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Preliminary studies on the systematics of deep-sea alepocephaloidea (pisces: salmoniformes)

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The College of William and Mary in Virginia,
Ph.D., 1976
Biological Oceanography

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PRELIMINARY STUDIES ON THE SYSTEMATICS OF DEEP-SEA ALEPOCEPHALOIDEA (PISCES: SALMONIFORMES)

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Doctor of Philosophy

by
Douglas F. Markle
1976

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Douglas F Markle

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ABSTRACT

This study has three objectives: determination of probable phylogenetic relationships of alepocephaloids; evaluation of generic groups; and determination of characters for the identification of western North Atlantic alepocephalids in conjunction with recent interest in deep-sea ecology. The approach is comparative, mainly anatomical but partly ecological. Comments are presented on alepocephalid ecology.

Arguments are presented which indicate that the crumenal organ may not be a shared, derived feature but, rather, a primitive epibranchial structure retained in alepocephaloid and argentinoid fishes. Conclusions reached herein tend to support ideas of mosaic evolution and, consequently, somewhat older salmoniform classifications.

Three families are recognized (Searsidae, Leptochilichthyidae and Alepocephalidae). The latter contains the bathylaconids, a group previously considered a separate family or suborder. Twenty-four alepocephalid genera are tentatively recognized, one of which is unnamed. Several previously recognized genera are synonymized: *Binghamichthys* with *Talismania*, *Lepogenys* with *Bathytroctes*, and *Torictus* with *Einara*. Changes are made in the nomenclature of *Bathytroctes* and *Nomoctes*.

Five generic groups are recognized within the alepocephalids; the *Aulastomatomorpha*-group with six genera, the *Bathyprion*-group with three genera, the genus A-group with five genera, the *Bathylaco*-group with four genera and the *Alepocephalus*-group with six genera. The main line of alepocephaloid evolution is postulated to have occurred on or near the deep-sea bottom. A characteristic of their evolution has been repeated invasions of the pelagic habitat.

A minimum of 25 alepocephalid species are known from the western North Atlantic. At least five, and possibly more, are also to be expected in this area.

Alepocephalids are known or suspected over a depth range from 100 to 5850 m. Off Virginia, four frequently encountered species are members of a lower continental slope community which is characterized by large fishes. Alepocephalid life histories are generally presumed to be accomplished over large geographic areas and may frequently include reproductive migrations.

PRELIMINARY STUDIES ON THE SYSTEMATICS OF DEEP-SEA ALEPOCEPHALOIDEA (PISCES: SALMONIFORMES)

INTRODUCTION

The first known alepocephaloid fish, Alepocephalus rostratus, was described in 1820 from deep water in the Mediterranean near Nice by Risso (1820:271) who considered it a member of Cuvier's (1817) pike family and placed it between the genera Microstome (Microstoma, Argentinidae) and Stomias (Stomias, Stomiatidae), but nearer the latter. Additional species were not described for 58 years, but with the beginning of national oceanographic expeditions, new species and genera were frequently described. From 1878 to 1899 an additional 42 species and 13 genus group names were published. At the end of the nineteenth century, Garman summarized the geographic and bathymetric distribution and speculated on the habits and habitat of the family (Garman, 1899:283-284).

Since then, from four to 12 species names have been published each decade, except in the 1930's when 21 names were introduced. In addition 30 generic level names have been published this century and four substitute names, so that there are now 111 nominal species and 43 valid names for genera and subgenera.

From Beebe (1933) to Parr (1952b), 20 species-group names were added to the family. Inevitably, species-groups were extracted from catch-all categories on the basis of an often ill-defined uniqueness or an extrapolation of inferred allometry (Parr 1951). The single attempt at a phylogenetic presentation of the family was superficial and inadequate (Gregory and Conrad 1936). To date, most concern has been with the identification of species and not with explicit, reasoned suprageneric classification.

The present study represents a preliminary attempt at a reasoned suprageneric classification. Stress has been placed on the study of selected anatomical structures. Interpretation of phylogeny and grouping of genera has been based on comparative morphology and, to a lesser extent, comparative ecology. Only one searsid, Mentodus rostratus, was examined in detail and the information obtained tended to support recognition of the Searsidae, Parr 1951. Of five other nominal family-level groups (Alepocephalidae, Cuvier and Valenciennes 1846; Aulastomatomorphinae, Fowler 1934; Bathylaconidae, Parr 1948; Bathyprionidae, Marshall 1966; and Leptochilichthyidae, Marshall 1966), preliminary recognition is given only to Alepocephalidae and Leptochilichthyidae.

The suprageneric groups within the Alepocephalidae are not recognized with formal nomenclature, even though for many a senior synonym exists. Instead they are referred to by the genus which forms the stem of the oldest available family-group name, if one exists. Thus, for example, reference is made to the Aulastomatomorpha-group.

Finally, this study was concerned with the identification of North Atlantic species and with alepocephalid ecology. Previous keys (such as Parr 1951) relied heavily on scalation, jaw dentition, body and fin form, and formulae of allometric growth. Except for the latter, these characters are still incorporated into the keys developed herein, but are reinforced with additional characters which will hopefully facilitate identification of often-damaged specimens.

SELECTIVE DESCRIPTIVE ANATOMY

Material and methods:

Study materials are listed in the Appendix. Cleared and stained specimens are noted with an asterisk. Radiographs were taken of most material.

Cheek muscles were examined from specimens subsequently sacrificed to enzyme digestion for skeletal preparation. This procedure was used because of the rarity of most species and did not allow reassessment of all original observations. When material was available, additional cheek dissections were made to confirm original drawings and notes. Names of muscles follow Winterbottom (1974a).

Skeletal preparation technique follows Taylor (1967a and b) except that whole fish were seldom digested. During this study it was noticed that: (1) many alepocephalids are available only in large sizes, and (2) ossification is sometimes delayed until a moderately large size is obtained. When these relatively large fish were digested, fins and superficial head bones often disarticulated before head and axial tissue was even moderately clear. To counter this problem specimens were dissected prior to digestion into 5 or 6 pieces following, in general, Weitzman's dissection technique (Paxton 1972, Weitzman 1974). This technique results in pieces with approximately uniform amounts of soft tissue each of which can be differentially digested. This dissection technique is highly recommended when the circumstances warrant. Names of bones follow Weitzman (1974).

For each anatomical unit discussed below an attempt is made to identify the primitive and any derived conditions within the Alepocephaloidea. The main purpose of this review is to outline probable sister group relationships (Hennig 1966) and monophyletic groups in the sense of Nelson (1973). A major limitation of the study is a lack of opportunity to study all species and genera for all character states and a lack of intraspecific comparative material. Thus, the resulting conclusions on phylogeny and classification are preliminary and tenative.

Cheek muscles:

The function of the cheek muscles is to move the opercular apparatus during respiration and open and close the mouth (Ballintijn and Hughes 1965, Ballintijn 1969a and 1969b, and Gosline, 1969). Their particular functions are as follows. The levator arcus palatini abducts the hyomandibular resulting in the lateral expansion of the buccal cavity, jaws, hyoid and opercle. The antagonists of this muscle are the adductor arcus palatini series and the adductor arcus palatini which mainly adducts the palatal complex. The adductor hyomandibulae, a derivative of the later, also acts antagonistically to the levator arcus palatini and adducts the hyomandibular. Three muscles act on the opercle. The levator operculi raises the posterior portion and the dilatator operculi abducts the opercle. These act through the other opercular elements to either the epihyal-mandibular or epihyal-interopercular-mandibular ligaments to lower the mandible. The levator operculi as well as the third opercular muscle, the adductor operculi, are part of the adductor arcus palatini-adductor hyomandibulae series. The adductor operculi closes the opercle.

In alepocephaloids the adductor mandibulae (A2) is in a stage of incipient subdivision which becomes realized in two genera. The bulk of the muscle appears to have two separate, though probably coordinated, functions.

The most obvious insertion is through an attachment, usually ligamentous, to the dorsal or lateral (Leptochilichthys) surface of the maxillary. It adducts the maxillary in the process of closing the mouth, although in carp, at least, the functions are more complex (Ballintijn *et al*, 1972). The maxillary ligament seems to be controlled by the lateral-most fibers while a second ligament seems controlled by the medial-most fibers. In most genera no distinction can be made between the masses of fibers. In Talismania careful dissection will show separate masses of muscles partially or completely separated by myocoma. In Leptochilichthys the separation is obvious.

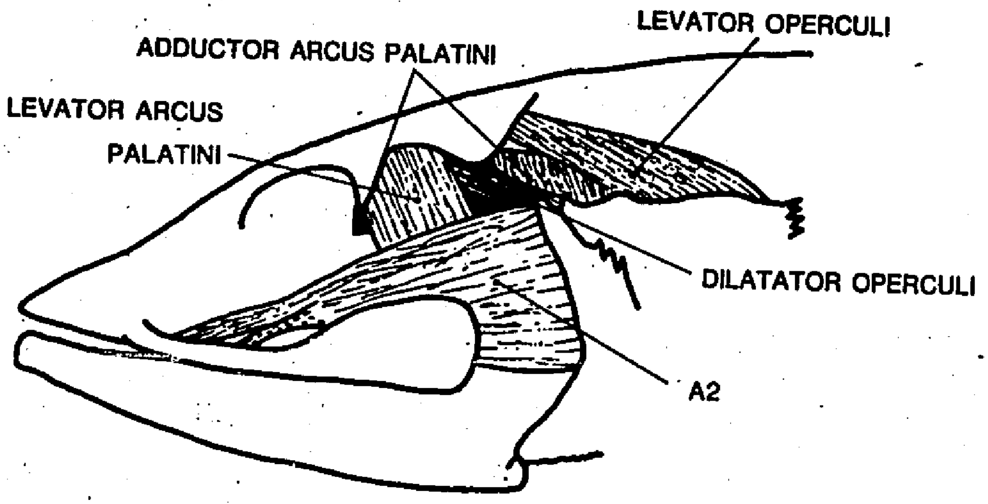
The medial mass of fibers inserts ligamentously on the coronomeckelian (sesamoid articular of Gosline 1969, Fig. 2). Through this ligament the adductor mandibulae (A2) adducts the mandible during the process of closing the mouth. A derivative of the adductor mandibulae found in all alepocephaloids is section AW which arises from the fibers lateral to the coronomeckelian ligament and inserts in the Meckelian fossa of the dentary. It is a thin, generally parallel muscle which also acts to raise or adduct the lower jaw.

In summary the single A2 muscle mass acts through a muscle (AW) broadly inserted on the lower jaw and a ligament with a point insertion on the coronomeckelian to control the lower jaw. It further acts through a ligament with a point insertion or through a broad musculous insertion (Bathylaco) to control the upper jaw. Physical separation of the muscle fibers controlling the two jaws has been determined in two genera.

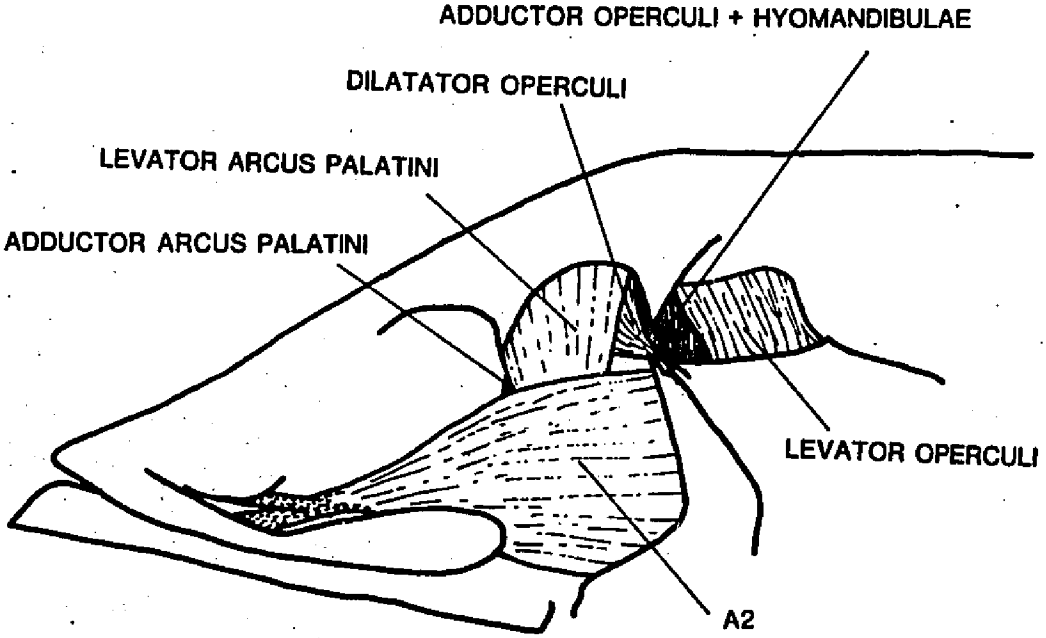
Fig. 1

A. *Narcetes stomias*, USNM 215515, 473 mm SL, cheek muscles.

B. *Bajacalifornia calcaratus*, UMML 15157, ca. 345 mm SL, cheek muscles.


LEVATOR OPERCULI
ADDUCTOR ARCUS PALATINI
LEVATOR ARCUS
PALATINI
DILATATOR OPERCULI
A2

A


ADDUCTOR OPERCULI + HYOMANDIBULAE
DILATATOR OPERCULI
LEVATOR ARCUS PALATINI
ADDUCTOR ARCUS PALATINI
LEVATOR OPERCULI
A2

B

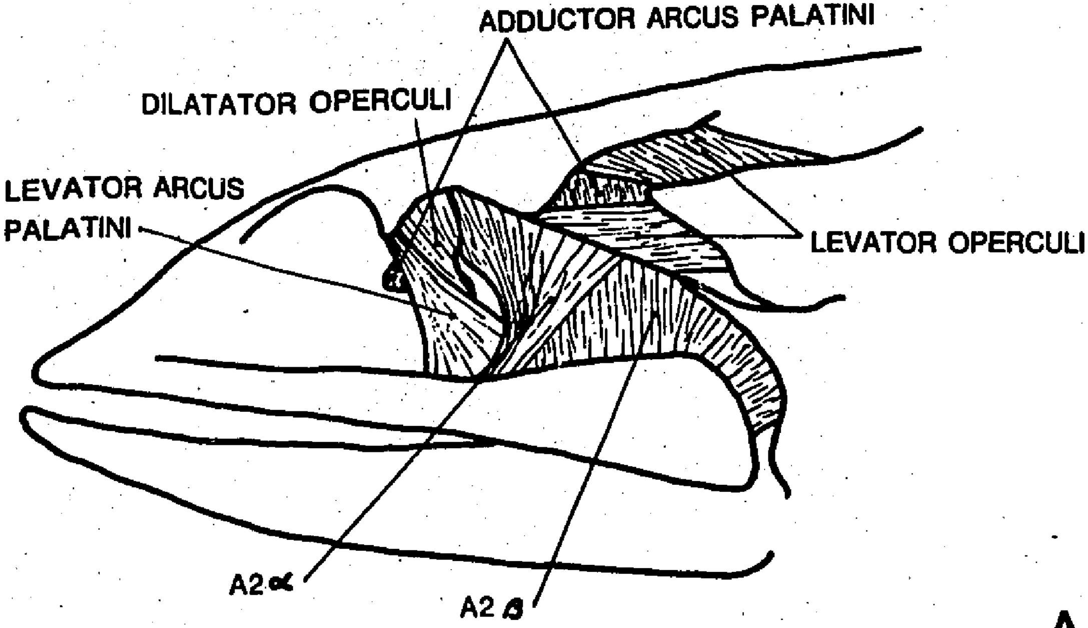
The cheek muscles of Narcetes (Fig. 1A) and Bajacalifornia (Fig. 1B) show a fairly primitive arrangement for alepocephaloids. In Narcetes, for example, the A2 section of the adductor mandibulae originates on the preopercle and hyomandibular and has both a tendinous insertion midway along the maxillary and a musculous insertion anteriad on the maxillary and also on the ventral surface of the lacrimal (not shown). The levator arcus palatini (LAP) in Narcetes originates on the sphenotic and pterotic and inserts on the metapterygoid and hyomandibular. The muscle fibers are essentially parallel rather than convergent upon a single point as is the case in pinnate muscles (Winterbottom 1974b). The dilatator operculi (DO) is a pinnate muscle whose apex points posteroventrally and which lies medial to the LAP which covers about half its base. The insertion of the DO is on the dilatator spine of the opercle near the hyomandibular-opercle joint. The levator operculi (LO) originates on the pterotic and inserts posteriorly on the dorsomedial surface of the opercle. The adductor arcus palatini (AAP) shows no evidence of a separate adductor operculi (AO) or adductor hyomandibulae (AH). In Bajacalifornia an adductor operculi plus hyomandibulae is separate from the AAP. Although the condition in Narcetes is probably primitive for alepocephaloids, it is derived over the salmonid condition (Ballintijn and Hughes 1965 and personal observations of an Oncorhynchus kisutch) in which the levator operculi is also a part of the adductor arcus palatini-adductor operculi-adductor hyomandibulae sheet and in which the adductor mandibulae inserts only on the dentary.

Bathylaco nigricans (Fig. 2A) probably has one of the more unusual arrangements of cheek muscles. The arrangement is due to the anterior movement of the orbit, associated with the evolution of rostral binoc-

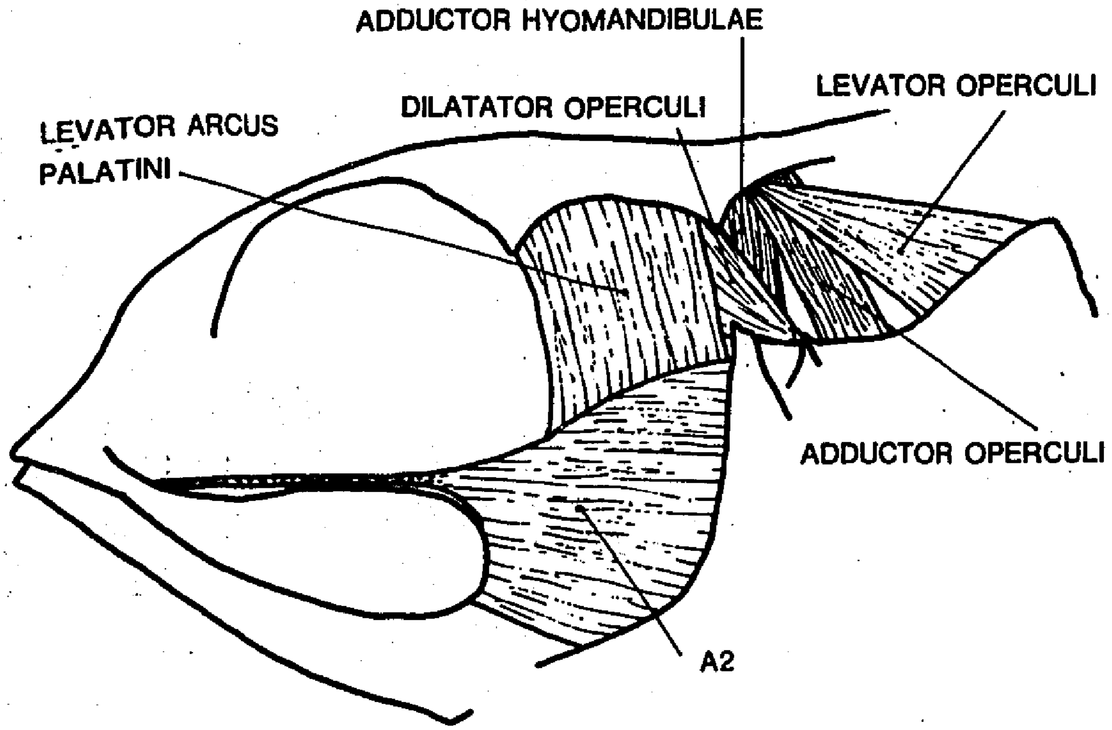
Fig. 2

A. Bathylaco nigricans, USNM 206693, 268 mm SL, cheek muscles.

B. Bathytroctes microlepis, USNM 215493, 276 mm SL, cheek muscles.


ADDUCTOR ARCUS PALATINI
DILATATOR OPERCULI
LEVATOR ARCUS PALATINI
LEVATOR OPERCULI
A2α
A2β

A


ADDUCTOR HYOMANDIBULAE
DILATATOR OPERCULI
LEVATOR OPERCULI
LEVATOR ARCUS PALATINI
ADDUCTOR OPERCULI
A2

B

ularity, and the increase in the size of the jaws. Both of these features are associated with the habits expected of a fast swimming bathypelagic predator (Nielsen and Larsen 1968). The adductor mandibulae (A2) is less pinnate than in other genera and has a musculous insertion on the maxillary. It originates on the preopercle, hyomandibular, and pterotic. The section labeled A2α has fibers oriented at a 35° angle to those in A2β with which they are continuous. Section A2α is an externally directed twist of superficial layers of A2β that origins on the hyomandibular and pterotic and inserts laterally adjacent to A2β on the maxillary. The LAP is more pinnate than other genera with the apex directed anterodorsally to the sphenotic and the base arising from the metapterygoid. The AAP is not inserted on the opercle and has an indistinct subdivision which might be an incipient AH. The DO no longer inserts on the opercle but rather on the medial face of the hyomandibular. The functional DO is the anterior subdivision of the levator operculi which is a parallel muscle arising from the pterotic and hyomandibular and inserting broadly on the anteroventral edge of the opercle thus eliminating the need for the dilatator spine which normally receives a point rather than a broad insertion. The posterior section of the LO is normally situated.

Bathylaco _nigricans_ apparently represents the most derived state with respect to cheek muscles in the genus. In a small specimen of Bathylaco "specimen" from Dana st. 1206 I the dilatator spine is present on the opercle and the dilatator operculi inserts on it.

In _Alepocephalus_ _agassizii_, _A_. _bairdi_, and _A_. _rostratus_ A2 inserts well forward on the maxillary with a weak sheet of connective tissue linking it to the ventral surface of the lacrimal. Skin and weak connective tissue also link the maxillary and angulo-articular.

This connective tissue is somewhat stronger in *A. rostratus* and is presumably the ligament found by Gosline (1969). The AAP is distinctly subdivided in *A. agassizii*, there being a separate LO, AO and AH. In *A. bairdi* the adductor operculi and adductor hyomandibulae are not very distinct, the two muscles being comprised of about six separate bundles with no obviously distinct groups. The broadly parallel LAP completely covers the base of the pinnate DO.

Bathytroctes microlepis (Fig. 2B) differs very little from *Alepocephalus*. The AAP is reduced and not visible in the illustrated view and there is a thicker adipose layer between the skin and muscles of *Bathytroctes*.

Xenodermichthys and *Rouleina* differ only slightly from Alepocephalus and *Bathytroctes*. The only obvious difference is that the base of the LAP only covers about half of the base of the DO in *Xenodermichthys* and *Rouleina*.

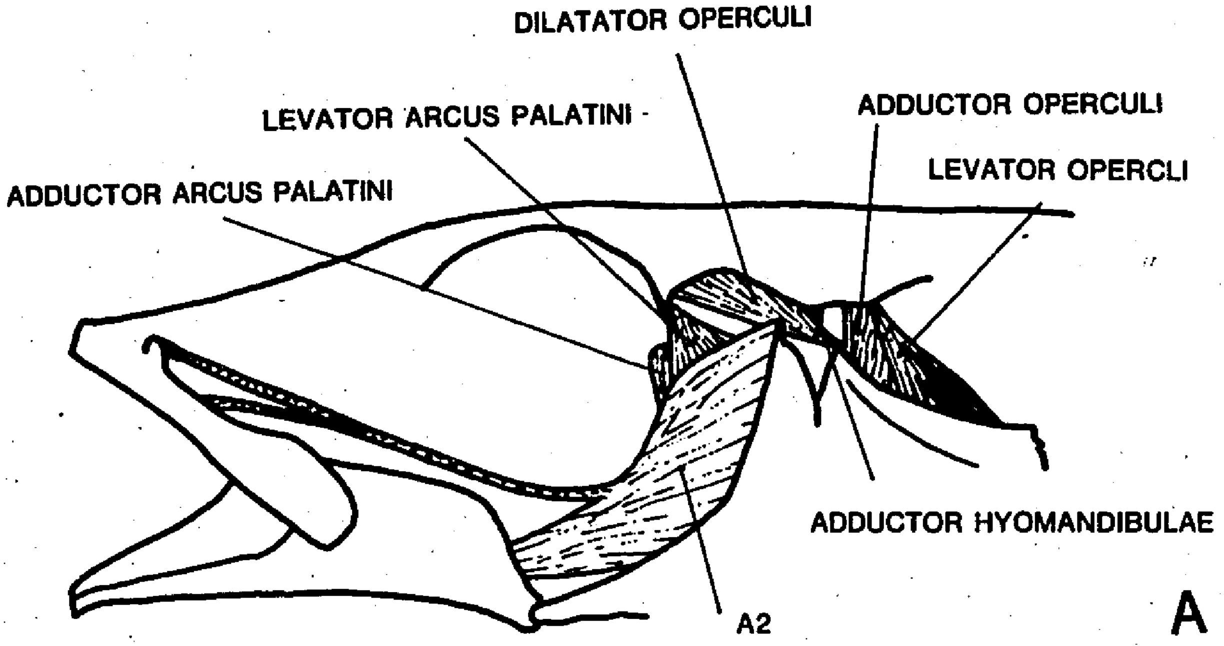
In *Ericara salmonea* and *Conocara mcdonaldi* (Fig. 3A) the base of the DO is exposed. The LAP is barrel-shaped in *Ericara*, pinnate in *Conocara*. In both the LO is subdivided distally into distinct bundles and separate AO and AH are present. I could find no AAP in *E. salmonea*. Section A2 inserts well forward on the maxillary in *Ericara* and two branches from the A2 ligament insert on the lacrimal and grade into the relatively well developed maxillo-angulo-articular connective tissue. In *Conocara* the subdivided A2 ligament attaches to the maxillary at two points (Fig. 3A).

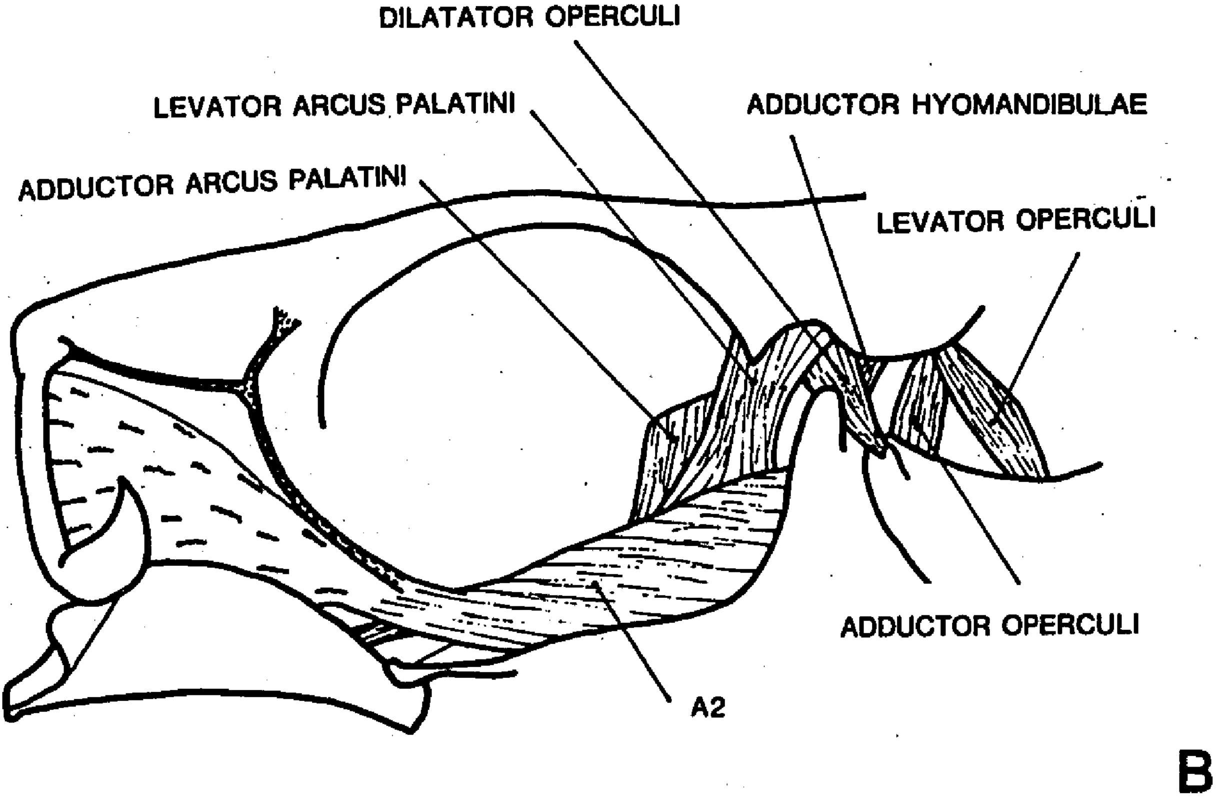
In *Leptoderma macrops* (Fig. 3B) section A2 grades into the broad sheet-like maxillo-articular connective tissue which is somewhat thickened

Fig. 3

A. *Conocara mcdonaldi*, USNM 215599, ca. 285 mm SL, cheek muscles.

B. *Leptoderma macrops*, USNM 215604, 188 mm SL, cheek muscles.


DILATATOR OPERCULI
LEVATOR ARCUS PALATINI
ADDUCTOR OPERCULI
LEVATOR OPERCLI
ADDUCTOR ARCUS PALATINI
ADDUCTOR HYOMANDIBULAE
A2
A


DILATATOR OPERCULI
LEVATOR ARCUS PALATINI
ADDUCTOR HYOMANDIBULAE
ADDUCTOR ARCUS PALATINI
LEVATOR OPERCULI
ADDUCTOR OPERCULI
A2
B

dorsally into a thin ligament which subdivides and inserts on the articular knob of the maxillary and the lateral ethmoid. The LAP encroaches over the base of the DO and the LO is not subdivided into bundles. Otherwise the muscles are as in Conocara.

Einara edentulus (Fig. 4A) and Bathyprion danae (Fig. 4B) are fairly similar and generalized in their muscle arrangement. The LAP only covers a small portion of the DO base. The AAP is present in both, but is part of the orbital floor only in Einara.

In the specimen of Photostylus pycnopterus there was a LAP similar to that of Leptoderma (Fig. 3B), an A2 section of the adductor mandibulae which inserted well forward on the maxillary, a pinnate DO uncovered by the LAP, and a pinnate LO whose apex was directed anterodorsally. I could find no indication or remnants of an AAP, AH or AO. The relatively small size and difficulty of determining the presence of these muscles leaves the question of their presence unanswered.

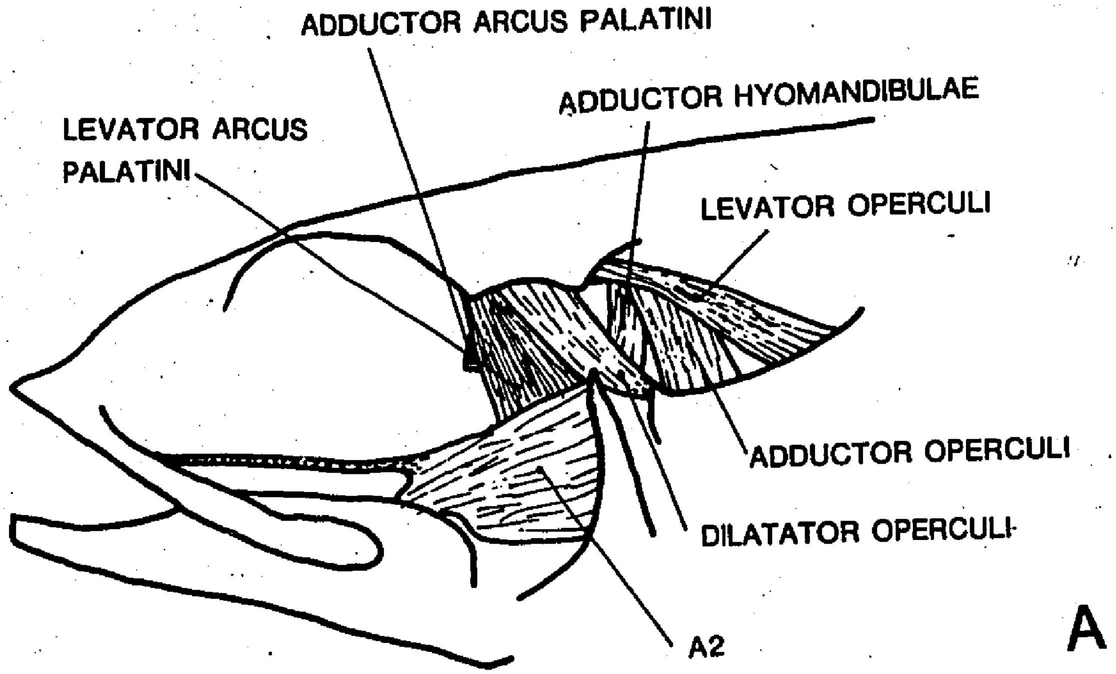
Two of the genera examined, Leptochilichthys and Talismania, have subdivided adductors mandibulae. In Leptochilichthys (Fig. 5A) both sections A1 and A2 arise almost exclusively from the hyomandibular which is somewhat modified to take over this function normally shared with the preopercle. Section A1 inserts ligamentously on the lateral surface about midway along the maxillary. Section A2 is indistinctly subdivided into $A2\alpha$ and $A2\beta$. An AAP is present although not apparent in the illustrated view. The AH is separate from the AAP but not from the AO which is subdivided into bundles distally. The LAP covers about half of the base of the DO.

The muscle arrangement in Talismania antillarum (Fig. 5B), T. aphos, and T. oregoni is very generalized for alepocephaloids except for the

Fig. 4

A. *Einara edentulus*, NIO uncatalogued, 116 mm SL, cheek muscles.

B. *Bathyprion danae*, ISH 1539/71, 252 mm SL, cheek muscles.


ADDUCTOR ARCUS PALATINI
ADDUCTOR HYOMANDIBULAE
LEVATOR ARCUS PALATINI
LEVATOR OPERCULI
ADDUCTOR OPERCULI
DILATATOR OPERCULI
A2
A

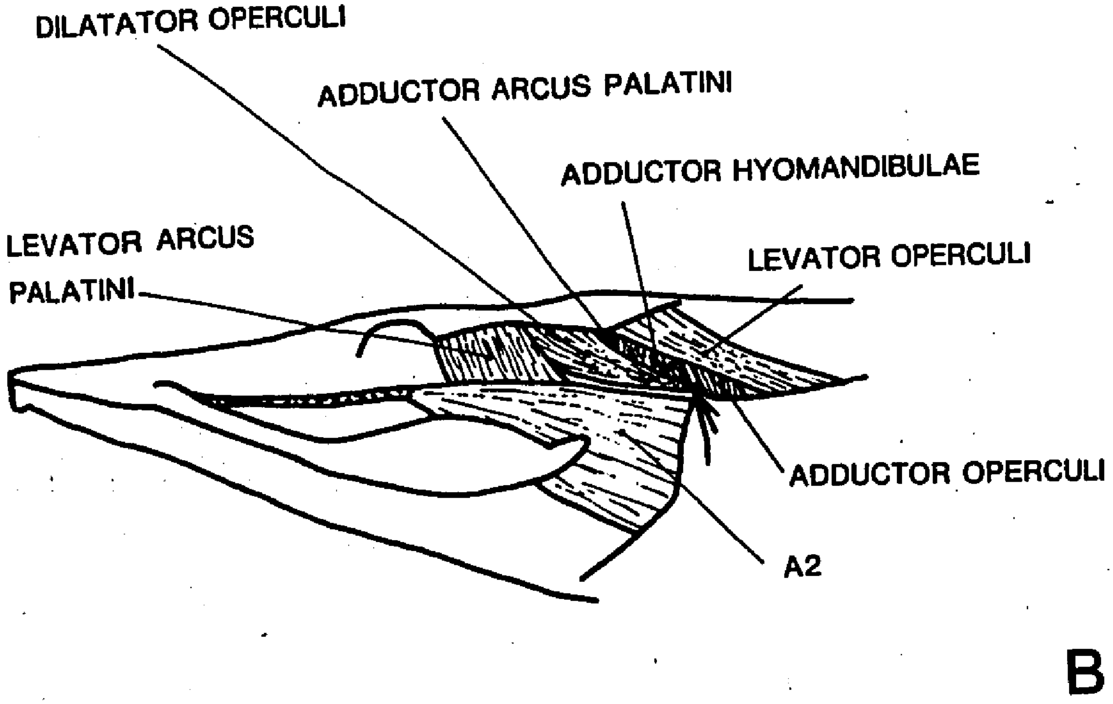
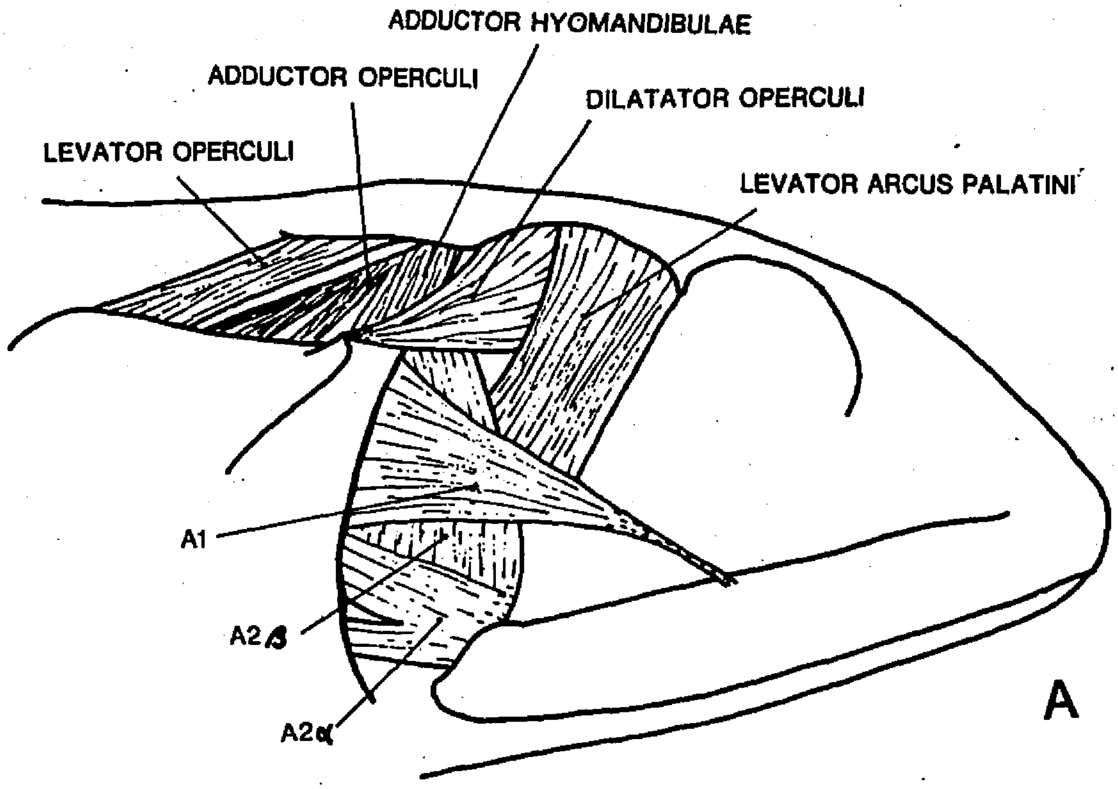
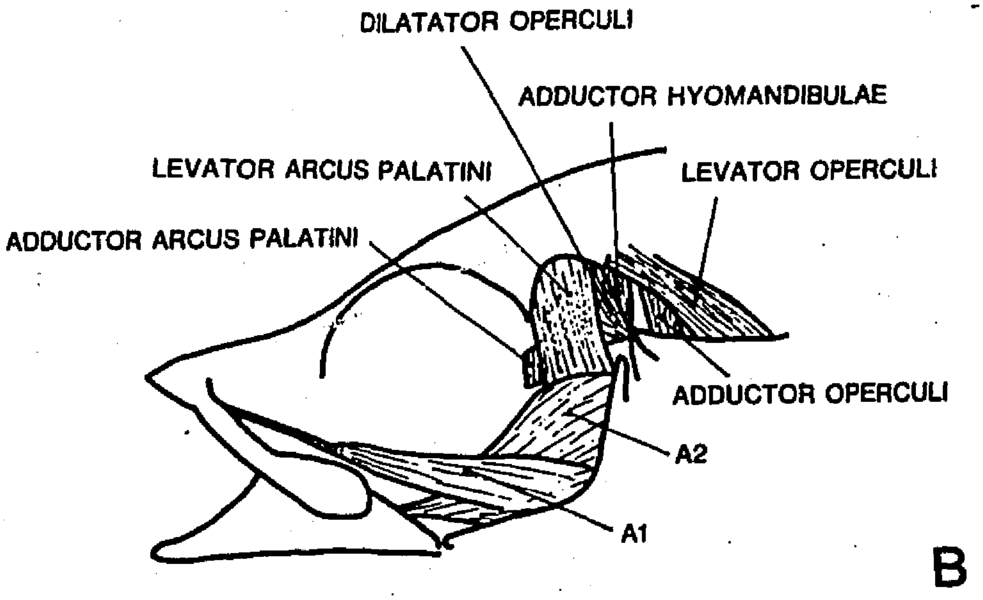

DILATATOR OPERCULI
ADDUCTOR ARCUS PALATINI
ADDUCTOR HYOMANDIBULAE
LEVATOR ARCUS PALATINI
LEVATOR OPERCULI
ADDUCTOR OPERCULI
A2
B

Fig. 5

A. Leptochilichthys agassizii, ISH 916/73, 255 mm SL, cheek muscles.

B. Talismania antillarum, USNM 215560, 140 mm SL, cheek muscles.


ADDUCTOR HYOMANDIBULAE
ADDUCTOR OPERCULI
DILATATOR OPERCULI
LEVATOR OPERCULI
LEVATOR ARCUS PALATINI
A1
A2β
A2α
A


DILATATOR OPERCULI
ADDUCTOR HYOMANDIBULAE
LEVATOR ARCUS PALATINI
LEVATOR OPERCULI
ADDUCTOR ARCUS PALATINI
ADDUCTOR OPERCULI
A2
A1
B

adductor mandibulae. In this genus the muscle fibers controlling the maxillary ligament are relatively distinct from those which insert on the coronomeckelian. Section A1 in _T_. _oregoni_ differs from that illustrated in _T_. _antillarum_ (Fig. 5B) since it completely covers A2 dorsally to the top of the preopercle. The LAP covers the base of the DO in both.

Gonads _and_ _Viscera_:

Testes:

It was noticed early in this study and has been observed in _Bathylaco_ (Nielsen and Larsen 1968), that the testes of alepocephalids are sometimes lobed. Males of all species and genera have not been seen and the intraspecific variation in gross testicular structure is incompletely known. However, some inductive generalizations about testicular structure have emerged from the present study.

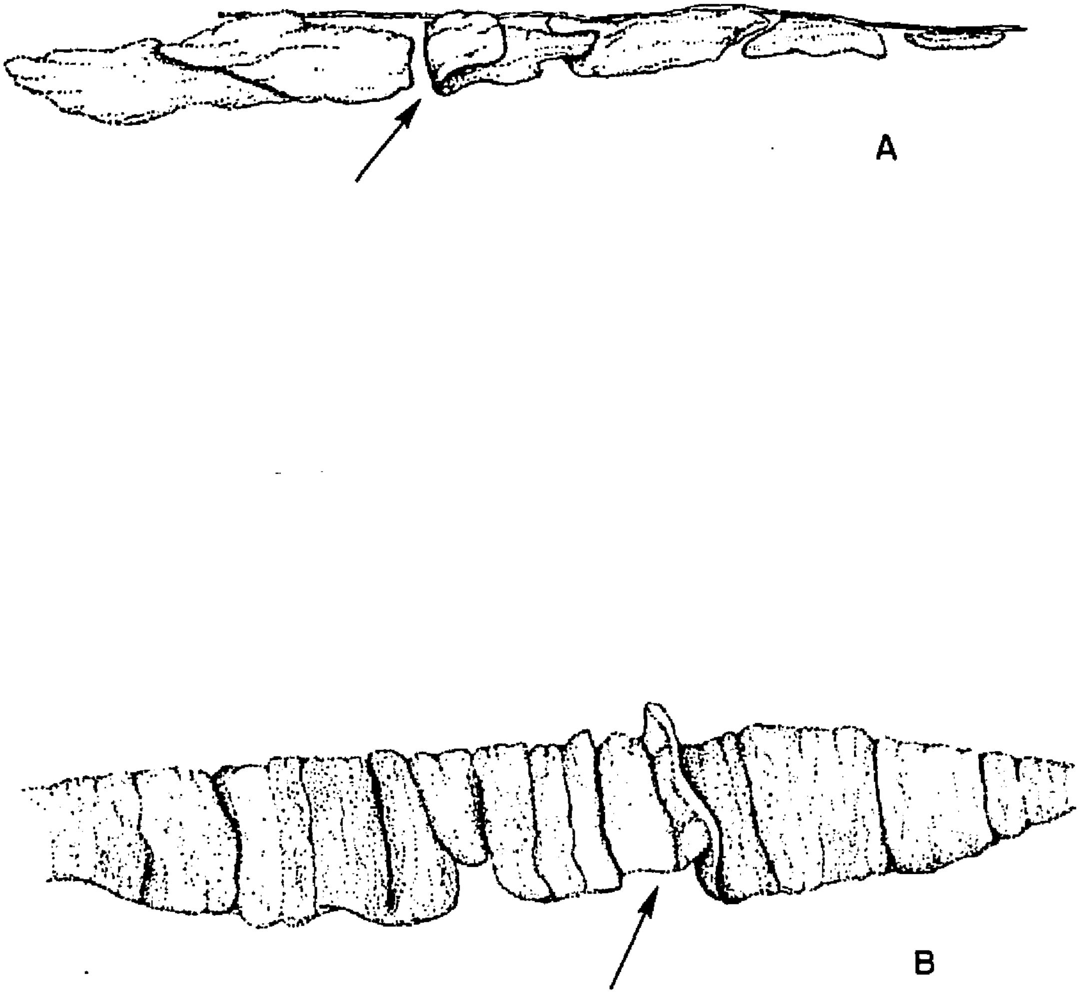
Testicular structure varies intragenerically and is sometimes valuable in distinguishing closely related species. In _Rouleina_, for example, _R_. _maderensis_ testes are distinct, separate lobes joined only along the dorsal seminiferous canal (Fig. 6A). Testes in the closely related _R_. _mollis_ are convoluted, often to the point of superficially resembling lobes, but there are never distinct, separate lobes. All sections of these testes are joined as shown in Figure 6B.

Testicular structure can be categorized as follows. Simple testes are bilaterally-paired organs without convolutions. The convoluted testes are as described for _R_. _mollis_ (Fig. 6B). The lobate testes are the most variable. In any individual the lobes are usually bilaterally symmetrical in number and shape. Lobe shape is variable and often species-specific. There are as few as two pairs of lobes in _Alepocephalus_ _bicolor_ and as many as 35 pairs in some _Bathylaco_ _nigricans_ (Nielsen and Larsen 1968).

Fig. 6

A. *Rouleina maderensis*, USNM 215476, ca. 275 mm SL, testes.

B. *Rouleina mollis*, USNM 215483, 369 mm SL, testes.


A
B

The lobes may be overlapping, adjacent and partly overlapping, or adjacent and non-overlapping. Further, individual lobes may be convoluted and in some individuals the lobes and convolutions make it impossible to categorize the structure.

No character phylogeny can be proposed for testicular structure. If the simple testes are presumed primitive, then there is no way of distinguishing them from the derived condition of adjacent non-overlapping lobes which have been reduced secondarily to one pair.

