygiophore is greatly expanded laterally; tendons from the protractor analis muscle insert onto it. The first anal ray articulates through a long cartilaginous radial in such a way that the fin base comes to lie close to the head of the second pterygiophore.

In *Bathylaco* the first anal ray articulation has shifted to the second pterygiophore, thus freeing the first from its function as a ray-bearer. As in *Talismania*, the head of this pterygiophore is expanded and lies almost horizontally, and a pair of protractor analis tendons are attached to it.

There is, in fact, very little difference between the preanal plate of the microstomatine *Nansenia oblita* and the first anal pterygiophore of *Bathylaco nigricans*, except for the longer shaft of the latter. In other argentinoids (for example, *Argentina brucei* and *Glossanodon pygmaeus*) the plate lies further anteriorly, and has lost all contact with the anal pterygiophores.

GENERAL FEATURES OF THE ANATOMY

Other anatomical details of argentinoids and alepocephaloids show similarities of a more general nature. Neither group, for example, has lower intermuscular bones anteriorly, and in most species the epineural bones are fused to the neural arch bases—both features that are primitive for teleosts as a whole. An exactly similar pattern of intermuscular bones occurs in the stomiatoid, *Gonostoma denudatum*. In salmonoids, osmeroids, and galaxioids, the lower intermuscular bones are present also, but extend over a greater length of the vertebral column, and the epineurals are autogenous. The only other group resembling the argentinoids and alepo-

cephaloids in this character is the Osteoglossomorpha. In argentinoids and alepocephaloids the posterior branchiostegal rays tend to be bladelike, at least proximally (figs. 19, 20), but so do they in clupeoids. The nasal bones, when present, are rather elongate in argentinoids and alepocephaloids (figs. 21-23), and are shorter in salmonoids, osmeroids, and galaxioids.

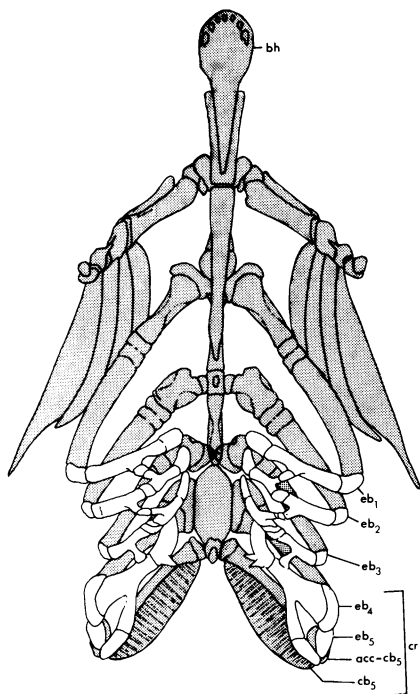


FIG. 19. Hyobranchial skeleton of *Nansenia oblita*, dorsal view.

Many similarities between argentinoids and alepocephaloids are simply the result of the retention of primitive teleostean features, such as the presence of supraorbitals and antorbitals (figs. 21-23), long, attenuate frontals and a small supraoccipital (figs. 21-24), the occurrence in both groups of *Ringfalten* in the gut (and see Cohen, 1958), the presence in many forms in both groups of extensive dermal basibranchial plates (toothed in various alepocephaloids), upper pharyngeal dentition, and unsutured anterior and posterior ceratohyals (figs. 19, 20), the relatively small, often feeble, premaxillaries, and the presence in most forms of more than six pelvic fin rays and as many as 17 branched caudal fin rays.