Ovaries:

Ovarian structure, in contrast to that of the testes, appears to offer two intelligible phyletic trends. The alepocephalid ovary is a bilaterally symmetrical organ, each half of which is primitively covered on its medial surface and ventral edge by the ovarian tunic (Fig. 7A). Posteriad, the tunic is continuous with the peritoneum dorsally, thus forming a common oviduct which receives the products of both ovaries and empties through a genital pore (dissections of several *Alepocephalus agassizii* showed that the archinephric duct emptied through a separate pore on the urinary papilla behind the genital pore). Ovarian structures more complex than this have basically tended toward enclosing the ovary. There are two different types of enclosed alepocephalid ovaries.

In some members of the *Aulastomatomorpha* group, as well as in *Talismania*, the tunic has fused with the peritoneum along the ventral edge of the ovary. Extant species show different degrees of fusion. In *Conocara macroptera* (Fig. 7B) and *Ericara salmonea* only the anterior portion has fused. In *C. mcdonaldi* (Fig. 7C) the anterior and most of the posterior edge have fused but there is a small unfused gap between the

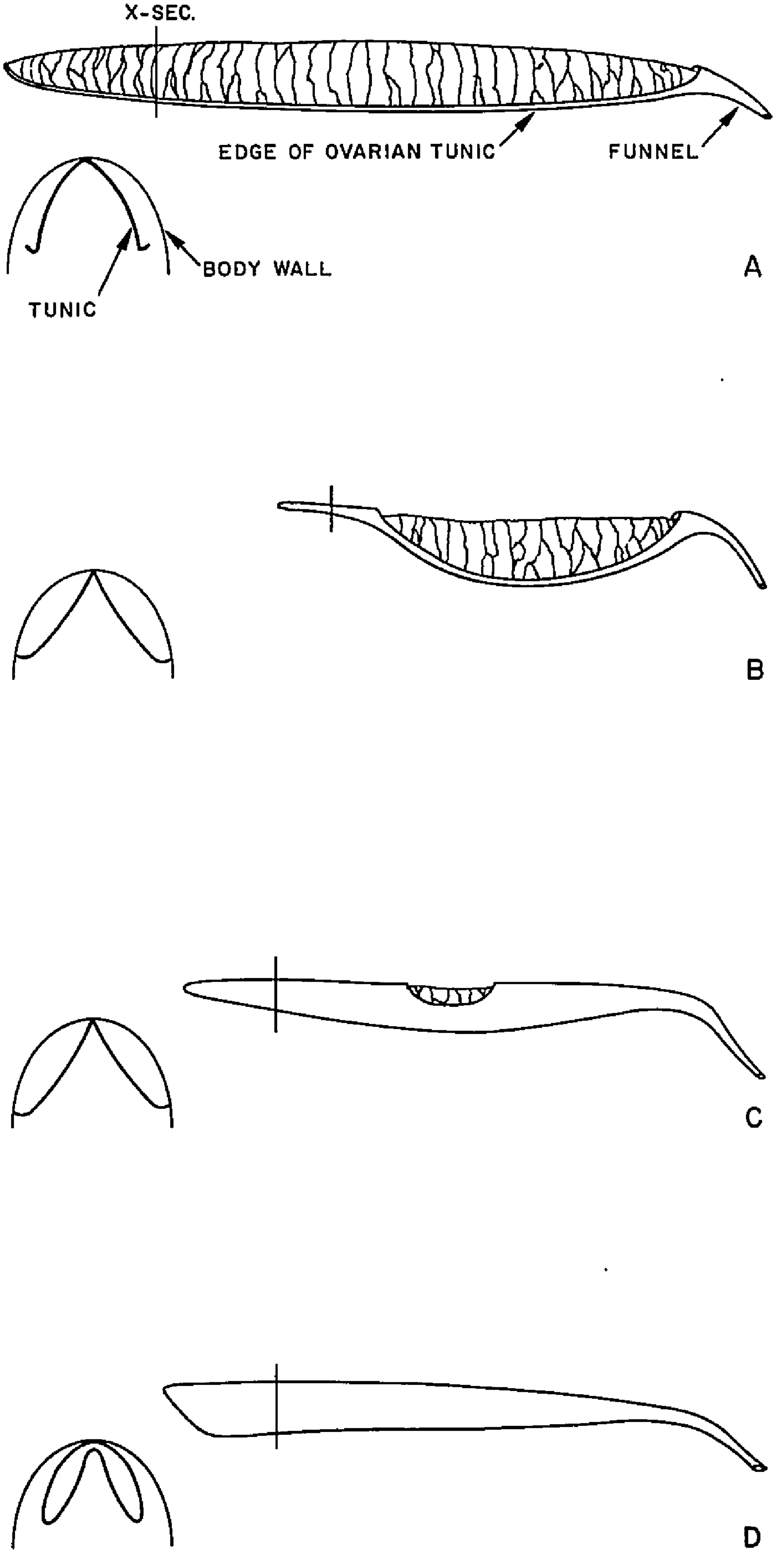
Fig. 7

A. *Bathytroctes microlepis*, UMML uncatalogued, 233 mm SL, ovary.

B. *Conocara macroptera*, NIO uncatalogued, 316 mm SL, ovary.

C. *Conocara mcdonaldi*, UMML 26713, 293 mm SL, ovary.

D. *Nomoctes michaelsarsi*, UMML 21628, 291 mm SL, ovary.


X-SEC.
EDGE OF OVARIAN TUNIC
FUNNEL
BODY WALL
TUNIC
A
B
C
D

two areas. In Leptoderma macrops, Talismania oregoni, T. aphos, and T. antillarum the tunic has fused with the peritoneum along the whole length of the ovary and there are no unfused gaps. In these enclosed ovaries the ovary is flush against the peritoneal wall, although in mature fish there is a noticeable medial bulge and the eggs are visible through the tunic.

In the species of Bathyprion, Mirognathus, and Nomoctes (Fig. 7D) and in Bathytroctes oligolepis the ovary has also been enclosed by the tunic. These ovaries differ from the primitive condition in the extent to which the tunic covers the lateral surface of the ovary. Compared to the other type of enclosed ovary these forms differ in that the ovaries hang from the mid-dorsal coelomic wall and are exposed to coelomic space on the lateral as well as the medial surface (Fig. 7).

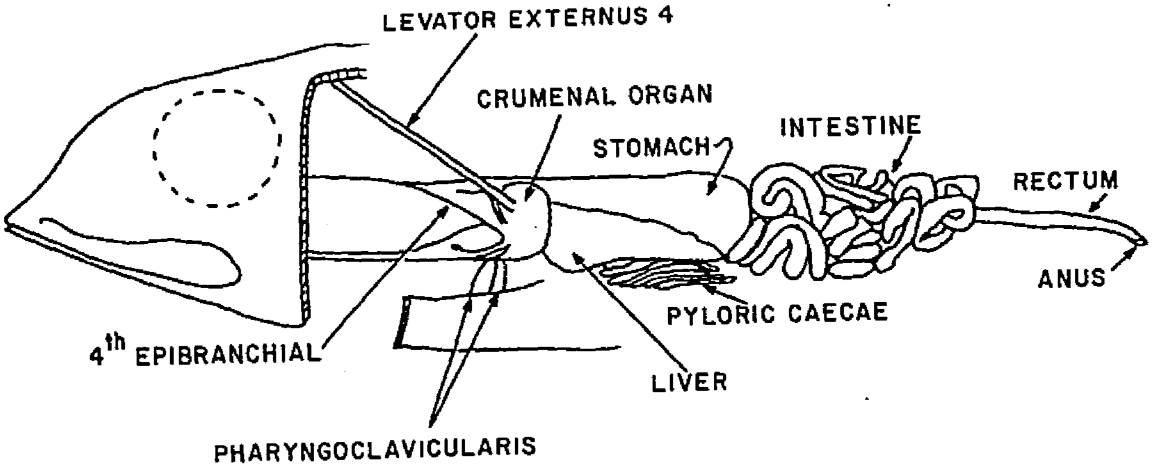
The phylogeny of alepocephalid ovarian structure can be interpreted as a trichotomy or a line with two bifurcations. If the latter, the first bifurcation should be one or the other of the enclosed ovaries since both structures are more easily derived from the simple ovary than from each other.

Alimentary system and viscera:

Based on many dissections of Alepocephalus agassizii, I offer the following gross description of its alimentary system which precedes summary notes of intrafamilial variation in some of the structures. The alimentary system in A. agassizii has a well developed crumenal organ (Fig. 8). The bulbous dorsal half of the organ is formed from the fifth epibranchial, accessory cartilage of the fifth ceratobranchial, and muscle and connective tissue which are continuous with the esophagus medially. In addition to two layers of perpendicular intrinsic muscles, the crumenal

Fig. 8

Alepocephalus agassizii, semi-diagramatic, composite drawing of alimentary system of typical 350 mm SL, specimen.


LEVATOR EXTERNUS 4
CRUMENAL ORGAN
STOMACH
INTESTINE
RECTUM
ANUS
PYLORIC CAECAE
4th EPIBRANCHIAL
LIVER
PHARYNGOCLAVICULARIS

organ is subject to two sets of extrinsic muscles. The fourth levator externus inserts on the expansion of the fourth as well as the fifth epibranchial, and both internal and external pharyngoclavicularis muscles, insert on the fifth ceratobranchial (Fig. 8). These muscles, acting on toothed pharyngeal bones (the fourth epibranchial and fifth ceratobranchial), may assist in manipulating food items (Nelson, 1967). They also act on the major hard portions of the crumenal organ (the fifth epibranchial and fifth ceratobranchial) and, therefore, may assist in expanding and contracting the cavity within the organ.

In A. agassizii there is a siphonal stomach (sensu Bertin 1958), numerous (15 to 23) pyloric caecae, a thin-walled coiled intestine and thick walled rectum (Fig. 8). At 300 mm SL the length of the intestine and rectum is around 115% SL. Within the posterior section of the rectum are 6 to 10 circular shelf-like structures which project into the lumen. These are the Ringfalten or so-called "spiral valves" which were found in Alepocephalus rostratus by Cuvier and Valenciennes (1846) and are also found in salmonids, clupeids, argentinins, and chirocentrids (see Cohen 1958). Longitudinal sections of the rectum of a 315 mm SL A. agassizii and a 490 mm SL Narcetes stomias showed that the former also had additional projections into the intestine that were perpendicular to and located between the Ringfalten. These may be analogous to the labyrinthine ridges described by Cohen (1958) in Argentina sphyraena. Although the Ringfalten areas are not located in the same parts of the intestine in Alepocephalus and Argentina, there is no reason to suspect different functions. It seems clear that Ringfalten and labyrinthine ridges slow the passage of food and increase the potential absorptive surface of the intestine (Cohen 1958).

In most alepocephalids the stomach is siphonal as in *A. agassizii*. In *Xenodermichthys* and *Asquamiceps* it is slightly caecal. In *Bathylaco*, *Bathytroctes*, *Bajacalifornia* and *Narcetes* it is caecal. Caecal stomachs (*sensu* Bertin 1958) appear to be more common in large-mouthed species and may be an adaptation for holding large, long prey such as fish. There is no obvious relationship between number of pyloric caecae and stomach type. The number of pyloric caecae is as low as 2 in *Mirognathus*, *Ericara* and *Leptoderma* and as high as 26 in *Bajacalifornia drakei*. There is also no relationship between intestine morphology and stomach type. Intestines vary from highly convoluted (Fig. 8) to straight tubes. In general, the visceral anatomy seems plastic and subject to autecological variations. Some genera which are obviously close relatives and otherwise difficult to distinguish, such as *Bathylaco* and *Herwigia*, have strikingly different visceral morphology (Nielsen 1972).

Liver morphology was not intensely surveyed but it appears to have potential taxonomic value. In *Einara macrolepis* and *E. edentulus* the liver is bilobed and the major branches of the hepatic vein are exposed and visible on the ventral surface of the liver. No other genus was seen which had exposed hepatic veins. All alepocephaloids lack a swimbladder.

Photophores:

Photophores are present on stalks on the body, and yellowish flaps of tissue are present in the gular region of the branchiostegal membrane in *Photostylus*. Irregularly parallel rows of photophores are prsent in genus A. Photophores arranged in quincunx are found in *Xenodermichthys* and some species of *Rouleina*.

Lendenfeld (1887), Matsubara and Iwai (1969), and Best and Bone (1976) have examined *Xenodermichthys* photophores. The latter list among the differences with other teleostean photophores, the following: absence of a guanine reflector, structure of photocytes and nervous relationship, and size and distribution on the body. Best and Bone (1976) further examined Photostylus photophores and found them "closely similar" to Xenodermichthys.

Photophores in genus A sp. nov. (Fig. 40C) are topographically more primitive than those in Xenodermichthys or Photostylus (Best and Bone 1976 and personal observations). In genus A sp. nov. the photophores lie under the epidermis and under scales (Fig. 40C). Except for lateral line scales in Rouleina, no other alepocephalid has both scales and photophores. In Rouleina maderensis vestigial photophores are present and appear to be covered by a thin epidermal layer (Fig. 40D). Photophores are absent in R. mollis. In Xenodermichthys and Photostylus the epithelial layer does not cover the photophore which is thus exposed (Best and Bone 1976).

Photophores in genus A sp. nov. (Fig. 40E and F) are more complex then those in Xenodermichthys and Photostylus (Best and Bone 1976). In genus A sp. nov. the core cells show an approximate radial arrangement proximally, and there is a space demarcating a distal group of cells. These cells are adjacent to dense basophilic structures which appear to line the distal surface of the photophore (Fig. 40E and F). In Xenodermichthys and Photostylus the core cells are relatively larger and less numerous and the proximal cells are modified as saucer-shaped reflectors (Best and Bone 1976).

The topography of the photophore in genus A suggests that it represents the primitive character state. The photophore position in the other genera suggests that body photophores have migrated distally to become circumscribed by epithelial tissue in R. maderensis and to lie surrounded though projecting through epithelial tissue in Xenodermichthys and Photostylus, The photophore stalks of Photostylus can be conceptualized as additional distal migration on epithelial tubes.

The structure of alepocephalid photophores suggests a reduction in cellular components from genus A to the others, including complete loss in Rouleina. Corellated with reduction in number of cellular components is an increase in specialized structures such as the cellular reflectors of Xenodermichthys and Photostylus.

Alepocephalid luminescence has only been observed in genus A by J. R. Paxton (personal communication) as areas of faint red under ultraviolet light. However, these areas did not correspond to the photophores.

As mentioned above, most alepocephalids with photophores are naked. In Xenodermichthys and Rouleina the integument is compartmentalized and the inner and outer layers are separated by a bouyant fluid within the compartments (Best and Bone 1976 and personal observations).

Best and Bone (1976) also consider the Photostylus integument to resemble that of Xenodermichthys. In the present study several well preserved Photostylus have been examined. No compartmentalized integument was seen. However, the integument readily separates into inner and outer sheets, the latter bearing the stalked photophores. It would be reasonable to assume that the Photostylus condition is derived, that compartments were lost, and that the nodulous Xenodermichthys-like photophore was raised on a stalk composed of tissue from the outer integument layer.

EYES:

Alepocephaloid eyes vary from rather small in Bathyprion danae to relatively large in Alepocephalus agassizii. There is, variously developed, an aphakic aperature formed by an increase in the size of the pupil relative to the lens. The aperture in *B. danae* is circumlental (Munk and Frederiksen 1974), that is, the width of the pupil being about twice that of the lens (Marshall 1966) results in a wide, circular gap between the edge of the lens and the edge of the pupil. In the majority of alepocephaloids the aphakic aperture is crescent-shaped and anteriad of the lens. The resultant oval shape of the pupil contributes an elliptical appearance to many alepocephaloid eyes.

Although the size of the eye relative to head and body size is important in distinguishing some species, eye size and aphakic aperture type are of little value in determining higher relationships. *Mirognathus*, the presumed closest relative of *Bathprion*, has a crescent-shaped aperture and *Ericara salmonea* has a poorly developed aperture unlike other members of the genus.

The so-called preorbital light organ of Bathylaco (Parr 1948) has been shown to be the rostral part of a palpebral (eyelid) fold composed of modified connective tissue (Munk 1968). However, a number of searsids do appear to have orbital photophores (Parr 1960). Some *Talismania* and *Alepocephalus owstoni* have whitish structures on or near the orbit. In *T. oregoni* the structure is simply thickened scleral tissue while in *T. bifurcata* it is on the edge of the orbital socket and may be luminous.

The only orbital structures which might offer phylogenetic information are the muscles of the eye. Winterbottom (1974a) mentions that teleost eye muscles are relatively constant; there are usually six. Munk (1968) has found only five in *Bathylaco nigricans*. Unfortunately, a study of eye muscles was not included in the present work.

Although no orbital structures are yet known to provide phylogenetic information within alepocephaloids, the eyes are important in any discussion of alepocephaloid evolution. The eye has apparently adapted to low light levels by an increase in the sensitivity of the retina. This has been achieved through aphakic apertures which allow light to fall directly on the retina (Munk 1966, Marshall 1971) thus increasing "the sensitivity of the eye by increasing the relative retinal illumination either in the caudally located area or fovea (in those with crescent-shaped apertures or all over the retina (in those with circumlental apertures)" (Munk and Frederiksen 1974). In addition, shallow sighting grooves in front of the eye and a tendency for eyes to be located far forward on the snout (Bathylaco) or near the dorsal outline of a shortened, narrow snout (Xenodermichthys) are specialized features for rostral binocularity. Binocular vision increases light sensitivity by about 10% (Weale 1955). The advantage of two monocular views of the surroundings is apparently lost in alepocephaloids. At the light intensity of their habitat it is apparently "better to be able to see a relatively small field than not to see a large one" (Weale 1955).

Superficial head bones and hyoid arch:

Parr (1951) used the number of supramaxillaries to distinguish two large groups of genera in his key to the Alepocephalidae. The number, however, is apparently variable in Rouleina (Parr 1951) as well as Mirognathus and Bathyprion since I find one or two supramaxillaries in the latter two genera instead of the two reported by Parr (1951) and Marshall (1966). The genera with only one (posterior) supramaxillary, the derived character state, are Bathylaco, Bathyprion sometimes, Mirognathus sometimes, Rouleina sometimes, Xenodermichthys, Ericara, Conocara, Leptoderma, Aulastomatomorpha, Einara, Leptochilichthys, Asquamiceps and

Photostylus. These probably do not form a monophyletic group; the anterior supramaxillary has been lost more than once in the evolution of the group.

The series of six infraorbital bones is complete in all genera except Leptoderma which has only four. The dorsal and ventral postorbitals are missing in Leptoderma, leaving a gap in the posteroventral part of the series.

In the specimens in which the following bones could be seen, there is typically a supraorbital, antorbital and nasal. The supraorbital is reduced in Ericara and absent in Bathyprion, Bajacalifornia, Alepocephalus, Narcetes, Rouleina, Xenodermichthys, Conocara, and Leptoderma. The antorbital is missing in Rouleina, Conocara, and Leptoderma.

The subopercle is broadly L-shaped to subrectangular and usually gives ventromedial support to the opercle and occasionally the preopercle (Bathyprion and Bathylaco). It is reduced to a small flat spine or subtriangular dagger-like blade in Rouleina, Xenodermichthys, Ericara, Conocara and Leptoderma.

The hyomandibula usually has a broad dorsal articular surface distinctly separate from the posteriorly directed opercular process. In Ericara (Fig. 9A), Conocara and Leptoderma the opercular process is less distinct and only barely separate from the dorsal articular surface. The opercular process is in the upper half of the hyomandibula in all genera except Bathyprion (Fig. 9B) in which it is found in the lower third. The process is near the half-way point in Mirognathus.

Near the hyomandibula-opercle joint the opercle may have a dorsal outgrowth (Bathylaco nigricans Fig. 9C), a notch similar to the osmerid-stomiatoid notch of Weitzman (1967, 1974) (Talismania antillarum, Fig. 9D), or a smooth dorsal surface. On the lateral surface near the joint

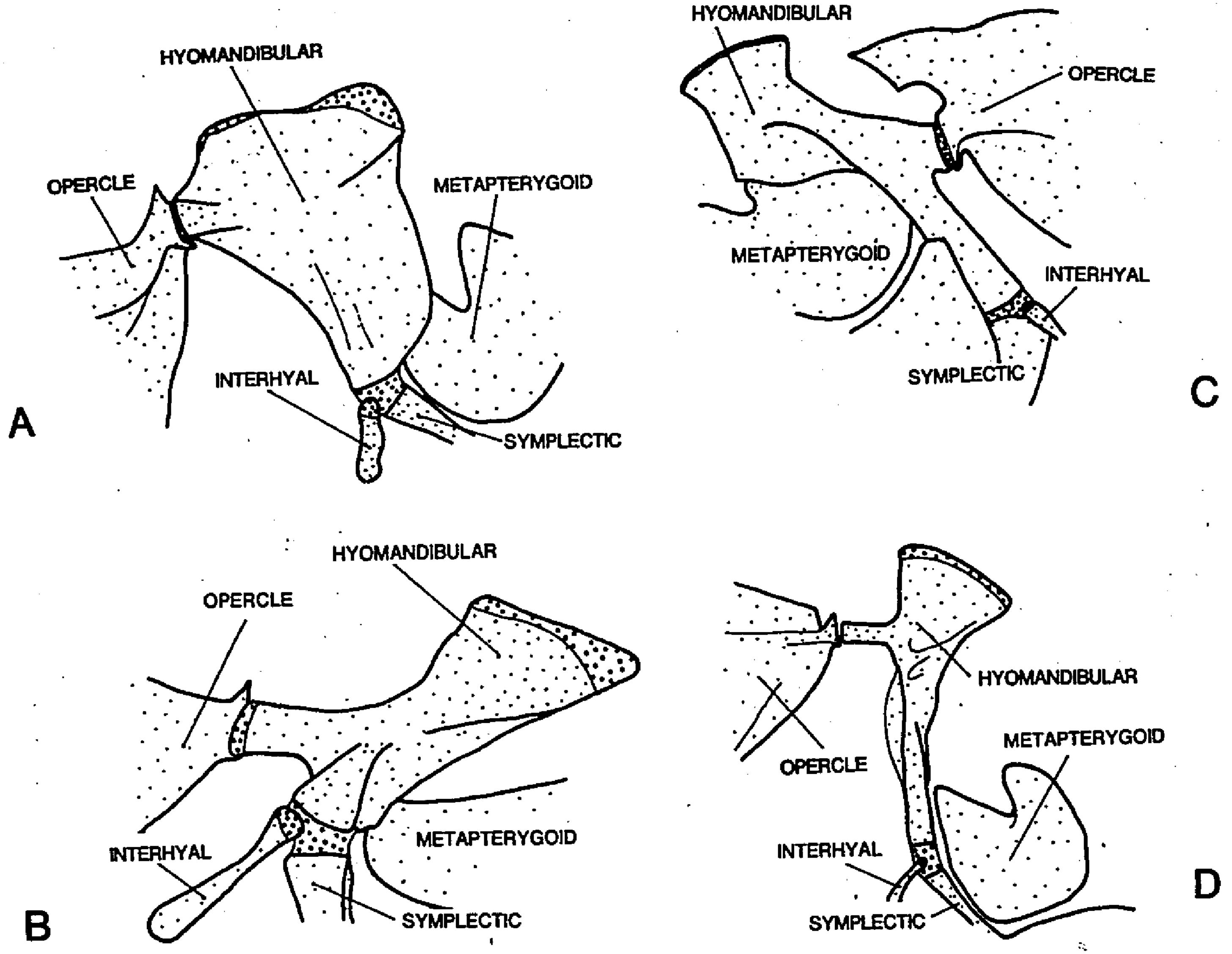
Fig. 9

A. *Ericara salmonea*, UMML 32354, ca. 305 mm SL, hyoid bones, medial view, left side.

B. *Bathyprion danae*, ISH 1539/71, 252 mm SL, hyoid bones, medial view, left side.

C. *Bathylaco nigricans*, USNM 206693, 268 mm SL, hyoid bones, medial view, right side.

D. *Talismania antillarum*, USNM 215560, 140 mm SL, hyoid bones, medial view, left side.


A
HYOMANDIBULAR
OPERCLE
METAPTERYGOID
INTERHYAL
SYMPLECTIC
C
HYOMANDIBULAR
OPERCLE
METAPTERYGOID
INTERHYAL
SYMPLECTIC
B
HYOMANDIBULAR
OPERCLE
INTERHYAL
METAPTERYGOID
SYMPLECTIC
D
HYOMANDIBULAR
OPERCLE
METAPTERYGOID
INTERHYAL
SYMPLECTIC

all alepocephaloid opercles (except *Bathylaco*, see above) have a spine which receives the insertion of the dilatator operculi. The dilatator spine can be seen in the medial views of *Bathyprion* (Fig. 9A) and *Ericara* (Fig. 9B).

McAllister (1968) gave 5 to 13 as the range of variation in branchiostegals. Marshall (1966) noted that most of the variation is due to the ceratohyal complement of rays and that all members of the group have only 3 or 4 rays on the epihyal. The species with four epihyal rays are *Talismania antillarum*, *T. aphos*, *T. oregoni*, *Bajacalifornia calcaratus*, *Mirognathus normani*, *Bathytroctes microlepis* and *Leptochilichthys agassizii*. In all cases the anteriad (fourth) epihyal ray articulates at the cartilagenous epihyal-ceratohyal junction. Most genera have three ceratohyal rays. *Ericara*, *Conocara*, and *Leptoderma* usually have two ceratohyal rays. *Einara* and *Mirognathus* have four, *Narcetes* has five, *Bathylaco* has six, *Leptochilichthys* has nine, and *Bathyprion* has 5, 6, or 8 ceratohyal rays.

Pharyngobranchial structure and dentition:

Crumenal organ:

The crumenal organ is a bilateral pharyngobranchial pair of pouches that are formed from the last two gill arches and the anterior limits of the esophagus (Greenwood and Rosen 1971). It is distinguished from epibranchial organs of other teleosts (Nelson 1967; Bertmar *et al*. 1969) by its position lateral rather than dorsal or dorsolateral to the esophagus, and by a unique accessory cartilage of the fifth ceratobranchial. Greenwood and Rosen (1971) consider the crumenal organ a synapomorphous character uniting the Alepocephaloidea and Argentinoidea.

The crumenal organ is, therefore, a primitive structure of alepocephaloids. Its function, implied by Greenwood and Rosen (1971), is analogous to epibranchial organs and is that of a collecting and temporary storage structure for filtered particles. In partial support of this, serial sections of crumenal organs of Alepocephalus agassizii, 295 mm and 315 mm SL, showed small amounts of siliceous material and a few diatom tests. However, macroscopically both fresh and preserved specimens usually show copious amounts of mucous exuding between the fourth and fifth arches and no indication of food. If food storage was also its primitive function, a justified but debatable assumption, then other branchial structures which would assist efficient filtration would have developed with the organ. It would be pointless to store filtered particles if there are no particles being filtered. Although I am not concerned with which came first, both the crumenal organ and the elaborate filtration system found in Leptochilichthys, Asquamiceps and a few other genera are probably very close to the primitive state for alepocephaloids.

The primitive filtration system of alepocephaloids probably was based upon interdigitating dentate gill rakers. In Leptochilichthys, for example, the gill rakers on antero-lateral surfaces are numerous, from 24 to 36 on each of the first four arches, and long, from 2.7 to 6.5% SL. These interdigitate with equally numerous but shorter rakers on the medial surfaces of the gill arches. Proceeding posteriad the lateral rakers decrease in size and the medial rakers increase in size so that the medial rakers of the fourth arch are usually as large as the lateral rakers of the fifth arch. Because of this, the posterior gill slit, between arches four and five, appears to be an effective final sieve through which few particles and little water would pass. No alepocephalid has lost the medial rakers of the fourth arch (Table 1), and consequently all possess this type of sieve in the posterior gill slit. Table 1 further shows that the medial rakers of the first three arches have been lost in many diverse genera. Conversely, the medial rakers are retained on the first and second arches of genera as disparate as the clupeid-like Leptochilichthys and the salmonid-like Bathylaco. Unfortunately, nothing is known of the food habits of either genus. Bathylaco is presumably a fast swimming predator (Nielsen and Larsen 1968) and the medial gill rakers, when present, are modified on the anterior arches to small tooth plates. Leptochilichthys with its long gill rakers and clupeid-like mouth is presumably a water strainer or filter feeder (the one stomach examined contained no identifiable remains). Therefore, the retention of the medial gill rakers on the first arch in these genera would seem not to be due to common ecological needs but rather to retention of common primitive characters which are slightly modified for different purposes.

The interdigitating rakers of the posterior gill slit form the floor of a generally shallow channel that leads to the crumenal organ. The walls of this channel are formed by the fourth and fifth ceratobranchials. The fifth ceratobranchial is expanded medially and meets its opposite along the midline thus forming a ridge continuous with the basibranchial. The "invariably" elevated medial ridge of the basibranchial tooth plate (Rosen 1974) is very high in Leptochilichthys and apparently serves to direct filtered particles into one shallow channel or another and thus to one crumenal organ or another. In all other genera the basibranchial ridge is slight to non-existent. Instead the basibranchials are slightly arched and the hypo- and ceratobranchials articulate ventrolaterally to

Table 1. Gill arches possessing complete or nearly complete rows of gill rakers on the medial surface of the lower limb (+ = present, ± = sometimes present, blank = absent).

Genus	Gill arch number			
	1	2	3	4
Asquamiceps	±	+	+	+
Einara		+	+	+
Ericara	+	+	+	+
Conocara		+	+	+
Leptoderma			+	+
Talismania	±	±	+	+
Leptochilichthys	+	+	+	+
Nomoctes		+	+	+
Alepocephalus	±	±	+	+
Bathylaco	±	±	+	+
Bajacalifornia			+	+
Narcetes			+	+
Bathytroctes			+	+
Rouleina			+	+
Xenodermichthys			+	+
Rinoctes			+	+
Bathyprion				+
Mirognathus				+
Photostylus				+

form a slightly rounded ridge which is accentuated by a medial fold of skin. Further changes are found in Ericara salmonea and Bathyprion in which the tooth plate is restricted to the basibranchial of the second arch only and Conocara mcdonaldi and Mirognathus which have no basibranchial tooth plate.

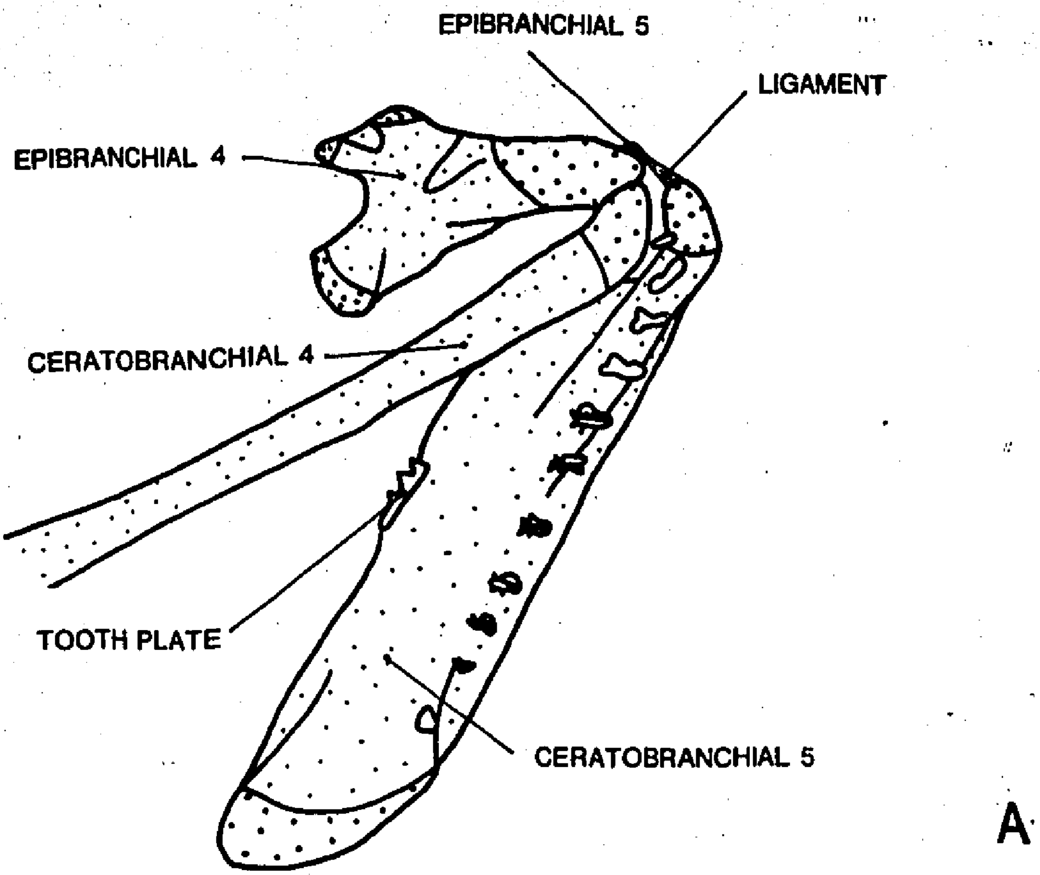
Once particles have been filtered and passed posteriad, they enter a simple blind sac, the crumenal organ. The organ empties dorsally into the esophagus. The apparent purpose of the organ is, as stated above, to store particles until a sufficiently large bolus is formed which is then squeezed into the esophagus and swallowed. In Alepocephalus agassizii there are two layers of muscles around the organ. The inner layer is approximately perpendicular to the fourth and fifth ceratobranchial and the outer layer is approximately perpendicular to the inner layer and parallel to the general C-shaped curve of the arches. Such a muscle system could easily constrict the blind sac and empty the contents of the crumenal organ.

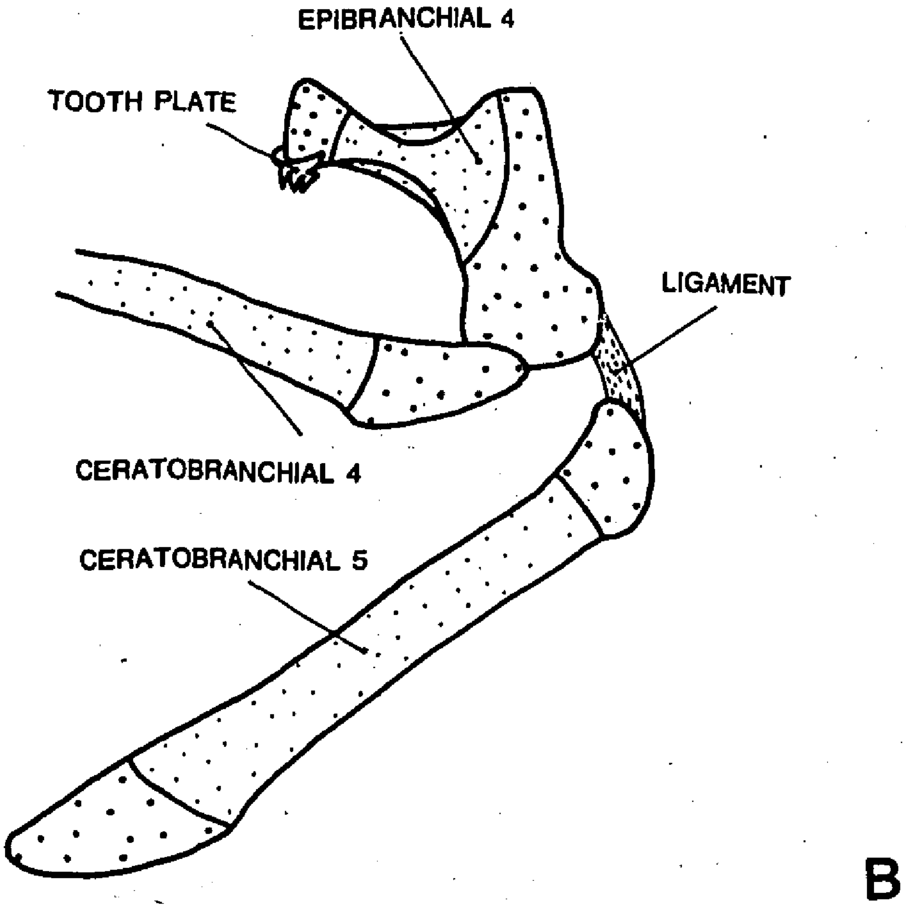
The osteology of the crumenal organ has been illustrated by Greenwood and Rosen (1971, Figs. 1, 2 and 3), but some important variations have not been noted. The accessory cartilage of the fifth ceratobranchial is absent and replaced by a loose ligament in Bathylaco, Bathyprion (Fig. 10A), Mirognathus and Photostylus (Fig. 10B). The cartilagenous fifth epibranchial is lost or fused to the fourth epibranchial in Photostylus (Fig. 10B) and Mirognathus. In Mirognathus the fifth epibranchial is in the same position medial to the fourth epibranchial as it is in Bathyprion (Fig. 10A), except the two are apparently fused. Although Greenwood and Rosen (1971) suspected that the crumenal organ gill rakers

Fig. 10

A. Bathyprion danae, ISH 1539/71, 252 mm SL, epibranchial bones, left side.

B. Photostylus pycnopterus, USNM 215518, 83 mm SL, epibranchial bones, left side.


EPIBRANCHIAL 5
LIGAMENT
EPIBRANCHIAL 4
CERATOBRANCHIAL 4
TOOTH PLATE
CERATOBRANCHIAL 5
A


EPIBRANCHIAL 4
TOOTH PLATE
LIGAMENT
CERATOBRANCHIAL 4
CERATOBRANCHIAL 5
B

of Bathyprion were edentate, they are slightly dentigerous and reduced (Fig. 10A). The gill rakers in Mirognathus are apparently edentate.

From the preceding paragraph and Table 1, it can be seen that three of the four genera which lack the accessory cartilage of the fifth ceratobranchial also lack medial gill rakers on the first three arches. All four genera are bathypelagic. The correlation may indicate that bathypelagic species generally lose the selective advantage of filter feeding. Apparently, the secondary development of tooth plates on the medial surfaces of Bathylaco's gill arches has been sufficiently useful to prevent their complete loss. Other genera with bathypelagic adults such as Einara, some Bajacalifornia, and possibly Xenodermichthys may be more recent recruits to the bathypelagic fauna. Leptochilichthys, if the scant data are correct, has apparently succeeded as a filter feeding bathypelagic alepocephaloid.

In Leptochilichthys (Greenwood and Rosen 1971, Fig. 3), Rouleina, Xenodermichthys, Asquamiceps, and Einara there are small autogenous patches of teeth located on the esophogeal lining of the crumenal organ. These plates vary from circular with one small tooth to longitudinal with several teeth. Usually these teeth form rows which parallel the rows of papillae which characteristically line the buccopharyngeal cavity.

Dentition:

The branchial dentition is relatively stable in the genera examined. The most extensive dentition is found in Talismania oregoni, Bathytroctes microlepis, Leptochilichthys agassizii and Mentodus rostratus. In these species tooth plates are present on the second, third, and fourth infrapharyngobranchials, fourth epibranchials and the fifth ceratobranchial.

All other species show a reduction of this pattern in the loss of teeth on the second infrapharyngobranchial. *Bathyprion*, *Mirognathus* and *Photostylus* are the only genera showing further reduction of branchial dentition. *Bathyprion danae* has only a few small teeth on the fifth ceratobranchial and extremely reduced dentition on the fourth epibranchial. *Photostylus pycnopterus* has only one small oval tooth plate mainly on the fourth epibranchial. *Mirognathus normani* is totally without teeth.

None of the species examined regularly has basihyal or basibranchial teeth. However, in the cleared specimen of *Bajacalifornia calcaratus* and several others from the same lot (UMML 15157) there are uniserial teeth along the midline of the basihyal. Some searsids, on the other hand, do have marginal fang-like basihyal dentition (Greenwood and Rosen 1971, Rosen 1974). In order to derive these two dentition patterns, a common ancestor would have had rather extensive basihyal dentition.

Although Weitzman (1967) reported mesopterygoid teeth in *Xenodermichthys*, none of the species I have examined, including *Xenodermichthys*, has mesopterygoid or ectopterygoid teeth. However, in *Narcetes stomias* the palatine tooth plate sometimes extends onto the ectopterygoid and may fragment to give the appearance of a separate ectopterygoid tooth patch.

The dentition of the jaws and palate are summarized in Table 2. In most alepocephaloids the primary bite involves the dentary acting against the palato-vomerine teeth (*Leptochilichthys*, *Alepocephalus*, and *Conocara*) or, more commonly, against the palato-vomerine and maxillary teeth (Table 2). In *Rouleina* and *Xenodermichthys* it acts against the premaxillary and maxillary or maxillary, respectively; in *Asquamiceps* (?), *Einara macrolepis* and *Leptoderma* against the premaxillary; and in *Einara edentulus* there is no dentition antagonistic to that of the dentary.

Table 2. Dentition of the jaws and palate. Sources other than this study are indicated: (1) Vaillant 1888, (2) Alcock 1890, (3) Garman 1899, and (4) Nielsen and Larsen 1970. (Presence of teeth in all examined species indicated by +, absence indicated by 0, variable dentition indicated by ±, no knowledge or questionable dentition indicated by ?).

	Vomer	Palatine	Dentary	Premaxillary	Maxillary
Searsidae:					
Mentodus	+	?	+	+	+
Leptochilichthidae:					
Leptochilichthys	+	+	+	0	0
Alepocephalidae:					
Narcetes	+	+	+	+	+
Bajacalifornia	+	+	+	+	+
Bathylaco	+	+	+	+	+
Herwigia[4]	+	+	0	+?	+?
Rinoctes	+	+	+	+	+
Nomoctes	±	±	+	+	+
Bellocia[1]	?	?	?	+	+
Photostylus	?	+	+	+	+
Talismania	±	+	+	+	+
Bathyprion	0	+	+	+	+
Bathytroctes	0	±	+	+	+
Rouleina	0	0	+	+	+
Xenodermichthys	0	0	+	+	0

Table 2 (cont'd).

	Vomer	Palatine	Dentary	Premaxillary	Maxillary
Alepocephalidae:					
Asquamiceps	0	0	+	?	0
Anomalopterichthys[1]	0	+	+	+	0
Alepocephalus	0	+	+	+	0
Brunichthys[3]	?	+	+	+	0
Ericara	0	+	+	+	0
Conocara	0	+	+	+	0
Leptoderma	0	0	+	+	0
Aulastomatomorpha[2]	0?	0?	+	+	0
Einara	0	0	+	±	0
genus A	0?	0?	+	0?	0
Mirognathus	0	0	0	0	0

Unlike the argentinoids, coregonines and Cretaceous *Guadryella* which have the primary bite between the toothed vomer and tongue, the alepocephaloids resemble the myctophiforms, higher teleosts, and Cretaceous *Humbertia* which have a primary grasping bite between the toothed jaws and a secondary gulping bite between the pharyngeals (Patterson 1970:265). However, the myctophiforms and other neoteleosts possess a retractor arcuum branchialium muscle (Rosen, 1973), not found in alepocephaloids, and tend to retain and develop the infrapharyngobranchial dentition (especially the third) (Rosen 1973). In alepocephaloids there is a tendency to lose the dentition on the second infrapharyngobranchial or to lose all branchial dentition as in *Mirognathus*. The dentition therefore indicates a distant relationship to Rosen's (1973) neoteleosts, but the evolutionary tendency of alepocephaloids to maintain the status quo or lose all the dentition is unlike that of the neoteleosts.

Vertebral column and vertical fins:

The total number of preural vertebrae in the species examined ranged from 37 in *Asquamiceps indigatio* to 81 in *Leptoderma macrops*. The relationship between the number of precaudal and preural caudal centra was quite variable within the superfamily. At present it does not seem possible to state with any degree of certainty whether the primitive condition involved more precaudal, more caudal or approximately equal numbers of precaudal and caudal vertebrae. However, one of the earliest teloests, *Leptolepis*, and some cretaceaus salmoniforms, *Ichthyotringa* (Goody 1969), *Humbertia* and *Gaudryella* (Patterson 1970) have at least seven more precaudal than caudal vertebrae. In primitive members of many extant lower teleostean groups, such as *Elops*, *Albula* (Lindberg and Legeza 1969), the osmerid *Spirinchus* (Weitzman 1967), the salmonids (Norden 1961), *Retropinna*, the galaxiids, the aplochitonids (McDowall 1969) and Argentina (Halliday 1969) there are seven or more precaudal than caudal vertebrae. It therefore seems reasonable to speculate that the primitive alepocephaloid also had more precaudal than caudal vertebrae. The derived character states would therefore be any other combination of vertebrae (i.e., approximately equal numbers of precaudal and caudal vertebrae, greatly increased numbers of precaudal vertebrae, or more caudal than precaudal vertebrae). Since it would not be prudent to speculate on whether the ancestral alepocephaloid had many more or only a few more precaudal than caudal vertebrae, only the condition of significantly more caudal than precaudal vertebrae can reasonably be identified as a derived state. Corroborative evidence on the position of the vertical fins strengthens this conclusion (see below).

The following forms have ten or more caudal than precaudal centra: Alepocephalus (Halisauriceps) longiceps, Conocara, Einara, Ericara, Leptoderma, Talismania (except T. aphos) and Xenodermichthys. Alepocephalus macrops, Asquamiceps longmani and Bathyprion danae have five to nine more caudal than precaudal centra. The remainder of Alepocephalus and Asquamiceps, plus Talismania aphos, Bathytroctes, Nomoctes, Rouleina, and Rinoctes have approximately equal (± 5 numbers of precaudal and caudal centra. Bajacalifornia, Bathylaco, Herwigia, Leptochilichthys, Narcetes and Photostylus have six or more precaudal than caudal centra.

Some, although not all of the members of the last two, presumably primitive, groups have the dorsal fin inserted distinctly in advance of the anal fin and located about 60% of the standard length behind the snout. In many, although again not all of the members of the first, presumably most derived group, the dorsal fin is inserted distinctly behind the anal fin and is located as much as 77% of the standard length behind the snout. The dorsal fin is inserted near the middle of the body and distinctly in advance of the anal fin in all the fossil and lower teleosts mentioned at the beginning of this section with the exception of *Retropinna* and the galaxiids. Therefore, as with the vetebrae, I consider the character state which is found in many unrelated "basal" lower teleosts to be the primitive condition. The ancestral alepocephaloid probably had a dorsal fin located around 50 to 60% of the standard length behind the snout and distinctly in advance of the anal fin.

In all specimens examined the fused proximal and middle radials of both the dorsal and anal fins were associated with neural or haemal spines at an average ratio of about three radials for every two spines. One fin ray is associated with each distal radial except for the first which is sometimes unsupported and the last two or three which are sometimes supported by one radial.

Pleural ribs begin on the second vertebral centrum except in *Bathyprion* where they begin on the third. Epineurals (dorsal intermuscular bones) are fused to the neural arches, begin on the first centrum and, like the epipleurals (ventral intermuscular bones), usually end near the origin of the anal fin around the fourth or fifth caudal centrum. Epipleurals are usually fused to a parapophysis or directly to a centrum but their commencement is variable. Epipleurals begin on the second vertebra in *Talismania oregoni*, *Bajacalifornia*, *Bathylaco*, and *Asquamiceps*; the third in *Rouleina*, *Leptochilichthys* and *Talismania antillarum*; the fourth in *Bathytroctes* and *Bathyprion*; the sixth in *Alepocephalus*; the eighth in *Ericara*; the eleventh in *Leptoderma*; and the twelfth in *Conocara* and *Xenodermichthys*.

The parapophyses are usually moderately developed. In Conocara and Leptoderma the parapophyses on the first centrum are elongated into dagger-like processes directed laterally in the same plane as the pleural ribs. The parapophyses of the first centrum of Talismania are also well developed but are triangular and not nearly as long as those in Conocara and Leptoderma.

From one to thirteen supraneurals are found in all genera except the following which have none: Leptoderma, Alepocephalus (excluding Lloydiella), Mirognathus and some species of Asquamiceps. When present supraneurals lie within the ligamentous connective tissue which joins the vertebrae with the supracarinalis muscle.

In Xenodermichthys, Rouleina and Leptochilichthys the first supraneural is expanded longitudinally and broadly articulates with the first neural arch. In Xenodermichthys the first centrum does not possess the unfused halves of the first neural spine typical of other genera.