In some respects alepocephaloids are more primitive than argentinoids,

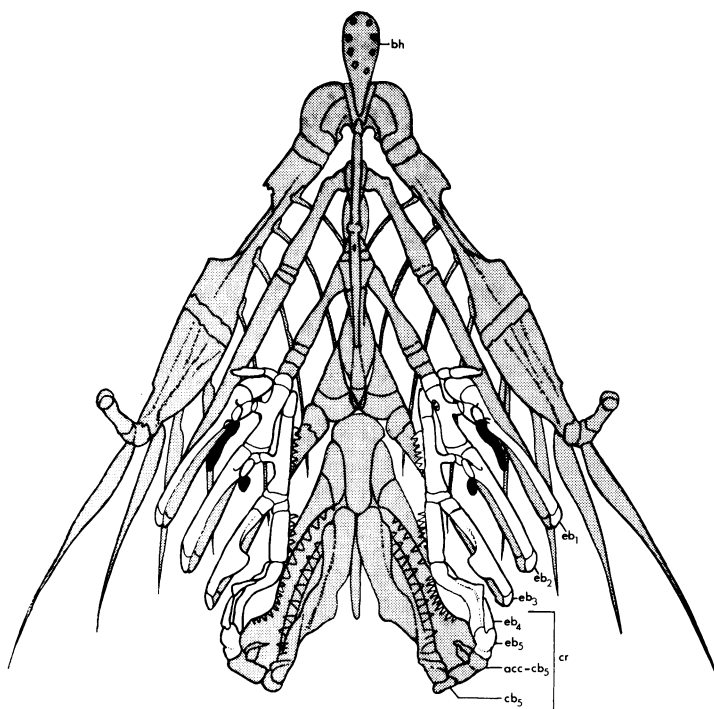


FIG. 20. Hyobranchial skeleton of *Searsia koefoedi*, dorsal view; suprapharyngobranchials in solid black. Basihyal teeth occur in various patterns in searsiids. *Mentodus rostratus* teeth are arranged as in *S. koefoedi*, but are larger and fanglike. *Barbantus curvifrons* has only two large fanglike teeth on each side; *Platyroctes apus* has but a single fanglike tooth distally on the basihyal.

and in others more specialized. The ways in which alepocephaloids are more primitive than argentinoids are:

1. One, sometimes two, suprapharyngobranchials (versus none); figures 19 and 20.
2. Basibranchial dentition present in some species (versus absent).
3. One or two supramaxillae (versus none).
4. Upper jaw dentition present (versus absent).
5. A first uroneural that is never ankylosed with a centrum (versus one that is sutured or ankylosed with PU_1).
6. Retention in most cases of three separate caudal centra, PU_1 , U_1 , and U_2 (versus the frequent fusion of PU_1 and U_1).

Argentinoids are more primitive than alepocephaloids in the following:

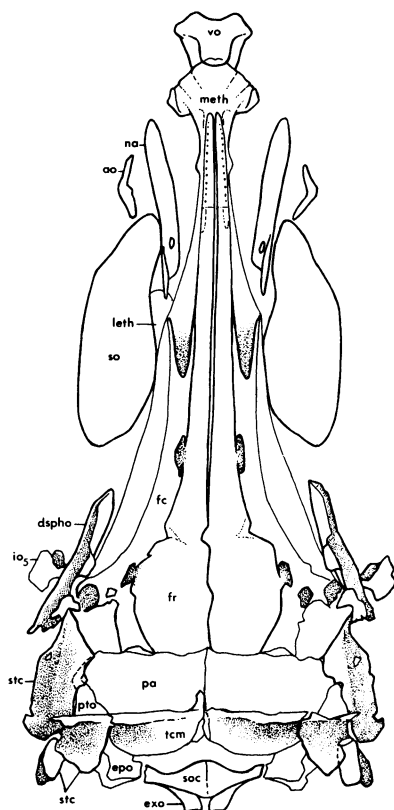


FIG. 21. *Glossanodon pygmaeus*, dorsicranium.

1. Frequent occurrence of basihyal dentition (versus its occurrence only in searsiids where it is reduced, fig. 20).

2. Adductor mandibulae muscle without a maxillary insertion (versus its presence); figures 17 and 18.

3. Parietals large and meeting in midline in most forms (versus their separation); figures 21 to 24.

4. Supraoccipital never contacting frontals, and, in most forms, confined to the posterior edge of the dorsicranium (versus one that contacts the frontals); figures 21 to 24.

5. An adipose fin present in most (versus absent).

6. A urodermal present in most species (versus absent).

Argentinoids and alepocephaloids are differently specialized in the following ways that do not involve the simple loss or growth of a primitive feature:

Argentinoids:

1. Small, terminal mouth with short oblongate maxilla; figure 18.
2. Anterior extension of the vomer beyond the ethmoid block to act as the forward biting surface (replacing the edentulous upper jaw); figures 21 and 22.