Caudal Skeleton:

The caudal skeleton has been used extensively in phylogenetic studies of lower teleosts (Gosline, 1960 and 1969; Greenwood, et al., 1966; Greenwood and Rosen, 1971; Nybelin, 1971 and 1973; Patterson, 1968 and 1970; Rosen, 1974; Weitzman, 1974 and others). According to Greenwood and Rosen (1971), as modified by Rosen (1974), the alepocephaloid caudal skeleton is characterized by the well-developed tendency to lose liminar bone from the posterior neural and haemal spines and the less-developed tendency to foreshorten the first uroneural. Thus, the primitive alepocephaloid condition is the presence of laminar bone on the posterior neural and haemal spines and a long first uroneural extending to the second preural centrum. Also, among primitive salmoniforms, the first uroneural had no laminar bone and the ural centra were separate (Rosen, 1974).

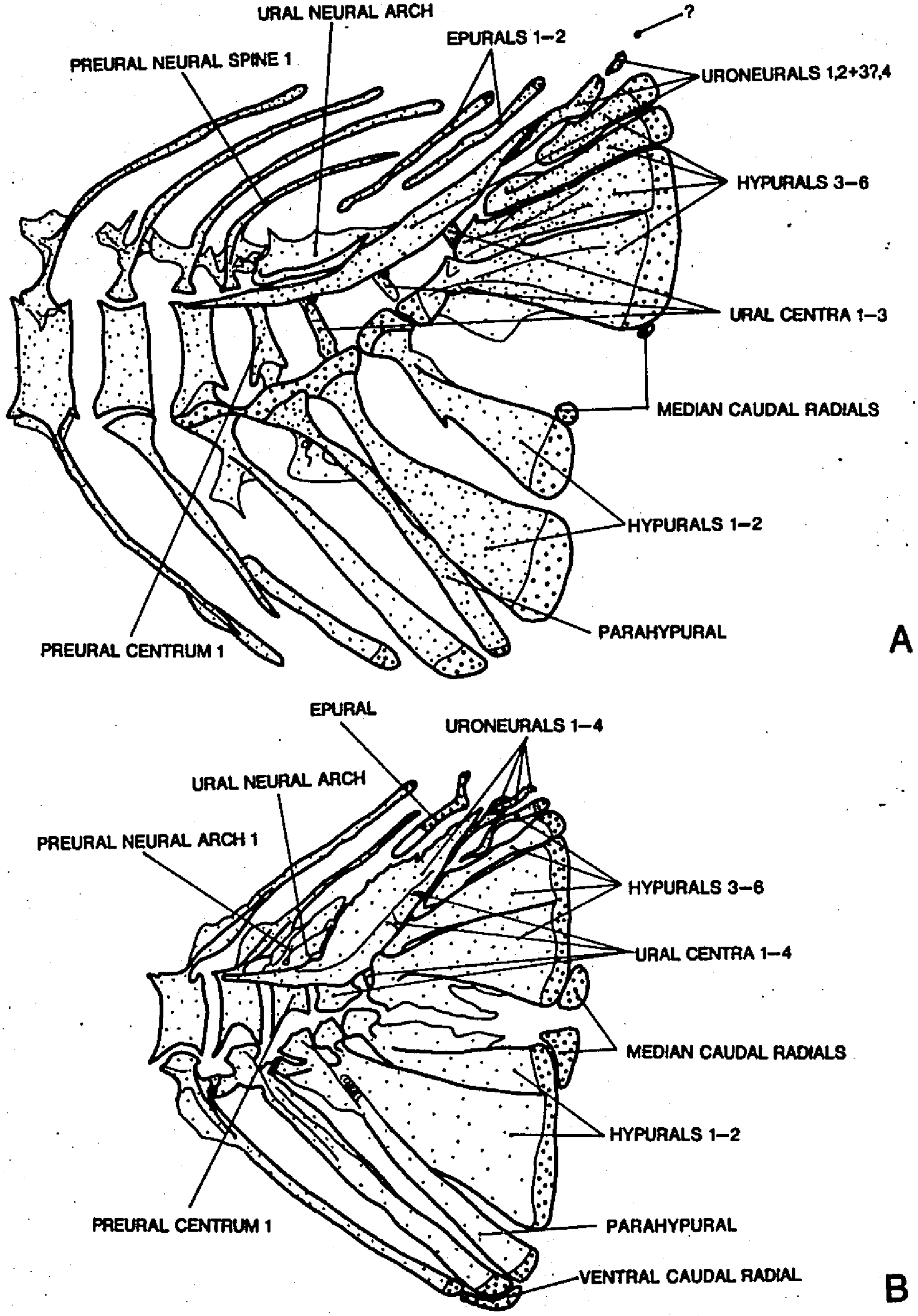
The alepocephaloid caudal skeleton represents a primitive teleostean grade. In the earliest teleosts, ossification of the ural and preural centra and forward extension of the uroneurals eliminated the oblique plane of weakness which separated the upper caudal skeleton along a line that could be drawn through the distal ends of the first three preural neural spines and the proximal ends of the epurals, the so-called "chondrostean hinge" (Patterson 1968). This produced a tail which could swing about a vertical rather than an oblique axis and which could develop internal symmetry (Patterson 1968). At the primitive alepocephaloid level, internal symmetry has not been well developed, ural centra are still upturned and additional stiffeners have been applied to the former plane of the "chondrostean hinge".

The primitive alepocephaloid grade is probably best represented in <u>Asquamiceps hjorti</u> (Fig. 11A). It has at least three ural centra, a primitive, generally considered aberrant, feature in teleosts (see Nybelin 1971 and Weitzman 1974 for other instances among teleosts). The uppermost and lowermost ural centra are completely ossified rings while the middle one is ossified on the right side and mostly unossified on the left side of this specimen. Between ural centra 1 and 2 on the right side is another small ossification completely hidden by the first uroneural. Since it is not possible to discern which centrum belongs to the single ural neural arch or if the arch is actually compound, it cannot be shown that these are either complete vertebrae or a pair of hemicentra (Greenwood, 1970). The uppermost centrum appears to be homologous with the second ural centrum of other alepocephaloids. The middle one, in spite

Fig. 11

A. Asquamiceps hjorti, ISH 2481/71, damaged, ca. 125 mm SL, caudal skeleton.

B. Leptochilichthys agassizii, ISH 916/73, 255 mm SL, caudal skeleton.


URAL NEURAL ARCH
?
EPURALS 1–2
PREURAL NEURAL SPINE 1
URONEURALS 1,2+3?,4
HYPURALS 3–6
URAL CENTRA 1–3
MEDIAN CAUDAL RADIALS
HYPURALS 1–2
PARAHYPURAL
PREURAL CENTRUM 1
A
EPURAL
URONEURALS 1–4
URAL NEURAL ARCH
PREURAL NEURAL ARCH 1
HYPURALS 3–6
URAL CENTRA 1–4
MEDIAN CAUDAL RADIALS
HYPURALS 1–2
PREURAL CENTRUM 1
PARAHYPURAL
VENTRAL CAUDAL RADIAL
B

of the fact that it appears to give partial support to the third hypural, apparently fused with the lower centrum in all other alepocephaloids to form a compound first ural centrum. Additional evidence for a compound origin can be seen in the two ventral facets of the first ural centrum, such as in *Conocara mcdonaldi* (Fig. 18A). Nybelin (1971 and 1973) has suspected a compound origin for the first ural centrum in the fossil leptolepids and *Elops*.

There are four uroneurals on the right side, three on the left and a fifth unpaired ossification (?) distally (Fig. 11A). There is no laminar bone on the strap-like first uroneural. The first ural neural arch is autogenous and has extensive development of laminar bone, which has developed uniquely in a longitudinal axis and crosses the top of the lowermost ural centra. It is not fused to the first uroneural. Laminar bone is present on the first four neural and first haemal preural spines and the parahypural. A structure which may be an ossified ventral caudal radial is cylindrical, blunt at each end, cartilagenous distally and free from its associated haemal spine.

The first and second hypurals are separate (Fig. 11A), unlike other alepocephaloids in which there is distal fusion of the cartilage. The distal edge of the lower hypurals is distinctly ahead of the distal edges of the upper hypurals and the first hypural is only slightly deeper than the second. Part of the internal symmetry that was acquired with the loss of the "chondrostean hinge" was the nearly vertical alignment of the edges of the upper and lower hypurals (Patterson, 1968). In alepocephaloids this has apparently been achieved by the disproportionate growth of the first hypural relative to the second. This has taken place through lengthening and the distal vertical expansion of the first hypural. Thus, the condition of the lower hypurals in Asquamiceps hjorti is primitive for alepocephaloids.

The median caudal radials each support a fin ray. The dorsal procurrent, upper principal, lower principal and ventral procurrent numbers of fin rays are, respectively: 9, 10+9, 8.

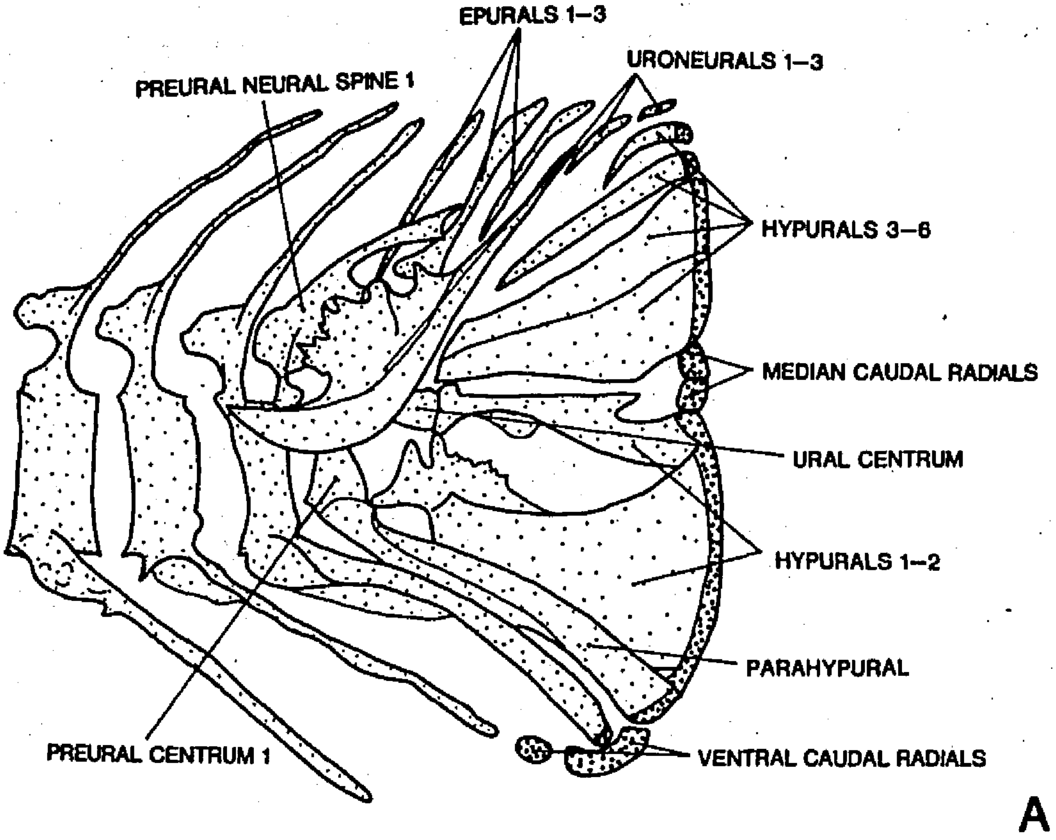
In Leptochilichthys agassizii (Fig. 11B), as well as all other alepocephaloids, the edges of the upper and lower hypurals lie in a vertical plane, or nearly so. In this specimen there are four pairs of uroneurals and a third and fourth ural centrum at the bases of the fourth and fifth hypurals, respectively. The latter lends additional support to Nybelin's (1971) hypothesis that "each hypural corresponds to an originally separate centrum" rather than Patterson's (1968) assertion that such centra never existed. Laminar bone on the first ural neural arch has apparently sutured with that on the first preural neural arch and the structures are both sutured to the first preural centrum. Laminar bone is present on the first four neural and three haemal spines. The parahypural and first haemal spine each have a peg on their anterior surface which abuts a similar smaller structure on the posterior surface of the preceding spine. There is no "peg and socket" joint as in salmonids or pholidophorids (Patterson 1968). The first hypural has fused proximally with the parahypural and distally with the second hypural. A cartilagenous ventral caudal radial is present. It is a primitive structure found in chondrosteans, generalized holosteans (Patterson 1968), Elops and an assortment of lower teleosts (Nybelin 1971). It is apparently lost among some alepocephaloid lineages. The median caudal radials each support a fin ray and the caudal formula is 10, 10+9, 9.

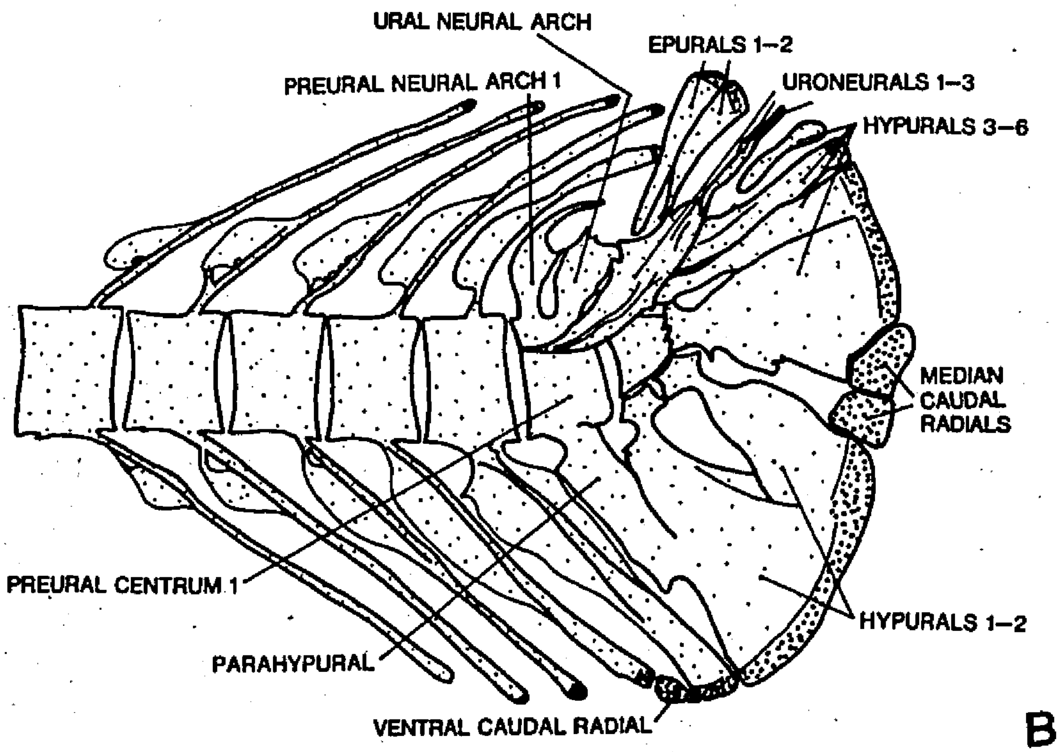
In Narcetes stomias (Fig. 12A) the second ural centrum is missing.

Fig. 12

A. Narcetes stomias, USNM 215515, 473 mm SL, caudal skeleton.

B. Bajacalifornia calcaratus, UMML 15157, ca. 345 mm SL, caudal skeleton.


EPURALS 1–3
URONEURALS 1–3
PREURAL NEURAL SPINE 1
HYPURALS 3–6
MEDIAN CAUDAL RADIALS
URAL CENTRUM
HYPURALS 1–2
PARAHYPURAL
PREURAL CENTRUM 1
VENTRAL CAUDAL RADIALS
A


URAL NEURAL ARCH
EPURALS 1–2
PREURAL NEURAL ARCH 1
URONEURALS 1–3
HYPURALS 3–6
MEDIAN
CAUDAL
RADIALS
PREURAL CENTRUM 1
HYPURALS 1–2
PARAHYPURAL
VENTRAL CAUDAL RADIAL
B

Both centra were present in 4 of 7 specimens examined. One specimen each showed fusion of the ural centra, first preural and ural centra, and first three preural and ural centra. Laminar bone was variously developed on zero to four neural spines and one to four haemal spines. In four cases there were two epurals and in three cases there were three. There are three uroneurals in the illustrated specimen. Typically, there is laminar bone on the first uroneural, which is aberrantly fused to the underlying centra in one specimen. Other important features common to all specimens are the tall preural centra with large interspaces, lack of ural neural arches, fused third and fourth hypurals, two ventral caudal radials and robust median caudal radials in contact with each other which together support the tenth principal (upper) fin ray. The caudal formula varies from 12, 10+9, 10 to 15, 10+9, 14.

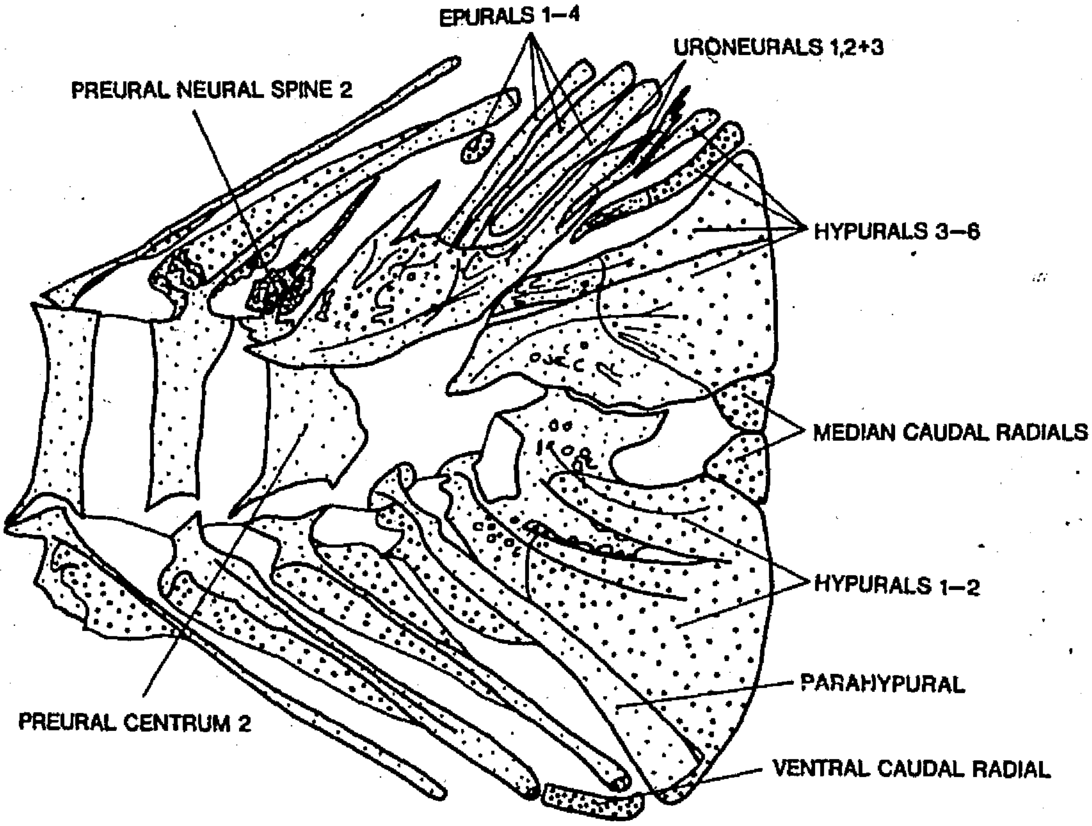
Bajacalifornia calcaratus (Fig. 12B) shows some advanced features over that of Narcetes, including foreshortening of the first uroneural to the first preural centrum, fusion of the ural centra, distal fusion of the first hypural with both the parahypural and second hypural, and two epurals. It retains primitive features such as laminar bone on seven neural and five haemal spines, a ural neural arch which however is ankylosed to the first preural centrum, and a short, arched second neural spine. Radiographs confirm the stability of the number of epurals and the short second neural spine in B. calcaratus and B drakei. The median caudal radials are again robust and in contact but each supports a principal ray. The caudal formula is 16, 10+9, 14.

The caudal skeleton of Bathylaco nigricans (Fig. 13A) is mostly cartilage. Laminar cartilage, or at least a non-alizarin staining structure, is present on two neural and three haemal spines. No ural

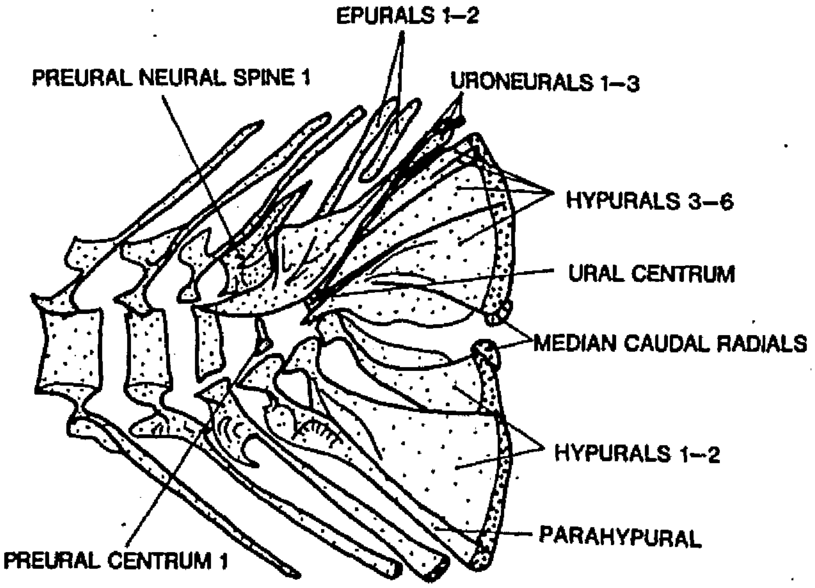
Fig. 13

A. *Bathylaco nigricans*, USNM 206693, 268 mm SL, caudal skeleton.

B. *Mentodus rostratus*, USNM 215612, ca. 135 mm SL, caudal skeleton.


EPURALS 1–4
URONEURALS 1,2+3
PREURAL NEURAL SPINE 2
HYPURALS 3–6
MEDIAN CAUDAL RADIALS
HYPURALS 1–2
PARAHYPURAL
VENTRAL CAUDAL RADIAL
PREURAL CENTRUM 2

A


EPURALS 1–2
PREURAL NEURAL SPINE 1
URONEURALS 1–3
HYPURALS 3–6
URAL CENTRUM
MEDIAN CAUDAL RADIALS
HYPURALS 1–2
PARAHYPURAL
PREURAL CENTRUM 1

B

or first preural arches are evident, although if the latter is present it has fused with the first uroneural. The second preural neural arch is reduced, I presume secondarily. Two of the three (four?) epurals have their proximal ends inserted between the expanded first uroneurals, an apparent stiffening device also found in Narcetes (Fig. 12A), Bathyprion (Fig. 14A), and Mentodus, and searsid (Fig. 13B). There are three uroneurals, the third fused with the second on the left side but free on the right. The ural and first preural centra are unossified and the first hypural has has fused and/or sutured with the parahypural and second hypural. There is a single ventral caudal radial and the two median caudal radials are in contact and support the tenth principal (upper) fin ray. The caudal formula is 18, 10+9, 16.

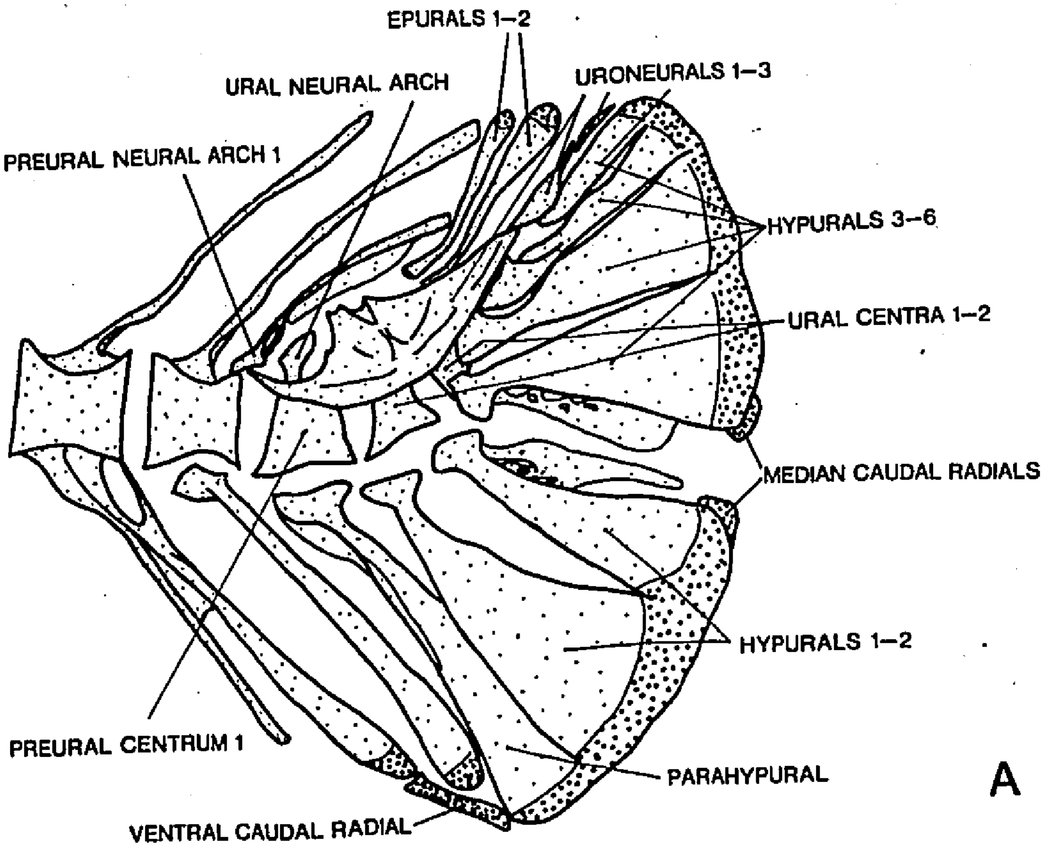
Similar to the last four genera in several respects is the searsid, Mentodus rostratus (Fig. 13B). Laminar bone is present on five neural and three haemal spines, the parahypural and the first uroneural. There is no visible ural neural arch, first ural centrum or ventral caudal radial. The fifth and sixth hypurals are fused proximally. The bases of the third and fourth hypurals extend along the side of the second ural centrum as a caudal stiffener. This type of caudal stiffener may be characteristic of searsids (Greenwood and Rosen, 1971, Fig. 11B), but a similar structure is also found in Photostylus (Fig. 16A). The median caudal radials are small and both support the tenth principal (upper) fin ray. The caudal formula is 15, 10+9, 13.

With the following minor exception, none of the remaining genera have laminar bone on neural spines and only a few have reduced amounts on the haemal spines and parahypural. Bathyprion danae (Fig. 14A) retains a small amount of laminar bone on the first preural neural spine and

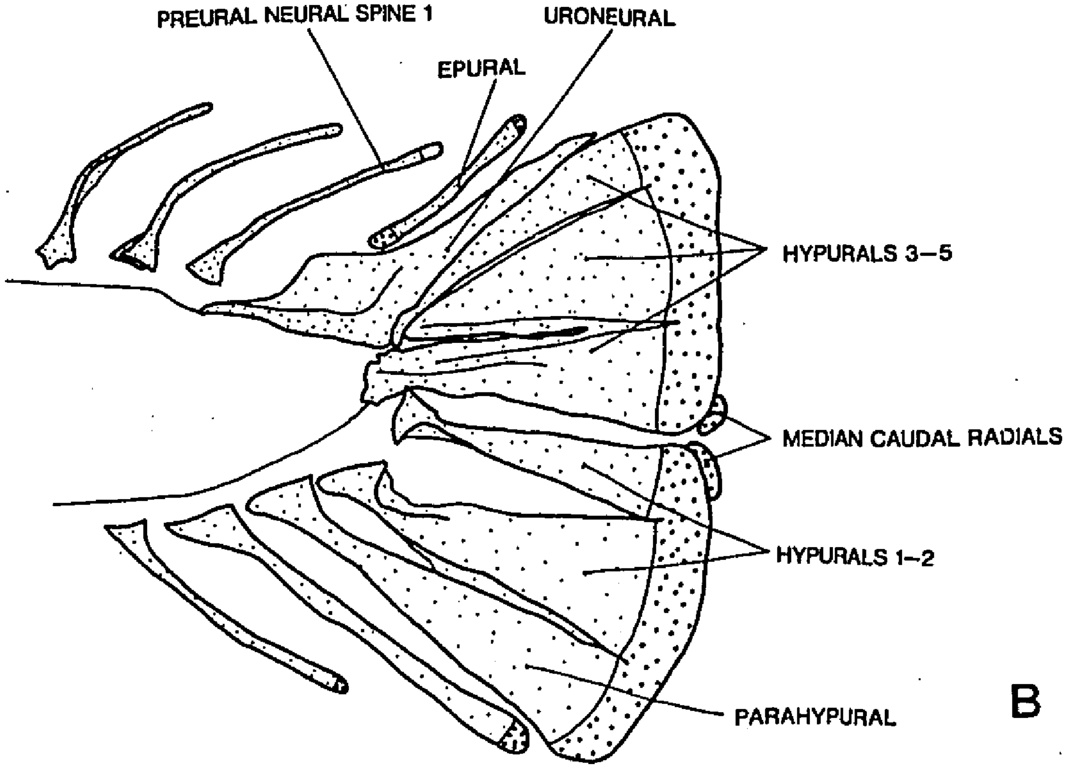
Fig. 14

A. *Bathyprion danae*, ISH 1539/71, 252 mm SL, caudal skeleton.

B. *Mirognathus normani*, ISH 917/73, 90 mm SL, caudal skeleton.


EPURALS 1–2
URONEURALS 1–3
URAL NEURAL ARCH
PREURAL NEURAL ARCH 1
HYPURALS 3–6
URAL CENTRA 1–2
MEDIAN CAUDAL RADIALS
HYPURALS 1–2
PREURAL CENTRUM 1
PARAHYPURAL
VENTRAL CAUDAL RADIAL

A


PREURAL NEURAL SPINE 1
URONEURAL
EPURAL
HYPURALS 3–5
MEDIAN CAUDAL RADIALS
HYPURALS 1–2
PARAHYPURAL

B

parahypural. The first uroneural is expanded and the proximal end of the second epural fits in between the two uroneurals. A ventral caudal radial is present as are two small median caudal radials, each supporting a separate fin ray. The caudal formula is 27, 10+9, 23.

In the specimen of Mirognathus normani (Fig. 14B) there is no vertebral ossification, no laminar bone except on the first (and only) uroneural, and only one epural. The sixth hypural is missing and the parahypural, expanded distally, is larger than the second hypural. Among alepocephaloids this type of caudal symmetry is unique. There is no ventral caudal radial and there are two small median caudal radials, each contributing minor support to a fin ray. The caudal formula is 12, 10+9, 13.

In Rouleina maderensis (Fig. 15A) laminar bone remains on the first uroneural, of which there are two, and there are two epurals. Otherwise this caudal looks simple and, except for the lack of laminar bone on the spines, primitive. There is no ventral caudal radial and the two median caudal radials each support a fin ray. The caudal formula is 13, 10+9, 13.

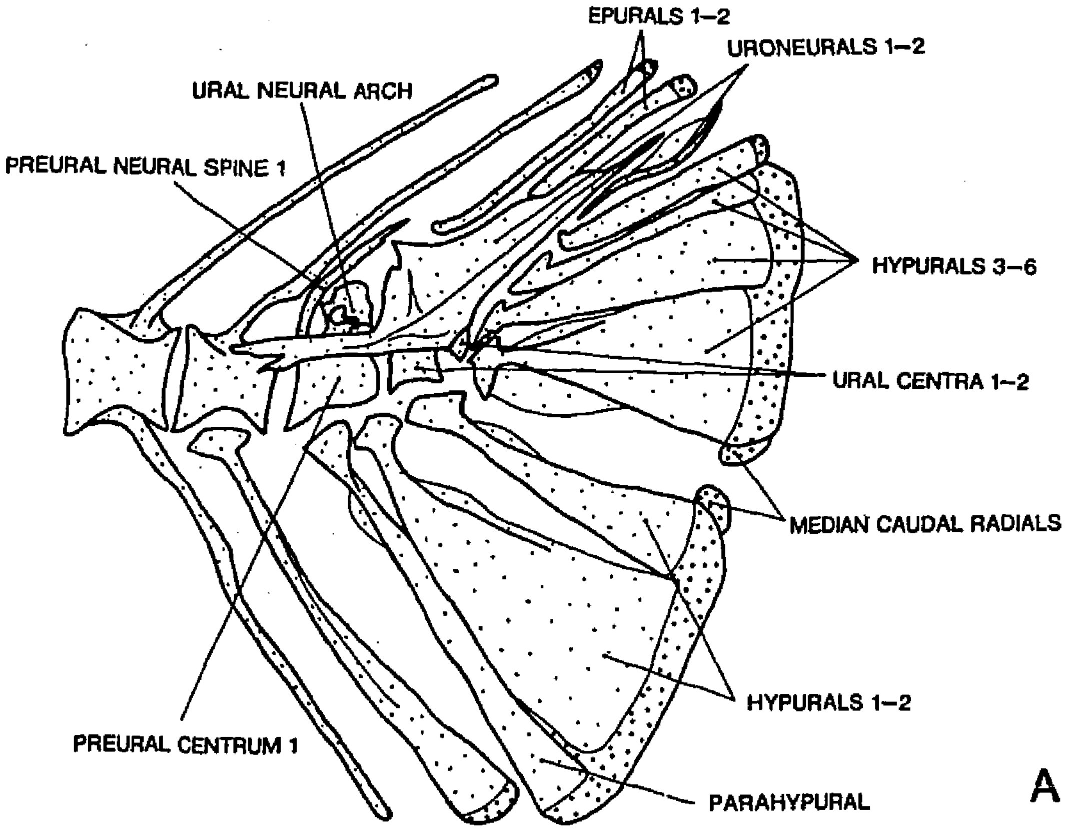
Xenodermichthys copei (Fig. 15B) is very similar to Rouleina. The illustrated specimen has fused first ural and preural centra but in a second specimen they are separate. In both specimens there are three uroneurals, two epurals, and no ventral or median caudal radials. The laminar bone on the first uroneural is consistently directed forward (Greenwood and Rosen, 1971, Fig. 9A). There are no ventral or median caudal radials. The caudal formula is 12, 10+9, 14.

Photostylus pycnopterus (Fig. 16A) has fused ural centra, upper hypurals, lower hypurals, and uroneurals. The first uroneural has an anteriorly-directed spine. There is no trace of a sixth hypural. The base of the fused upper hypurals extends down along the side of the fused

Fig. 15

A. Rouleina maderensis, USNM 215473, ca. 230 mm SL, caudal skeleton.

B. Xenodermichthys copei, USNM 215539, 151 mm SL, caudal skeleton.


EPURALS 1–2
URONEURALS 1–2
URAL NEURAL ARCH
PREURAL NEURAL SPINE 1
HYPURALS 3–6
URAL CENTRA 1–2
MEDIAN CAUDAL RADIALS
HYPURALS 1–2
PREURAL CENTRUM 1
PARAHYPURAL
A

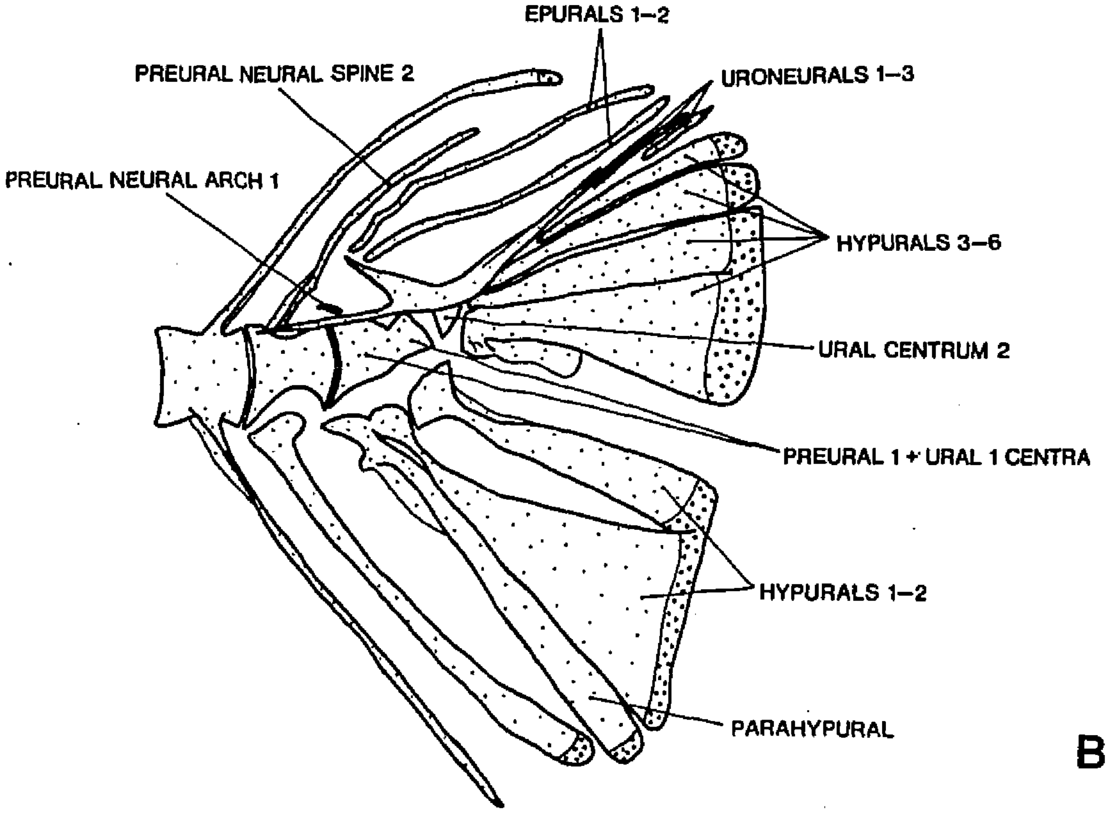
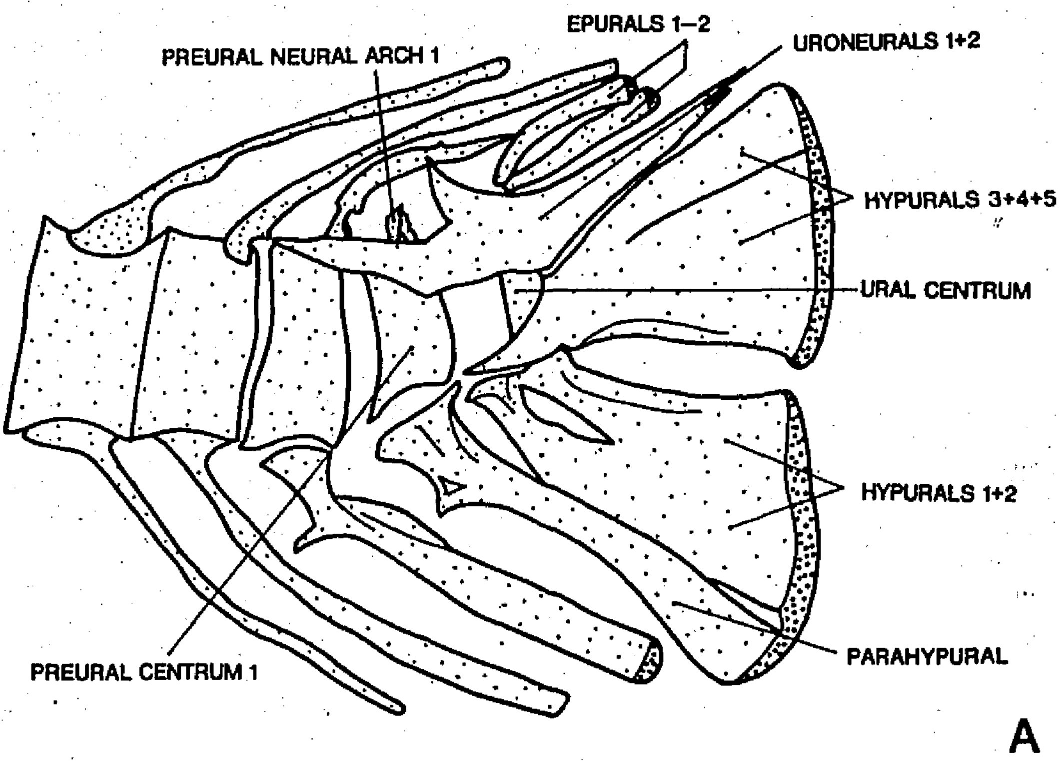
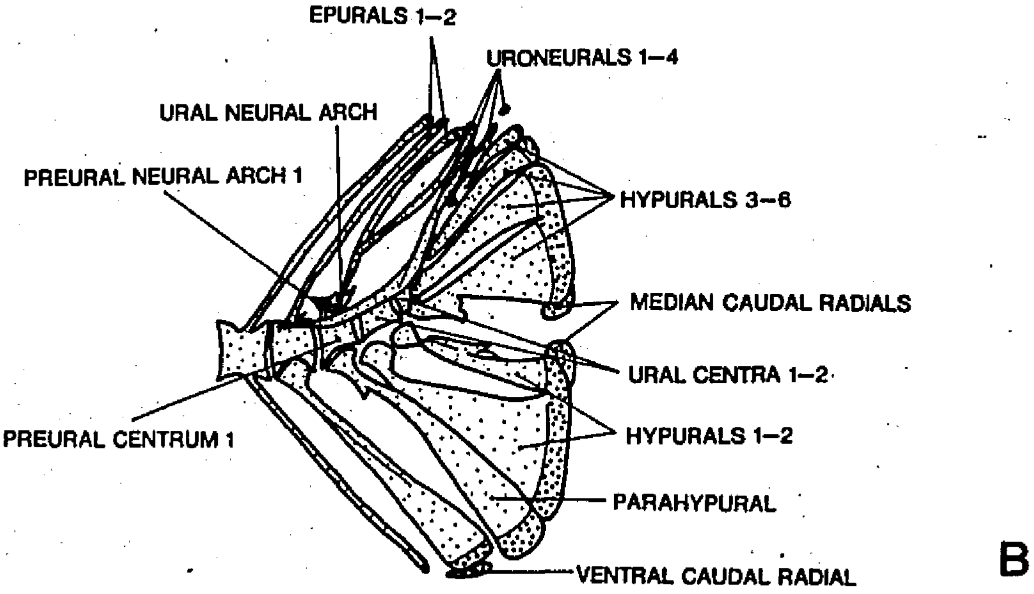

EPURALS 1–2
PREURAL NEURAL SPINE 2
URONEURALS 1–3
PREURAL NEURAL ARCH 1
HYPURALS 3–6
URAL CENTRUM 2
PREURAL 1 + URAL 1 CENTRA
HYPURALS 1–2
PARAHYPURAL
B

Fig. 16

A. *Photostylus pycnopterus*, USNM 215518, 83 mm SL, caudal skeleton.

B. *Talismania oregoni*, USNM uncatalogued, 265 mm SL, caudal skeleton.


EPURALS 1–2
PREURAL NEURAL ARCH 1
URONEURALS 1+2
HYPURALS 3+4+5
URAL CENTRUM
HYPURALS 1+2
PARAHYPURAL
PREURAL CENTRUM 1
A


EPURALS 1–2
URONEURALS 1–4
URAL NEURAL ARCH
PREURAL NEURAL ARCH 1
HYPURALS 3–6
MEDIAN CAUDAL RADIALS
URAL CENTRA 1–2
PREURAL CENTRUM 1
HYPURALS 1–2
PARAHYPURAL
VENTRAL CAUDAL RADIAL
B

ural centra and external to the base of the second hypural. This would appear to be an elaboration of the condition found in Mentodus (Fig. 13B) and acts to further stiffen the caudal base along the former plane of the "chondrostean hinge".

None of the remaining genera has a dorsal expansion of laminar bone on the first uroneural, all possess two ural centra, and only the first two genera have ural neural arches. With respect to the first two characters, all of these genera are primitive, although secondary loss of laminar bone on the first uroneural is possible. The loss of ural neural arches is a derived feature.

Talismania oregoni (Fig. 16B) has a ural neural arch fused to the first preural neural arch and two long thin epurals (see also Greenwood and Rosen, 1971, Fig. 8A). There are four pairs of uroneurals, the uppermost very minute, a ventral caudal radial and two median caudal radials each supporting a fin ray. The caudal formula is 16, 10+9, 15.

In two species of the Binghamichthys subgenus of Talismania (Fig. 17A), there are two epurals, three uroneurals, separate ural and first preural neural arches, and two median caudal radials supporting fin rays. The caudal formula for T. antillarium is 13, 10+9, 13 and for a specimen of T. aphos it is 15, 10+9, 13.

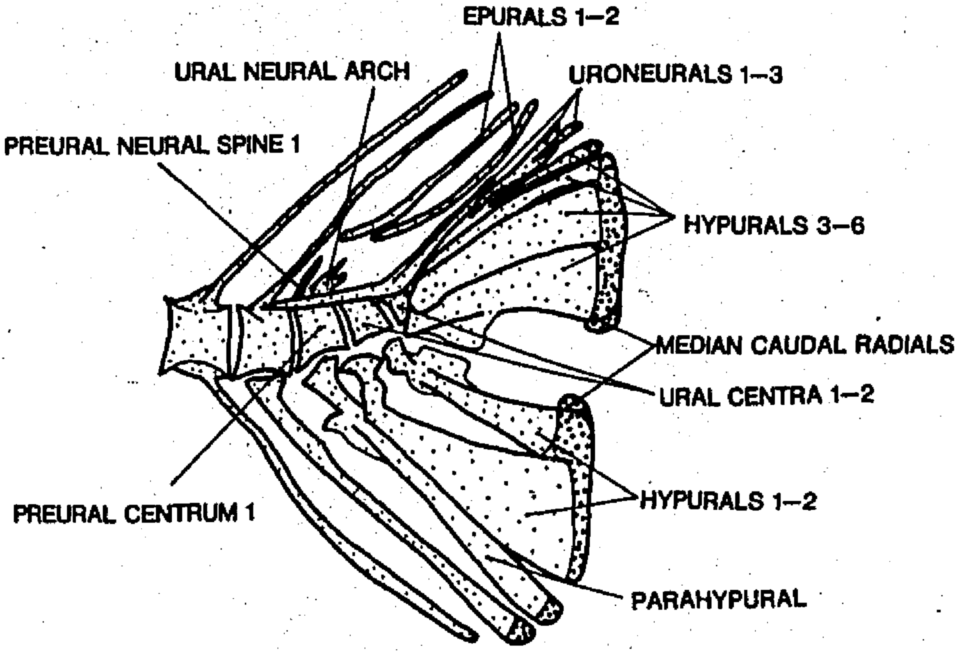
Ericara salmonea (Fig. 17B) retains laminar bone on the parahypural and one haemal spine and retains the fourth or possibly fifth pair of minute uroneurals. The second uroneural is forked on both sides. There is one epural. There is one, possibly aberrant, ventral caudal radial and no median caudal radials. The caudal formula is 16, 10+9, 16.

Conocara mcdonaldi (Fig. 18A) has a forked second uroneural on both sides, one epural, no caudal radials, and laminar bone on the parahypural

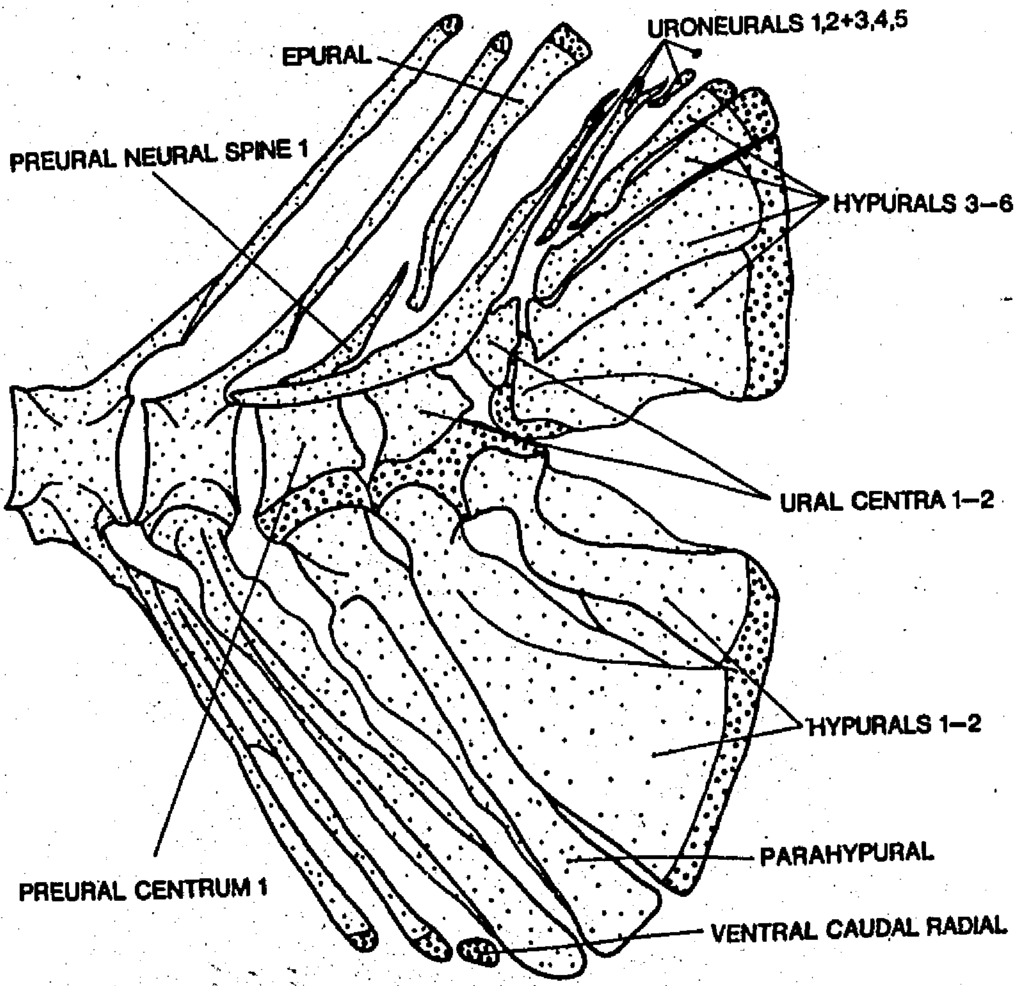
Fig. 17

A. <u>Talismania antillarum</u>, USNM 215560, 140 mm SL, caudal skeleton.

B. <u>Ericara salmonea</u>, UMML 32354, ca. 305 mm SL, caudal skeleton.


EPURALS 1–2
URAL NEURAL ARCH
URONEURALS 1–3
PREURAL NEURAL SPINE 1
HYPURALS 3–6
MEDIAN CAUDAL RADIALS
URAL CENTRA 1–2
PREURAL CENTRUM 1
HYPURALS 1–2
PARAHYPURAL

A


URONEURALS 1,2+3,4,5
EPURAL
PREURAL NEURAL SPINE 1
HYPURALS 3–6
URAL CENTRA 1–2
HYPURALS 1–2
PARAHYPURAL
PREURAL CENTRUM 1
VENTRAL CAUDAL RADIAL

B

formed into a peg that fits in a socket on the preceding haemal spine. The parahypural is similar to that described above for Leptochilichthys. The caudal formula is 17, 10+9, 16.

The caudal of Leptoderma macrops is reduced (Fig. 18B). A consistent feature in two specimens of L. macrops and the one of L. lubricum-complex examined and in the Leptoderma illustrated by Greenwood and Rosen (1971, Fig. 9B) is the accessory parahypural. They also found an epural and a second uroneural which I did not find. There is no sixth hypural, only a remnant of the fifth, and no caudal radials. The caudal formula in the specimen illustrated is 7, 6+7, 6. In L. lubricum-complex the formula is 26, 9+10, 23.

Einara edentulus (Fig. 19A) is more primitive than the last three genera in having two epurals and two median caudal radials. It is more advanced in having only two pairs of uroneurals; the minute third one is a single median ossification. The caudal formula is 8, 10+9, 8.

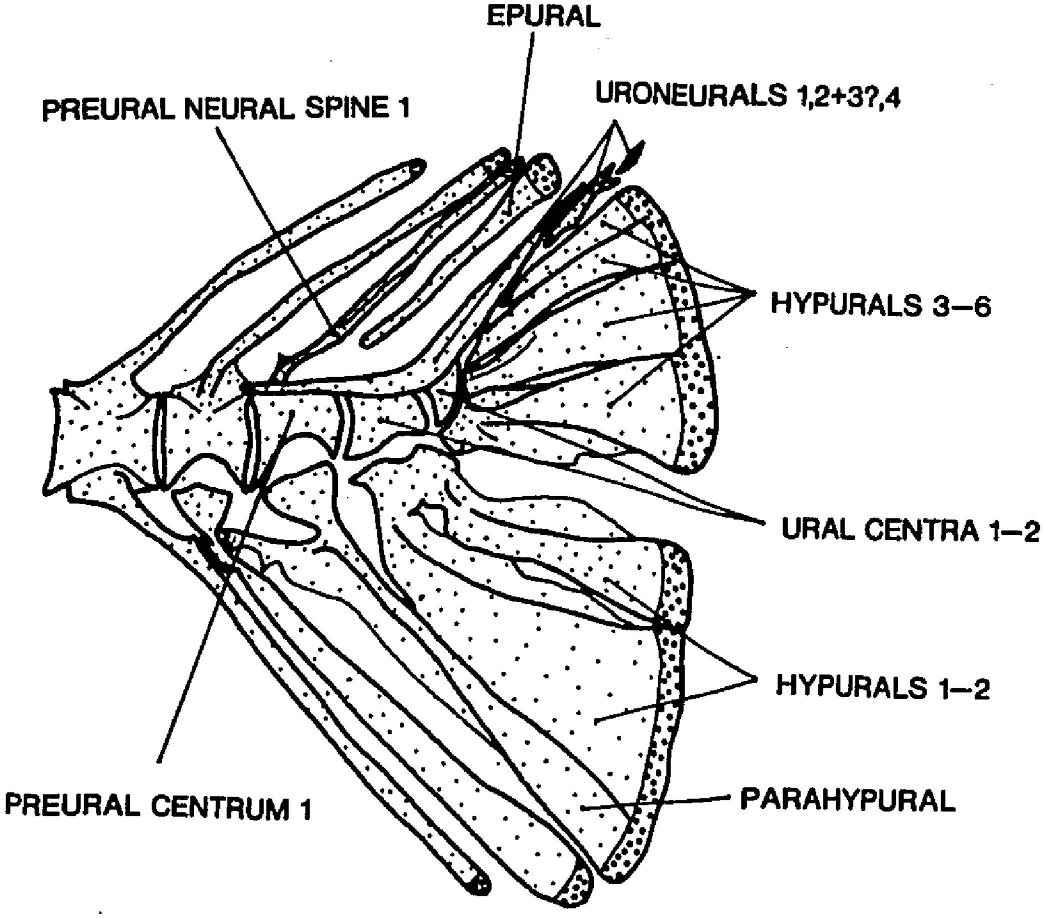
Bathytroctes microlepis (Fig. 19B) retains the minute fourth uroneural, laminar bone on three haemal spines and the parahypural, and the median and ventral caudal radials. The parahypural has a small peg-like process and the base of the fused third and fourth hypural is expanded below and along the side of the second ural centrum. The caudal formula is 14, 10+9, 12.

Alepocephalus agassizii (Fig. 20A) has a peg-like process on the parahypural and the base of the third hypural is variously expanded below the second ural centrum. There is one long epural and a small circular ossification anteriad, two pairs of uroneurals and a minute third ossification, the remains of at least one ural neural arch, and both ventral and median caudal radials. The latter each support a fin ray. The caudal formula is 15, 10+9, 15.

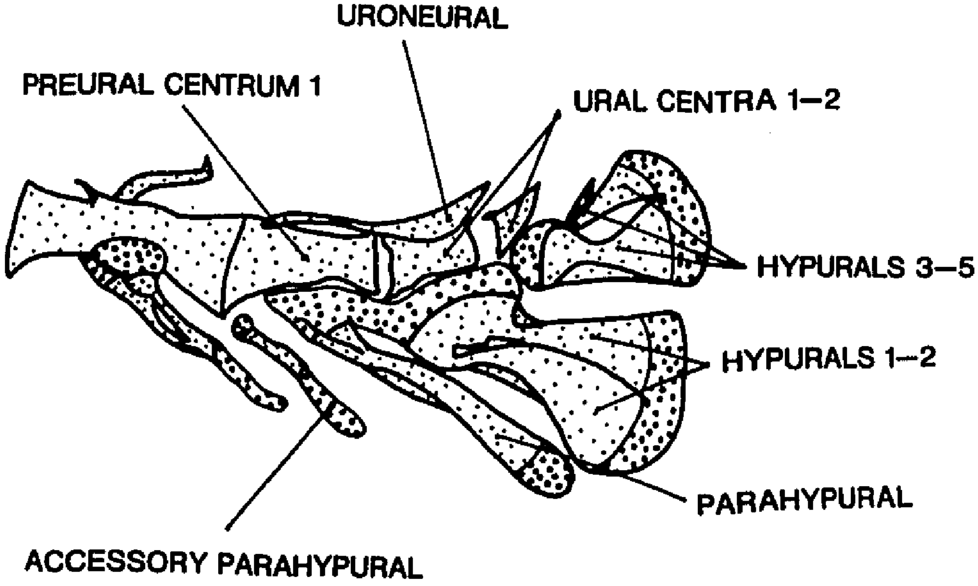
Fig. 18

A. Conocara mcdonaldi, USNM 215599, ca. 285 mm SL, caudal skeleton.

B. Leptoderma macrops, USNM 215605, 195 mm SL, caudal skeleton.


EPURAL
PREURAL NEURAL SPINE 1
URONEURALS 1,2+3?,4
HYPURALS 3–6
URAL CENTRA 1–2
HYPURALS 1–2
PARAHYPURAL
PREURAL CENTRUM 1

A

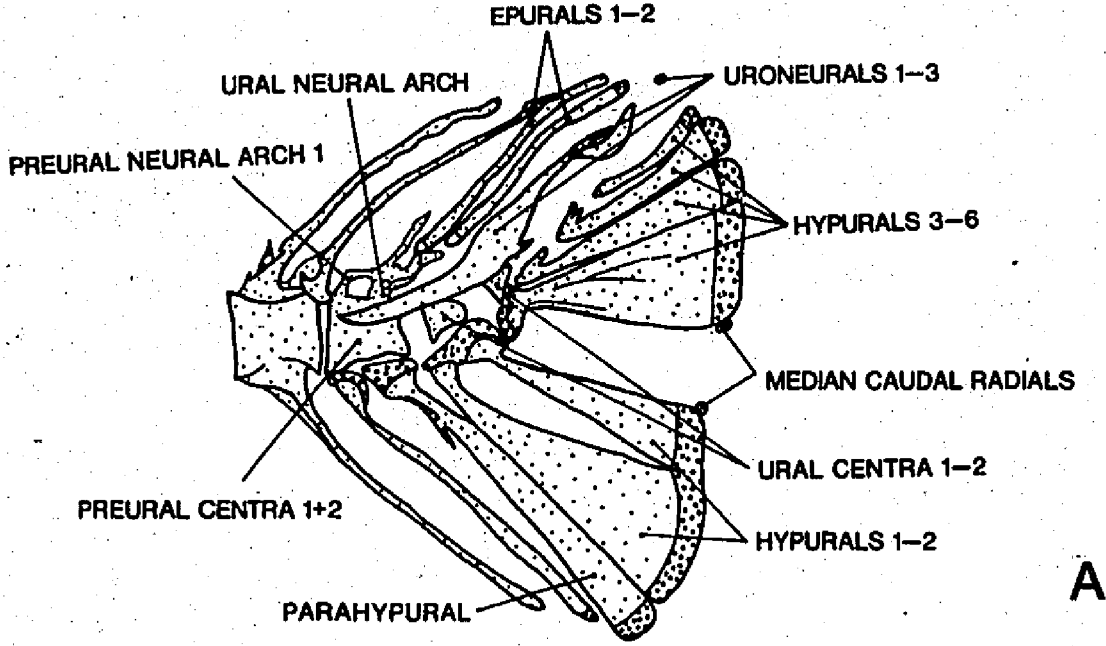

URONEURAL
PREURAL CENTRUM 1
URAL CENTRA 1–2
HYPURALS 3–5
HYPURALS 1–2
PARAHYPURAL
ACCESSORY PARAHYPURAL

B

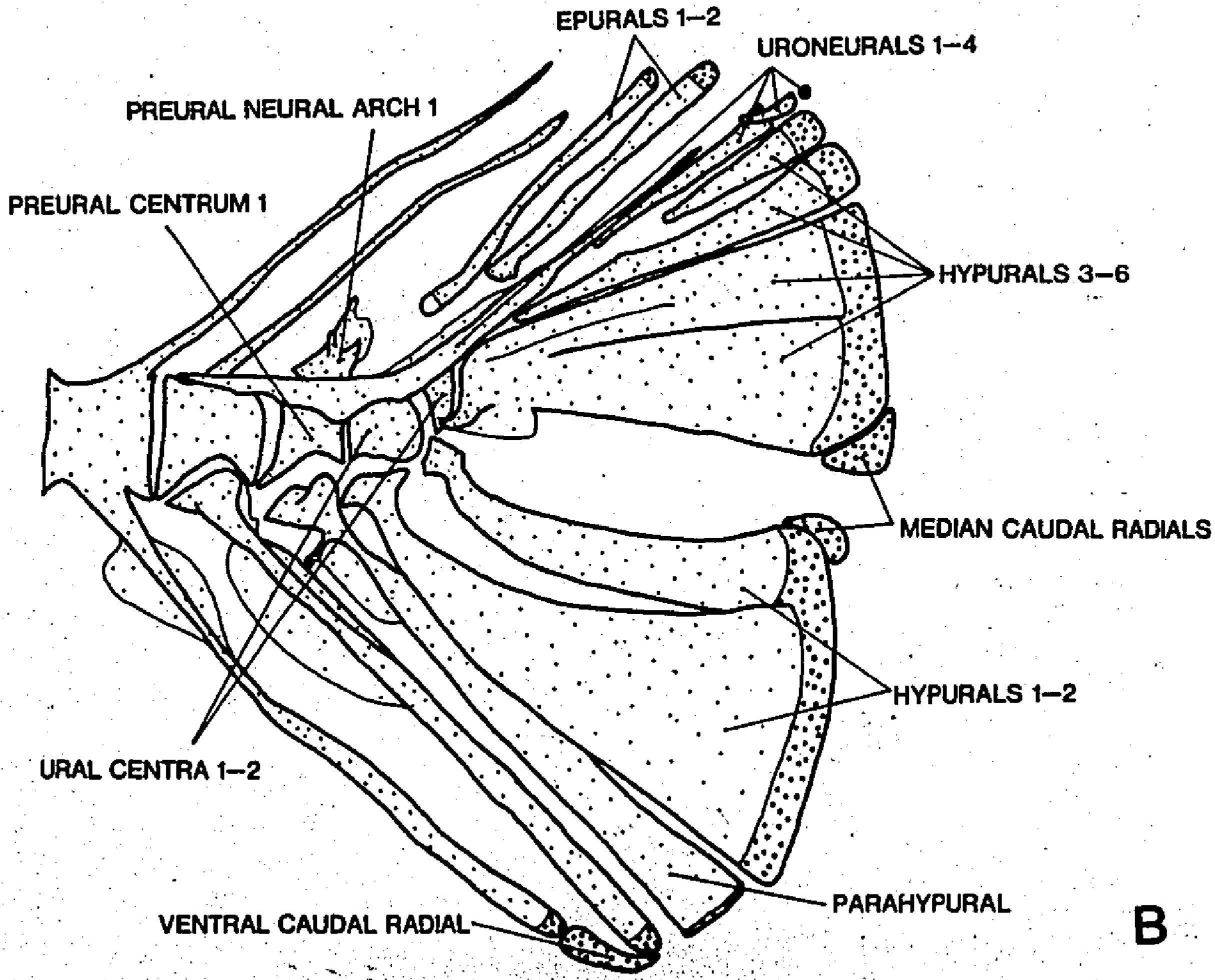
Fig. 19

A. *Einara edentulus*, NIO uncatalogued, 116 mm SL, caudal skeleton.

B. *Bathytroctes microlepis*, USNM 215493, 276 mm SL, caudal skeleton.


EPURALS 1–2
URONEURALS 1–3
URAL NEURAL ARCH
PREURAL NEURAL ARCH 1
HYPURALS 3–6
MEDIAN CAUDAL RADIALS
URAL CENTRA 1–2
PREURAL CENTRA 1+2
HYPURALS 1–2
PARAHYPURAL

A


EPURALS 1–2
URONEURALS 1–4
PREURAL NEURAL ARCH 1
PREURAL CENTRUM 1
HYPURALS 3–6
MEDIAN CAUDAL RADIALS
HYPURALS 1–2
URAL CENTRA 1–2
PARAHYPURAL
VENTRAL CAUDAL RADIAL

B

In the subgenus Lloydiella, represented by a specimen of Alepocephalus bicolor (Fig. 20B), there are two epurals, three pairs of uroneurals and the ural and first preural neural arches have fused. A peg-like process on the parahypural is present and the base of the fused third and fourth hypurals produces another peg-like process which meets a similar structure from the second hypural in a flat cartilagenous joint. No ventral caudal radial was found and the two small median caudal radials each support a fin ray. The caudal formula is 18, 10+9, 15.

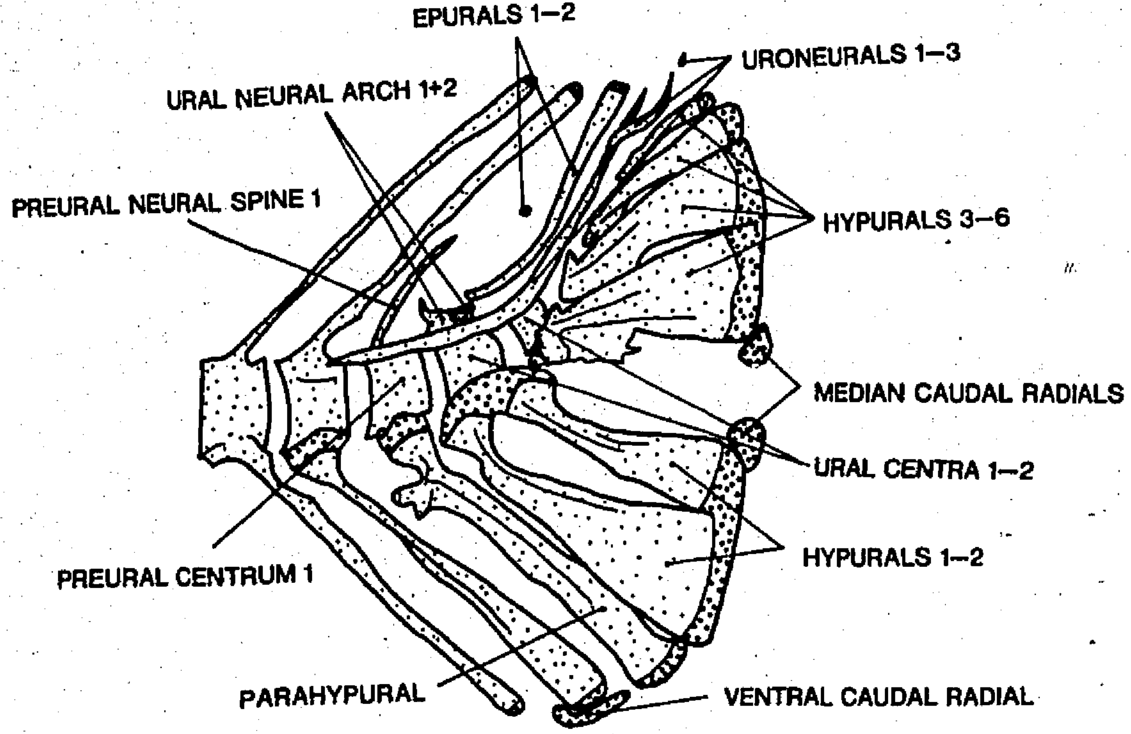
It should be apparent from the emphasis in some of the preceding descriptions that I consider the elimination of the oblique plane of flexion or "chondrostean hinge" important. Patterson (1968) has commented on the functional significance of the elimination of the "hinge" and considered it the essential change in the tail at the pholidophorid/leptolepid transition, i.e. as a distinguishing feature of the Teleostei.

At the alepocephaloid level further stiffening of the "hinge" has occurred. One method has been through the ventral expansion of the base of the third or third and fourth hypurals. This has led to a structure which either provides rigidity and support to the base of the second hypural (Mentodus, Fig. 13B, and Photostylus, Fig. 16A) or sutures to a similar basal process from the second hypural (Alopecephalus, subgenus Lloydiella, Fig. 20B). A second stiffening device has involved the expanded first pair of uroneurals and one or more epurals which insert between the bony plates of the uroneurals (Narcetes, Fig. 12A; Bathyloco, Fig. 13A; Mentodus, Fig. 13B; and Bathyprion, Fig. 14A). The latter device may be the fortuitous result of two separate developments. One is the lengthening of epurals and preural neural spines which is associated with the loss of the "chondrostean hinge" in many early teleosts

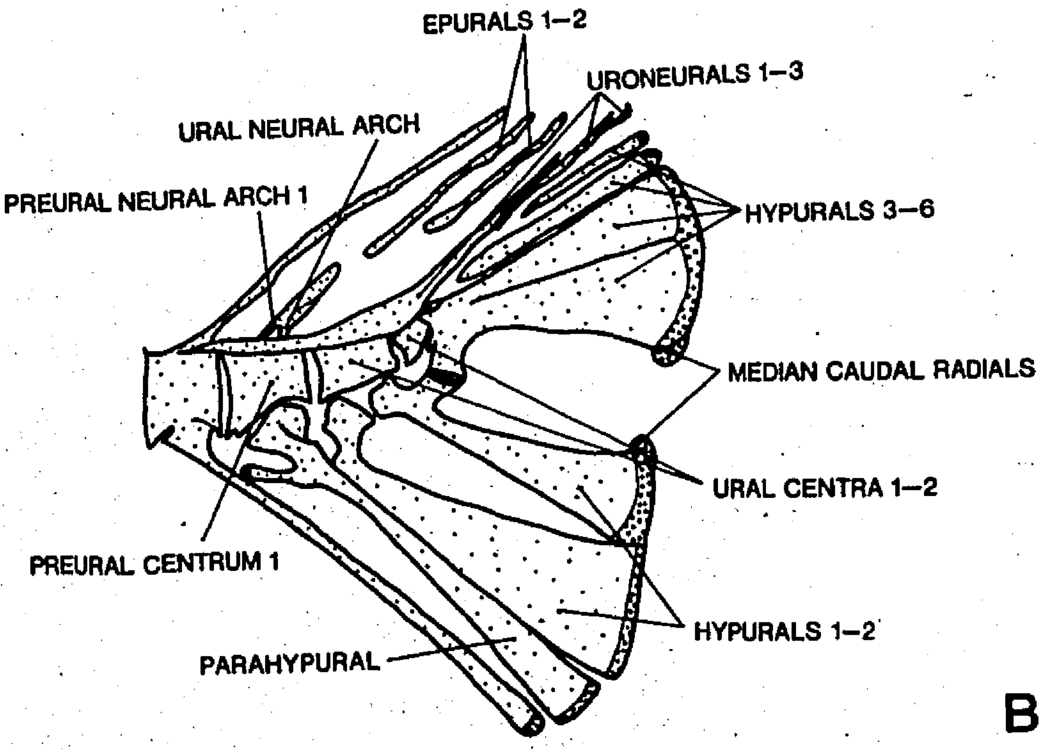
Fig. 20

A. *Alepocephalus agassizii*, USNM 215579, 345 mm SL, caudal skeleton.

B. *Alepocephalus* (*Lloydiella*) *bicolor*, USNM 215607, caudal skeleton.


EPURALS 1–2
URONEURALS 1–3
URAL NEURAL ARCH 1+2
PREURAL NEURAL SPINE 1
HYPURALS 3–6
MEDIAN CAUDAL RADIALS
URAL CENTRA 1–2
HYPURALS 1–2
PREURAL CENTRUM 1
PARAHYPURAL
VENTRAL CAUDAL RADIAL

A


EPURALS 1–2
URONEURALS 1–3
URAL NEURAL ARCH
PREURAL NEURAL ARCH 1
HYPURALS 3–6
MEDIAN CAUDAL RADIALS
URAL CENTRA 1–2
PREURAL CENTRUM 1
HYPURALS 1–2
PARAHYPURAL

B

(Patterson 1968), and the other is the outgrowth of laminar bone on the first uroneural, an advanced feature, which is also associated with stiffening the tail.

Pectoral girdle:

The pectoral fin is moderately high on the side of the body in most alepocephaloids. Exceptions are Bathylaco which has reduced fins located relatively low on the side and Leptochilichthys which has a ventrolateral pectoral base and fin rays aligned horizontally.

Typically in alepocephaloids, there is a forked post-temporal, a supracleithrum, and no postcleithra. In Leptochilichthys agassizii Fig. 21A), a mesocoracoid is present; the cleithrum has a slight expansion of laminar bone dorsolateral to the scapula; the ventral process of the coracoid (VPC) is directed sub-horizontally, about parallel to the posterior (ventral) primary radial; and there is a sheet-like ligament (not shown) from the ventro-medial area of the cleithrum to the VPC. There are nine pectoral rays supported by six cartilagenous distal radials in turn supported by four ossified proximal radials. The anterior (dorsal) distal radial has a proximal groove which fits over the scapular cartilage in a saddle joint arrangement, a condition found in all alepacephaloids.

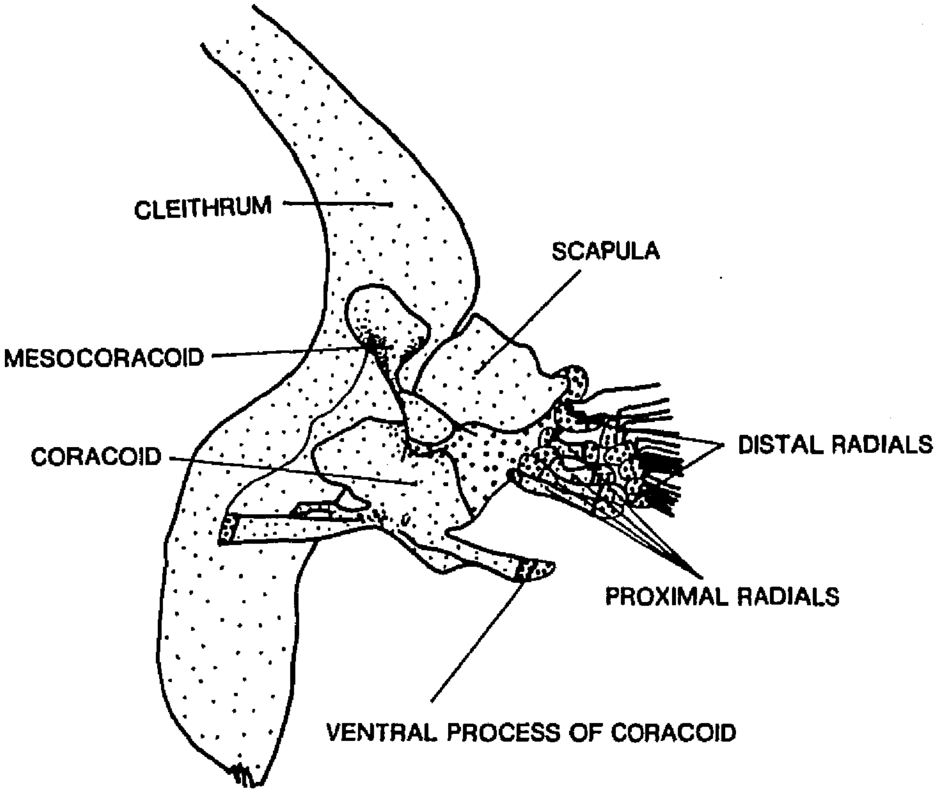
The pectoral girdle of the searsid Mentodus rostratus (Fig. 21B) is similar to that of L. agassizii, but the VPC is much shorter and has no ligament. Further, the expanded cleithrum in M. rostratus is crenellated.

In Bathytroctes microlepis and Narcetes stomias (Fig. 22A & B) there is little departure from the Leptochilichthys condition. Notably, the ventral process of the coracoid and associated ligament are little changed, there are still four proximal radials and the dorsal distal radial articulates with the scapula by a saddle joint. They differ from

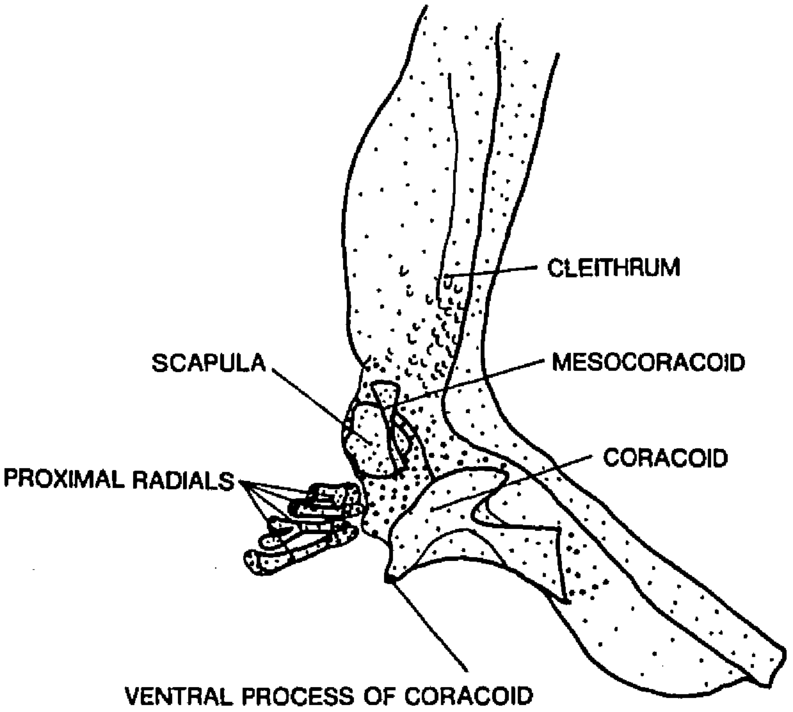
Fig. 21

A. *Leptochilichthys agassizii*, ISH 916/73, 255 mm SL, pectoral girdle, medial view, right side.

B. *Mentodus rostratus*, USNM 215612, ca. 135 mm SL, pectoral girdle, medial view, left side.


CLEITHRUM
SCAPULA
MESOCORACOID
CORACOID
DISTAL RADIALS
PROXIMAL RADIALS
VENTRAL PROCESS OF CORACOID

A

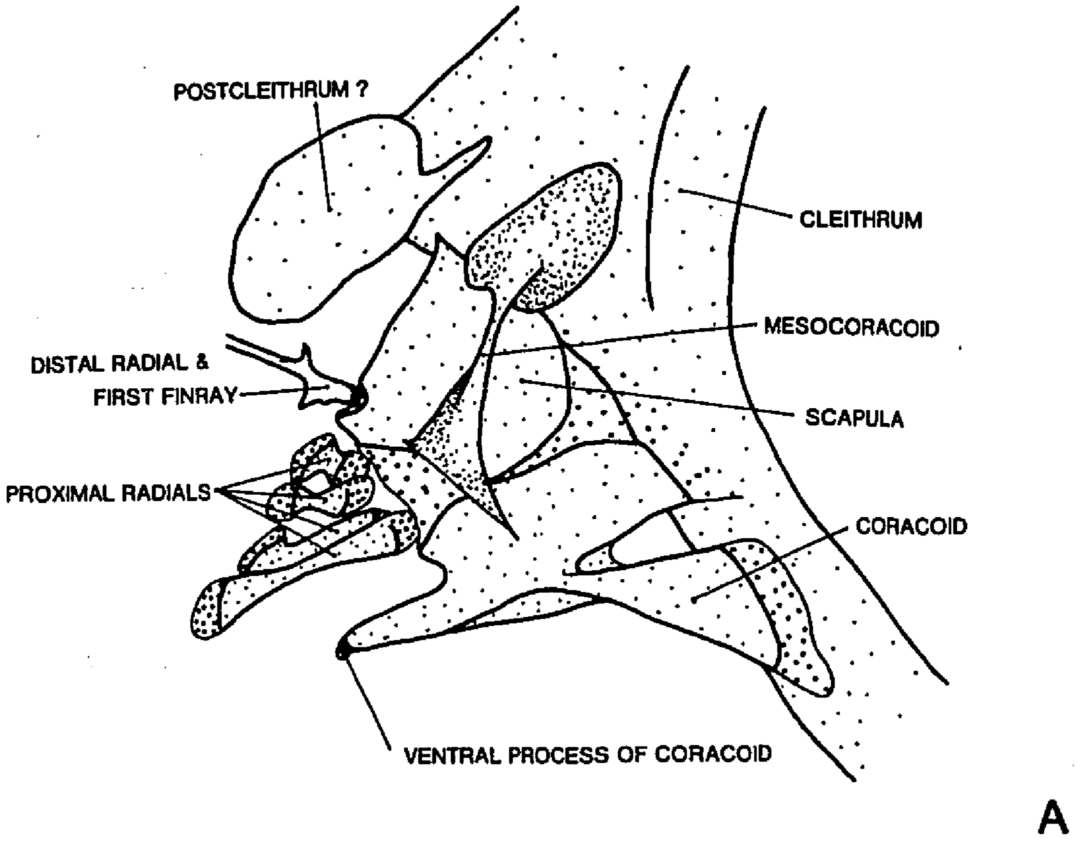

CLEITHRUM
SCAPULA
MESOCORACOID
CORACOID
PROXIMAL RADIALS
VENTRAL PROCESS OF CORACOID

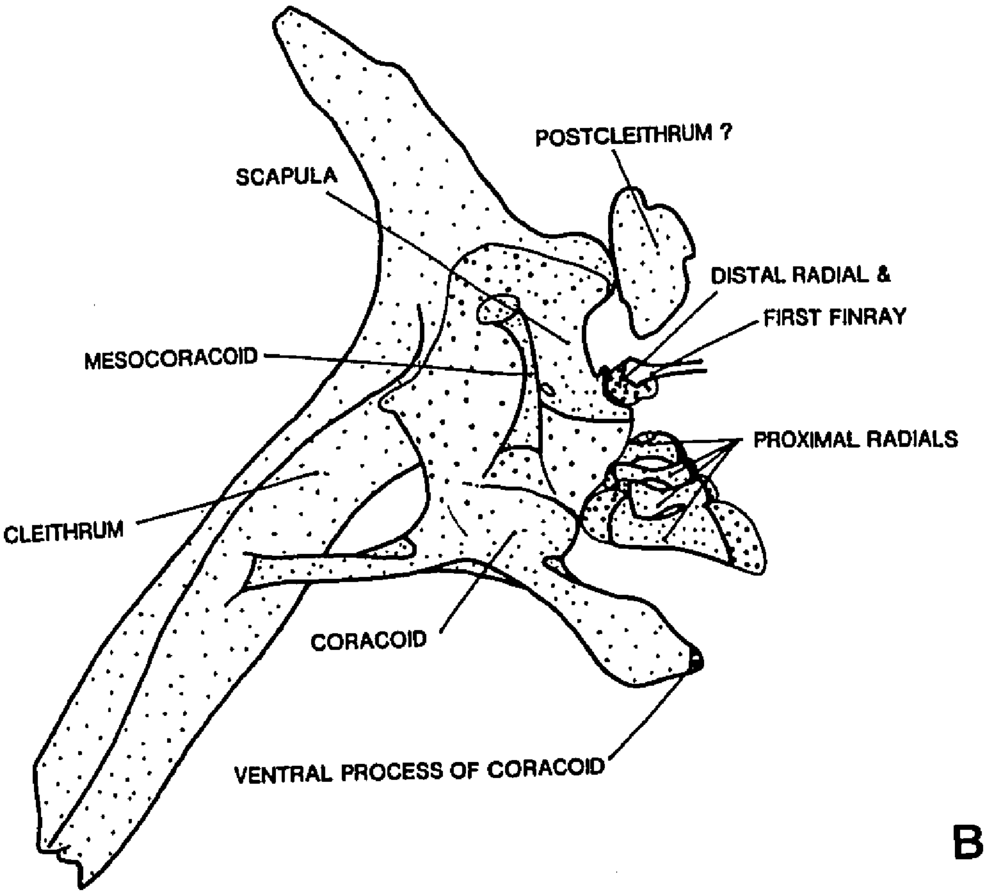
B

Fig. 22

A. *Bathytroctes microlepis*, USNM 215493, 276 mm SL, pectoral girdle, medial view, left side.

B. *Narcetes stomias*, USNM 215515, 473 mm SL, pectoral girdle, medial view, right side.


POSTCLEITHRUM ?
CLEITHRUM
MESOCORACOID
DISTAL RADIAL &
FIRST FINRAY
SCAPULA
PROXIMAL RADIALS
CORACOID
VENTRAL PROCESS OF CORACOID
A


POSTCLEITHRUM ?
SCAPULA
DISTAL RADIAL &
FIRST FINRAY
MESOCORACOID
PROXIMAL RADIALS
CLEITHRUM
CORACOID
VENTRAL PROCESS OF CORACOID
B

Leptochilichthys in the noticeably expanded cleithrum dorsolateral to the scapula and the thin scale-like structure tentatively identified as a remnant of a dorsal postcleithrum. In Bathytroctes microlepis there are 12 rays, each supported by a small distal radial, and in Narcetes stomias there are 11 rays supported by 9 distal radials.

Bajacalifornia calcaratus and Bathylaco nigricans (Fig. 23A & B) begin to show specializations found in many other genera. The postcleithrum is a small remnant on the right pectoral and is missing on the left pectoral of B. calcaratus (Fig. 23A), but is retained in B. nigricans (Fig. 23B). In both, the cleithrum is perforated as is the scapula in B. calcaratus. The ventral process of the coracoid is directed ventrally and is aligned almost perpendicular to the plane of the ventral proximal radial. The ligament of the VPC is retained in Bathylaco and possibly in Bajacalifornia but this could not be positively verified. In B. calcaratus there are 14 rays supported by 12 distal radials, the dorsal most articulating with the scapula by a saddle joint. In B. nigricans there are 8 rays, six distal radials and only two proximal radials. Again there is a saddle joint between the dorsal distal radial and the scapula.

In Alepocephalus rostratus and A. agassizii (Fig. 24A & B), as well as A. bairdii and A. (Lloydiella) bicolor, the ventral process of the coracoid is largely cartilagenous. However, the degree of ossification of the VPC appears size dependent in A. agassizii since it is totally cartilagenous in an 87.9 mm SL specimen and has just begun to ossify in a 142 mm SL specimen. No sheet like ligament could be found associated with the VPC in any Alepocephalus. Instead, the space between it and the cleithrum is bridged by thin connective tissue. The scapula in Alepocephalus has a groove (A. agassizii and A. bairdii) or foramen (A. rostratus

Fig. 23

A. Bajacalifornia calcaratus, UMML 15157; ca. 345 mm SL, pectoral girdle, medial view, left side.

B. Bathylaco nigricans, USNM 206693, 268 mm SL, pectoral girdle, medial view, right side.

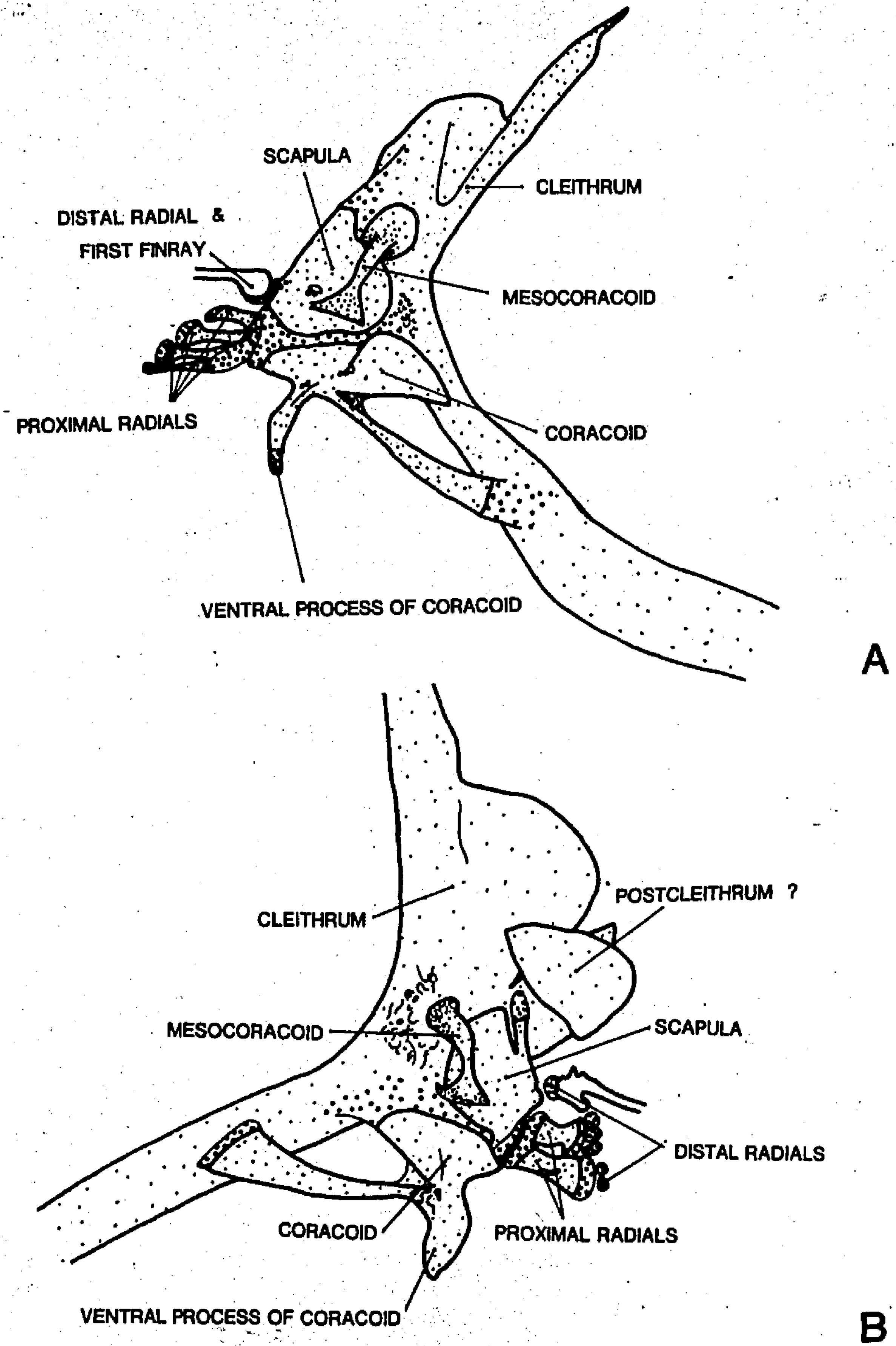
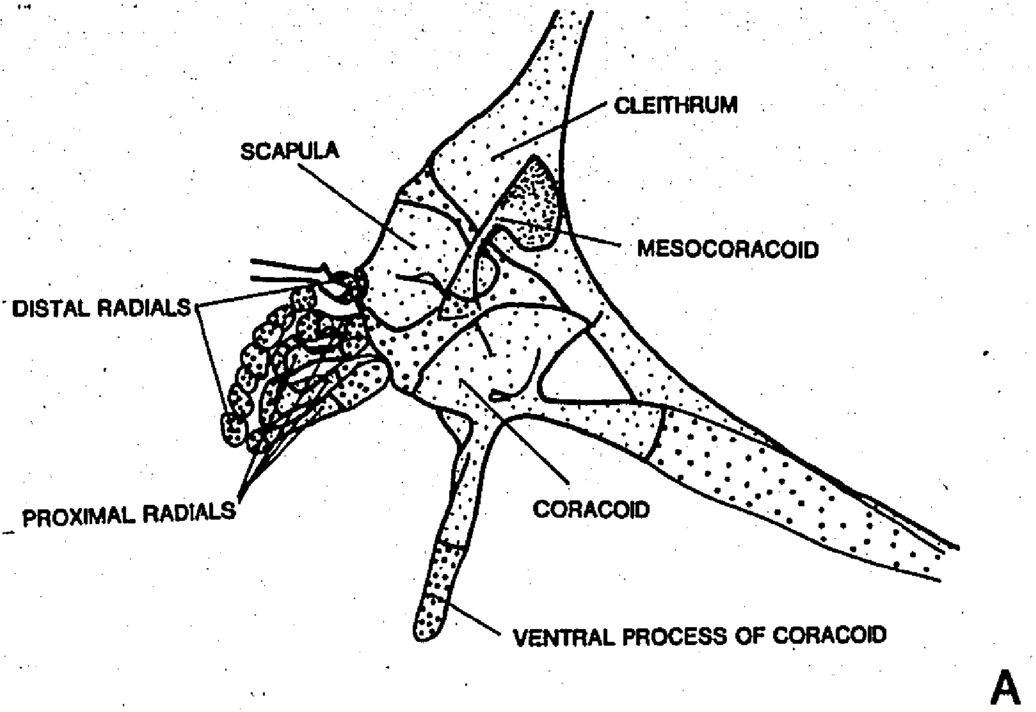
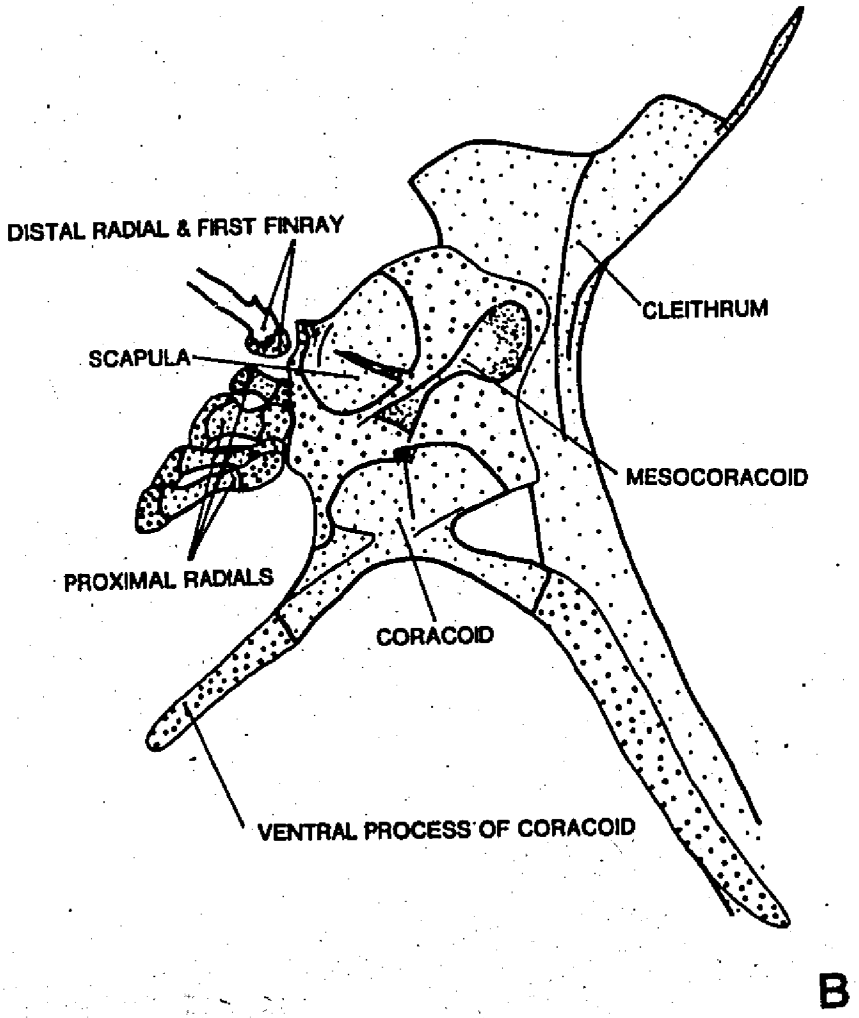

SCAPULA
CLEITHRUM
DISTAL RADIAL &
FIRST FINRAY
MESOCORACOID
PROXIMAL RADIALS
CORACOID
VENTRAL PROCESS OF CORACOID
A
POSTCLEITHRUM ?
CLEITHRUM
MESOCORACOID
SCAPULA
DISTAL RADIALS
CORACOID
PROXIMAL RADIALS
VENTRAL PROCESS OF CORACOID
B

Fig. 24

A. <u>Alepocephalus</u> <u>rostratus</u>, NIO uncatalogued, 271 mm SL, pectoral girdle, medial view, left side.

B. <u>Alepocephalus</u> <u>agassizii</u>, USNM 215579, 345 mm SL, pectoral girdle, medial view, left side.


CLEITHRUM
SCAPULA
MESOCORACOID
DISTAL RADIALS
PROXIMAL RADIALS
CORACOID
VENTRAL PROCESS OF CORACOID
A


DISTAL RADIAL & FIRST FINRAY
SCAPULA
CLEITHRUM
MESOCORACOID
PROXIMAL RADIALS
CORACOID
VENTRAL PROCESS OF CORACOID
B

and *A.* (*Lloydiella*) *bicolor*. The dorsal distal radial is joined to the scapula by a saddle joint although the groove in the radial is sometimes not well pronounced. In the specimens examined there were 9 rays on 8 distal radials in *A. rostratus* and 11 rays on 10 distal radials in *A. agassizii*. A remnant of the postcleithrum was found in *A. bairdii* and *A.* (L.) bicolor.