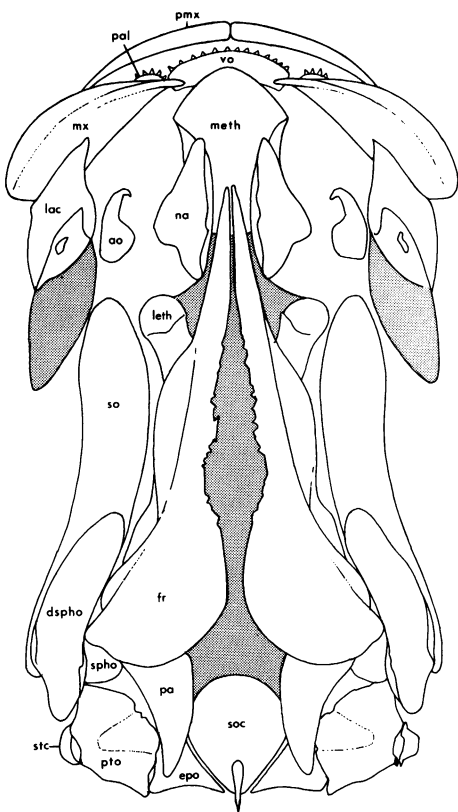


FIG. 22. *Bathylagus stilbius*, dorsocranium. Note large cartilaginous appendage (shaded) on lacrimal (lac).

3. Freeing of the premaxilla from its ethmoid articulation.
4. Greatly elongate basihyal with specialized distal dentition in most (see Cohen, 1964; Nelson, 1970).
5. Dermosphenotic greatly elongate and troughlike; figures 21 to 23.
6. A small plate of bone formed from the first anal pterygiophore, except in the opisthoproctids, which have reduced anal fins.
7. First uroneural fused or sutured with the anterior portion of centrum PU_1 (whether or not PU_1 and U_1 are fused).
8. Large, leaflike plates of bone (the supraneural laminae) associated

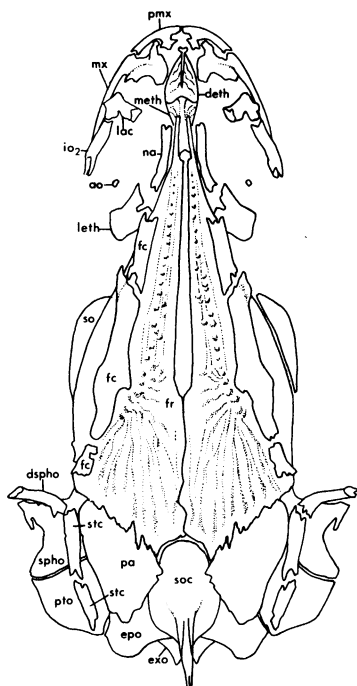


FIG. 23. *Leptoderma* sp., dorsicranium.

with the rudimentary neural arches on caudal centra PU_1 and U_1 ; figure 12.

Alepocephaloids:

1. Development of a shallow, sloping opercular with a usually deeply incised posterior margin.

2. Dorsal fin posterior in position, situated partly or entirely over the anal fin.

3. Reduction of laminar bone associated with the caudal fin skeleton, and the probable secondary elongation of the first uroneural.

For many features that separate argentinoids and alepocephaloids it is difficult to decide which of the contrasting character states is primitive and which advanced. One may suppose, for example, that the bifid condition of the fourth epibranchial of argentinoids (figs. 4-6) is advanced, as all of the representatives of primitive teleostean groups studied by Nelson (1967) have an undivided posterior articular surface on the fourth epibranchial. But are dentate or edentate gill rakers primitive? One cannot decide until the matter is surveyed, and at this time we can only note that in our osmerid material the rakers are dentate as in alepocephaloids.

DISCUSSION AND CONCLUSIONS

The comparative evidence presented above, especially that of the pharyngobranchial apparatus and caudal fin skeleton, warrants the hypothesis that argentinoids and alepocephaloids are descended from a common ancestor and that they are more closely related to each other

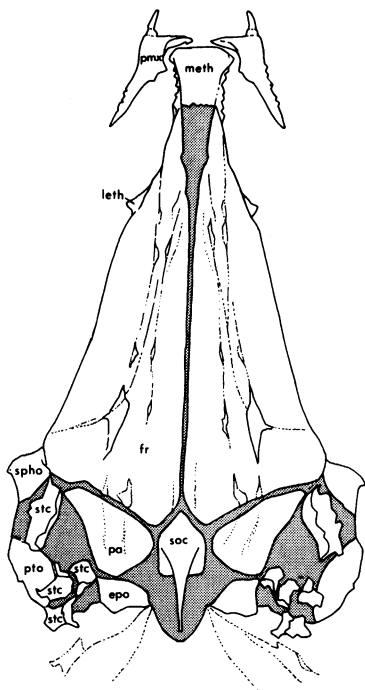


FIG. 24. *Searsia koefoedi*, dorsicranium.

than to any other group of extant fishes; that is, they are sister groups that together form a monophyletic assemblage. The hypothetical common ancestor of these fishes may be visualized as a protacanthopterygian euteleostean, in body and fin form like an argentinid, with an internal caudal skeleton structure more like those of argentinoids and searsiids than alepocephalids, and in jaw anatomy like that of an alepocephaloid. Such a common ancestor probably also possessed an opercular apparatus and skull roof of argentinid type, and a basically salmonoid-osmeroid-galaxioid pattern of basihyal teeth which seems to have persisted in searsiids (fig. 20). A crumenal organ of simple form, as in *Argentina*, or, at the very least, an accessory cartilage on the fifth ceratobranchial, was probably also present.

From such a hypothetical ancestor, generalized argentinids might have evolved by reducing the gape and losing upper jaw teeth, with associated enhancement of the palato-vomerine dentition and elongation of the basihyal so that the anterior fanglike basihyal teeth came to oppose the palato-vomerine dentition; the formation of a preanal plate of bone associated with the tendons of the protractor analis muscles; and the strengthening of the caudal skeleton by consolidation of the first preural and ural centra, the fusion of the first uroneural to PU_1 , and filling of the sub-epural space directly above the rudimentary neural arches of

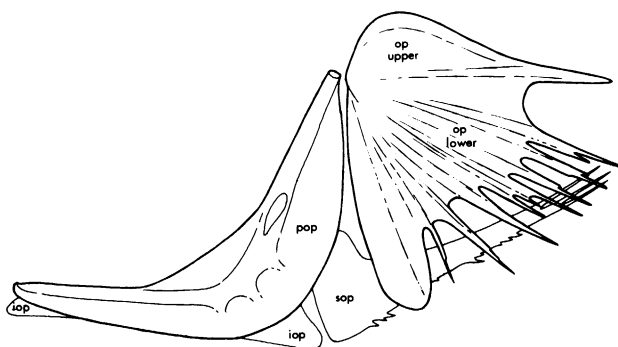


FIG. 25. *Bathylagus stilbius*, left opercular apparatus.

PU_1 and U_1 by the supraneural laminae that, in their best developed state, bind together the spine of PU_1 , the compound centrum ($PU_1 + U_1$), and the first uroneural (and hence strengthen the support of the upper and lower hypurals).

The direction of evolution in alepocephaloids seems to have involved loss of the swimbladder, a reduction in the quantity and density of bone, perhaps related to invasion of the abyssal environment, and the backward migration of the dorsal fin (with the consequent loss of the adipose fin), possibly also related to an environmental shift. Bone reduction in alepocephaloids is particularly evident in the opercular apparatus where the peculiar opercular seems to represent a residual ventral section of that bone when it undergoes a reduction as in *Bathylagus* (fig. 25). Bone reduction also is evidenced in the caudal skeleton by the loss of a urodermal, reduction of the preural flanges on the posterior neural and hemal spines, and of the supraneural laminae on the rudimentary neural arches on U_1 and PU_1 ; urodermals and preural flanges both are features typically present in the more primitive euteleosteans, including argentinoids. The

jaws seem to have been emphasized in alepocephaloid evolution, as evidenced by the large gape present in some forms (e.g., *Bathylaco* and various alepocephalids) and by the specialized premaxillary teeth present in many searsiids (fig. 24). The supposed concurrent emphasis on dermal jaw development and general bone reduction, may also have been directly related to the reduction or loss, not only of basihyal teeth, but of the ossified basihyal itself as in *Leptoichthys* and *Rouleina*.