Talismania antillarum (Fig. 25A), *T. aphos*, and *T. oregoni* (Fig. 25B) have a foramen in the coracoid and the former two also have a foramen in the scapula. On both sides of the specimen of *T. antillarum* the ventral proximal radial is split distally. In *T. aphos* there are five separate proximal radials, the second from the bottom about two-thirds the length of its neighbors. An additional minute radial (?) is present on both sides of *T. antillarum*. In *Talismania oregoni* there is an opposite trend to consolidate proximal radials. On the left side of the specimen illustrated the two dorsal radials fused and on the right side the two ventral radials fused. The dorsal distal radial forms a saddle joint with the scapula. There are 16 rays supported by 16 distal radials in *T. antillarum* and 13 rays on 12 distal radials in *T. oregoni*.

In *Xenodermichthys copei* and *Rouleina maderensis* (Fig. 26A& B) there is a general reduction in ossification. The cleithrum is not expanded dorsolateral to the scapula and both have reduced numbers of radials. In *X. copei* there are three proximal radials, 6 distal radials (including the saddle joint), and 8 rays. In *Rouleina maderensis* there are two proximal radials, 6 distal radials (including the saddle joint) and 6 rays.

With the exception *Photostylus*, none of the remaining genera has a mesocoracoid. In *Ericara salmonea* (Fig. 27A), *Conocara mcdonaldi* (Fig. 27B), and *Leptoderma macrops* (Fig. 28A) there is a triangular expansion of the

Fig. 25

A. *Talismania antillarum*, USNM 215560, 140 mm SL, pectoral girdle, medial view, left side.

B. *Talismania oregoni*, USNM uncatalogued, 265 mm SL, pectoral girdle, medial view, left side.

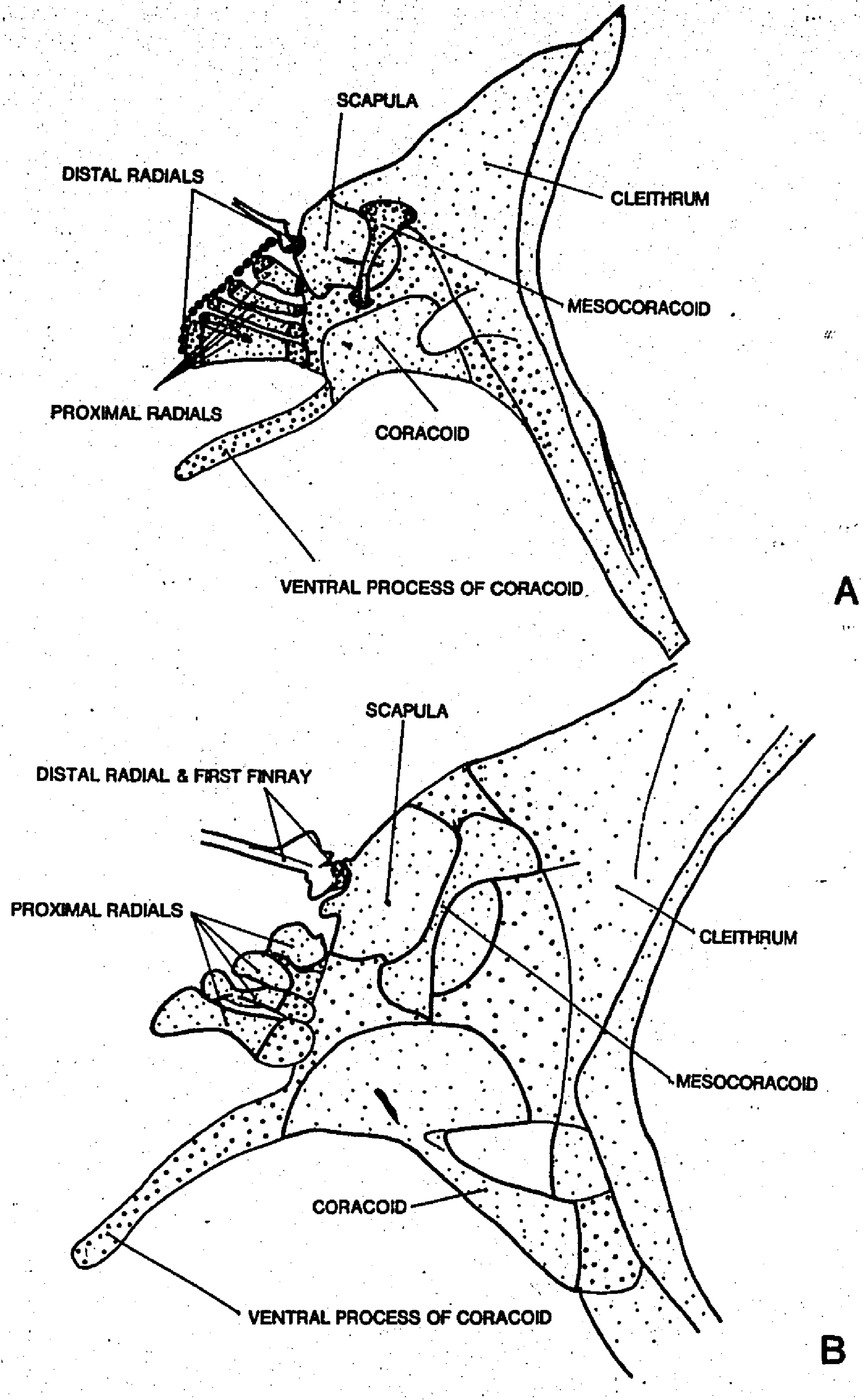
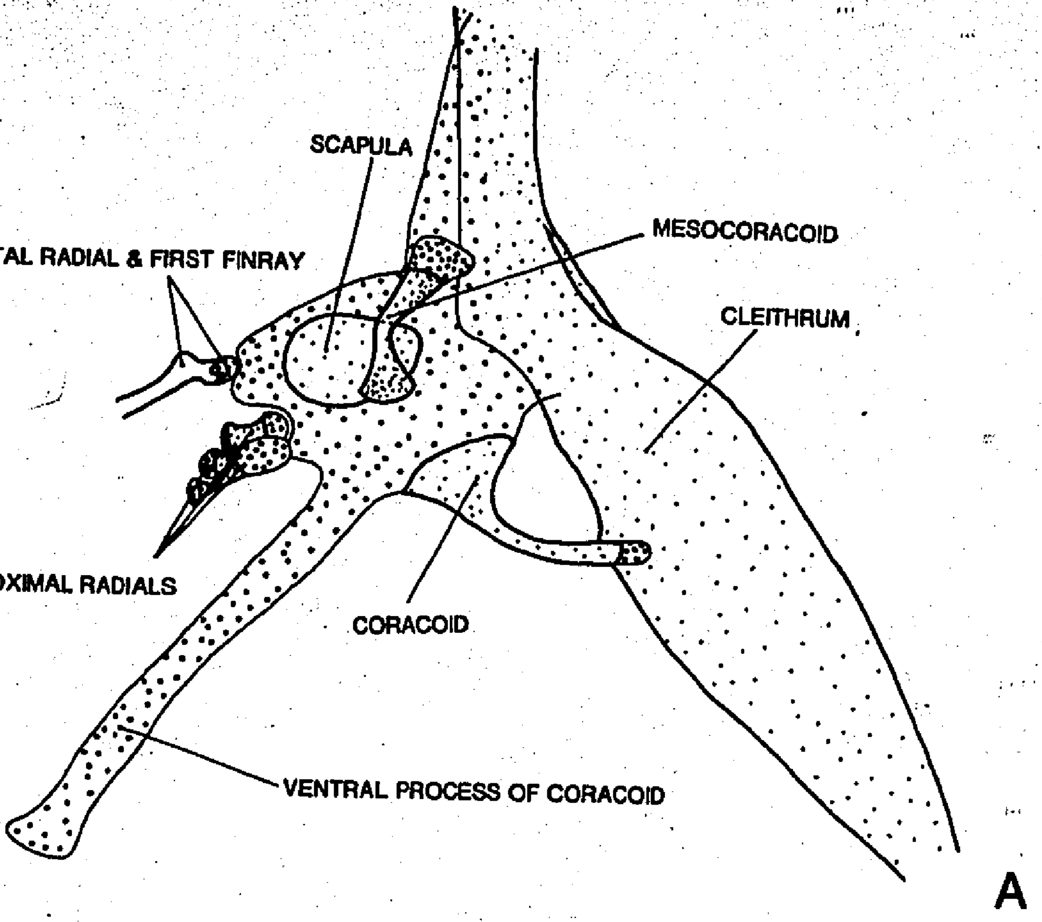

SCAPULA
DISTAL RADIALS
CLEITHRUM
MESOCORACOID
PROXIMAL RADIALS
CORACOID
VENTRAL PROCESS OF CORACOID
A
SCAPULA
DISTAL RADIAL & FIRST FINRAY
PROXIMAL RADIALS
CLEITHRUM
MESOCORACOID
CORACOID
VENTRAL PROCESS OF CORACOID
B

Fig. 26

A. *Xenodermichthys copei*, USNM 215539, 151 mm SL, pectoral girdle, medial view, left side.

B. *Rouleina maderensis*, USNM 215473, ca. 230 mm SL, pectoral girdle, medial view, left side.


SCAPULA
DISTAL RADIAL & FIRST FINRAY
MESOCORACOID
CLEITHRUM
PROXIMAL RADIALS
CORACOID
VENTRAL PROCESS OF CORACOID
A

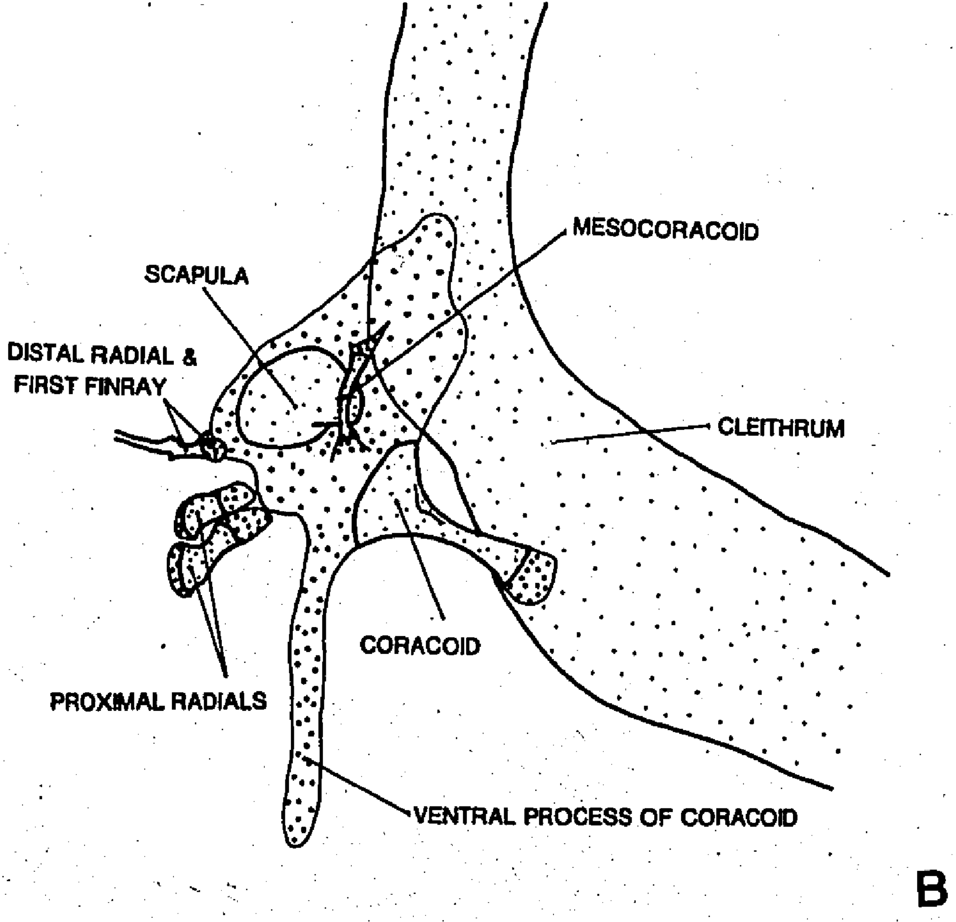
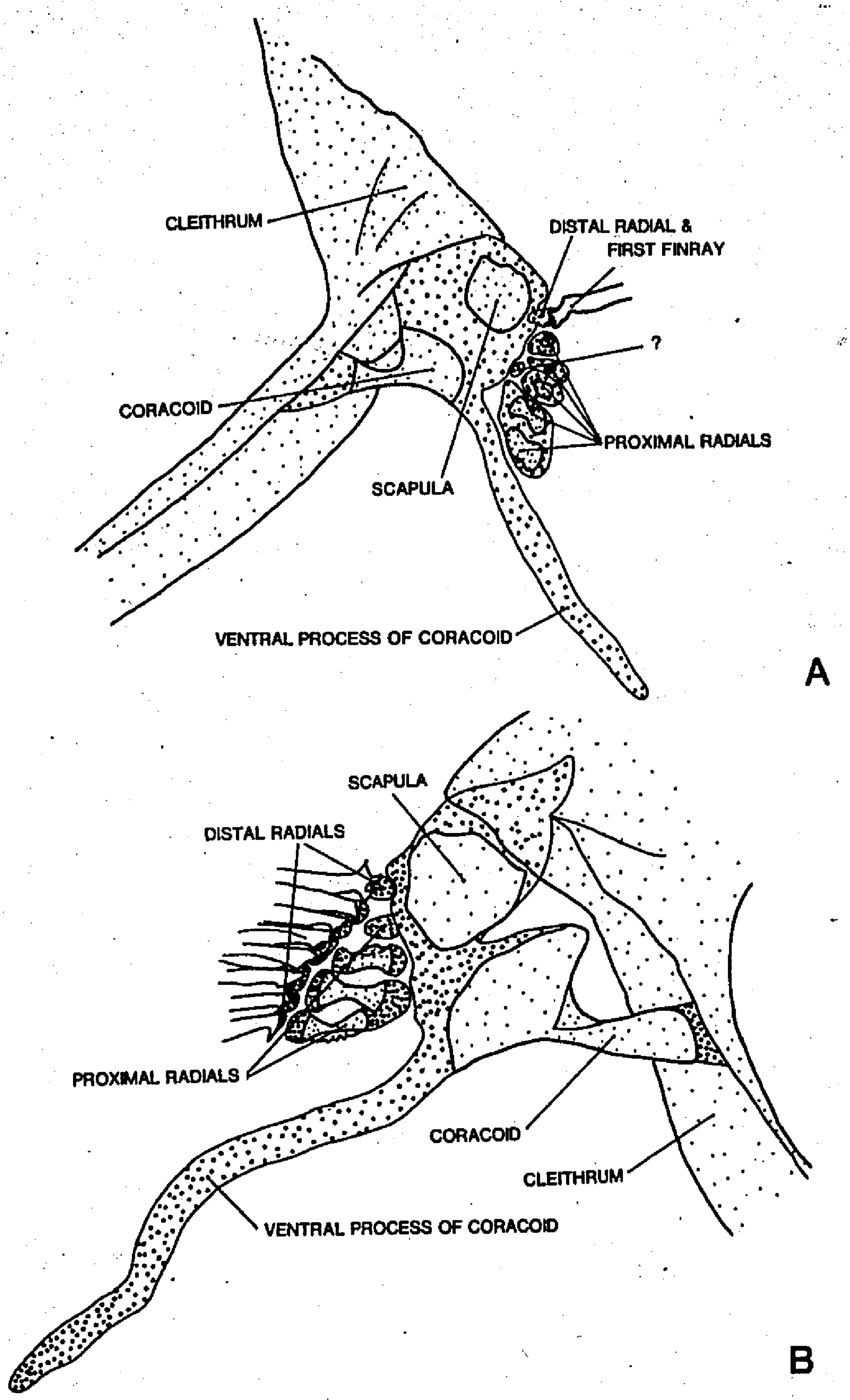

MESOCORACOID
SCAPULA
DISTAL RADIAL &
FIRST FINRAY
CLEITHRUM
CORACOID
PROXIMAL RADIALS
VENTRAL PROCESS OF CORACOID
B

Fig. 27

A. <u>Ericara</u> <u>salmonea</u>, UMML 32354, ca. 305 mm SL, pectoral girdle, medial view, right side.

B. <u>Conocara</u> <u>mcdonaldi</u>, USNM 215599, ca. 285 mm SL, pectoral girdle, medial view, left side.


CLEITHRUM
DISTAL RADIAL &
FIRST FINRAY
?
CORACOID
PROXIMAL RADIALS
SCAPULA
VENTRAL PROCESS OF CORACOID
A
SCAPULA
DISTAL RADIALS
PROXIMAL RADIALS
CORACOID
CLEITHRUM
VENTRAL PROCESS OF CORACOID
B

cleithrum dorsolateral to the scapula and a relatively elongate cartilagenous VPC. There are five ossified proximal radials on the right side and four on the left side of E. salmonea. An unidentified piece of cartilage (?) lies at the base of the third cartilage on both sides. In E. salmonea there are 8 distal radials including the saddle joint and 12 rays. Conocara mcdonaldi has three ossified and one cartilagenous proximal radial, 7 distal radials including the saddle joint and 8 rays. Leptoderma macrops has three ossified proximal radials (usually autogenous), five distal radials and 8 rays.

Einara edentulus (Fig. 28B) lacks laminar bone on the cleithrum and the specimen examined lacks ossification of the coracoid and scapula. There are three ossified and greatly expanded proximal radials which support 9 fin rays. Two cartilagenous radials are labelled distal radials though this identification is arguable. A specimen of Einara macrolepis has a pectoral girdle very similar to that of E. atlanticus in that it also lacks an expanded cleithrum and ossified coracoid and scapula and has three expanded proximal radials and at least two other cartilagenous radials (the precise number could not be determined).

A specimen of Asquamiceps hjorti was examined but pectoral girdle development was incomplete. However, the following features of this pectoral were noted: a mesocoracoid appeared to be absent, the scapula and coracoid were unossified, a VPC was present, four ossified proximal radials were present, two cartilageous distal radials of approximately equal size were present in a position as in E. edentulous (Fig. 28B) but unlike Einara, each of the 11 or 12 fin rays also had a distal radial.

In Bathyprion danae (Fig. 29A) and Mirognathus normani the pectoral fin is reduced and absent, respectively. In B. danae there are 9 rays

Fig. 28

A. Leptoderma macrops, USNM 215605, 195 mm SL, pectoral girdle, medial view, right side.

B. Einara edentulus, NIO uncatalogued, 116 mm SL, pectoral girdle, medial view, left side.

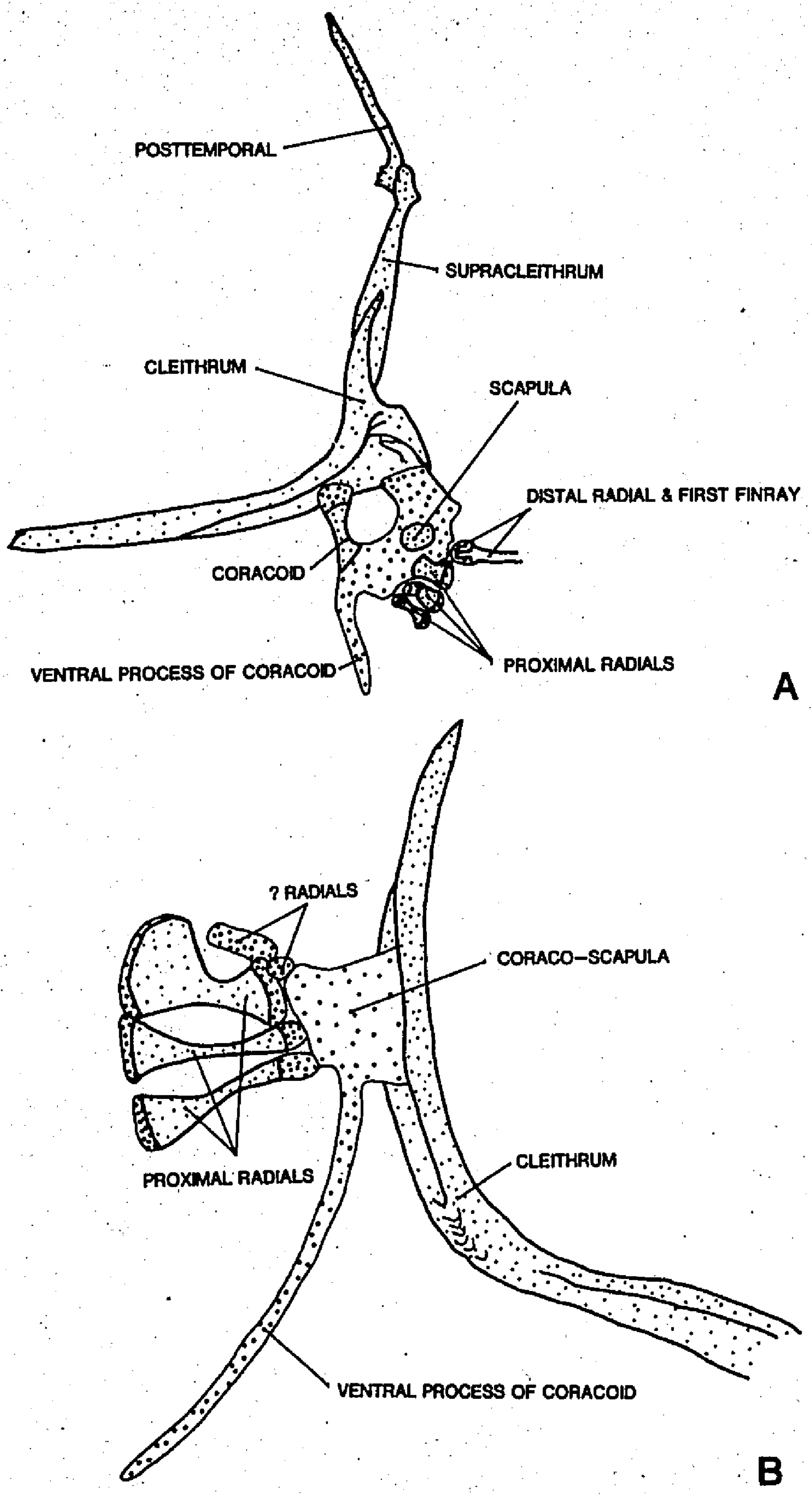
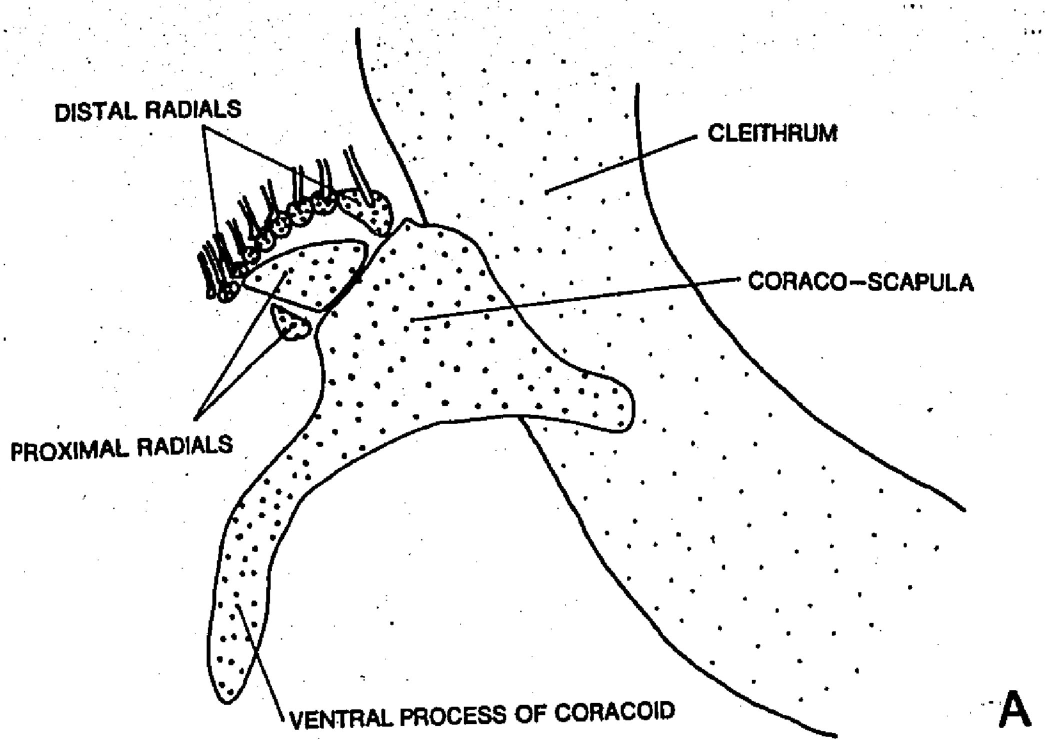
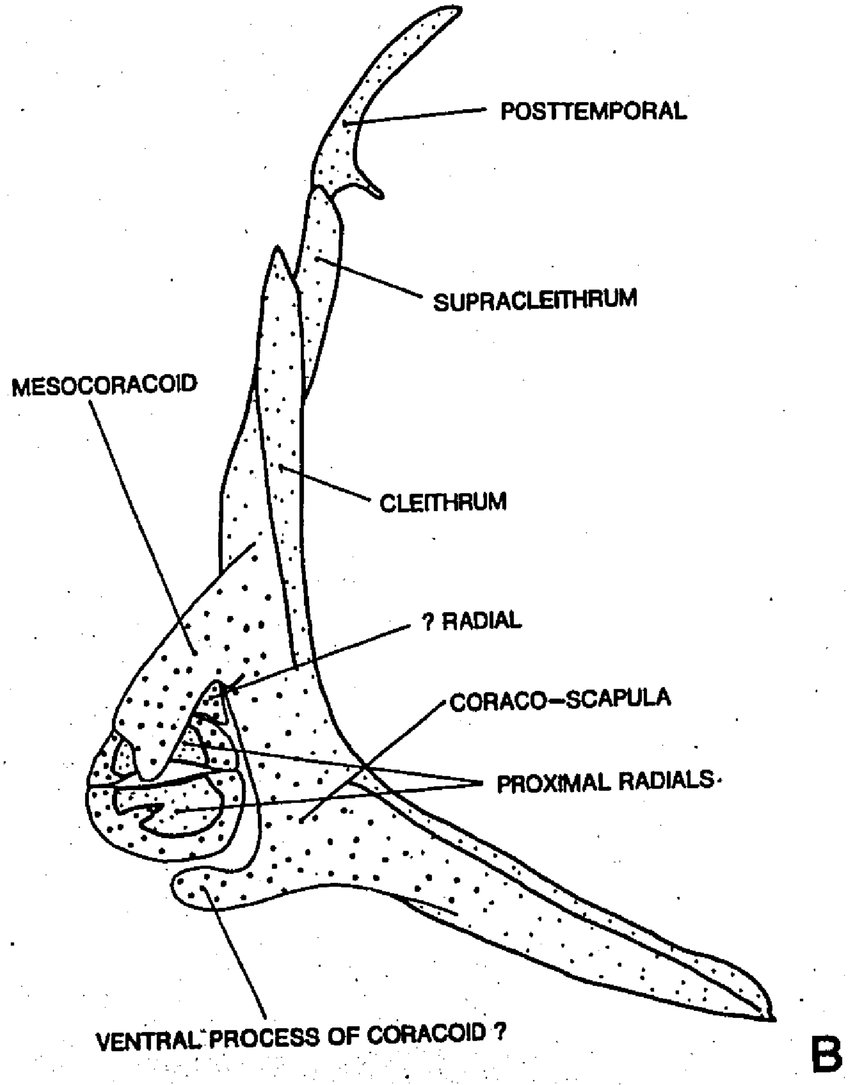

POSTTEMPORAL
SUPRACLEITHRUM
CLEITHRUM
SCAPULA
DISTAL RADIAL & FIRST FINRAY
CORACOID
VENTRAL PROCESS OF CORACOID
PROXIMAL RADIALS
A
? RADIALS
CORACO–SCAPULA
PROXIMAL RADIALS
CLEITHRUM
VENTRAL PROCESS OF CORACOID
B

Fig. 29

A. Bathyprion danae, ISH 1539/71, 252 mm SL, pectoral girdle, medial view, left side.

B. Photostylus pycnopterus, USNM 215518, 83 mm SL, pectoral girdle, medial view, left side.


DISTAL RADIALS
CLEITHRUM
CORACO–SCAPULA
PROXIMAL RADIALS
VENTRAL PROCESS OF CORACOID
A


POSTTEMPORAL
SUPRACLEITHRUM
MESOCORACOID
CLEITHRUM
? RADIAL
CORACO–SCAPULA
PROXIMAL RADIALS
VENTRAL PROCESS OF CORACOID ?
B

on 8 distal radials, all supported by one of two proximal radials. Like the radials the coraco-scapula and VPC are cartilagenous. In M. normani (ISH 917/73) no rays or radials were seen, but a VPC and reduced cartilagenous coraco-scapula are present.

A damaged pectoral from a specimen of Rinoctes nasutus was dissected and stained. There was no mesocoracoid, but there appeared to be a remnant of the postcleithrum, four proximal radials, and a well developed VPC.

The pectoral of Photostylus pycnopterus (Fig. 29B) differs noticeably from all other alepocephaloids thus far examined. There are no distal radials. The 17 to 20 pectoral rays are supported by the two ossified proximal radials which together form a nearly circular articular surface. A third cartilagenous radial is also present. The VPC is short, not directed ventrally, and together with the cartilagenous radial appears to provide dorso-ventral support to the two ossified radials. The mesocoracoid, if the structure in P. pycnopterus is homologous, is unique among teleosts. The proximal end arises from the coraco-scapular cartilage. The structure then arches towards the ossified radials where it ends unattached.

Pelvic fin and girdle:

Alepocephaloids can be divided into two grade groups on the basis of pelvic structure. In the first group (Leptochilichthys, Alepocephalus, Narcetes, Bajacalifornia, Bathylaco, Bathyprion, Bathytroctes, Nomoctes, and, presumably, Herwigia, Bellocia, and Brunichthys) are those genera that have 8(7-9) rays plus a pelvic splint. The others (Mentodus, Photostylus, Rinoctes, Mirognathus, Talismania, Rouleina, Xenodermichthys, Asquamiceps, Ericara, Conocara, Leptoderma, Einara, genus A, and presumably Anomalopterichthys, and Aulastomatomorpha) have 6(5-8) rays and no pelvic splint. The latter condition is derived although probably not indicative of common ancestry for the group, i.e. the pelvic splint has been lost and fin ray numbers have been reduced repeatedly.

Typically each half of the pelvic girdle consists of an elongate pubic process with a cartilagenous tip, an ossified pubic plate on either side of the proximal end of the pubic process, a large ischial cartilage with a variously ossified ischial plate, a generally poorly developed iliac process, a median distally ossified radial and zero to two additional radials. In addition there are sometimes various ischial processes within, above and below the plane of the ischial plate.

In *Bathytroctes* (Fig. 30A), *Alepocephalus*, and *Narcetes* the ischial processes are well developed. In species of these genera a cartilagenous dorsal ischial process is directed posteriad, sometimes past the ossified radial (Fig. 30A), and located above the plane of the ischial plate. There is also a cartilagenous ventral ischial process directed slightly posteroventrally which meets its opposite member at the midline (except in *Narcetes*). In these genera the pubic plate is expanded and well ossified medially as is the ischial plate posteriorly, there is a pelvic splint and seven or eight rays. There are usually one or two cartilagenous radials although in *B. microlepis* (Fig. 30A) the posterior surface of the two radials is ossified.

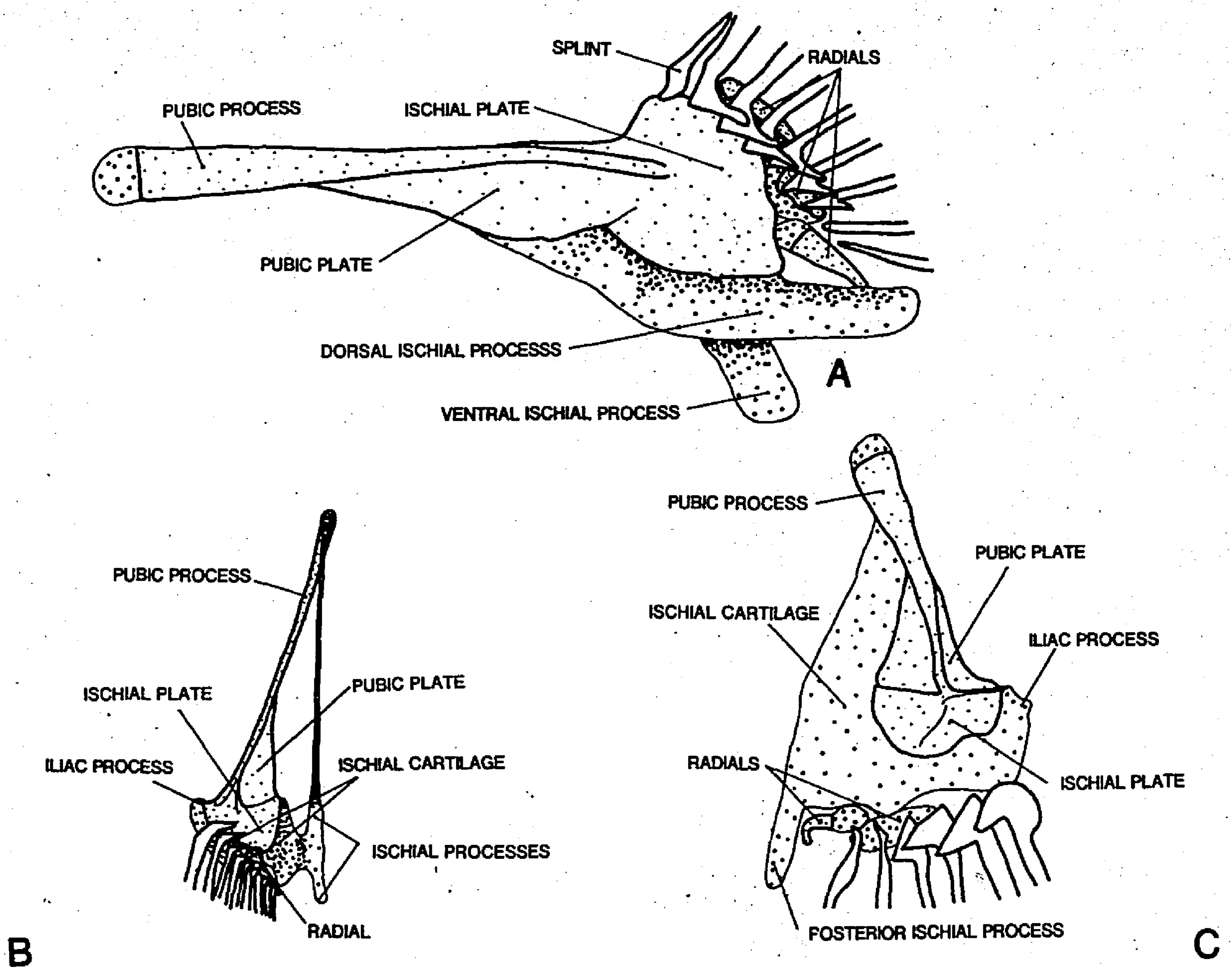
Bajacalifornia calcaratus and *Bathylaco nigricans* are very similar to the above genera except that the posteroventrally directed ischial process which is merely a small knob. *Bathylaco* has seven and *Bajacalifornia* has eight rays plus a splint. The ventral hemitrich of the innermost ray is rigidly attached to but not fused to the ossified medial radial in *Bathylaco*, similar to the condition in *Alepisaurus* (Gosline, et al, (1966).

Fig. 30

A. *Bathytroctes microlepis*, USNM 215493, 276 mm SL, pelvic girdle, dorsal view, right side.

B. *Talismania antillarum*, USNM 215560, 140 mm SL, pelvic girdle, dorsal view, left side.

C. *Ericara salmonea*, UMML 32354, ca. 305 mm SL, pelvic girdle, dorsal view, right side.


SPLINT
RADIALS
PUBIC PROCESS
ISCHIAL PLATE
PUBIC PLATE
DORSAL ISCHIAL PROCESSS
VENTRAL ISCHIAL PROCESS
A
PUBIC PROCESS
ISCHIAL PLATE
PUBIC PLATE
ILIAC PROCESS
ISCHIAL CARTILAGE
ISCHIAL PROCESSES
RADIAL
B
PUBIC PROCESS
PUBIC PLATE
ISCHIAL CARTILAGE
ILIAC PROCESS
RADIALS
ISCHIAL PLATE
FOSTERIOR ISCHIAL PROCESS
C

Leptochilichthys agassizii has nine rays plus a splint. Otherwise it differs from the above genera only in the cartilagenous ischial processes. The ventral process is moderately long and broad and meets its opposite member at the midline as in Bathytroctes (Fig. 30A). However, the dorsal process is very broad based and instead of being elongate posteriad, it arches away from the midline as a plate-like structure.

Bathprion danae has 8 rays plus a splint, but unlike the other forms with a splint, it has no median ossified radial and no dorsal or ventral ischial processes. The ischial cartilage is expanded medially and has a small posteriorly-directed process in the same plane as the ischial plate. The pubic plate is small. There are three cartilagenous radials, with the posterior surface of the outermost ossified.

Mirognathus normani is one of the few remaining forms without a median ossified radial. It has 5 rays, no splint, and no radials. Like Bathyprion it has a small pubic plate, a medially expanded ischial cartilage and a small posterior ischial process.

Mentodus rostratus has 8 rays, no splint, a well developed pubic plate and an ischial cartilage expanded medially where it contacts its opposite member. The ischial cartilage has a small dorsal process but no ventral process.

Asquamiceps hjorti, Einara edentulus, Rouleina mollis, R. maderensis, Xenodermichthys copei and Photostylus pycnopterus are all characterized by their small pubic plates, poorly developed or absent iliac process, no pelvic splint, and medially expanded ischial cartilage in contact, or nearly so, with its opposite member and small posteriorly-directed process. There are six rays in Photostylus, Xenodermichthys, Rouleina and Torictus and five in Asquamiceps.

With the exception of the searsid *Mentodus*, *Talismania* is the only genus without pelvic splints that has ischial processes outside the plane of the ischial plate (Fig. 30B). In this genus the pubic plate and iliac process are well developed. The medially expanded ischial cartilage has both a posterior and anterior process, the latter of which connects to the anterior tip of the pubic process through a ligament. There is a short posteriorly directed dorsal process in the subgenus *Talismania* and a fold in the ischial cartilage in the subgenus *Binghamichthys*. *Talismania* oregoni has 7 rays, *T. antillarum* has 8 and *T. aphos* has 6 or 7.

Ericara salmonea (Fig. 30C) has 6 rays, no pelvic splint, two radials including the median ossified one and a long posterior ischial process. In *Conocara mcdonaldi* which also has 6 rays and no splint, the pubic process is reduced and almost indistinguishable from the pubic plate. None of three radials in *Conocara* are ossified. In *Leptoderma macrops* which has 5 rays and no splint there is no pubic process, no posteriorly directed ischial process, and only one cartilagenous radial. The iliac process of *Leptoderma* is relatively well developed and directed dorsally as a small knob.

NARRATIVE PHYLOGENY AND OUTLINE CLASSIFICATION

Interfamilial relationships:

At the beginning of this study, as can be determined in some previous sections, I made the a priori assumption that the sister group of alepocephaloids was the argentinoids as proposed by Greenwood and Rosen (1971). Although other lower teleosts were examined during the course of this study (Appendix), their relationship to alepocephaloids was not critically reviewed. However, the cornerstone of the alepocephaloid-argentinoid relationship , the crumenal organ, requires comment. As preface to these comments, it should be noted that Greenwood and Rosen (1971) admit that many of the similarities between the two groups are the result of retention of primitive characters, to which list one can also add Ringfalten. That they could spend several pages listing characters that are more primitive in one group and more specialized in the other presumably indicates the distance of the proposed relationship and the differing selection pressures on the two groups. Acceptance of the crumenal organ as indicative of common ancestry of the two groups requires one to believe that the structure is complex, that it was evolved but once, and, by implication, that other epibranchial structures or the lack thereof in other fishes could not, parsimoniously, be derived from this structure.

According to Greenwood and Rosen (1971:5) "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". Rosen

(1974:274) tried to further establish the complexity of the structure in the statement, "In argentinoids the basibranchial tooth plate is invariably elevated medially into a sharp ridge..." It is obvious from the paragraph from which the latter was extracted that "argentinoids" refers to the suborder, not just the superfamily. As shown above, the accessory cartilage is not present in all alepocephalids and the sharp medial basibranchial ridge is virtually absent in every alepocephalid.

The idea of complexity associated with the crumenal organ rests primarily on the assumption that the accessory cartilage evolved <u>de novo</u> in a common ancestor of the two groups. Another possibility is that the accessory cartilage is a primitive, perhaps salmoniform, character which has remained, along with many other characters, almost unchanged in these two groups. Concerning loss of endoskeletal gill-arch elements, Nelson (1969:520) wrote, "A normal sequence of events seems to be an initial loss of ossification, resulting in an independent cartilaginous element, and its gradual reduction with loss of the resulting rudiment or its fusion with the cartilaginous articular areas of an adjacent ossified element". Within alepocephalids such a sequence has resulted in a <u>Bathyprion-Mirognathus</u> condition of no accessory cartilage plus a minute or fused fifth epibranchial (Fig. 11A) and a <u>Photostylus</u> condition in which neither element is present (Fig. 11B). Thus, within alepocephalids Nelson's regressive sequence is confined to some specialized bathypelagic members. These genera have probably been resident in a bathypelagic habitat for a long time and thus under selection pressures which differ from the benthic/engybenthic habitat of the main line of alepocephalid evolution.

Goody (1969) presents a useful outline of early teleost evolution which is germain to the previous statement. He postulates that: (1)

initial evolution of a salmoniform ancestor was in freshwater in the late Triassic and early Jurassic; (2) they reentered the seas at the close of the Jurassic; (3) they rapidly diversified in the Cretaceous in the more productive inshore and equatorial surface waters of the ocean; and (4) they were subjected to stern competition towards the close of the Cretaceous by beryciforms and their relatives which resulted in numerous extinctions and forced other salmoniform lineages into less favorable habitats. Although Goody (1969) mentioned only the deep pelagic habitat, the salmoniforms were forced into high latitudes as well. The Esocoidei and Salmonoidea are mainly high latitude freshwater groups and the Osmeroidea are high latitude coastal, estuarine and freshwater (Bigelow and Schroeder 1963, Rosen 1974). Only the Argentinoidea (Cohen 1964) and Alepocephaloidea are exclusively marine with benthic or engybenthic adults. Marshall (1963) logically assumes that early colonizers of deep water would live not far under the productive photic zone, i.e. mesopelagically. Among the groups forced into less favorable habitats by the Cretaceous beryciforms were also the structurally advanced (relative to salmoniforms) stomiatoids and myctophiforms (Goody 1969). From present distributions it can be assumed that these groups were competitively superior to argentinoids and alepocephaloids in this habitat. The latter apparently took up deep benthic residences on the upper and lower slope, respectively. In both groups specialized lineages subsequently took to the pelagic habitats secondarily. A few, although not all, of these pelagic forms indicate the ease with which the accessory cartilage and crumenal organ can be lost (see above).

If the crumenal organ is a primitive salmoniform character, its absence in only a few of the marine species but in all of the fresh-water groups may be indicative of habitat rather than phylogenetic similarity among its owners. A noticeable difference between freshwater, especially lotic, and marine habitats is the relative lack of plankton in the former. Even in estuaries planktonic organisms are at the mercy of currents and specialized behavioral mechanisms are needed to retain planktonic forms (Sandifer, 1975). A filtering mechanism for plankton could easily be lost during evolution in freshwater, although some lacustrine forms might be expected to retain or secondarily acquire a filtering mechanism.

As a prelude to further discussion, note that it is generally agreed that epibranchial organs (analogues of crumenal organs) are structural adaptations independently evolved in many microphagus lower teleosts (Nelson 1967, Bertmar, Kapoor and Miller 1969). Further, the autogenous patches of teeth or papillae on the esophogeal lining of the crumenal organ and the dentigerous gill rakers (Greenwood and Rosen 1971) bear a close resemblance to the pharyngeal sac papillae and gill rakers of stromateoids (Haedrich 1967). Stromateoids have relatively unspecialized, perhaps opportunistic, diets, which include jellyfishes (Haedrich 1967). The few alepocephalid stomachs examined in this study, as well as some examined by T. McLellan (Harvard) and Golovan and Pakhorukov (1975) also indicate unspecialized, opportunistic feeding, including frequent consumption of ctenophores and jellyfish. All of this suggests that an "ecological" explanation of the crumenal organ may be credible.

Where food is a potentially scarce resource, as is the case in the deep-sea in general (Dayton and Hessler 1972), a generalized opportunistic feeding "strategy" might have a selective advantage. The filtering and storage of diatoms and perhaps radiolarians (see above) during the course of normal respiration might represent a small additional metabolic expense that could increase the potential food supply of the species with this ability. If the crumenal organ is used for this purpose, its loss within specialized bathypelagic alepocephalids must be interpreted as an indication that the metabolic expense of the organ outweighed any advantage that it may have conferred upon its owner. Conversely, the retention of the organ in searsids and its aggrandizement, with associated structures, in leptochilichthyids (both bathypelagic groups) must be interpreted as an indication that the equation worked the other way. Thus, for example, the fact that the epibranchial structure of Photostylus (Fig. 11B) strongly resembles the esocoid (Rosen 1974:Fig. 8) lepidogalaxiid (Rosen 1974:Fig. 14) epibranchial skeleton suggests that the structure has undergone similar regressive evolution in different lineages. Furthermore, accessory structures such as the esophogeal papillae and teeth and the dentigerous gill rakers in stromateoids and alepocephaloids suggests that they are the result of convergence due to common ecological needs (microphagy or omnivory).