Among argentinoids, many of the apparent reductional changes that are characteristic of alepocephaloids may be noted in the deeper water forms such as microstomatines, bathylagids, and opisthoproctids (as in the opercular apparatus of *Bathylagus* mentioned above). For example, swimbladders have been reduced or lost. The urodermal has been lost in at least some *Bathylagus*. Perhaps even the fact that the parietals are relatively small in alepocephaloids and bathylagids, and that they fail to meet in the midline (figs. 22–24), is related to similar reductional influences associated with a bathypelagic existence. Bathylagids, microstomatines, and opisthoproctids, which show numerous adaptations to life in the deep sea (Cohen, 1964), also have reduced the basihyal, or the basihyal teeth, or both.

Opisthoproctids may represent an early, independent invasion of the deep sea by argentinoids, as suggested by the failure of opisthoproctids to have consolidated the caudal centra as in all other argentinoids. But opisthoproctids have many resemblances to microstomatines and bathylagids, and in microstomatines caudal centra PU_1 and U_1 , although fused, are still distinguishable as separate elements (fig. 13). Opisthoproctids, microstomatines, and bathylagids also have exceedingly similar, and highly specialized, crumenal organs (figs. 5, 6), and some bathylagids and opisthoproctids develop similar optical specializations. As bathylagids currently are separated from microstomatines only on the basis of a lesser development of their parietals, and the pharyngobranchial and caudal evidence indicates that these fishes are intimately related, it is reasonable to infer that microstomatines, bathylagids, and opisthoproctids are a monophyletic assemblage within the argentinoids that represents a single argentinoid contribution to the deep water habitat. If that phylogenetic inference is valid, it follows that the microstomatines and bathylagids have advanced a bit farther in the caudal region and a good deal less in the cephalic region than the related opisthoproctids.

We propose that all of the relationships hypothesized above be incorporated into a revised taxonomic plan of the argentinoid fishes. By way of preamble to our proposed taxonomic scheme and to summarize what we have found, it may be noted that we have uncovered no phyletic

evidence to separate the bathylaconids from the alepocephalids (nor, in our opinion, have Nielsen and Larsen, 1968), but we have discovered reasons for uniting microstomatines, bathylagids, and opisthoproctids as an argentinoid assemblage distinct from the Argentinidae. We should also note that our reasoning is based on the concept of genealogy, and on the idea that a classification should not be primarily an attempt to demonstrate degrees of adaptational divergence of its component taxa. In other words, we believe that a classification should reflect propinquity of descent, a view first formulated by Darwin (see Ghiselin, 1969) and later expanded by Hennig and Brundin (see Brundin, 1966) and, most elegantly, by Crowson (1970).

It is on this basis that we have united, at the hierarchical level of the family, the opisthoproctid, bathylagid, and microstomatid fishes. We do not deny that the opisthoproctids show many and bizarre structural modifications; we also believe that a detailed study of these modifications is essential to an understanding of the evolution of this group. But, we know of no objective way of indicating taxonomically the sum of these adaptations except by arbitrary definition. To be effective, a system incorporating adaptational information requires a prearranged consensus as to which characters or character combinations qualify for a given rank. We do not believe that, in general, such an enduring consensus can ever be achieved—witness the already checkered history of the taxa we now include in the Bathylagidae (see Cohen, 1964). We therefore advance the following phyletic classification:

Suborder Argentinoidei

Superfamily Argentinoidea^{1, 2}

Family Argentinidae

Family Bathylagidae

Subfamily Bathylaginae (including Microstomatidae)

Subfamily Opisthoproctinae (including Macropinnidae, Dolichopterygidae, Winteriidae)

Superfamily Alepocephaloidea³

¹ We agree with Hubbs (1953) that the argentinoids are a compact group, but find, nevertheless, two distinct lineages within the group.

² Nelson (1970) has recently provided a classification of the Salmoidei which included the Argentinidae but did not consider the alepocephaloids or bathylaconoids. This classification is based on certain aspects of gill arch morphology; when he proposed this classification, Nelson was unaware of the features of the gill arches and caudal skeleton that are used here to relate argentinoids and alepocephaloids.

³ Subfamily classifications have been proposed for alepocephaloids by Parr (1951, 1960) and others.

Family Alepocephalidae (including Bathylaconidae, Leptoichthyidae [Marshall, 1966], Anomolopteridae)

Family Bathyprionidae¹

Family Searsidae (including Mirorictidae, Platytrictidae)

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¹ Our recognition of the Bathyprionidae (Marshall, 1966) is tentative, as we have examined only one specimen in a partial dissection of its pharyngobranchial apparatus.

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