If the crumenal organ is accepted as a shared derived feature of alepocephaloids and argentinoids, one would hope for additional corroborative evidence. To date I know of no such evidence. I believe there are three possible interpretations of the crumenal organ: (1) it is a shared derived feature of the Argentinoidei; (2) it is a primitive feature at the salmoniform level which has been retained in Argentinoidea and Alepocephaloidea; (3) it represents a genetic potential which may or may not be developed within all members of a monophyletic group. The latter statement implies the possibility of secondary acquisition. I favor the second interpretation.

Prior to discussion on the possible higher relationships of alepocephaloids, the following summarizes the above anatomical information as it relates to an hypothetical ancestral alepocephaloid. The following are the most advanced features such an ancestor could be expected to have:

1. The adductor mandibulae had a thin section (AW) which inserted in the Meckelian fossa of the dentary.

2. Posteriad of AW the coronomeckelian received a ligament which passed medial to AW and arose from the medial fibers of the adductor mandibulae.

3. Through a ligament the lateral fibers of the adductor mandibulae inserted on the maxillary.

4. The levator operculi was a separate muscle.

5. The adductor arcus palatini-adductor hyomandibulae-adductor operculi was a single undivided muscle sheet.

6. The ovarian tunic covered the medial surface of the ovary only.

7. A crumenal organ was present.

8. *Ringfalten* were present.

9. A swimbladder was absent.

10. There were two supramaxillaries.

11. The hyomandibula had a dorsal articular surface separated from an opercular process.

12. Tooth plates were present on the second, third and fourth infrapharyngobranchials, fourth epibranchials, and fifth ceratobranchial.

13. The basihyal had teeth, with a minimal arrangement around the margins and along the midline.

14. The basibranchial, mesopterygoid, and ectopterygoid had no teeth.

15. The vomer, palatine, dentary, premaxillary and maxillary had teeth.

16. There were more precaudal than caudal vertebrae.

17. The dorsal origin was in advance of the anal origin and 50-60% SL behind the snout.

18. There were probably two ural centra, the first most likely of compound origin.

19. There were as many as two ural neural arches, four epurals, four uroneurals, and six hypurals.

20. Laminar bone was probably present on the posterior neural and haemal spines.

21. There were 19 principal caudal rays.

22. A mesocoracoid was present.

23. Postcleithra were absent.

24. The coracoid had a small ventral process.

25. The pelvic fin had a splint.

26. Intermuscular (epipleural and epineural) bones were present.

27. The retractor arcuum branchialium muscle was absent.

Other characters mentioned in the previous section or by Gosline (1960, 1969), Greenwood, Rosen, Weitzman and Myers (1966), Greenwood and Rosen (1971) and Rosen (1973, 1974) are of debatable information content and are not included above. Most of the above characters are primitive. Only points 3, 4, 9, 14 and 23 represent derived character states over the basal salmoniform condition (Greenwood, Rosen, Weitzman and Myers, 1966 as modified by Rosen and Patterson, 1969 and Rosen 1973, 1974). Only the insertion of the adductor mandibulae on the maxillary (point 3) is a nonreductional character.

Evolution of adductor mandibulae control of the maxillary probably came about through encroachment on the maxillo-mandibular ligamentous sheet. This is the type of maxillary connection found in <u>Oncorhynchus</u>, Salvelinus and Bathysaurus. This condition appears to have given rise to three derived character states. In one group, which includes Elops and most alepocephaloids, the lateral fibers of the adductor mandibulae tend to converge on a ligament which has a point insertion of the maxillary. In the second group, which includes the engraulid, Anchoa and Bathylaco, the adductor mandibulae has a broad musculous insertion on the maxillary which in Bathylaco has an antero-lateral twist also inserting on the maxillary.

A completely different type of adductor mandibulae control has evolved within the neoteleosts (see Rosen 1973). Most aulopiforms, including Bathysaurus, apparently lack such control except for what is gained through encroachment on the maxillo-mandibular ligamentous sheeth. Among aulopiforms only Saurida and Harpadon (Rosen 1973: Fig. 38 and 39, Saurida brasiliensis are known to have maxillary control. In these aulopiforms the maxillary is under the control of lateral adductor mandibulae fibers which could have evolved through an antero-lateral twist similar to that in Bathylaco. Unlike Bathylaco, these genera do not have A2 fibers inserting on the maxillary. Rosen (1973) and Winterbottom (1974a) apparently believe that the A1 section in neoteleosts arose through dorsal subdivision of an A2 which had encroached upon the maxillo-mandibular ligament. Once this occurred, expansion of A2 medial to A1 could, if the A1 insertion became musculous, produce the Saurida-Harpadon configuration. Among other neoteleosts A2 expansion lateral to A1 could produce the common stomiatoid arrangement where the muscle controlling the maxillary is usually medial to A2 and is called A1β. Alternatively, subdivision of A1 could preceed A2 expansion between the resulting two muscles with the lateral most of these (A1α) subsequently lost. Rosen (1973) apparently favored the latter because of the arrangement in Argyropelecus.

In alepocephaloids, and especially noticeable in those in which physical subdivision of the adductor mandibulae has occurred (Leptochilichthys and Talismania, Fig. 5), the fibers controlling the maxillary are lateral to A2. The medial fibers are always connected to the coronomeckelian ligament and are never involved with maxillary. The alepocephaloid adductor mandibulae is, therefore, derived over both basal salmoniform (sensu Rosen 1974) and basal neoteleostean (sensu Rosen 1973) states. Within salmoniforms there is a progression from Osmerus, Argentina and Bathylagus which do not seem to have a maxillary connection, to the salmonids which encroach upon the maxillo-mandibular ligament, to alepocephaloids which have a musculous or ligamentous insertion on the maxillary.

This character, a derived feature expected in the ancestor, does not provide convincincing evidence of relationship. Goody (1969:242) believes "several of the salmoniform suborders have the potential, latent or expressed, to produce a more advanced structural complex which in most cases approaches the myctophiform (=neoteleost) grade". Since they are relatively primitive, salmoniform lineages may not be easily discerned. Most seem to be distinguished by the presence or absence of one or more primitive characters sometimes in combination with advanced character states, i.e. mosaic evolution (Goody 1969). Although no formal higher classification is adopted herein, the best classification of alepocephaloids within the salmoniforms seems, at this time, to be the least structured classification as exemplified by Greenwood et al 1966).

Searsidae:

The searsids form an easily defined, monophyletic group characterized by the presence of a post-cleithral organ. This is a large round sac located medial to the upper portion of the cleithrum which discharges luminescent granules through a black-lined tube (Parr 1960, Herring 1972). Searsids differ further from the rest of the superfamily in the presence of a relatively characteristic photophore arrangement in some genera which, further, is subject to ontogenetic changes (Matsui and Rosenblatt 1971). Additional distinguishing characters are the dermal pits found in most, or all members (Parr 1960), a tendency towards thickening of the ventral abdominal wall, a tendency to develop horizontal forward-directed tusks (Parr 1951), and the presence of a short uncinate process on the fourth epibranchial (Greenwood and Rosen 1971).

With respect to the several characters examined in Mentodus during this study, the ancestral searsid can be hypothesized to coincide with an ancestral leptochilichthyid-alepocephalid. In an ancestral searsid the adductor mandibulae, dorsal fin position, precaudal-caudal vertebral arrangement, pectoral girdle, caudal skeleton, oral and pharyngeal dentition cannot be considered to have been more advanced than in the other two groups. Further, none of the derived features characteristic of some members of the latter families could have been present in the ancestral searsid since the condition in Mentodus, at least, is more primitive. For example, the adductor mandibulae is not subdivided; the dorsal origin is anteriad of the anal insertion; the precaudal vertebrae outnumber the caudal; the mesocoracoid is present; the ventral process of the coracoid is poorly developed; laminar bone is retained in the caudal; the oral and branchial dentition are, with the exception of questionable palatine teeth, as extensive as the most primitive members of the other families. Only the loss of the pelvic splint parallels a derived feature in some alepocephalids.

The present indication is that searsids represent an early invasion of the bathypelagic habitat. They are well defined and nothing has been found to alter the _a priori_ assumption that the group should be treated as anything less than a family.

Leptochilichthyidae:

Leptochilichthys is tentatively recognized as a family. It is distinguished by complex subdivision of the adductor mandibulae, loss of the basihyal, an edentate premaxillary and maxillary combined with a dentate vomer and palatine, a high bony basibranchial ridge and deep clupeoid-like maxillary which receives a lateral insertion of the adductor mandibular (A1).

The Leptochilichthyidae represents a second early invasion of the bathypelagic habitat. It is apparently unique as a bathypelagic filter-feeding alepocephaloid; its success apparently due to the above specializations. Except for these specializations, _Leptochilichthys_ displays a vast array of primitive features and shows none of the specializations found in some alepocephalid or searsid groups.

Among the primitive character states which are derived in some alepocephalids and searsids, _Leptochilichthys_ retains numerous (13) branchiostegal rays, the presumed primitive gill raker filtration system, primitive branchial dentition, more precaudal than caudal vertebrae, four pairs of uroneurals, four ural centra, laminar caudal bone, a dorsal insertion in advance of the anal insertion, a ventrolateral pectoral base, horizontally aligned pectoral rays, a mesocoracoid and a pelvic splint.

Leptochilichthys is very likely not far removed in most character states from the ancestral condition. However, it is not considered possible or even desirable at this time to speculate on any supposed sequence of early alepocephaloid phyletic bifurcations. In fact there is no known reason why evolution should or must proceed by bifurcations anyway.

Alepocephalidae:

Alepocephalids do not have a postcleithral organ, premaxillary tusks, dermal pits or a searsid photophore arrangement. They do not have a complex adductor mandibulae and do not look like herrings. They can be diagnosed from other alepocephaloids but, to date, no derived unifying character state is known although many trends are apparent.

Among the most apparent trends are: subdivision and specialization of the adductor arcus palatini series; development of completely enclosed ovaries; reduction in pyloric caecae; loss of medial surface gill rakers; loss of maxillary and palato-vomerine dentition; reduction in pharyngeal dentition; increase in number of caudal vertebrae relative to precaudal vertebrae; migration of dorsal origin behind anal origin; reduction and loss of laminar bone from neural and haemal spines; application of stiffening devices to "chondrostean hinge" including development of laminar bone on the first uroneural; loss of the mesocoracoid; development of a long ventral process of the coracoid; loss of the pelvic splint; reduction in pelvic finray numbers; increase in number and loss of scales; and development of photophores.

The main line of alepocephalid evolution appears to have taken place on or near the bottom and most likely below 1000 m. However, there have been repeated invasions of the pelagic habitat by adults. Some genera, such as Bathyprion and Bathylaco, contain only bathypelagic species and are presumed to have been in that habitat a long time. Other genera, such as Bajacalifornia, contain both near-bottom (B. calcaratus) and bathypelagic (B. drakei) adults which are presumably more recent midwater recruits.

Generic groups are discussed below. They are not taxonomic equivalents. Their main value, I believe, is as a starting point for further work. In general the order of arrangement is from the best defined group, including possible relatives which may not be so well defined, to the most tentative group.

Aulastomatomorpha group:

Although no specimens were examined, the descriptions and illustrations (Fig. 35B) of Aulastomatomorpha (Alcock 1890 and 1899, Lloyd 1906, and Illustrations of the Zoology of the Investigator pt. 1) leave little doubt that it is a close relative of Ericara, Conocara and Leptoderma. The dorsal and anal fin positions, small non-imbricate scales, and naked strip between the pectoral base and gill cavity are all features collectively unique to these genera. Aulastomatomorpha is therefore treated with this group which has had only one family level name applied, Aulastomatomorphinae Fowler 1934. Six genera are included: Asquamiceps, Aulastomatomorpha, Conocara, Einara, Ericara and Leptoderma.

The group is easily diagnosed as alepocephalids with no mesocoracoid but with well developed pectorals, one supramaxillary, no maxillary or vomerine teeth, and characterized by trends (least, if at all, developed in some species of Asquamiceps and Einara) as follows: migration of dorsal insertion behind origin of anal which tends to be elongate; tendency to reduce size and increase number of scales culminating in a naked genus, Leptoderma; reduction in number of proximal pectoral radials; a tendency (not unique) to lose tubular lateral line scales and proliferate sensory papillae on head, body, and caudal fin; loss of the pelvic splint, and loss of caudal radials.

None of the members of this group possess laminar bone on the first uroneural as is found in some other groups. In Asquamiceps some laminar bone is primitively retained on the neural and haemal spines. Asquamiceps and Ericara are probably close to the ancestral condition with respect to many character states. For example: median caudal radials retained in A. hjorti; a ventral caudal radial in E. salmonea; dorsal origins over or near anal insertions in both genera; about equal numbers of precaudal and caudal vertebrae in some Asquamiceps; four or five proximal pectoral radials in both genera; a relatively simple ovary in E. salmonea; a complete row of medial gill rakers on the lower limb of the first arch in both genera; and an overall primitive caudal in A. hjorti.

Although similar in many primitive features, Asquamiceps and Ericara belong to two different lineages within the Aulastomatomorpha group. Asquamiceps and Einara appear to form a monophyletic group distinguished by the lower jaw ending behind the posterior margin of the orbit, a short narrow caudal peduncle, two epurals, and a lack of the trends apparent in the other four genera. Einara and, possibly, some Asquamiceps are bathypelagic.

Ericara, Conocara, Leptoderma and Aulastomatomorpha are probably equivalent to Asquamiceps and Einara as monophyletic groups, Aulastomatomorpha possesses the unique characters mentioned above plus a lower jaw which ends before the posterior margin of the orbit and, according to Alcock (1899), a fold of skin along the dorsal midline and dorsal and ventral caudal peduncle. The skin folds are typical of Ericara and Conocara as well. The sequence Ericara to Conocara to Leptoderma illustrates trends to reduce numbers of precaudal and increase numbers of caudal vertebrae, reduce or eliminate scales, reduce maximum body depth, reduce epurals from one to none, reduce the number of uroneurals, generally reduce the caudal skeleton, reduce the number of proximal pectoral radials, develop an enclosed ovary, and (not in the above sequence) reduce pyloric caecae number and reduce pelvic radial number. In addition these genera all have a triangular cleithral shield above the coracoscapular cartilage, a relatively indistinct opercular process on the hyomandibular, and two ceratohyal branchiostegal rays. Although little evidence is available for most species, the commonly encountered species in this group (*E. salmonea*, *C. mcdonaldi*, and *L. macrops*) are benthic or engybenthic.

Bathyprion group:

This is an ill-defined group in which I tentatively include *Bathyprion*, *Mirognathus* and *Rinoctes*. These are elongate bathypelagic or abyssal (pelagic?) fishes with no mesocoracoid; a reduced or absent pectoral; a complete ovary of the type exposed to the coelom on both sides and in which the ovarian tunic is thin, closely adherent to the ova and in which the whole ovary is slightly convoluted; premaxillae elongate anteriorly; the fifth epibranchial on the postero-medial surface of the fourth epibranchial, fused or not; and no gill rakers on the medial surfaces of the lower limbs of the first two (*Rinoctes*) or three (*Bathyprion* and *Mirognathus*) arches.

Rinoctes is tentatively aligned with this group. Parr (1952) removed *Rinoctes* from *Bathytroctes* primarily because of its premaxillae, "which meet dorsally in a long, firm symphysis so as to form a hard beak-like snout". The elongate snouts of *Bathyprion* and *Mirognathus* could reasonably be derived from *Rinoctes* which is more primitive than the others in its forward dorsal fin position, complete oral dentition, and complete row of gill rakers on the median surface of the third gill arch. Rinoctes agrees with this group in its lack of a mesocoracoid which is unknown in Bathytroctes and related genera.

Ovarian structure is by far the most useful character with which to describe this group. Although only one female of each genus has been examined, the ovaries appear similar as described above and agree with Bertelsen's illustration of the ovary of the holotype of B. danae (Marshall 1966).

This group may be closely related to the Aulastomatomorpha group and shows several parallel or convergent developments (depending on recency of common ancestry). These developments are: lack of a mesocoracoid; restriction of basibranchial toothplate to second arch (Ericara and Bathyprion); loss of basibranchial toothplate (Conocara and Mirognathus); increase in number of caudal relative to precaudal vertebrae (Bathyprion); reduction of pyloric caecae number to two (Mirognathus). None of these characters are very convincing. However, convergence due to similar ecological requirements can probably be ignored since their habitats are rather different. Although both lack a mesocoracoid the pectoral is strong and well developed in the Aulastomatomorpha group and weak or absent in the Bathyprion group, thus emphasizing that the loss of the mesocoracoid was probably not due to similar physical responses to external forces.

Genus A group:

This group contains all of the alepocephalid genera which have photophores in some or all of their species (Anomalopterichthys, Rouleina, Xenodermichthys, Photostylus, and genus A). In addition these genera are characterized by a lack of scales and, except for some Rouleina, are bathypelagic. Since some of these are very rare, little can be said about the group as a whole.

The pectoral and caudal skeleton as well as the epibranchial structure of Photostylus are substantially different from Xenodermichthys and Rouleina. It is tentatively included in this group because of the evidence provided by Best and Bone (1976). It can be inferred from their work that Photostylus photophore stalks were likely derived from the outer integument layer of a Xenodermichthys-like ancestor. Although they show a more highly organized structure in the photophore of Photostylus, they further state that its photophore and that of Xenodermichthys are closely similar. Otherwise, there is little anatomical evidence to place Photostylus in this group and future work will likely show it to be an early independent lineage.

Genus A is probably the most primitive member of this group since one species possesses scales and its photophores are arranged in horizontal rows rather than in quincunx. Unfortunately the two known species are represented by a total of four small specimens. Consequently, any obvious information about the relationships of this group must come from the more specialized Xenodermichthys, Rouleina and Photostylus.

These all possess two epurals, laminar bone on the first uroneural directed anteriorly as a spine, no laminar bone on haemal and neural spines, two or three proximal pectoral radials, and no pelvic splint. Some species, such as R. mollis, are grossly similar to Alepocephalus, but until more is learned of genus A and Anomalopterichthys this is not very significant.

Bathylaco group:

The genera presently placed in this group are Bajacalifornia, Bathylaco, Herwigia and Narcetes. This group has many primitive characteristics including more precaudal than caudal vertebrae; a dorsal inserted in advance of the anal insertion; a considerable amount of laminar bone on neural and haemal spines; ventral caudal radial(s); robust median caudal radials; a single undivided adductor arcus palatini (Bajacalifornia with beginning of adductor hyomandibulae + operculi); a mesocoracoid; remnant of a dorsal postcleithrum; generally poorly developed but extensively ossified ventral process of the coracoid; basihyal teeth in Bajacalifornia calcaratus; extensive oral dentition; and a pelvic splint.

The group has only a few derived characters: laminar bone on the first uroneural, a condition which it shares with Leptochilichthyidae, Searsidae, Bathyprion group and genus A group; generally large mouths with upper and lower jaws ending well behind the moderate to small orbit; a trend to develop a musculous adductor mandibulae insertion associated with trends to move the orbit rostrally and increase the mouth size; and approximately square or rectangular vertebral centra separated by broad spaces of unossified chorda.

The Bathylaco group may be the most primitive alepocephalid group overall. Narcetes is probably closest to the basal alepocephalid. Herwigia and Bathylaco are specialized bathypelagic genera as are some species of Bajacalifornia.

Alepocephalus group:

This group of primarily benthic genera includes Alepocephalus, Bathytroctes, Nomoctes, Talismania and probably Brunichthys and Bellocia. The group shows several progressions from primitive, usually in Nomoctes and Bathytroctes, to derived characters, usually in Alepocephalus and Talismania. These include characteristics of the dorsal origin, vertebral number, pharyngeal and oral dentition, adductor mandibulae, pectoral girdle and pelvic splint. The ovary in Nomoctes and one Bathytroctes is of the type exposed on both surfaces to the coelom but enclosed by the tunic. The ovary in Talismania is of the Aulastomatomorpha group type.

This group seems very artificial. A unifying feature is the absence of laminar bone from the first uroneural, a character also shared by the Aulastomatomorpha group. The members of this group are a transitional grade between the Bathylaco group and both the Aulastomatomorpha and genus A groups. Much remains equivocal.

TAXONOMY

Coverage:

All genera are included in the following keys and all nominal species are accounted for in the generic synonymies. The generic synonymies therefore serve both to establish the valid genus name and to list nominal species. Generic names which were used in the publication of a nominal species names but which are not available for a particular genus are followed by "not of" and the appropriate author. Some species which were not examined and which could not be confidently placed are indicated with question marks.

For purely arbitrary and convenient reasons only species known from the western North Atlantic are definitely diagnosed. Small comparative collections from outside this region have been examined and where possible the keys and/or diagnoses will distinguish all known species. One notable exception is the genus Alepocephalus, the key to which is applicable only in the western North Atlantic.

Methods:

Standard taxonomic measurements and counts were made (Hubbs and Lagler 1958) with the following clarifications and additions. The last two dorsal or anal rays may show one of three states: (1) bases distinctly separate, (2) bases adjacent yet distinct, and (3) a single base with a split ray. Only in the latter case is a ray counted as one. Caudal vertebrae were distinguished from precaudal vertebrae by the presence of a haemal arch and spine in the former. On radiographs the pleural ribs on precaudal vertebrae are all approximately parallel as are the haemal spines. Usually there is a sharp demarcation between the two which is characterized by a reduction in the length of the pleural rib on the last precaudal vertebrae and/or the apparent intersection of the last pleural rib with the first haemal spine. The last caudal vertebrae counted is that which articulates with the parahypural. The one or more ural centra are variable intergenerically and sometimes intraspecifically and are not counted.

Measurements over 100 mm were taken to the nearest millimeter with dial calipers or dividers and those less than 100 mm were taken to the nearest tenth of a millimeter with dial calipers or a calibrated ocular micrometer on a dissecting microscope. Slight departures from standard methods were made in taking orbit diameter measurements, which was taken as the diagonal measurement between the point of the sphenotic and the dorsal surface of the cartilaginous palatine near the antorbital. This bony measurement is the most precise orbit measurement.

Most species are soft with a high water content in their flesh. Transfer of preserved specimens to 70% ethanol usually causes additional shrinkage and dehydration beyond that which occurs in 10% formalin. This plus the damage inflicted on most specimens during capture causes a noticeable amount of variation in most measurements of a species or even in repeated measurements of an individual. The precision of alepocephalid morphometrics is therefore relatively low. In addition most alepocephalid morphometrics exhibit definite allometry (Parr 1949, 1956 and 1960). Although the allometry of morphometrics will eventually prove useful in describing larvae and small juveniles, it will require a large amount of material. The allometric formulae of Parr were often based on too few specimens so that even the direction of allometric change, such as the head length in the genus Leptoderma (Parr 1951), was incorrectly stated (Fig. 31A). Morphometrics and associated allometry are, therefore, not stressed in the following keys.

Key to Families of Alepocephaloidea

(Cuvier and Valenciennes 1846)

1a. A luminous sack at the shoulder girdle which exits through a dark tube above the pectoral fin.. Searsidae.

1b. No luminous sack and no dark tube above pectoral fin...2.

2a. Premaxillary and maxillary edentate; vomer palatine and dentary dentate; maxillary deep, giving mouth "clupeoid" appearance; basihyal absent; basibranchial toothplates with a high bony ridge down midline; adductor mandibulae subdivided into sections A1 and A2, the latter further subdivided into A2 and A2B .... Leptochilichthyidae.

2b. Premaxillary and/or maxillary dentate or if both edentate so also are vomer and palatine; basihyal present, sometimes reduced; basibranchial toothplates without or with very slight medial ridge or completely absent; adductor mandibulae subdivided only in <u>Talismania</u>, but section A2 never further subdivided.. Alepocephalidae.

Key to genera of Alepocephalidae

1a. Dorsal fin origin distinctly behind anal fin origin or, if approximately opposite, either the body is scaled and an area or strip anteriad of the pectoral is naked or the liver has conspicuously exposed portal veins.. 2.

1b. Dorsal fin origin distinctly ahead of anal fin origin or, if approximately opposite, the body and area anteriad of pectoral both scaled or both naked and the liver is without exposed portal veins. .... 7.

2a. Body very elongate; completely naked and covered by darkly pigmented skin; circumorbital bones incomplete.. <u>Leptoderma</u> (p.147).

2b. Body scaled.. 3.

3a. Snout produced, tubular; lower jaw ends distinctly before anterior margin of orbit.. <u>Aulastomatomorpha</u> (p.120).

3b. Snout not produced, not tubular; lower jaw ends under or behind orbit .... 4.

4a. Lower jaw ends under orbit; peritoneum darkly pigmented; palatine with teeth.. 5.

4b. Lower jaw ends behind posterior margin of orbit; peritoneum unpigmented or only slightly pigmented; palatine without teeth... 6.

5a. A complete or nearly complete row of short, stubby gill rakers on the back (medial surface) of lower limb of first gill arch: premaxillary with sharp bony visor piercing the skin.. Ericara (p.143).

5b. No gill rakers on medial surface of lower limb of first gill arch; premaxillary normal, without sharp bony visor...Conocara (p.137).

6a. Area anteriad of pectoral base naked; dorsal and anal approximately equal and opposite, D 15-19, A 15-20; pectoral with 14-18 rays..Asquamiceps (p.117).

6b. Pectoral base and area anteriad scaled; dorsal distinctly or barely behind anal which always has more rays, D 22-27, A 26-34; pectoral with 9-10 rays...Einara (p.140).

7a. Body naked usually with gelatinous covering, some species with modified ring-like lateral line scales; if body scaled (one species) photophores present... 8.

7b. Body scaled or presumed so, without gelatinous covering; never with photophores...12.

8a. Photophores present on raised stalks; ventral outline of upper jaw with obtuse angle at end of premaxillary; no pseudobranch; acentrous vertebrae behind head in adults causing some downward flexure.. Photostylus (p. 158).

8b. Photophores, if present, not on raised stalks; ventral outline of premaxillary and maxillary approximately straight; pseudobranch present; acentrous vertebrae unknown in adults.....................9.

9a. Dorsal and anal fins each with 15-23 rays.. 10.

9b. Dorsal and anal fins each with 25-32 rays.. 11.

10a. Maxillary edentate; pelvic fin with 9 rays.. Anomalopterichthys (p.116).

10b. Maxillary dentate; pelvic fin with 6-7 rays.. Rouleina (p.162).

11a. Pelvic rays 6; photophores on body arranged in quincunx... Xenodermichthys (p.176).

11b. Pelvic rays 7; photophores on body arranged in horizontal rows... genus A. (p.112).

12a. Premaxillae elongate anteriorly, meeting each other broadly along the midline; no mesocoracoid; ovary complete..13.

12b. Premaxillae not elongate, only the anterior tips meeting along midline; mesocoracoid present; ovary incomplete.. 15.

13a. Dorsal fin origin in advance of anal fin origin; vomer dentate.. Rinoctes (p.160).

13b. Dorsal and anal fins approximately opposite; vomer edentate.. 14.

14a. All oral and branchial bones edentate; pectorals absent or rudimentary; 2 pyloric caecae.. Mirognathus (p.152).

14b. Conical, fang-like teeth present on palatine, premaxillary, maxillary and dentary; pectorals small with 10-12 rays; 7-8 pyloric caecae.. Bathyprion (p. 133).

15a. One supramaxillary...
....16.

15b. Two supramaxillaries...
....19.

16a. Origin of dorsal fin in advance of anal fin origin and closer to the vertical through the pelvic fin insertion than to the vertical through the anal fin origin...
....17.

16b. Origin of dorsal fin approximately opposite origin of anal fin.....
.... *Brunichthys* (p.136).

17a. Teeth present in lower jaw...
.... 18.

17b. No teeth in lower jaw..
.... *Herwigia* (p.146).

18a. Upper jaw ending approximately below posterior margin of orbit; anus about midway between insertion of pelvic fins and origin of anal fin
.... *Bellocia* (p.135).

18b. Upper jaw ending well behind posterior margin of orbit; anus adjacent to anal fin origin...
.... *Bathylaco* (p.123).

19a. Origin of dorsal fin distinctly in advance of anal fin origin......
.... 21.

19b. Dorsal and anal fins approximately equal and opposite.............
.... 20.

20a. Maxillary dentate; a black wart-like spot near base of sixth dorsal ray (sometimes abraded); ovary completely enclosed in tunic; adductor mandibulae subdivided...
.... *Talismania* (p.167).

20b. Maxillary edentate; no black wart-like spot on dorsal fin; ovary incomplete; adductor mandibulae no subdivided... *Alepocephalus* (p.113).

21a. Total preural vertebrae 38-48.. 22.

21b. Total preural vertebrae 48-60; dentary teeth near symphysis pluriserial or dentary with prominent knob directed antero-ventrally... 23.

22a. Number of caudal vertebrae 22-26; 13-17 anal fin rays; more than 29 gill rakers on first arch... *Bathytroctes* (p.124)

22b. Number of caudal vertebrae 16-19; 9-11 anal fin rays; less than 31 gill rakers on first arch... *Nomoctes* (p.130).

23a. Teeth in both jaws uniserial; pyloric caecae 13-26; usually 7 branchiostegal rays; 22-31 gill rakers on first arch; dentary with prominent antero-ventral knob... *Bajacalifornia* (p.121).

23b. Premaxillary and dentary teeth pluriserial; pyloric caecae (6?) 8-14; usually 8 branchiostegal rays; 14-22 gill rakers on first arch.. *Narcetes* (p.154).

Leptochilichthys Garman 1899

Leptochilichthys Garman 1899:284 (Type species: Leptochilichthys agassizii Garman 1899 by monotypy). Roule and Angel 1931:6 (macrops)

Leptochilichthys agassizii Garman 1899

Figure 38A

?synonym: Leptochilichthys agassizi macrops Roule and Angel 1931.

Diagnosis:

Monotypic, same as family in above key.

Remarks:

Three specimens were examined in detail, including Garman's type(which lacks pelvics and from which dorsal, anal, pectoral, branchiostegal and scale counts could not be reliably taken), a second eastern Pacific specimen, and a north Atlantic specimen. The Atlantic specimen differed from the Pacific specimens in number of gill rakers on the first but not the subsequent arches (11+1+20 vs. 9-10+1+15-16) and in vertebrae (29+19=48 vs. 29-30+20-21=50). The differences in eye size and number of scales above and below the lateral line, reported to differentiate Atlantic specimens (Roule and Angel 1931 and Fowler 1936) did not exist. The number of scales from the lateral line to the dorsal and anal were, respectively, (4)-5 and (5)-6. If Roule and Angel's specimen has 8 scales above and 5 below the lateral line as reported by Fowler (1936), two Atlantic species may exist. The present material, however, provides no positive support of this.

Morphometrics of the three specimens, 149-255 mm SL, expressed as a percent SL, were: head length 38.8-41.0, snout length 7.8-8.4, snout to top of opercular opening 28.8-31.9, prepectoral length 38.6-40.0, prepelvic length 59.5-63.9, preanal length 72.4-78.8, predorsal length 63.5-67.0, maximum orbit diameter 8.2-8.9, interorbital width 5.2-6.4, upper jaw length 23.1-24.1, lower jaw length 24.6-25.0, pectoral fin length 10.9, pelvic fin length 12.8, dorsal base length 11.8-13.2, anal base length 9.4-10.1, caudal peduncle depth 7.4-9.6, caudal peduncle length 25.3-26.4, maximum body depth 20.2-21.8, sphenotic width of skull 11.5-13.8.

In the SIO and ISH specimens there were 51-52 lateral line scales, about 4 of which were on the caudal fin, and about 19-21 transverse scale rows above the lateral line before the dorsal. Part of the isthmus anteriad of the pectoral symphysis is scaled. Meristic variation of the material: D 12-14, A 11, P_1 9-10, P_2 8-9 plus a splint, br 4+9=13; gill rakers on second, third and fourth arches 12-13+1+20-21, 12-14+1+20-21, 8-9+1+14-19; gill rakers long, on the 149 mm SL SIO specimen the length of the rakers in the angle of the arch were 9.8, 7.0, 5.7 and 4.0 mm, respectively; gill rakers present on the medial surface of all arches, about 28 on the lower limb of the first arch; teeth present on vomer, palatine and mandible; none on premaxillary or maxillary; 10 pyloric caecae; 29-30 + 19-21 = 48-50 vertebrae.

<u>Distribution</u>: Known from the eastern Pacific between 01°07'N (Garman 1899) and 38°24'N (SIO 66-55) and from the eastern Atlantic between 14°11'N and

48°30'N (ISH records). Twelve eastern Atlantic ISH specimens were caught in midwater between 490-3100 m, 11 from below 2000 m, and 9 from below 2650 m. Bathypelagic.

Genus "A"

Figure 40 A&B

Aleposomus (not of Gill 1884). Angel and Verrier 1931: 121 (schmidti).

Diagnosis:

In key.

Remarks:

Parr's (1951) treatment of the species in the Xenodermichthys - Rouleina group helped clarify a confusing list of nominal species. However, he omitted the Indo Pacific species Aleposomus schmidti Angel and Verrier (1931). In Parr's key A. schmidti would fall somewhere between Rouleina and Xenodermichthys. I have recently obtained three specimens of two species, one of which agrees with Angel and Verrier's (1931) description.

The unnamed species in this unnamed genus has thin scales covering its regular rows of photophores. It would, on this basis seem to be more primitive than the genera it most closely resembles, Xenodermichthys, Rouleina and Anomalopterichthys. Until more material becomes available the interrelationships of these genera will be problematical. However, if the presence of scales and regular rows of photophores is established as primitive for the group, then the loss of scales and the quincunxial arrangement of photophores in Xenodermichthys and some species of Rouleina would serve as additional features uniting these genera. Since this genus is presently known only from the Indo-Pacific region, it will not be treated further.

Alepocephalus Risso 1820

Alepocephalus Risso 1820:270 (Type species Alepocephalus rostratus Risso 1820 by monotypy).

Mitchillina Jordan and Evermann 1896:453 (Type species Alepocephalus bairdii Goode and Bean 1879 by original designation).

Halisauriceps Fowler 1934:247 (Type species Alepocephalus longiceps Lloyd 1909 by original designation).

Narcetes (not of Alcock 1890). Fowler 1934:255 (part. garmani only).

Alcockella Fowler 1934:255 (Type species Narcetes garmani Fowler 1934 by original designation).

?Normania Parr 1937:5 (Type species Alepocephalus andersoni Fowler 1933 by original designation).

?Proditor Whitley 1940:407 (new name to replace Normania Parr 1937, preoccupied by Normania Brady 1866, an ostracod; Normania Bowerbank 1869, a sponge; and Normania Boeck 1871, an amphipod).

?Noriona Strand 1942:401 (new name to replace Normania Parr 1937, thrice preoccupied).

Bathytroctes (not of Gunther 1878). Parrott 1948:143 (?antipodiana).

Lloydiella Parr 1952:256 (Type species Alepocephalus bicolor Wood-Mason and Alcock 1891 (not Alcock 1892) by original designation).

Diagnosis:

No teeth on vomer or maxillary; teeth present on premaxillary, palatine and dentary; mesocoracoid present; dorsal and anal fins approximately equal and opposite; body completely scaled.

Remarks:

The identification of species of Alepocephalus is difficult due to poor original descriptions and the damaged condition of many specimens. In his key to the genus Parr (1952) recognized the importance of scale counts in distinguishing species. But, because of their damaged condition, especially the very frequent loss of scales on the caudal peduncle, the number of scales in a longitudinal series (Parr's character) is almost impossible to count. Much more frequently, one is able to make a count of transverse scale rows (directed up and backwards) above the lateral line before the dorsal. Also vertebral counts are useful in distinguishing species. These characters are therefore incorporated into the following provisional key to known western North Atlantic species.

Western North Atlantic Distribution and comments:

Alepocephalus bairdii is known from the type locality on the Grand Banks (Goode and Bean 1879) to west Greenland (Krefft 1973) in the western North Atlantic. *Alepocephalus productus* is known from three specimens (Krefft 1973), two are from the western North Atlantic at 39°26'16"N and 70°02'37"W (Gill 1883) and 28°47'N and 87°50'W (Grey 1958). The specimen of *A. productus* reported by Haedrich and Polloni (1974) is not that species. *Alepocephalus australis* is the name I tentatively apply to Haedrich and Polloni's specimen, as well as to two specimens from off Virginia and one from *Oregon* II station 11242 (10°10'N, 76°14'W). All four specimens as well as two from the Gulf of Guinea (UMML 21680) agree with *A. australis* in head size according to Parr's (1952) key. *Alepocephalus agassizii* is the most common western Atlantic *Alepocephalus*. Krefft (1973) reports it from Davis Strait to 15°N in the western North Atlantic.

Key to North Atlantic Species of *Alepocephalus*

1a. Anal fin with 21-25 rays; total vertebrae 62-64.. *Alepocephalus bairdii* Goode and Bean 1879.

1b. Anal fin with less than 20 rays; total vertebrae 50-57.. 2.

2a. Transverse scale rows above lateral line and before dorsal fin origin greater than 40, usually around 48; pyloric caecae 15-23; vertebrae 25-28+26-28=53-55...................................... *Alepocephalus agassizii* Goode and Bean 1883 (Fig. 39A).

2b. Transverse scale rows above lateral line and before dorsal fin origin less than 40.. 3.

3a. Pyloric caecae 23-24; juveniles with unpigmented strip along dorsal and anal fin bases; maximum body depth of adults at dorsal and anal fin origins.. *Alepocephalus rostratus* Risso 1820.

3b. Pyloric caecae 13-16; bases of dorsal and anal fins of juveniles with same pigmentation as rest of fins; little change in body depth from pectorals to dorsal in adults.. 4.

4a. Transverse scale rows above lateral line and before dorsal origin 33-34; vertebrae 24+26-28=50-52.. *Alepocephalus productus* Gill 1884.

4b. Transverse scale rows above lateral line and before dorsal origin 26; vertebrae 24-27+28-30=53-57; males with tri-libed testes.................................... *Alepocephalus australis* Barnard 1923.

Anomalopterichthys Whitley 1940

Anomalopterus Vaillant 1888:160 (Type species: *Anomalopterus pinguis* by monotypy).

Anomalopterichthys Whitley 1940:242 (Substitute name for *Anomalopterus* Vaillant 1888, preoccupied by *Anomalopterus* Gray 1855, a bird).

Remarks:

The genus is monotypic and only known from Vaillant's 61 mm type specimen. Parr (1951) said the upper jaws were toothless while Vaillant said the premaxillary and dentary had very small teeth and only the maxillary and possibly vomer were edentate. Vaillant's dentition pattern distinguishes *Anomalopterichthys* from all genera but *Alepocephalus*, *Ericara* and *Conocara* from which it differs in the insertion of the dorsal in advance of the anal. It appears most similar to genus "A" although its small eye is unlike the species of genus "A". When additional material becomes available, it will be desirable to consider relationships of *Anomalopterichthys* with genus "A", *Xenodermichthys* and *Rouleina*.

The genus and species are known only from the eastern North Atlantic.

Asquamiceps Zugmayer 1911

Figures 34A and 35A

Asquamiceps Zugmayer 1911:2 (Type species: Asquamiceps velaris Zugmayer 1911 by monotypy). Fowler 1934:248 (longmani). Parr 1954:1-8 (indagatio and pacificus).

Alepocephalus (not of Risso) Koefoed 1927:43 (in part, hjorti only).

Megalepocephalus Fowler 1934:248 (Type species: Asquamiceps longmani Fowler 1934 by original designation).

Diagnosis:

Alepocephalids with voluminous opercles covering base of pectoral which is large and fan-like; area anteriad of pectoral base naked; peritoneum unpigmented or very lightly pigmented; lower jaw with minute uniserial teeth and ending behind posterior margin of orbit; palatine, maxillary and vomer edentate, premaxillary with or without teeth; gill rakers present on lateral and medial surfaces of first four arches, a well developed flap of skin on the anterior surface separating the two sets of rakers; body compressed, covered with scales with or without a lateral line; head naked, some with reticulated pattern approximating scale pockets (A. longmani); dorsal and anal approximately equal and opposite; total vertebrae 37-53, the number of precaudal about equal to or up to 8 less than the number of caudal vertebrae; A 15-20, D 15-19, $P_1$14-18, $P_2$5-6, br 5-6.

Remarks:

The genus Asquamiceps is now represented by three species in the North Atlantic. Asquamiceps velaris is known only from the holotype taken at $36^{\circ}06'$N and 09°W (Zugmayer 1911). Asquamiceps hjorti is known from the holotype taken at 34°59'N and 33°01'W (Koefoed 1927) and several other specimens taken between 20°N and 20°S in the eastern Atlantic (Krefft, personal communication). Asquamiceps species A is known only from the holotype taken in the Gulf of Mexico and is the only member of the genus known from the western Atlantic. Species of Asquamiceps are rare in collections (Krefft 1973). The shoalest capture depth is 1110 m for the type of A. longmani Fowler 1934 but most captures are from below 2000 m, an infrequently sampled habitat.

Key to species of Asquamiceps

(adapted from Parr, 1954)

1a. Upper jaw ends well in advance of posterior margin of orbit... 2.

1b. Upper jaw reaches about to the vertical through the posterior margin of orbit.. 4.

2a. Four pyloric caecae; 15-17 gill rakers in first arch; lateral line indistinct... 3.

2b. Eight pyloric caecae; 25 gill rakers in first arch; lateral line very distinct... Asquamiceps pacificus Parr 1954.

3a. Five branchiostegal rays; more than 70 scales in "longitudinal series" .... Asquamiceps velaris Zugmayer 1911.

3b. Six branchiostegals; about 65 scales in "longitudinal series"...... .... Asquamiceps indagatio Parr 1954.

4a. Twenty-six caudal vertebrae; orbit about 20% of head length; males lobed testes...
.... *Asquamiceps longmani* Fowler 1934.

4b. Twenty-one to twenty-two caudal vertebrae; orbit about 14% of head length; known male with convoluted testes..........................
.... 5.

5a. Lateral line present; about 50 transverse scale rows above lateral line to caudal base; anus midway between pelvic insertion and anal fin origin...
.... *Asquamiceps hjorti* Koefoed 1927.

5b. Lateral line absent; about 80 transverse scale rows above lateral line to caudal base; anus adjacent to anal fin origin.............
.... *Asquamiceps* species A. (Fig. 35A).

Aulastomatomorpha Alcock 1890

Figure 35B

Aulastomatomarpha Alcock 1890:307 (Type species: *Aulastomatomorpha phospherops* Alcock 1890 by monotypy). Lloyd 1906:308 (*caeruleiceps*). *Aulastomomorpha* Alcock 1899:178 (incorrect emendation of *Aulastomatomorpha* Alcock 1890). Alcock 1899:178 (*phosphorops*, incorrect emendation of *A. phospherops* Alcock 1890).

Diagnosis:

In key.

Remarks:

Two species known only from the Indian Ocean.

Bajacalifornia Townsend and Nichols 1925

Figure 36 A-C

Bathytroctes (not of Gunther 1878) Weber 1913:11 (calcaratus). Beebe 1929:6 (drakei).

Bajacalifornia Townsend and Nichols 1925:8 (Type species: Bajacalifornia burragei Townsend and Nichols 1925 by original designation).

Diagnosis:

Teeth in both jaws uniserial, dentary not expanded laterally but with a prominent knob directed antero-ventrally; vertebrae 26-39+18-23=50-60 with 11-18 more precaudal than caudal vertebrae; vertebral interspaces not noticeably enlarged; pyloric caecae 13-26, long; br usually 7; gill rakers on first arch 5-7+1+15-23=22-31. Two North Atlantic species.

Key to Species of Bajacalifornia

1a. Precaudal vertebrae 26-27; 10 pelvic rays; 17 pectoral rays.........
.................Bajacalifornia burragei Townsend and Nichols 1925.

1b. Precaudal vertebrae 31-39; 7-9 pelvic rays; 12-15 (16?) pectoral rays
.... 2.

2a. Vertebrae 36-39+20-23=57-60; orbit relatively small 4.2-10.8% SL or 55-90% of snout (negatively allometric)..........................
.... Bajacalifornia calcaratus (Weber 1913).

2b. Vertebrae 31-32+19-20=50-51; orbit relatively large 7.2-10.8% SL or 90-130% of snout (negatively allometric)..........................
.... Bajacalifornia drakei (Beebe 1929).

Bajacalifornia calcaratus (Weber 1913)

Figure 36B

Bathytroctes calcaratus Weber 1913:11

Bajacalifornia calcaratus Parr 1952:265.

Diagnosis:

Vertebrae 36-39+20-23=57-60; orbit relatively small, 4.2-10.8% SL, 55-90% of snout, negative lenear allometry between 75.8 and 345 mm SL. Known from four localities in the North Atlantic, all in the Gulf of Guinea from bottom trawls in 350-730 m.

Bajacalifornia drakei (Beebe 1929)

Figure 36C

Bathytroctes drakei Beebe 1929:6

Bajacalifornia drakei Parr 1937:25.

Diagnosis:

Vertebrae 31-32+19-20=50-51; orbit relatively large, 7.2-10.8% SL, 90-130% of snout, negatively allometric, although probably not linear between 28.7 and 223 mm SL; testes apparently with only one or a few pairs of long lobes. Juveniles less than 90mm SL and larvae from midwater trawls known from the eastern Pacific between 11°S and 35°S, the western Atlantic (Beebe 1929, 1933), and the eastern Atlantic at 53°N from nets towed as shallow as 250 m and as deep as 3182 m. Two adults, 180 and 223 mm SL, known from bottom trawls in the western Atlantic at 39°N and 40°N between 820 and 1425 m.

Bathylaco Goode and Bean 1896

Bathylaco Goode and Bean 1896:57 (Type species *Bathylaco nigricans* Goode and Bean 1896 by monotypy).

Macromastax Beebe 1933a:161 (Type species *Macromastax gymnos* Beebe 1933a by monotypy).

Diagnosis:

Orbit far forward on snout; jaws extending well behind posterior margin of orbit; dorsal profile of head relatively straight with slight arch over snout; testes lobed; lower jaw dentigerous; modified gill rakers sometimes present on medial surface of first gill arch; vertebrae 26-32(?)+17-19; gill raker on first arch 3-4+1+7-10=11-17' P_1 4-11; vertebral centra tall, rectangular with relatively wide intervertebral spaces of unossified chorda. Two or three species, one from the western North Atlantic.

Bathylaco nigricans Goode and Bean 1896

Figure 38B

Bathylaco nigricans Goode and Bean 1896:57.

Macromastax gymnos Beebe 1933a:162.

Diagnosis:

No dilatator spine on opercle; A 10-13.

Distribution:

Circumglobal between 40°N and 10°S (Nielsen and Larsen 1970) from 450-4376 m, usually from midwater trawls between 1750 and 2200 m (Nielsen and Larsen 1968, 1970 and Nielsen 1972).

Classification of Bathytroctes and Nomoctes:

Krefft (1970 and personal communication) has expressed reasonable doubt about the validity of separate genera for Bathytroctes and Nomoctes as here restricted. Although more material is needed for some species, four characters appear to offer some justification for maintaining separate genera. Two characters, number of caudal vertebrae and number of anal rays, distinguish two groups (vertebrae unknown for B. grimaldi, B. microlepis, B. danae, B. zugmayeri and N. macrolepis). Two additional characters, number of gill rakers on the first arch and structure of the ovary, separate the two groups except that B. oligolepis falls into the Nomoctes group for both characters and N. michaelsarsi falls into the Bathytroctes group with respect to number of gill rakers. Obviously, the classification adopted here is tentative. Furthermore, the diagnoses of the two genera are strictly applicable only to the known western North Atlantic species.

Bathytroctes Gunther 1878

Bathytroctes Gunther 1878:249 (Type species: Bathytroctes microlepis Gunther 1878 by subsequent designation of Jordan 1919:395) Alcock 1890:303 (squamosus). Zugmayer 1911:1 (grimaldi). Fowler 1934:250 (part. zugmayeri). Parr 1951:12 (part. danae).

Lepogenys Parr 1951:5 (Type species: Bathytroctes squamosus Alcock 1890 by original designation).

Grimatroctes Parr 1952:265 (Type species: Bathytroctes grimaldi Zugmayer 1911 by original designation). Grey 1958:150 (bullisi). Krefft 1970:40 (oligolepis).

Nomenclature:

Gunther (1878) introduced the genus Bathytroctes to include (in order) B. microlepis and B. rostratus. He did not designate a type species. In his 1887 work, Gunther added another species, *B. macrolepis*, and listed it first.

The earliest designation of a type species for *Bathytroctes* is by Goode and Bean (1896:40) who state, "The type of this genus is *Bathytroctes macrolepis*, Gunther,..." Since *B. macrolepis* was not originally included in Gunther's genus, this designation is not valid. Subsequently, Jordan and Evermann (1896:454) list in their standard format, "*Bathytroctes*, Gunther, Ann. Mag. Nat. Hist., 1878, 249, (*microlepis*)". *Bathytroctes microlepis* has since been recognized as the type species by by Jordan (1919) and Fowler (1936a), who incorrectly attributed the designation to Goode and Bean. Parr (personal communication) accepted the statement by Goode and Bean (1896) that the type species of *Bathytroctes* was *B. macrolepis*. He then erected a new genus, *Grimatroctes*, Parr 1952, with type species *Bathytroctes grimaldii* Zugmayer 1911, but containing *Bathytroctes microlepis*.

The nomenclature presently in use, therefore recognizes *Bathytroctes* Gunther 1878, containing *B. macrolepis* Gunther 1887 as type species. Of the two species originally described in *Bathytroctes*, *rostratus* Gunther 1878 is a searsid and *B. microlepis* Gunther 1878 has been referred to the genus *Grimatroctes*, where it is a senior subjective synonym of the type species. Thus, neither of the two species originally included in *Bathytroctes* are now considered to be included within it.

According to article 69 of the International Code of Zoological Nomenclature, subsequent designation of a type species must be from one of the originally included species; therefore, *B. macrolepis* is not available. *Bathytroctes* with *B. microlepis* as its valid type species becomes a senior synonym of *Grimatroctes* Parr 1952.

The oldest available genus-group name for Bathytroctes (not of Gunther 1878, but of Parr 1952) is Nomoctes Parr 1952 (see below).

Diagnosis:

Number of caudal vertebrae 22-26, total 44-48; anal fin rays 13-17; ovary incomplete (except in B. oligolepis); more than 29 gill rakers in first arch (except B. oligolepis); palato-vomerine teeth feeble to absent; dorsal profile of head arched over eye (relatively straight in oligolepis). Two western North Atlantic species; three Atlantic species, all diagnosed below.

Key to Species of Bathytroctes

1a. Branchiostegal rays 6; 24-26 gill rakers on first arch, 6 on upper limb; usually 7 pelvic rays.. ....Bathytroctes oligolepis (Krefft 1970).

1b. Branchiostegal rays 7-8; 29-36 gill rakers on first arch, 8-12 on upper limb; usually 8 pelvic rays.. .... 2.

2a. Scales present on cheeks and/or opercles; scales above lateral line approximately same size as lateral line scales; 48-61 transverse scale rows above lateral line; orbit diameter 1.6-1.9 times larger than snout length... .... Bathytroctes squamosus Alcock 1890.

2b. Scales not present on cheeks or opercles; scales above lateral line noticeably smaller than lateral line scales; 59-77 transverse scale rows above lateral line; orbit diameter 1.2-1.6 times larger than snout length.. .... Bathytroctes microlepis Gunther 1878.

Bathytroctes squamosus Alcock 1890

Figure 37 D-F

Bathytroctes squamosus Alcock 1890:303.

Bathytroctes zugmayeri Fowler 1934:250.

Lepogenys squamosus Parr 1951:5.

Grimatroctes bullisi Grey 1958:150 (part. see under B. microlepis).

Diagnosis:

Branchiostegals 7-8; 29-34 gill rakers on first arch, 8-10 on upper limb; P_2 8; scales present on cheeks and/or opercle; 48-51 lateral line scales; scales above lateral line approximately same size as lateral line scales; 48-61 transverse scale rows above lateral line (Table 3); orbit diameter 1.6-1.9 times larger than snout length, Arabian Sea, Celebes Sea and western North Atlantic.

Remarks:

The twenty-four available western North Atlantic specimens differ from Alcock's (1890) description, given in parentheses: P_1 11-13 (10); P_2 8 (9); anal origin under last 3 dorsal rays (under third dorsal ray, although illustration shows the anal origin under the last dorsal ray); intestine with one, usually two, flat loops (intestine coiled in a spiral); and pyloric caecae 10-15 (5-6). All of these differences could indicate some genetic differences between Arabian Sea and western North Atlantic specimens. However, in view of the large amount of variability in scale size and counts found within western North Atlantic specimens (Table 3), these differences should be confirmed through reexamination of the holotype and examination of more Arabian Sea specimens before they are attributed to different species.

Bathytroctes microlepis Gunther 1878

Figure 37 A-C

Bathytroctes microlepis Gunther 1878:249.

Bathytroctes grimaldi Zugmayer 1911:1.

Bathytroctes danae Parr 1951:12.

Grimatroctes bullisi Grey 1958:150 (part. see below).

Nomenclature:

The descriptions of the above species provide no way of distinguishing them from each other. Bathytroctes grimaldi was reported to have 11 anal rays (Zugmayer 1911), but Parr (personal communication) reexamined the holotype and found 15 anal rays in agreement with the observed variation in B. microlepis.

At least one of the paratypes of Grimatroctes bullisi (the second 203 mm SL specimen in Grey's (1958) Table 1, a female) is very likely a specimen of B. squamosus. Although I cannot confirm scale counts in any of Grey's type material, I believe I am able to see remnants of scale pockets on the upper opercle in this specimen. Further, her scale counts (listed as lateral line but quite obviously of the rows above the lateral line) show the specimen in question to have about 60 scales (rows above the lateral line) while the holotype and two other paratypes have about 64 scales. It is clear with respect to this character that the specimen in question falls in the area of overlap between B. microlepis and B. squamosus. The remaining type material is in the low range for B. microlepis. Also, the orbit in this specimen is 1.64 times as large as the snout (Grey 1958 and my measurements agree exactly on this). Thus, with respect to the three known characters which separate B. microlepis and B. squamosus this paratype appears to agree with B. squamosus.

Table 3: Number of transverse scale rows above lateral line in nominal species of Bathytroctes.

	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
B.microlepis														2		1	1	1			1	1	2	1				1	1	1		1
B.squamosus			1	1	2	2	1	3	5	1				2		3																
Type material of:																																
B.microlepis																									├┤							
B.squamosus					├┤																											
B.grimaldi																														├┤		
B.zugmayeri													├┤																			
B.danae															├─	──	─┤															
B.bullisi															├─	──	──	──	─┤													
B.oligolepis	├─	──	──	─┤																												

Diagnosis:

Branchiostegals 7-8; 32-36 gill rakers on first arch, 9-12 on upper limb; P_2 (7)-8-9; no scales present on cheeks or opercle; 47-49 lateral line scales; scales above lateral line smaller than lateral line scales, 59-77 transverse scale rows above lateral line (Table); orbit diameter 1.2-1.6 times larger than snout length. North Atlantic, South China Sea and southeast Pacific.

Bathytroctes oligolepis (Krefft 1970)

Grimatroctes oligolepis Krefft 1970:40.

Diagnosis:

Branchiostegals 6; 2-26 gill rakers on first arch, 6 on upper limb; P_2 7(8); no scales present on cheeks or opercle; 46-48 lateral line scales scales above lateral line about same size as lateral line scales (counts unavailable); orbit diameter 1.2-1.4 times larger than snout length. Known only from equatorial central Atlantic.

Nomoctes Parr 1952

Bathytroctes (not of Gunther 1878). Gunther 1887:225 (macrolepis only). Garman 1899:286-288 (alvifrons and inspector only). Koefoed 1927:48 (michaelsarsi). Parr 1951:11 (koefoedi only).

Narcetes (not of Alcock 1890). Fowler 1934:253 (part. pappenheimi only).

Nomoctes Parr 1952;266 (Type species: Bathytroctes michaelsarsi Koefoed 1927 by original designation). See Bathytroctes above for discussion of nomenclature.

Diagnosis:

Number of caudal vertebrae 16-19, total 38-45; A 9-11; ovary completely enclosed by ovarian tunic (known only in *michaelsarsi* and *koefoedi*); gill rakers 19-31 on first arch; palato-vomerine teeth usually well developed; body relatively flacid; dorsal profile of head relatively straight with little curvature over eye. Two western North Atlantic species.

Key to western North Atlantic Species of *Nomoctes*

1a. Pectoral with 16 rays; gill rakers in first arch 7-9+1+19-21=27-31.
.... *N. michaelsarsi* (Koefoed 1927).
1b. Pectoral with 11-12 rays; gill rakers in first arch 5-6+1+14-17=21-23.
.... *N. koefoedi* (Parr 1951).

Nomoctes michaelsarsi (Koefoed 1927)

Figure 38C

Bathytroctes michaelsarsi Koefoed 1927:48.

Diagnosis:

Total vertebrae 38-39; gill rakers in first arch 7-9+1+19-21=27-31; P_1 16.

Remarks:

In addition to the four specimens in the type series, *N. michaelsarsi* is known from two other eastern North Atlantic specimens and one western North Atlantic specimen. It has been caught between 2010 and 2933 m, only in the North Atlantic.

Nomoctes koefoedi (Parr 1951)

Figure 38D

Bathytroctes alvifrons (not of Garman 1899) Koefoed 1927:45.

Bathytroctes koefoedi Parr 1951:11.

Diagnosis:

Total vertebrae 39; gill rakers in first arch 5-6+1+14-17=21-23; P_1 11-12.

Remarks:

The holotype was collected along with 18 other specimens southwest of the Azores. An additional specimen from near the type locality and one from the Gulf of Mexico are also known. It has been caught between 2865 and 5850 m.

Bathyprion Marshall 1966

Bathyprion Marshall 1966:4 (Type species Bathyprion danae by original designation).

Diagnosis:

Vomer edentate; uniserial, conical, fang-like teeth on palatine, premaxillary, maxillary, and dentary; pectoral small with 10-12 rays; 7-8 pyloric caecae.

Bathyprion danae Marshall 1966

Figure 39B

Morphometric measurements from two specimens, one from the North Atlantic (378 SL, MMF 22053) and the other from the South Atlantic (252 SL, ISH 1539/71), expressed as a percent SL: head length 25.0-25.4, snout length 9.1-10.4, maximum orbit diameter 2.5, prepectoral length 25.7, prepelvic length 38.9-41.3, preanal length 54.7-57.5, predorsal length 54.3-57.9, interorbital distance 6.5-6.8, upper jaw length 15.0-16.0, lower jaw length 16.3-17.1, sphenotic width of skull 7.5-8.0, dorsal base length 22.6-25.0, anal base length 23.4-23.6 caudal peduncle depth 4.0-4.2, postdorsal length 20.3-21.3

Meristic variation noted: pyloric caecae 7-8, P_1 10-12, P_2 8-9, D 24-25, A 24-25, epihyal branchiostegal rays 2-4, ceratohyal branchiostegal rays 5-9 (usually 8-9), total branchiostegals 8-12 (usually 11-12), vertebrae 22+30, gill rakers on first four arches (MMF specimen) 4-1-13, 5-1-13, 7-1-13, 4-1-15.

Distribution:

In Atlantic from 64°N to 21°S ("Walther Herwig" data).

Holotype from west Pacific off Australia. Caught in depths of 1100 to 2100 m from 600 to 2300 m above the bottom. Unknown in western North Atlantic although not unexpected there. Bathypelagic.

Bellocia Parr 1951

Bathytroctes (not of Gunther 1878). Vaillant 1888:155-158 (part. description but not figure of Bathytroctes melanocephalus).

Bellocia Parr 1951:6, 12 (Type species: Bellocia vaillanti by monotypy).

Remarks:

The nominal genus and species Bellocia vaillanti are difficult to understand from the literature. The only information is contained in Vaillant's (1888) and Parr's (1951) descriptions (see Parr (1960:66) for a summary of the comedy of errors associated with descriptions of this species).

It is my guess based on these descriptions, there being no published illustration and no material presently available, that Bellocia vaillanti is closely related to Nomoctes or possibly Herwigia. It differs from known species of Nomoctes in having one supramaxillary rather than two. It is presently known only from the eastern North Atlantic.

Brunichthys Parr 1951

Alepocephalus (not of Risso 1820). Garman 1899:291 (in part, asperifrons only).

Brunichthys Parr 1951:8 (Type species: Alepocephalus asperifrons Garman 1899 by original designation).

Remarks:

This genus was introduced without comment in Parr's (1951) key. The only known materials are the type collections which I have not examined. The species was apparently removed from Alepocephalus on the basis of the number of supramaxillaries. In spite of this weak evidence the genus is tenatively recognized on the weight of Parr's indicated preference. The genus must eventually be critically compared with Alepocephalus.

Conocara Goode and Bean 1896

Alepocephalus (not of Risso 1820). Vaillant 1888:150 (part. macropterus only). Koefoed 1927:41 (part. murrayi only).

Conocara Goode and Bean 1896:39 (Type species: Conocara mcdonaldi Goode and Bean 1896 by subsequent designation of Jordan 1919:467.

Benthosphyraena Cockerell 1919:172 (reference to scales of Conocara macropterus apparently using a manuscript name found in a jar, see Jordan 1920).

Diagnosis:

In key.

Remarks:

Two western North Atlantic species, C. mcdonaldi and C. murrayi, the former found usually shoaler and the later deeper than 2000 m.

Key to Species of Conocara

1a. Four to 5 gill rakers on upper limb of first arch; 26-27 anal rays; vertebrae 21-23+31-33=52-56..Conocara murrayi (Koefoed 1927). (Fig.32C).

1b. One or two gill rakers on upper limb of first arch; 35-40 anal rays; vertebrae 18-21+35-38=54-57.. 2.

2a. Ovarian tunic discontinuous with peritoneum ventrally; dorsal rays 20-21; anal rays 36-40; vertebrae 18-19+35-38=54-57............................... Conocara mcdonaldi Goode and Bean 1896.

2b. Ovarian tunic continuous with peritoneum ventrolaterally, except for a short section anteriorly; dorsal rays 19-22; anal rays 35-38; vertebrae 19-21+34-37=54-57.. *Conocara macroptera* Viallant 1888.

Conocara murrayi (Koefoed 1927)

Only a single western Atlantic specimen is known (Grey 1958). It differs from an eastern Atlantic "Discovery" specimen from N.I.O. in the following (N.I.O. specimen in parentheses): vomerine teeth 0 (two groups of five); vertebrae 23+33 (21+31); and pyloric caecae 7(5). Although these differences are very suggestive and possibly indicative of genetic differences, the rarity of this form and the fact that the western Atlantic specimen is a juvenile dissuades me from describing it as a new species.

Proportional measurements expressed as a percent of SL for the two specimens (151 and 268 mm SL are: head length 37.7-41.0, snout length 12.6-15.2, prepelvic length 55.3-58.2, preanal length 66.9-70.9, predorsal length 70.2-76.5, maximum diameter of orbit 9.2-9.5, upper jaw length 15.0-16.2, dorsal base length 13.3-16.3, anal base length 18.0-21.4, sphenotic width of skull 13.0-13.5. Meristic counts were D 21-22, A 26-27, P_1 8-9, P_2 6, br 6-7, gillrakers in first arch 4-5+1+15-16, pyloric caecae 5-7.

Conocara mcdonaldi Goode and Bean 1896

Conocara mcdonaldi is difficult to distinguish from eastern Atlantic *C. macroptera*. As pointed out in the above key, the main distinguishing feature is the structure of the ovary.

Although C. mcdonaldi is very common in the Gulf of Mexico and Caribbean few preserved specimens offer reliable measurements or scale counts. The following proportions expressed as a percent of S.L. are from two specimens only: head length 30.4-33.0, snout length 9.4-10.1, prepelvic length 52.1-53.2, preanal length 63.7-63.8, predorsal length 75.8-75.9, maximum diameter of orbit 9.4-10.3, sphenotis width of skull 11.7-13.1, upper jaw length 10.4-11.2, dorsal base length 10.7-11.5, anal base length 25.0-25.8, lower jaw length 12.8-15.6. Meristic variation, from as many as 20 specimens, was D 19-22, A 35-38, P_1 8-9, P_2 6, vertebrae 19-21+34-37, pyloric caecae 5-7, and branchiostegal rays (4)-5-(6).

Krefft (1973) lists the range of C. macroptera. (=C. mcdonaldi) in the western Atlantic as extending from off Brazil at 24°S to the Gulf of Mexico in depths of 865 to 2115 m.

Einara Parr 1951

Figure 34 B-D

Alepocephalus (not of Risso 1820). Alcock 1892:358 (part. edentulus only). Roule and Angel 1931:5 (atlanticus). Koefoed 1927:44 (part. macrolepis only).

Einara Parr 1951:10 (Type species: Alepocephalus macrolepis Koefoed 1927 by original designation).

Torictus Parr 1951:10 (Type species: Alepocephalus edentulus Alcock 1892 by original designation).

Nomenclature:

Parr's (1951) genus Torictus was based on examination of an obviously damaged specimen of E. edentulus. Alcock (1892) did not mention, his arttist did not illustrate, and I cannot find in the specimens at hand (USNM 200522 and MCZ 49348) any indication that the "posterior portion of the maxillary {might normally be} twisted almost 90 degrees" (Parr 1951). The main differences then between E. macrolepis and E. edentulus are in the size of the head and degree of development of the ethmoid and premaxillary. These differences are slight in my opinion and insufficient to warrant generic separation in view of the large number of similarities indicative of recent common ancestry.

The original descriptions and figures of both A. macrolepis Koefoed 1927 and A. edentulus Alcock 1892 are adequate. Both holotypes are extant but since that of A. macrolepis is accessible to more deep-sea ichthyologists, and since that of A. edentulus was for a time considered lost, and since Einara has line precedence over Torictus, the former is chosen as the name of this genus.

Diagnosis:

Body compressed, rather elegant, covered with moderate to large sized scales; isthmus scaled or partly scaled; pectoral fan-like as in *Asquamiceps* but pectoral base and area anteriad of base scaled; with or without lateral line (one reported by Koefoed (1927) in type of *E. macrolepis*); caudal peduncle very slender and short, its height less than 5% and its length less than 11% SL; lower jaw ends behind posterior margin of orbit; peritoneum unpigmented; teeth in premaxillary and mandible, none on maxillary, vomer or palatine; most of first gill arch without gill lamellae; a complete row of 10-15 gill rakers on back of lower limb of second arch; A 26-34, D 22-27, $P_1$9-10, P_2 (5)-6, br 7, vertebrae 18-21+29-36=47-55.

Key to Species of *Einara*

1a. A32 or more; vertebrae 19-21+33-36=54-55..........................
.... *E. edentulus*.

1b. A28 or less; vertebrae 18-19+29=47-48..............................
.... 2.

2a. Anus slightly in front of anal fin and separated by about 2 scales, P_2 origin to A origin 12.5-15.1% SL, snout to anal 59-64% SL, pyloric caecae 3..
.... *E. macrolepis*.

2b. Anus about midway between pelvic base and anal origin and separated from anal fin by about 5 scales, P_2 origin to A origin 21% SL, snout to anal about 68% SL, pyloric caecae 5........................
....*E. species*.

There are no western North Atlantic records of *E. macrolepis*. *Einara species* is from the Indian Ocean (USNM 200465) and may be conspecific with

E. macrolepis. The differences noted in the key may be due to the larger size (217 SL) or sex (male) of the Indian Ocean specimen when compared to the holotype (175 SL) and an eastern Atlantic specimen from 'Discovery' st. 7824 #21 (172 SL, female).

There is only one western Atlantic specimen of E. edentulus from off Georges Bank in 490-520 fms. at 42° 39'N 63° 58'W (MCZ 49348). It is rather damaged but reliable meristic counts showed no significant difference with an Indian Ocean specimen (USNM 200522), which follow in parentheses: male (female), pyloric caecae 6 (6), P_1 9-10 (10-10), $P_2$5-6? (-5), gillrakers on first arch 7-1-13 (7-1-14), vertebrae 19+36 (19+35), scales from anal origin up and back to D base 19 (about 18), transverse scale rows from D origin to the point where the opercle meets the body 22 (23).

Ericara Gill and Townsend 1897

Figure 32 A&B

Alepocephalus (not of Risso 1820). Gunther 1878:248 (niger). Lloyd 1909:146 (part. microlepis only).

Pterothrissus (not of Hilgendorf 1877). Goode and Bean 1896: Figure 52 only which is of E. niger.

Ericara Gill and Townsend 1897:232 (Type species Ericara salmonea Gill and Townsend 1897 by monotypy).

Xenognathus Gilbert 1915:311 (Type species Xenognathus profundorum Gilbert 1915 by monotypy).

Whitleyidea Fowler 1934:247 (Type species Alepocephalus niger Gunther 1878 by original designation).

Diagnosis:

In Key.

Remarks:

Only one species, E. salmonea, known from the western North Atlantic.

Key to Species of Ericara

1a. Two pyloric caecae; 11 pectoral rays; 17-18 dorsal rays; 25-27 anal rays.. Ericara salmonea Gill Townsend 1897.

1b. Four to eight pyloric caecae; 9-10 pectoral rays; 19-22 dorsal rays; 27-33 anal rays...2.

2a. Anal with 27 rays; 4 pyloric caecae.. Ericara niger (Gunther 1878).

2b. Anal with 30-33 rays; 8 pyloric caecae............................ .... 3.

3a. Six pelvic rays; body elongate, height 16.8% SL; vertebrae 22+34=56 .... Ericara microlepis (Lloyd 1909).

3b. Seven pelvic rays; body stout, height about 25.9% SL, vertebrae 18+35=53.. .... Ericara werneri (Nybelin 1946).

Ericara salmonea Gill and Townsend 1897

Xenognathus profundorum Gilbert 1915.

Remarks:

Anteriorly, lateral line scales appear separated from each other by body scales; posteriorly they are not. There are a total of 50-60 pored lateral line scales; about 50-55 transverse rows above the lateral line before the dorsal. D 17-18, A 25-27, P_1 11, P_2 (5)-6, vertebrae 20-21 + 31-33 = 51-53, gillrakers on first arch 1-2+1+11, 9-12 gillrakers on back of lower limb first arch (16 in Pacific holotype of E. salmonea), brH 5, pyloric caecae 2.

The following proportions from specimens 266-437 mm SL are expressed as a percent of SL: head length 34.2-35.9, snout length 8.5-10.3, prepelvic length 52.6-53.2, predorsal length 74.4-76.5, preanal length 67.7-68.6, snout to anus 60.6-64.0, maximum diameter of orbit 10.3-11.8, upper jaw length 13.6-14.5, lower jaw length 16.3-16.8, dorsal base length 11.2-15.0, anal base length 18.3-21.4 sphenotic width of skull 14.1-16.8.

The western Atlantic material is from the Atlantic side of the Antilles. The holotypes of E. salmonea and X. profundorum, both from the eastern Pacific are in bad condition and difficult to distinguish from

Atlantic specimens. The type of _E_. _salmonea_ has more gillrakers (16) on the back of the lower limb of the first gill arch than the Atlantic specimens. Better eastern Pacific material must be examined to determine if they are conspecific with western Atlantic specimens. At present, there is no convincing evidence that Atlantic specimens differ from their Pacific counterparts.

Herwigia Nielsen 1972

Bathylaco (not of Goode and Bean 1896) Nielsen and Larsen 1970:35.

Herwigia Nielsen 1972:30 (Type species Bathylaco kreffti Nielsen and Larsen 1970 by original designation).

Diagnosis:

Orbit forward on snout; jaws extending well behind posterior margin of orbit; dorsal profile of head with moderate arch from orbit to snout; testes convoluted but without distinct lobes; lower jaw edentate; modified gill rakers not present on medial surface of first two gill arches; vertebrae reported as 26-27+20=46-47; gill rakers on first arch 7+1+13-14=21-22; P_1 17-18; vertebral centra tall, rectangular to hour-glass-shaped with relatively wide intervertebral spaces of unossified chorda. One species presently known only from the eastern North and South Atlantic (Nielsen 1972).

Leptoderma Vaillant 1886

Leptoderma Vaillant 1886:1239 (Type species: *Leptoderma macrops* Vaillant 1886 by monotypy). Vaillant 1888:165 (macrops). Alcock 1899:182 (*affinis*). Fowler 1943:55 (*retropinna*). Mead and Bohlke 1953:265 (*springeri*). Abe, Marumo and Kawaguchi 1965:69 (*lubricum*).

Diagnosis:

Dorsal origin distinctly behind anal origin; body slender, elongate, completely scaleless; lower jaw ends under orbit; circumorbital bones incomplete; peritoneum pigmented; pyloric caecae 2, short and stubby on either side of pyloric arm of intestine; ovary completely enclosed by ovarian tunic; vertebrae 15-19+48-65=63-84.

Key to Atlantic Species of *Leptoderma*

1a. Body tapers to a fine almost stringy point; dorsal and anal fins continuous with caudal; caudal vertebrae 56-64.................... .... *Leptoderma macrops* Vaillant 1886.

1b. Distinct dorsal and anal fins, each separated from a "second" fin which is composed of increased numbers of lengthened procurrent caudal rays; caudal fin base without fine tapering point.......... ..... *Leptoderma lubricum* - complex Abe, Marumo and Kawaguchi 1965.

Remarks:

There are two distinct forms of *Leptoderma*. One, represented by *L. macrops* and including the nominal species *L. affinis*, *L. retropinna* and *L. springeri*, has a body which tapers to a fine almost stringy point and has single dorsal and anal fins continuous with the caudal (Fig. 33). The other form, *L. lubricum*, has distinct dorsal and anal fins, each separated from a "second" fin which is composed of increased and lengthened procurrent caudal rays, and has a less pronounced taper to the caudal fin base (Fig.33C). Further, the L. lubricum form has generally fewer caudal vertebrae 48-59 than does the L. macrops form, 56-64.

West Pacific specimens of the L. macrops form, including the holotype of L. retropinna but not that of L. affinis, were examined for differences with a large series of western Atlantic L. macrops. West Pacific specimens have somewhat larger heads and generally have lateral line canal segments rather than papillae. However, a specimen from off Shiono Misaki, Japan (USNM 150073) has canal segments anteriorly, papillae posteriorly and both together over the middle part of its lateral line. In addition, occasional western Atlantic specimens sometimes have a solitary canal segment instead of lateral line papillae. Present material is insufficient to determine the status of Indo-west Pacific Leptoderma.

Leptoderma macrops Vaillant 1886

Figure 33A

Leptoderma springeri Mead and Bohlke 1953.

Remarks:

Examination of a paratype (BMNH 1890-6-16-44), radiographs of three syntypes (MNHN 85-233, 85-234, and 85-235), and Tucker's (1954) specimen (BMNH 1963 -3-6-5-7) of L. macrops revealed no differences between them and numerous western Atlantic specimens, a conclusion previously reached by Krefft (1973).

Leptoderma macrops has a loose, dark filmy to semi-glossy black skin covering the head, body and fins. Numerous small dark papillae (about

0.3 mm in a 200 mm SL specimen) are regularly arranged along the lateral line, anal fin and dorsal fin bases, mid-line of the back and over the head (Fig. 33Aand B). On the specimen illustrated there were about 120 along the anal base, about 80 along the dorsal and 97 on the lateral line which ended about 20 mm before the caudal base. The system of lateralis pores and papillae on the head were as illustrated (Fig.).

Morphometric measurements were taken from 35 specimens from one locality, 29°14'N, 87°33'W (USNM 215614). Spot comparison with other north Atlantic specimens showed no significant differences in the measurements taken. As shown in Figure for head length, the variation of most measurements was great. The range of measurements was as follows: standard length, 141-210 mm (subsequent measurements expressed as a percent standard length); head length, 16.7-20.8; snout length, 3.8-5.3; maximum orbit diameter 5.8-8.1; bony interorbital, 1.6-2.5; upper jaw length 4.6-5.8; prepelvic length, 31.0-40.3; predorsal length, 47.3-56.3; preanal length, 35.5-44.2. Preanal length (y) was related to predorsal length (x) by $y=11.55+0.53x$, $r=0.64$, $r^2=0.41$. Thus, 41% of the variation in preanal length was associated with the predorsal length. Maristic variation was as follows: br(4)-5-(6), pyloric caecae 2, P_1(7)-8-9, $P_2$5-(6), gillrakers on first arch, 0-1+11-14, vertebrae 17-19+62-65, D 57-67, A 78-85. The last 3-6 dorsal and anal rays were usually rudimentary and without basal pterygiophores.

Distribution:

In western Atlantic from Brazil (25°13'S, Krefft 1973), throughout the Gulf of Mexico and Caribbean in 530 to 1200 m. Krefft (1973) indicated a depth range in the North Atlantic of 650-2330 m with a distribution center between 1000 and 2000 m. Gulf of Mexico and Caribbean records of the R/V *Oregon* cruises indicate a narrower range with a distribution center between 700 and 1000 m.

A 194 SL female caught 9 February 1961, 530-585 m, and part of the large lot used in the morphometric study above had three size classes of eggs with diameters of about 0.6, 1.3, and 2.2 mm. There were only 41 of the large eggs.

Leptoderma lubricum Abe, Marumo, Kawaguchi 1965

As treated here *L. lubricum* may be a composite species. In addition to the holotype caught in a large plankton net from 1300 m in Suruga Bay, Japan, there are now two specimens from the southeast Pacific off northern Peru in 1815-1860 m (4°10'S, 81°27'W) and off Valparaiso, Chile in 1170-1480 m (33°39'S, 72°09.5"W) as well as four specimens from two 'Discovery' stations near the Azores in 2283-2287 m. Except for the holotype all specimens were caught in bottom nets.

In general the meristics from all three areas overlapped. The holotype, however, had more dorsal rays (37 vs. 27-33), anal rays (51 vs. 42-47) and caudal vertebral (59 vs. 48-52) than the specimens from the southeastern Pacific or Azores. Other meristics for all specimens were: dorsal procurrent rays 22-25, ventral procurrent rsys 20-26, $P_1$7, P_2(4)-5, precaudal vertebrae 15-17, br. 4-6, and gill rakers on first arch 0+1+15-16. Morphometric variation, expressed as a percent SL, of specimens 109-208 SL were: head length 23.5-24.8, snout length 5.7-7.4, maximum orbit diameter 8.6-10.0, prepectoral length 26.5-27.8, prepelvic length 38.7-40.2, preanal length 44.0-47.5, predorsal length 54.8-61.4, upper jaw length 7.4-8.2, lower jaw length 8.4-9.2, and sphenotic width of skull

9.4-11.6. The distribution of pores and papillae were described by Abe *et al* (1965) but except for the lateral line papillae these could not be verified with the present material. The arrangement described by them is similar in many respects to that illustrated for *L. macrops*.

Distribution. Unknown in the western Atlantic but present near the Azores Islands in the eastern Atlantic. All known capture localities are near oceanic islands (Japan, Azores) or a continental trench (Peru-Chile Trench). Western Atlantic sites near the Antilles may yield this species.

Mirognathus Parr 1951

Mirognathus Parr 1951:4 (Type species *Mirognathus normani* Parr 1951 by original designation).

Diagnosis:

In key; monotypic.

Mirognathus normani Parr 1951

Mirognathus normanii Parr 1951:4 (incorrect spelling).

Mirognathus normani Parr 1951:10.

Diagnosis:

All oral and branchial bones edentate; pectorals absent or rudimentary; two pyloric caecae.

Remarks:

Morphometric measurements from a female 91.9 mm SL from $42^{\circ}56'$N $13^{\circ}29'$W (ISH 917/73), expressed as a percent SL: head length 28.6, snout length 12.9, maximum orbit diameter 6.0, prepelvic length 46.8, preanal length 62.2, predorsal length 62.2, upper jaw length 17.0, dorsal base length 22.1, anal base length 19.8, caudal peduncle depth 7.3, postdorsal length 19.4, sphenotic skull width 9.2. Meristics: $P_2 5$, D 16, A 16, br 8, gill rakers on first four arches 7-1-22, 7-1-20, 6-1-17, 6-1-13. Scaleless; in preservative, body anteriad of pelvic symphysis dark, posteriod of pelvic symphysis light; stomach and intestine dark anteriorly, light posteriorly also.

Distribution:

Known only from the Atlantic between 58°N ("Walther Herwig" data) and 48°S (Parr 1951) from three ISH specimens and the holotype. Caught in depths of 1500 to 3100 m from 300 to 2300 m above the bottom. Unknown from the western North Atlantic although not unexpected. Bathypelagic.

Narcetes Alcock 1890

Bathytroctes (not of Gunther 1878). Gilbert 1890:52 (*stomias*). Garman 1899:287 (part. *alveatus* only).

Narcetes Alcock 1890:305 (Type species: *Narcetes erimelas* Alcock 1890 by monotypy). Garman 1899:289 (*pluriserialis*). Lloyd 1906:308 (*affinis*). Fowler 1934:253 (part. *lloydi* only). Herre 1935:126 (*wonderi*).

Diagnosis:

Premaxillary and dentary teeth (especially near symphysis) pluriserial; dentary expanded laterally and with an edentate gap at symphysis; vertebrae 26-33+18-25=48-56 with 3-14 more precaudal than caudal vertebrae; moderately large spaces of unossified chorda between centra; pyloric caecae (6?) 8-14, long; br usually 8; gill rakers on first arch 3-6+1+10-17=14-22. A single Atlantic species.

Narcetes stomias (Gilbert 1890)

Figure 36 D&E

Bathytroctes stomias Gilbert 1890:53.

Narcetes pluriserialis Garman 1899:289.

Nomenclature:

The types of *B. stomias* (USNM 43081) and *N. pluriserialis* (MCZ 28474) are both from the eastern Pacific and are indistinguishable except for the palatine teeth. However, as shown below, palatine teeth change from basically uniserial to pluriserial with age. Since the type of *B. stomias*, which has uniserial teeth, is one of the smallest known specimens (283 mm

SL), the two nominal species are considered conspecific. As pointed out by Grey (1958), N. affinis Lloyd 1906 may also be conspecific with N. stomias. However, the reported number of pectoral rays, 13, is outside the known variation in eastern Pacific and North Atlantic N. stomias, 9-11.

Diagnosis:

Cephalic lateralis pores not unusually numerous; head covered with smooth tough skin, its lateralis pores not raised and not giving head a rough appearance; P_1 9-11; A 14-17.

Description:

Body long, compressed, salmon-like, greatest depth about 20% SL at a point near the pectoral about 30% SL from snout; caudal peduncle 6.0-8.3% SL, almost rectangular in cross section in fresh and well preserved specimens; premaxillary and anterior triangular part of supraethmoid form projection over lower jaw.

Dentary teeth pluriserial, an edentate gap at symphysis; vomer with 1-5 pairs of teeth; premaxillary pluriserial; maxillary and palatine uni- to pluriserial becoming pluriserial with increase in size and beginning anteriorly on each bone (palatine uniserial in all four specimens less than 370 mm SL, pluriserial in 84% of those larger than 370 mm SL); basibyal edentate.

Scales deciduous, seldom present except on isthmus, in flap above pectoral and lateral line; lateral line scales extremely variable 53-73 (counts based on 10 specimens with all l. l. scales intact), a few scales extend onto caudal; one mature male, 504 mm SL, with two additional pit scales above and below ultimate lateral line scale; from 30 to 47 transverse scale rows above lateral line before dorsal; reportedly (Grey 1958), 100-105 scale rows above lateral line.

Counts, made in parentheses: D 18-20(19), A 14-17(16), P_1 9-11(11) P_2 8-9 (9), br 8-9, gill rakers first arch 3-5+1+10-14=14-19, vertebrae 25-28+21-23=47-50.

Pyloric caecae 8-11 (9), long, not quite reaching to end of thick-walled, pyloric stomach; intestine with only two or fewer small loops posteriad of stomach; ovary simple; testes with several large lobes on each side completely separate, only joined dorsally by mesentery and vas deferens.

Five measurements showed significant negative allometry when expressed as a percent of SL and regressed on SL: maximum head length = 0.378-0.0002 SL, r (coefficient of regression) = -0.80, n=19 (Fig. 31B); minimum head length (to top of gill opening) = 0.308-0.00018 SL, r= -0.74, n=19; snout length = 0.112-0.00007 SL, r = -0.75, n=19; sphenotic width = 0.142-0.00009 SL, r= -0.75, n=16; upper jaw length = 0.216-0.00012 SL, r= -0.66, n=19 (Fig. 31C). Less significant negative allometry was found in the prepelvic length = 0.600-0.00009 SL, r= -0.45, n=16; preanal length = 0.753-0.00008 SL, r= -0.43, n=17; predorsal length = 0.684-0.00009 SL, r= -0.38, n=17; dorsal base = 0.154-0.00001 SL, r= -0.08, n=13; and anal base = 0.115-0.00002 SL, r= -0.26, n=13.

Figures 31B and 31C are misleading. The significance of both regressions is due to an apparently sudden change in the physiognomy of the skull and jaws (Fig. 36). In specimens of both sexes larger than 410 mm SL the ventral profile of the upper jaw is distinctly concave rather than straight as in smaller specimens. At this size the snout and upper jaw become markedly arched (Fig.36E) so that the straight line measurements of head length and upper jaw length become actually, and relatively, smaller. These changes are very similar to the secondary sexual changes found in spawning salmonids. According to Davidson (1935 cited in Vladykov 1962: 52), complete development of male secondary sexual characters in *Oncorhynchus gorbuscha* requires only 35 to 45 days. Thus the very sudden change in proportions in Figures 32B and 32C probably reflects a real and rapid morphological change most likely associated with the onset of sexual maturity.

Known from the Atlantic and eastern Pacific from 1510 to 2334, with most from 1800 to 2100 m.

Photostylus Beebe 1933

Photostylus Beebe 1933a:163 (Type species: Photostylus pycnopterus Beebe 1933a by monotypy).

Diagnosis:

Acentrous vertebrae behind head in adults; head often flexed downward; photophores located on raised stalks over head and body; intermandibular membrane with bilateral rows of luminous (?) flaps (sometimes difficult to see); ventral outline of upper jaw with obtuse angle at end of premaxillary; no pseudobranch. Monotypic.

Remarks:

Beebe (1933a) implicated Anomalopterichthys, Rouleina and Xenodermichthys as genera closely related to Photostylus. Subsequent authors (Parr 1951, Grey 1958, Goodyear 1969 and Quero 1975a) have placed Photostylus in the Alepocephalidae without comment. Photostylus shares several characters with two other pelagic groups, the stomiatoids and the cetomimiform mirapinnatoid families Megalomycteridae and Entaeniophoridae. It differs from both groups by its lack of a retractor arcuum branchialium muscle (presumed present in megalomycterids and eutaeniophorids, Rosen 1973:491), and in its separate first preural and ural centra (fused in the other two groups, Rosen 1973, Weitzman 1974, personal observations).

Photostylus resembles the stomiatoids in its lack of a fifth epibranchial and separate fifth pharyngobranchial tooth plate (Fig.10B) (Weitzman 1974), toothless second infrapharyngobranchial and basihyal, lack of a pseudobranch and lack of ossification of the anterior vertebrae. All of these are loss characters, probably convergent. There is no synapomorphous character by which Photostylus may be placed in the stomiatoids.

Photostylus resembles the megalomycterids and eutaeniophorids in general appearance (Fig.41A), in the antero-ventral extension of the third hypural and along side the ural centrum of Photostylus (Fig.16A) or under the ultimate centrum in the megalomycterid, Ataxolepis (Rosen 1973, Fig. 57), and in the rounded lobate pectorals. A damaged pectoral from Eutaeniophorous (Dana st. 3731 XIV) resembled the pectoral of Photostylus (Fig.29B) in having two large proximal radials supporting the fin rays and an arched portion of the coraco-scapula ending blindly behind the radials. In Eutaeniophorus the arch, however, did not correspond to a mesocoracoid but rather to the ventral process of the coracoid. Again these similarities appear to be convergent specializations, probably to nutrient-poor epi and bathypelagic habitats.

Photophore histology indicates little difference with those of Xenodermichthys (Best and Bone, 1976). This is the most positive evidence of relationship available.

The reasonable assumption of a gelatinous covering in Photostylus (Beebe 1933a, Goodyear 1969, Best and Bone 1976) remains an assumption as it has yet to be seen.

Photostylus pycnopterus Beebe 1933

Photostylus pycnopterus Beebe 1933a:163.

Diagnosis:

Same as genus.

Distribution:

Circumglobal between about 40°N and 35°S, with records from the Indian Ocean, Tasman Sea, Central Pacific, east Pacific and both sides of the Atlantic.

Rinoctes Parr 1952

Bathytroctes (not of Gunther 1878). Koefoed 1927: 50 (in part, nasutus only).

Rinoctes Parr 1952: 263 (type species Bathytroctes nasutus Koefoed 1927 by original designation).

Diagnosis:

In key, monotypic.

Rinoctes nasutus (Koefoed 1927)

Figure 39A

Bathytroctes nasutus Koefoed 1927: 50.

Diagnosis:

Dorsal inserted distinctly before anal insertion, directly above or slightly in advance of anus; no mesocoracoid; possibly completely scaleless; teeth on vomer, palatine, premaxillary, maxillary and mandible; those on premaxillary in two rows, the outer larger; those near symphysis of mandible pluriserial but mandible not expanded so teeth spread over lateral surface and project out laterally; yellowish substance present in mandibular canal of both examined specimens; one acentrous vertebra behind skull.

Description:

Morphometric measurement, expressed as a percent SL, from two Gulf of Mexico specimens 69.0 and ca. 122 mm SL (USNM 189010 and USNM 215517): head length ca. 32.0-33.6, snout length ca. 11.1-12.3, maximum orbit diameter ca. 10.0- ca. 10.1, prepectoral length 38.1, prepelvic length ca.

57.4-60.9, preanal length ca. 71.3-75.4, predorsal length ca. 65.6-66.7, snout to anus ca. 61.5-65.9, upper jaw length ca. 16.8-19.1, lower jaw length ca. 17.0-19.1, dorsal base length ca. 14.2, anal base length 10.6, caudal peduncle depth 5.5-ca. 6.9, caudal peduncle length 18.6.

Meristic variation: P_1 8, P_2 7, D7, A 11, br 6-7, gill rakers on first arch 4+1+15-17, 11 gill rakers on back of lower limb of third arch, 8 pyloric caecae, vertebrae 22-24+18-19=41-42.

Distribution:

Known from around the Azores (Koefoed 1927) and Cuba (Parr 1952) as well as two new localities off Yucatan, 24°42'N 92°18'W and 27°06'N 89° 13'W. Respective capture depths were 2865, 3886, 3658 and 2012-2195 m. U.S.N.M. 215517 from Oregon st. 2199, 24 June 1958, 24° 42'N, 92° 18'W, 3658 m is a mature male about 122 mm SL. Benthic.

All specimens have been reported as being damaged to some extent. The holotype had no scales or skin yet Koefoed (1927) estimated that it had 50 lateral line scales. Parr (1952) implied that his MCZ specimen had scales which could not be counted. Both USNM specimens have colorless skin which provides no indication of scales or scale pockets. There are slight differences in some reported proportions (snout and orbit lengths, fin base lengths and positions) and meristics (pyloric caecae) for which no significance can be attached at present.

Rouleina Jordan 1923

Bathytroctes (not of Gunther 1878), Vaillant 188:158 (part. *attritus* only), Koehler 1896:517 (part. *mollis* only), Goode and Bean 1896:44 (part. *aequatoris* only), Fowler 1934:250 (Part. *harperi* only).

Xenodermichthys (not of Gunther 1878), Alcock 1892:359 (*guentheri*). Alcock 1898:148 (*squamilaterus*). Fowler 1943:53 (*funebris*).

Aleposomus (not of Gill 1884). Brauer 1908:21 and 22 (*lividus* and *nudus*). Tanaka 1909:14 (*watasei*).

Talismania (not of Goode and Bean 1896). Fowler 1934:250 (part. *harperi* only).

Rouleina Jordan 1923:122 (Type species: *Aleposomus guntheri* = (*guentheri*) Alcock 1892 by original designation), Whitley 1940:407, Maul 1948:7 (*maderensis*).

?*Anomalopterus* (not of Vaillant 1888) Beebe 1933a:159 (*megalops*).

Bathypropteron Fowler 1934:256 (Type species: *Aleposomus nudus* Brauer 1908 by original designation).

Caudania Roule 1935:2 (Type species: *Bathytroctes mollis* Koehler 1896 by *monotypy*).

Auchenalepoceps Fowler 1943:53 (Type species *Xenodermichthys funebris* Fowler 1943 by original designation).

Diagnosis:

Body scaleless, except for lateral line tube which is sometimes supported by modified ring-like scales standing on end; skin smooth silky black; the body with or without nodular photophores, with or without papillae, and with or without a thick epidermal gelatinous layer supported by oblong walled "cells"; photophores, when present, approach the approximately regular, quincunxial arrangement; D18-22, A 15-23, P_1 6-10, P_2 6-7; vertebrae 19-24+24-28=44-50; teeth on premaxillary, maxillary and dentary, none on palatine or vomer.

Remarks:

The available North Atlantic material of Rouleina consists of two species tentatively referred to *R. mollis* and *R. maderensis*. Beebe's (1933a) *Anomalopterus megalops* may represent a small juvenile of one of these species but examination of the holotype did not resolve the problem.

Key to North Atlantic Species of Rouleina

1a. No photophores; testes ribbon-like with many convolutions in mature specimens but folds always connected, never with separate lobes; lateral line with 44-48 modified ring-like scales, undetectable in specimens less than 155 mm SL; preural vertebrae 19-22+22-26=44-46; papillae on body especially near lateral line, along bases of vertical fins and along all finrays, mature around 250-300 mm SL... *R. mollis* (Koehler 1896).

1b. Flat superficial photophores present, commonly abraded; testes discrete, separate lobes even when immature; lateral line with 50-56 modified ring-like scales, undetectable at 131 mm SL; preural vertebrae 20-22+26-28=47-50; papillae restricted to fins and fin bases, always peripheral to photophores... *R. maderensis* Maul 1948.

Rouleina mollis (Koehler 1896)

Figure 41B

Bathytroctes attritus Vaillant 1888:158, nomen dubium according to Quero 1975b:437.

Bathytroctes mollis Koehler 1896:517.

Bathytroctes aequatoris Goode and Bean 1896:44.

Diagnosis:

Table 4 . No photophores; papillae on body, especially near lateral line, dorsal, anal and caudal fin bases, and along finrays of dorsal, anal, pectoral, pelvic and caudal fins; lateral line a tube enclosed within the gelatinous covering of the skin and supported by 44 to 48 modified ring-like scales standing on end (the lateral line scales and gelatinous skin covering were not detectable in four well preserved specimens less than 155 mm SL); vertebrae 19-22+22-26=44-46; D 18-21, A 18-21, P_1 6-7, P_2 6-7, gill rakers on first arch 7-8+1+16-20; testes ribbon-like with many convolutions in mature specimens but folds always connected, never with separate lobes; upper jaw 15.3-18.0% SL, lower jaw 16.5-20.0% SL; moderately large species up to 382 mm SL, mature around 250-300 mm SL.

Distribution:

In the eastern Pacific from 04°10'S to 29°29.5'S; western Atlantic from 09°00.2'N to 39°17.5'N; eastern Atlantic from Morocco to Bay of Biscay and Azores (Krefft 1973); and one locality in the Indian Ocean at 21°18'S 36°18'E. All available specimens are from bottom trawls made between 950 and 1960 m. It has been captured with its congener, R. maderensis, once in the western Atlantic and once in the southeast Pacific.

Rouleina maderensis Maul 1948

Rouleina maderensis Maul 1948:7

Diagnosis:

Table 4. Photophores on body in approximately regular quincunxial arrangement; papillae restricted to dorsal, anal and caudal fins and always peripheral to photophores; lateral line with 50-56 modified ring-like scales (Undetectable at 131 mm SL); vertebrae 20-22+26-28=47-50; D 20-22, A 20-22, P_1 6-7, P_2 6-7, gill rakers on first arch 6-7+1+17; testes discrete lobes even when immature; upper jaws 12.9-18.3% SL, lower jaws 14.4-19.8% SL; moderately small species up to about 323 mm SL, mature around 230-250 mm SL.

Distribution:

In the southeastern Pacific at 24°29.5'S 70°40'W; western Atlantic from 09°05'N - 37°04.4'N; and in the eastern Atlantic near Azores and Madeira. One specimen, the smallest known (86.7 mm SL), was captured in a *Dana* midwater net at st. 1183^{I}. The depth was 3025 m and there was 4500 meters wire out. All others were captured with bottom trawls between 595 and 1460 m. Six of the eight western Atlantic collections were made in less than 1000 m of water.

Table 4. Selected meristic differences between Rouleina mollis and Rouleina maderensis (^{1}indicates holotype of Bathytroctes aequatoris: ^{2}indicates paratypes of R. maderensis).

LATERAL LINE PORES

	44	45	46	47	48	49	50	51	52	53	54	55	56	57
R. mollis	1	4	1		1									
R. maderensis							2		1	1	1	1^{2}	2	1^{2}

VERTEBRAE

	Precaudal				Caudal							Total						
	19	20	21	22	22	23	24	25	26	27	28	44	45	46	47	48	49	50
R. mollis	4	20^{1}	7	2	1		12^{1}	15	4			12^{1}	15	7				
R. maderensis		2	17^{2}	17					19^{2}	15^{2}	3				8^{2}	22^{2}	8	1

FINRAYS

	Dorsal					Anal				
	18	19	20	21	22	18	19	20	21	22
R. mollis	5	9	10^{1}	1		6	10	9^{1}	1	
R. maderensis			3	8^{2}	5^{2}			5	6^{2}	4

Talismania Goode and Bean 1896

Bathytroctes (not of Gunther 1878). Vaillant 1888:153 (in part, homopterus only). Brauer 1902:277 (longifilis). Fowler 1934:249 (in part, hataii only).

Talismania Goode and Bean 1896:41 (in part, homopterus Vaillant 1888 and antillarum Goode and Bean 1896 only) (Type species Bathytroctes homopterus Vaillant 1888 by subsequent designation of Jordan 1919: 467. Parr 1952:269 (oregoni). Sulak 1975:88 (mekistonema). Quero 1975c:439 (grandisquamis).

Nemabathytroctes Fowler 1934:252 (Type species Bathytroctes longifilis Brauer 1902 by original designation). Parr 1951:10 (bifurcatus).

Binghamia Parr 1937:7 (Type species Binghamia microphos Parr 1937 by monotypy).

Binghamichthys Whitley 1941:4 (nomen novum replacing Binghamia Parr 1937 preoccupied by Binghamia Tutt 1908, a butterfly). Bussing 1965:189

Diagnosis:

Alepocephalids with subdivided adductor mandibulae muscle; a black wart-like spot in the vicinity of the base of the sixth dorsal ray (sometimes abraded); ovary completely enclosed in tunic; teeth present on premaxillary, maxillary, palatine, mandible, and usually vomer; dorsal and anal approximately equal and opposite with 17-24 rays; P_2 7-(8), P_1 10-13, Br(6), 7, (8), pyloric caecae 7-11; vertebrae 16-21 + 25-32 = 43-50. Composed of two evolutionary lineages herein recognized as the subgenera Talismania Goode and Bean 1896 with four or five species and Binghamichthys Whitley 1941 with two species.

Key to Species of Talismania

1a. Upper pectoral ray elongate, usually noticeably thickened; diameter of orbit less than snout length; A1 section of adductor mandibulae covers A2 section to top of preopercle............................ subgenus Talismania.. 2.

1b. Pectoral rays not elongate; diameter of orbit greater than snout length; A1 section of adductor mandibulae leaves exposed most of A2 section above bend in preopercle............................ subgenus Binghamichthys....................................... 5.

2a. Thick whitish arcs of luminous(?) tissue on the anterodorsal and posteroventral rims of the orbit (not to be confused with the whitish thickened scleral tissue on the back of the eyeball in *T. oregoni*), 17+26=43 vertebrae,.. *T. bifurcata*.

2b. No arcs of whitish luminous(?) tissue around orbit, 45 or more vertebrae.. 3.

3a. Head length 40-41% SL, lower jaw length 22.7% SL, about 90-100 lateral line scales.. *T. longifilis*.

3b. Head length 31-38% SL, lower jaw 14-18% SL, about 46-55 (64?) lateral line scales.. 4.

4a. Vomerine dentition reduced to two small widely separated patches of minute teeth; 46-48 lateral line scales; 19+28-29=(46)-48 vertebrae; 7-8 pyloric caecae.. *T. mekistonema*.

4b. Vomerine dentition strong, on one tooth plate, forming a straight line across anterior tips of palatine teeth; 52-55(64?) lateral line scales; 17-19+29-32=47-50 vertebrae; 10-11 pyloric caecae.......... .... T. homoptera - T. oregoni.

5a. Pectoral rays 15-16, 18-19 transverse scale rows above lateral line before dorsal, 16-17+28-31=44-48 vertebrae........................ .... T. antillarum.

5b. Pectoral rays 10-12, 32-37 transverse scale rows above lateral line before dorsal, 19-21+25-28=44-48 vertebrae........................ .... T. aphos.

Remarks:

There are three western North Atlantic species of Talismania, T. oregoni, T. mekistonema and T. antillarum. Talismania oregoni may be synonymous with T. homoptera, a problem which is discussed first in the following summaries of the species.

Talismania homoptera (Vaillant 1888)

This species is known only from the damaged holotype captured in 1013-1113 m off northwest Africa, 22°03'N 17°33'W (Bauchot, et al 1971). Although I have not seen the specimen it is rather obvious that its description includes some misinformation which may falsely differentiate this from T. oregoni.

Vaillant (1888) listed under the new species Bathytroctes homopterus "D.19; A.19+ V.9." Goode and Bean (1896) stated about B. homopterus "D.19; A.19+; B.9". Sulak (1975) listed for T. homoptera 9 pelvic and 9 branchiostegal rays. Parr, who examined the holotype, stated in his diagnosis of the genus that there are 6-7 pelvic and 6-8 branchiostegal rays (Parr 1952).

Therefore, if Parr is correct the pelvic and branchiostegal counts of T. homoptera cannot be more than 7 and 8, respectively, and may not be different from T. oregoni (see below). The number of dorsal rays seems to be erroneous from Vaillant (1888) on. In the description and illustration of the holotype (pl. XII, fig. 1) Vaillant (1888) indicates 19 dorsal rays, the first as long as the second. In all other species of Talismania the first two or three rays are considerably shorter than shown, each subsequent ray being progressively longer than its predecessor until the fourth or fifth ray. Therefore, neither the dorsal nor anal ray count can be considered less than that for T. oregoni. Another supposed meristic difference between T. oregoni and T. homoptera is the number of scales. Vaillant (1888) noted, "Ecailles. 6/64/14", which indicates 6 above and 14 below the lateral line and 64 scales in the lateral line. The specimen must have been badly damaged for he states on the next page, "L'etat de l' individu ne permet pas de determiner exactement la situation de la ligne latērale" (Vaillant 1888). Furthermore, the illustration only shows 48 scales corresponding to a lateral line and no more than 18 scales from the dorsal to the pelvics. I therefore find it impossible to accept any published meristic figure on T. homoptera.

Some morphometrics have been used recently to distinguish species of Talismania (Sulak 1975, table 1). The single specimen of T. homoptera has produced different morphometrics, expressed as a percent of SL, by Vaillant (1888)=V, Vaillant's (1888) artist=A, Parr (1952)=P and Sulak (1975)=S. The significant observations are head length - 32.3(V), 32.4(A), less than 36.8(P), and 37.4(S); snout length - 10.6(V), 10.7(A), 12.1(S), diameter of eye - 8.1(V), 7.0(A); and diameter of orbit - 9.3(S). If Sulak's (1975) measurements are incorrect, as the weight of the evidence would seem, then only Parr's 1952) three key characters can separate *homoptera* and *oregoni*. One is the dorsal finray count mentioned above which will not work. Another is the distance of the snout to pelvics 17 percent of SL more than the snout to pectoral distance. This will not separate the species either (see below). Only the measurement of the length of the upper jaw as two percent of SL shorter than the lower jaw will distinguish *T. homoptera* from *T. oregoni* whose upper jaw is less than 1 percent of SL shorter than the lower jaw. If the specimen is as damaged as Vaillant (1888) and Goode and Bean (1896) indicate, then it would not be surprising if the very delicate posterior part of the upper jaw was also damaged, thus effectively shortening the upper jaw.

Resolution of this problem must await direct examination of the holotype of *T. homoptera*. Of interest, however, is the fact that in an appendix to his report, Vaillant (1888 : 386) incorrectly considered *B. homopterus* a junior synonym of *B. rostratus* Gunther.

Talismania oregoni Parr 1952

Numbers of scales or scale pockets are very important for the easy identification of species of *Talismania*. They are deciduous however and rarely intact. In specimens from which reasonably accurate scale counts could be obtained there were 52-55 lateral line scales, about 10 in a transverse series from the lateral line to the dorsal or anal, and 22-26 transverse rows above the lateral line before the dorsal. Some body scales have a triangular flap of black skin on the posterior edge which resembles that frequently seen in T. aphos. None possessed enough scales to determine the arrangement of these scale types. Other meristic counts were D21-24, A20-24, $P_1$11-13, $P_2$7, br 7-8. Modal gill raker counts for the first four arches were 8-1-17, 10-1-19, 11-1-19, and 5-1-14. There were 15 rakers on the back of the lower limb of the third arch. 17-19+29-32=47-50 vertebrae..

Morphometrics of five relatively undamaged specimens, expressed as a percent of S.L., were: head length -31.8-37.2, snout length 10.1-11.8, maximum orbit diameter 5.5-6.9, prepectoral length 33.4-37.6, prepelvic length 43.2-52.9, preanal length 60.3-68.4, predorsal length 62.3-67.9, upper jaw length 14.7-17.3, lower jaw length 14.8-17.5, dorsal base length 17.5-20.0, anal base length 16.8-18.9, caudal peduncle depth 6.2-7.3, postdorsal length 20.1-21.3 and sphenotic width of skull 9.7-11.7.

Sulak (1975) reported T. oregoni from the west coast of Africa, the western Atlantic off Surinam, the Caribbean and Gulf of Mexico. Additional records are mainly in the Gulf of Mexico off the Mississippi delta, in the Caribbean off Panama and Colombia, and the largest single catch of 18 specimens on the antillean side of the Caribbean at 17°47'N, 63°09'W. All specimens have been captured in bottom nets between 565 and 1690 m. A cursory examination of gonadal states of the limited material showed females with large orange eggs and males with large full testes from May through November.

Talismania mekistonema Sulak 1975

Talismania grandisquamis Quero 1975.

Remarks:

Only one reliable series of scale counts could be obtained in the two specimens examined. There were 48 lateral line scales, about 6 in a transverse series from the lateral line to the dorsal or anal, and about 19 transverse rows above the lateral line before the dorsal. Other meristic counts were D18-22, A21, $P_1$12, P_2 7-8, br 7. Modal gill raker counts for the first four arches were 6-1-18, 9-1-20, 10-1-21, 5-1-16. There were 15-18 rakers on the back of the lower limb of the third arch. 19+28-29=47-48 vertebrae.

Morphometrics, expressed as a percent of SL, were: head length 32.0-32.9, snout length 9.8-10.0, maximum orbit diameter 8.4-8.6, prepectoral length 32.6-32.7, prepelvic length 47.9-51.4, preanal length 61.5, predorsal length 61.8-62.8, upper jaw length 14.7-16.9, lower jaw length 16.0-16.8, dorsal base length 18.4-19.2, anal base length 18.4-19.6, caudal peduncle depth 7.7, postdorsal length 18.5-19.3, sphenotic width of skull 10.5-10.9.

In addition to the 11 specimens reported by Sulak (1975), two additional specimens caught at 26°53'N, 14°15'W (Quero, 1975c) and 25°51.7'N, 16°02.4'W (N.I.O. specimen) extend the known range of *T. mekistonema* in the eastern Atlantic north to 26°53'N. With the exception of two specimens reported by Sulak (1975) all other specimens have been caught in bottom trawls between 604 and 1518 m.

Talismania antillarum (Goode and Bean 1896)

Figure 39C

Bathytroctes hataii Fowler 1934

Binghamia microphos Parr 1937

Remarks:

Reliable scale counts were 45 lateral line scales, 5 or 6 in a transverse series from the lateral line to the dorsal or anal, and 18-19 transverse rows above the lateral line before the dorsal. D19-22, A20-22, $P_1$15-16, $P_1$7-9, br 7. Modal gill raker counts for the first four arches were 8-1-21, 9-1-21, 9-1-18, 4-1-11. There were 11-13 rakers on the back of the lower limb of the third arch. Uniserial teeth were present on the premaxillary, maxillary, palatine and mandible. The vomer varied from edentate to two separate patches of 0-2 teeth. External laterally directed premaxillary teeth are sometimes present. 16-17+28-31=44-48 vertebrae.

Morphometrics expressed as a percent SL were head length 29.1-34.4, snout length 7.1-9.7, maximum diameter of orbit 9.1-11.7, prepectoral length 31.7-35.0, prepelvic length 44.6-49.0, preanal length 61.7-69.4, predorsal length 63.0-68.7, upper jaw length 8.5-12.9, lower jaw length 12.9-14.0, dorsal base length 15.4-20.4, anal base length 15.8-21.5, caudal peduncle depth 7.6-9.2, postdorsal length 19.4-23.2, sphenotic width of skull 9.8-12.7.

The above measurements include the types of Bathytroctes antillarum and Binghamia microphos. Parr (1937) was incorrect about the dentition of B. microphos; there are palatine teeth and two teeth on the left side may be vomerine although it is difficult to say with certainty. At any rate the specimen is indistinguishable from other specimens of T. antillarum.

Two N.I.O. specimens and two USNM lots extend the known range of this species to the eastern Atlantic off Spanish Sahara and the Gulf of Guinea. Other material is from the western Atlantic off Surinam, the Caribbean from Colombia to Nicaragua, the antillean Caribbean, the Gulf of Mexico off the Mississippi delta and the Bahamas. All Atlantic specimens have been caught in bottom nets between 455 and 958 m. Females with large 2 mm eggs have been caught in October and November. A female caught in May also had some large size eggs, though she appeared to have more smaller eggs (less than 1 mm) than the ones captured in the fall.

Bussing (1965) reported a juvenile, as B. microphos, in the southeastern Pacific off Chile. An additional specimen (USNM 201160) from 23°29'S, 70°53'W confirms the presence of T. antillarum in the southeastern Pacific. An additional specimen (USNM 200521) extends the known range to the Indian Ocean, 10°01'S, 64°19'E. The nominal Phillippine species, Bathytroctes hataii Fowler 1934, also belongs to the subgenus Binghamichthys. After cursory examination of the type series (USNM 92331, 93390, 93389) and a 'DANA' specimen from 3°40.5'N, 137°53'E, I am unable to distinguish these from T. antillarum. The southeastern Pacific specimen showed the greatest variation from the Atlantic material. It had 9 rather than 7-8 pelvic rays, 48 rather than 44-46 vertebrae and an upper jaw equal to 8.5 rather than 10.9-12.9 percent SL. Analysis of population differences must await more and better material from all oceans.

Xenodermichthys Gunther 1878

Xenodermichthys Gunther 1878, p. 250 (Type species: Xenodermichthys nodulosus Gunther 1878 by monotypy).

Aleposomus Gill 1884, p. 433 (Type species: Aleposomus copei Gill 1884 by monotypy).

Diagnosis:

Body scaleless, covered with an adherent, transparent gelatinous sheath which supports photophores and papillae; photophores on body arranged in approximately parallel rows running diagonally backward from dorsal to ventral midline; dorsal and anal fins long with 27-32 rays; vertebrae 16-19+30-32=47-50; teeth on premaxillary and dentary, none on maxillary, palatine or vomer.

Remarks:

Two species, X. nodulosus and X. copei, are recognized. The former is known from the holotype, a Dana specimen from the Philippine Sea and 2 specimens reported by Matsubara and Iwai (1969). The latter is known from many Atlantic specimens as well as one from the Southwest Pacific and one from the Indian Ocean. Xenodermichthys copei has 27-31 dorsal and 26-30 anal finrays, 46-50 vertebrae and an unrestricted gill opening. Xenodermichthys nodulosus has 32-33 dorsal and anal rays, 50 vertebrae (18+32), and a dorsally restricted gill opening which begins at the upper base of the pectoral. Parr (1951) distinguished Xenodermichthys and Rouleina primarily on the basis of dorsal and anal fin ray counts. Although the differences are not well understood, the two genera are closely related. The species of Xenodermichthys appear monophyletic and are tentatively accepted as a generic group.

Xenodermichthys copei (Gill 1884)

Figure 41D

Aleposomus copei Gill 1884:433.

Xenodermichthys socialis Vaillant 1886:1239, nomen nudum.

Xenodermichthys socialis Vaillant 1889:162.

Aleposomus cyaneus Zugmayer 1914:1.

Nomenclature:

The name Aleposomus copei Gill 1884 was introduced in a preliminary note with the following description, "Another interesting fish, from the same collection, is an alepocephalid, with the body as well as heads caleless (typographical error - should read, head scaleless), which I shall describe as Aleposomus copei" (parenthetical statement mine). This inadequate statement introduced a new genus and species name both of which were considered available by Goode and Bean (1896) who published the first detailed description of Gill's holotype (USNM 33551) as well as by most subsequent workers (Jordan and Evermann 1896, Jordan 1923, Parr 1937 and others). Krefft (1973), however, has considered A. copei Gill 1884 a nomen nudum, but this seems debatable on two points. Gill's (1884) sentence clearly refers to an alepocephalid with a naked head and body, and in 1884 that was a sufficient amount of information to clearly distinguish A. copei from all known alepocephalids with the possible exception of X. nodulosus. In Gunther's (1878) description of Xenodermichthys he noted "minute, rudimentary, scale-like productions are imbedded in the skin, especially on the trunk". Although I have seen one excellent specimen of X. nodulosus, I cannot say with any confidence what Gunther was describing. There certainly are no scales on Xenodermichthys. Thus, Gunther's misleading statement would have provided sufficient detail to (incorrectly) distinguish X. nodulosus from A. copei in 1884.

Description:

The following description is based primarily on a 157 mm SL female specimen from Dana station 1296[I] as well as 14 other eastern Atlantic Dana specimens, 25 western Atlantic specimens, are Indian Ocean specimen (MCZ 45287), and one southwest Pacific specimen from Dana station 3630[II].

Head and body compressed; dorsal and anal fins located on posterior half of body, about equal and opposite; caudal peduncle about twice as long as deep, procurrent caudal rays well developed. Orbit large, surrounded by whitish scleral tissue; aphakii space present; interorbital narrow; snout small. Lower jaw moderate extending beyond midpoint of orbit, the symphysis with an anteroventrally directed point; upper jaw shorter extending to midpoint of orbit.

Body and branchiostegal membranes dark brown or black; fins light brown, their bases with light gray margin; pectoral fin base with an unpigmented strip connecting it to unpigmented gill cavity; head lightly pigmented. Twenty-three rows of body photophores from pectoral to caudal base; two ill-defined rows of photophores on dorsal, anal and pelvic fins, one on pectoral fin, the proximal row on the anal, pelvic and pectoral fin normal sized, others smaller; four photophores in vertical row at caudal base; one along midline between anus and anal origin; many smaller photophores or photophore-like structures on the primary caudal rays, especially the outermost, none on the procurrent rays. Small sensory papillae lining primary caudal rays, especially dense on innermost rays; papillae irregularly scattered over body, two rows along dorsal midline most noticeable; a compact group of papillae located on a raised portion of gelatinous membrane adjacent to dorsal origin. Photophores on head located near tip of each branchiostegal ray, in a group on each branchiostegal membrance near where they overlap, and in the following series: opercular-mandibular (9), preopercular-mandibular (9), adductor mandibular (4), circumorbital (7), and opercular (7). Rows of papillae along same series as well as in an interrupted supratemporal, a supraorbital and lacrimal series. Pores along preopercular-mandibular, circumorbital and supraorbital series.

Selected morphometric measurements of 22 North Atlantic Specimens 84.0 to 170 mm SL, expressed as a percent SL: head length 20.2-25.4, orbit diameter 6.4-9.0, predorsal length 55.1-63.9, preanal length 58.4-65.1, prepelvic length 47.7-52.7, dorsal base length 25.3, maximum body depth 15.0-19.4, and sphenotic skull width 7.3-9.2.

Meristic variation in genus shown in Table 5 as well as the following: P_1 7-8, P_2 6, pyloric caecae 4-7, gill rakers first arch 6-8+1+16-18.

Gonads. The testes are lobed, each lobe conical and resembling stubby pyloric caecae. Ovaries are simple, the ovarian tunic is incomplete except anteriorly where it is continuous with the peritoreum as in _Conocara_ _macroptera_ (Fig. 7) Markle and Wenner (in prep.) have recently presented evidence that _X_. _copei_ is mesopelagic for only part of its life. Their evidence suggests that ripe adults migrate to or very near to the bottom to spawn in the fall.

Table 5. Selected counts from radiographs of *Xenodermichthys*.

	D RAYS					
X. copei	27	28	29	30	31	32
western Atlantic		7	4	4		
eastern Atlantic	3	3	3	2	1	
Indian			1			
southwest Pacific	1					
X. nodulosus						
Philippine Sea						1

	A RAYS						
X. copei	26	27	28	29	30	31	32
western Atlantic	1	3	10	2	1		
eastern Atlantic		5	3	2			
Indian		1					
southwest Pacific		1					
X. nodulosus							
Philippine Sea							1

	VERTEBRAE										
	Precaudal				Caudal			Total			
X. copei	16	17	18	19	30	31	32	47	48	49	50
western Atlantic	1	4	11	4	4	15	1	2	4	11	3
eastern Atlantic		6	8		3	8	3		7	6	1
Indian			1			1				1	
southwest Pacific		1					1			1	
X. nodulosus											
Philippine Sea			1				1				1

Fig. 31

A. Relationship between head length, expressed as a fraction of standard length, and standard length in western North Atlantic *Leptoderma macrops*. Dashed lines are limits of variation as given by Parr (1951), less than (30-0.5 SL) percent of SL and more than (25-0.5 SL) percent of SL. Regression equation fits observed points.

B. Relationship between head length, expressed as a fraction of standard length, and standard length in *Narcetes stomias*. Brackets denote groups of points showing little or no allometry above and below 400 mm SL, associated with shortening and arching of the snout and upper jaw.

C. Relationship between upper jaw length, expressed as a fraction of standard length, and standard length in *Narcetes stomias*. Brackets as in Fig. 31B.

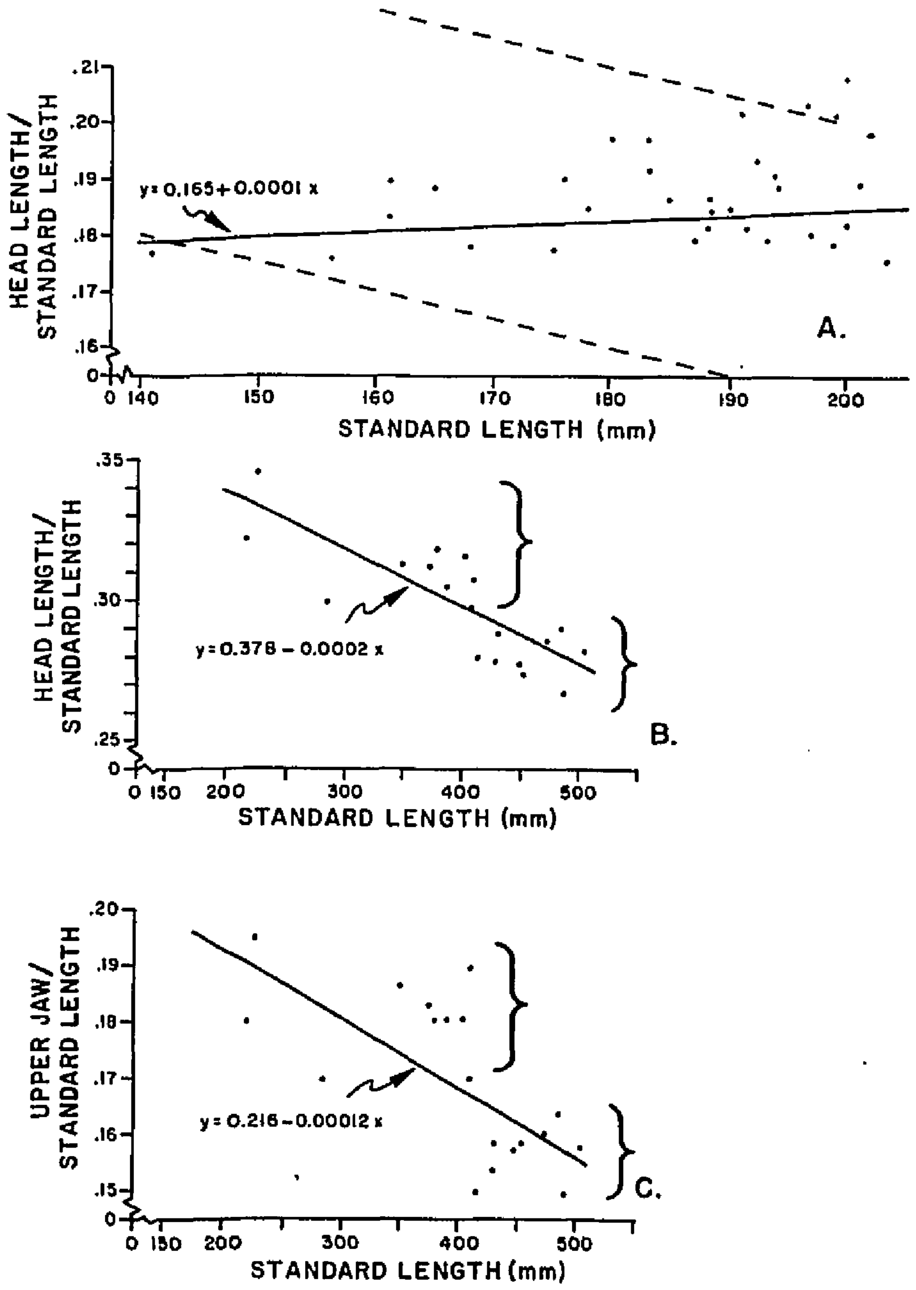

HEAD LENGTH/
STANDARD LENGTH
.21
.20
.19
.18
.17
.16
0
y= 0.165+0.0001 x
A.
0 140
150
160
170
180
190
200
STANDARD LENGTH (mm)
HEAD LENGTH/
STANDARD LENGTH
.35
.30
.25
0
y= 0.378 – 0.0002 x
B.
0 150
200
300
400
500
STANDARD LENGTH (mm)
UPPER JAW/
STANDARD LENGTH
.20
.19
.18
.17
.16
.15
0
y= 0.216–0.00012 x
C.
0 150
200
300
400
500
STANDARD LENGTH (mm)

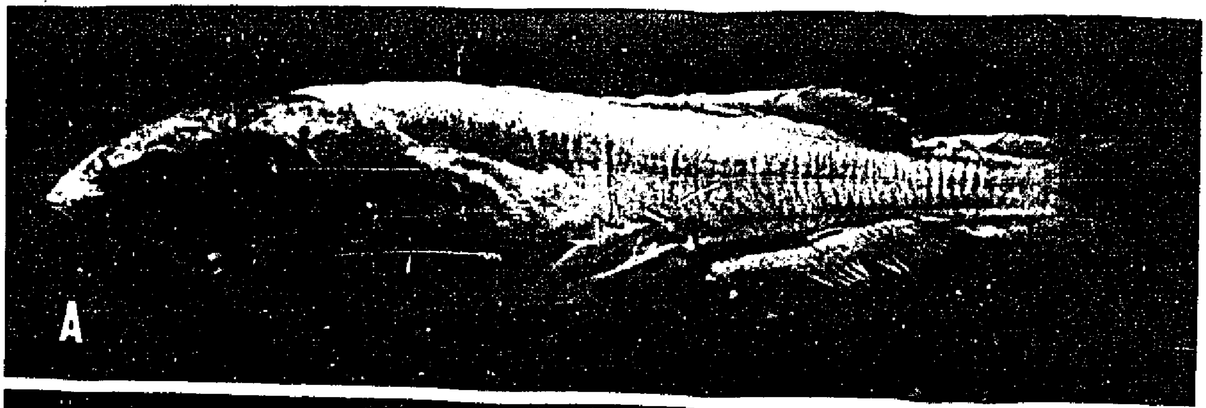
Fig. 32

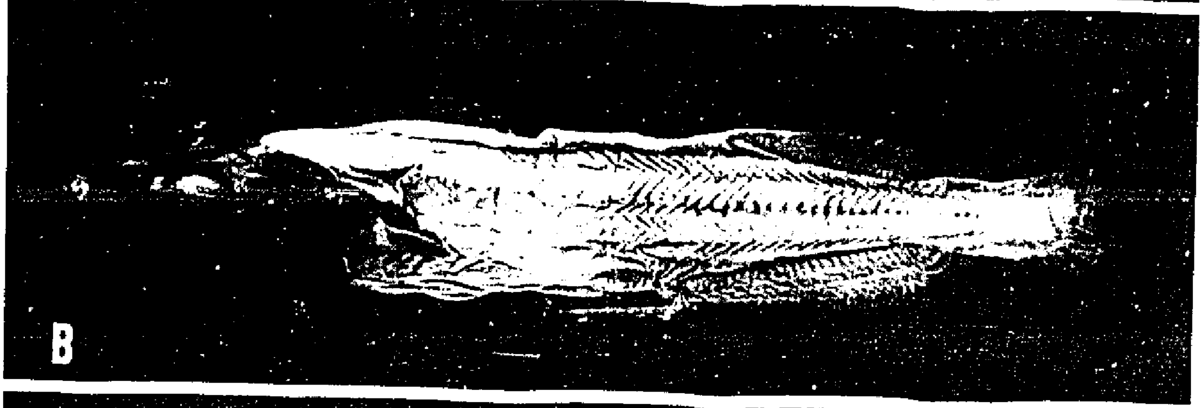
A. *Ericara salmonea*, UMML 32360, 266 mm SL.

B. *Ericara microlepis*, USNM 215601, 268 mm SL.

C. *Conocara murrayi*, NIO, Discovery st. 7424, 268 mm SL.

D. *Conocara murrayi*, FMNH 64071, 151 mm SL.


A


B


C


D

Fig. 33

A. Leptoderma macrops, USNM 215614, 194 mm SL.

B. Same as A, showing detail of cephalic lateralis pores and papillae.

C. Leptoderma lubricum, NIO, Discovery st. 7423, 165 mm SL.

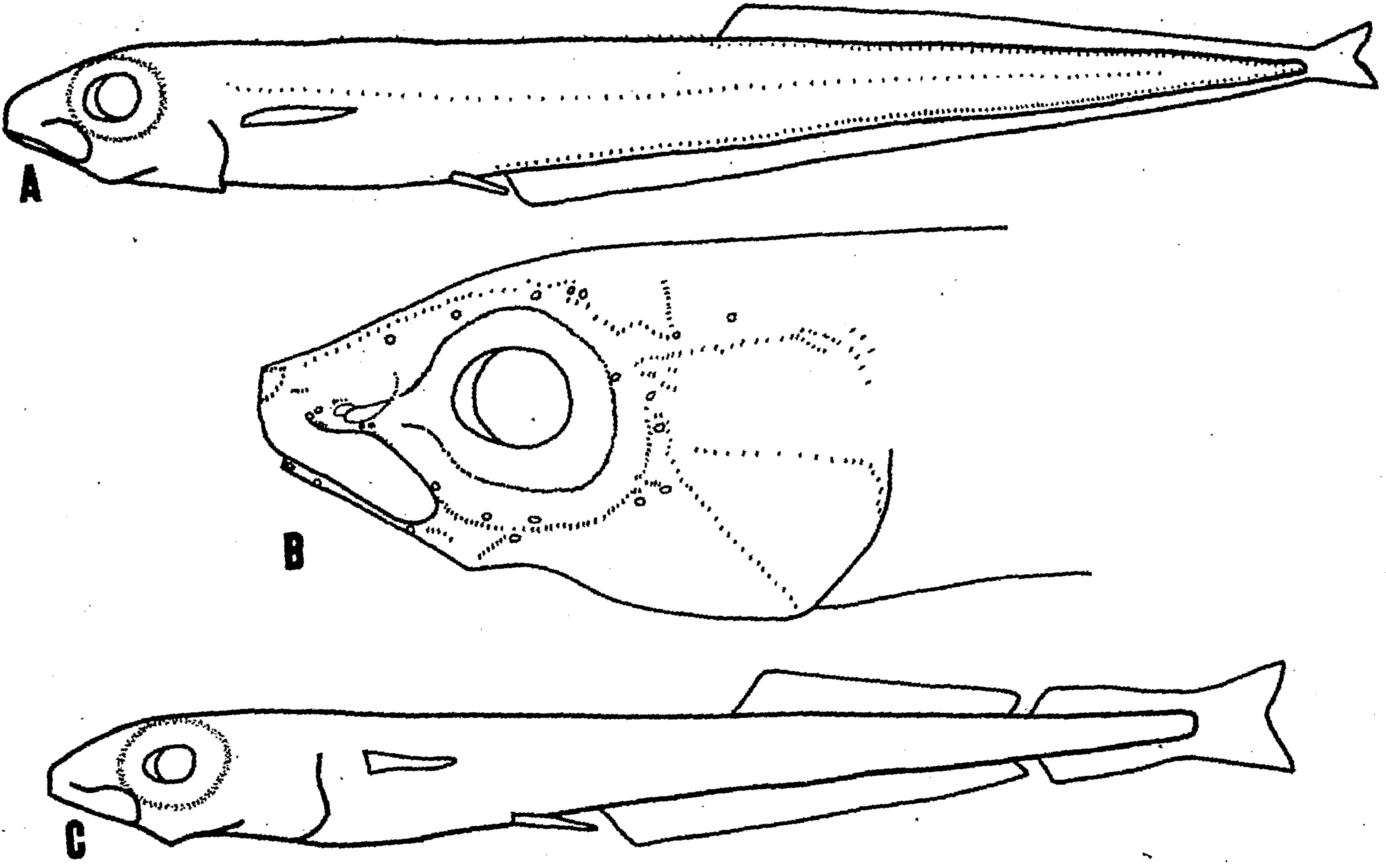

A
B
C

Fig. 34

A. *Asquamiceps indagatio*, SIO 64-11, 97.5 mm SL.

B. *Einara macrolepis*, NIO, Discovery st. 7824 #21, 172 mm SL.

C. *Einara* sp., USNM 200465, 217 mm SL.

D. *Einara edentulus*, USNM 200522, 132 mm SL.

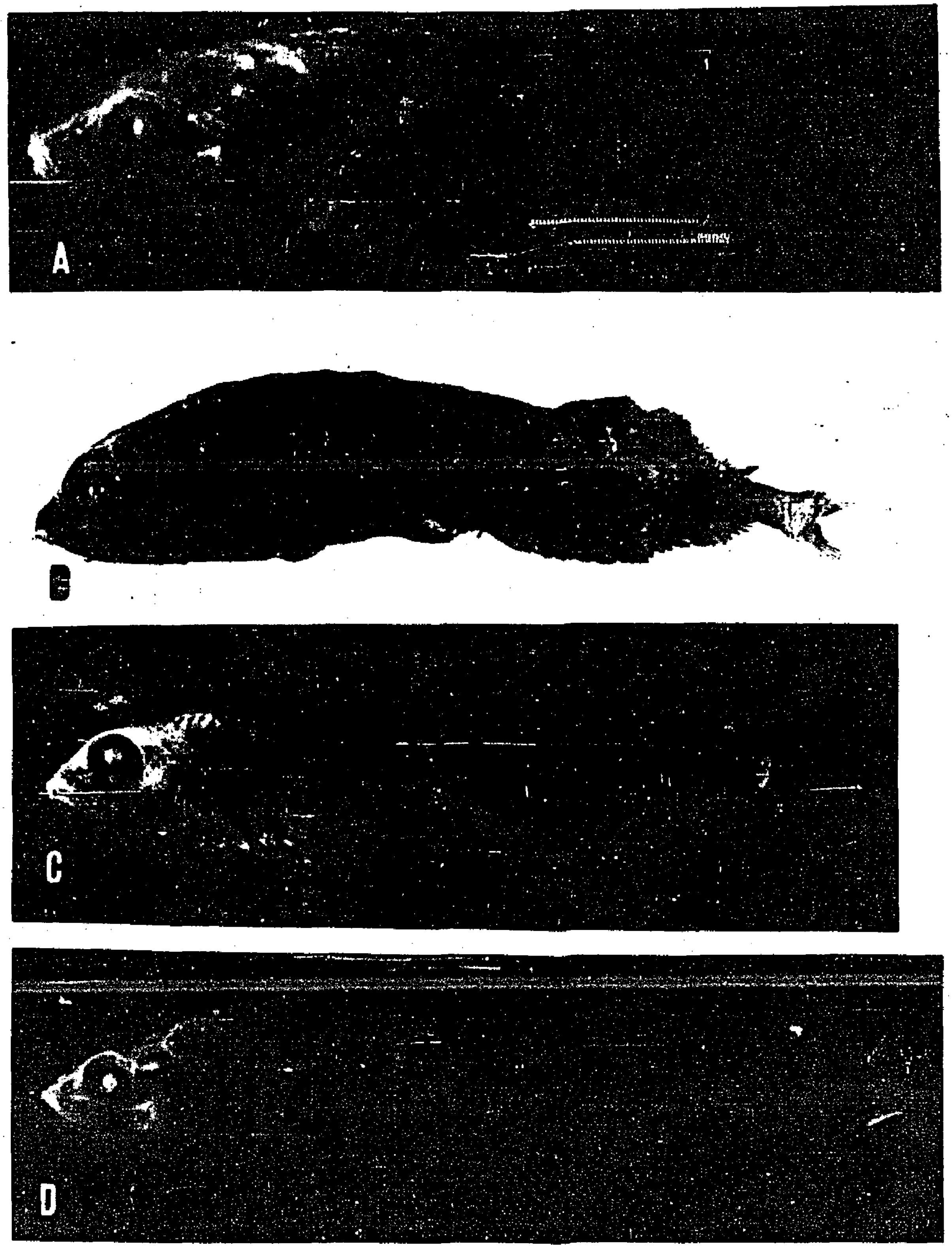
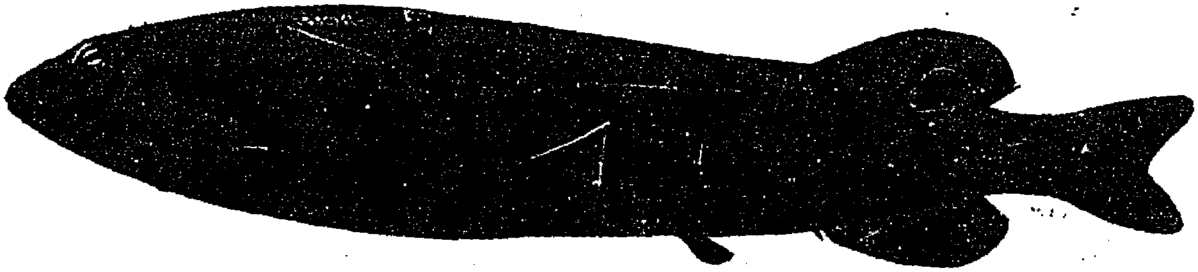

A
B
C
D

Fig. 35

A. Asquamiceps sp. A, USNM 214938, 315 mm SL.

B. Aulastomatomorpha phospherops, reprinted from "Illustrations of the Zoology of the Investigator, Fishes", pt. 1, pl.5, 1892.



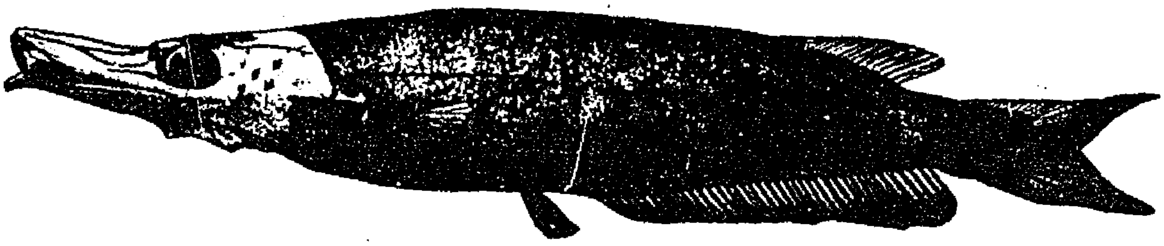


Fig. 36

A. Bajacalifornia burragei, USNM 215610, 112 mm SL.

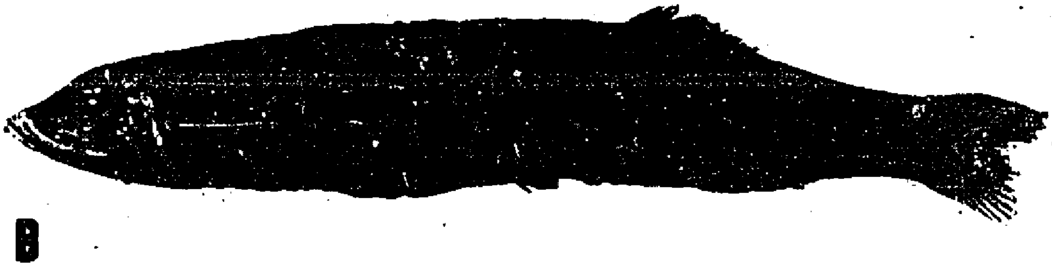
B. Bajacalifornia calcaratus, USNM 215506, 312 mm SL.

C. Bajacalifornia drakei, USNM 215504, 223 mm SL.

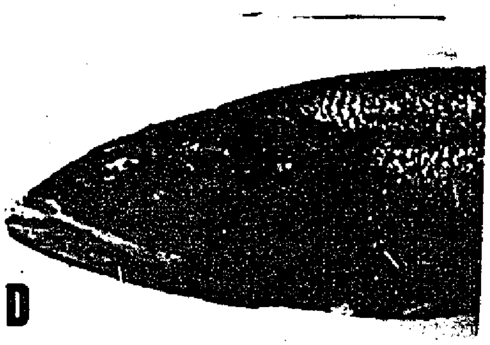
D. Narcetes stomias, USNM 215513, 428 mm SL, showing straight jaws.

E. Narcetes stomias, USNM 215513, 504 mm SL, showing arched jaws.


A


B


C


D

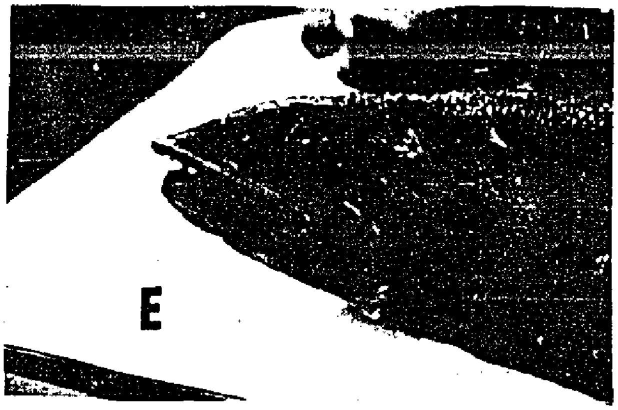

E

Fig. 37

A. <u>Bathytroctes</u> <u>microlepis</u>, USNM 215496, 263 mm SL.

B. <u>Bathytroctes</u> <u>microlepis</u>, USNM 215492, 260 mm SL, showing snout variation.

C. <u>Bathytroctes</u> <u>microlepis</u>, USNM 215492, 278 mm SL, showing snout variation.

D. <u>Bathytroctes</u> <u>squamosus</u>, UMML uncatalogued, st. CI-160, 186 mm SL,

E. <u>Bathytroctes</u> <u>squamosus</u>, same as D above, showing normal cheek scalation.

F. <u>Bathytroctes</u> <u>squamosus</u>, UMML 30957, 168 mm SL, showing reduced cheek scalation.

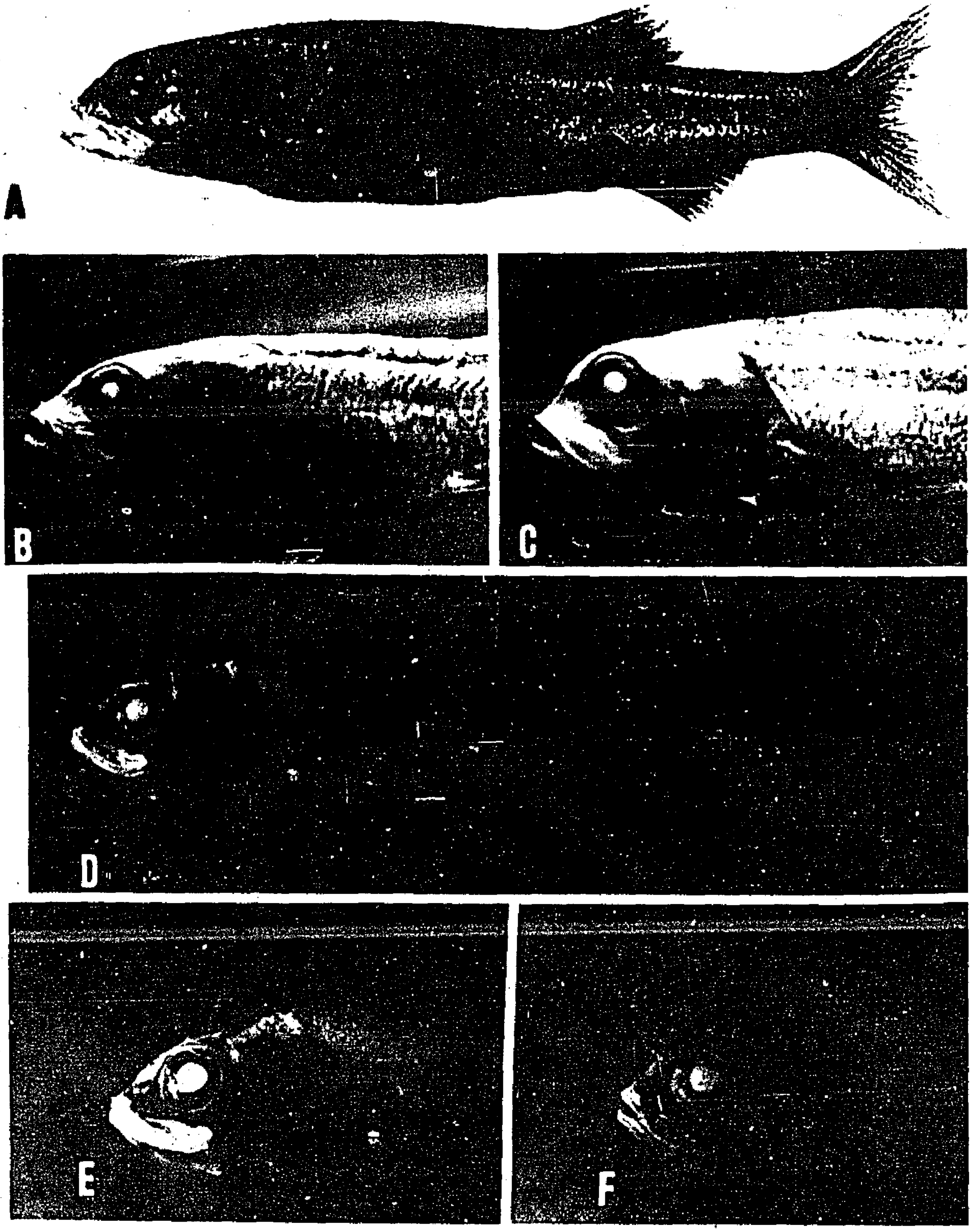

A
B
C
D
E
F

Fig. 38

A. Leptochilichthys agassizii, SIO 66-55, 149 mm SL.

B. Bathylaco nigricans, USNM 206694, 233 mm SL.

C. Nomoctes michaelsarsi, USNM 215501, 244 mm SL.

D. Nomoctes koefoedi, MCZ 36636, 132 mm SL.

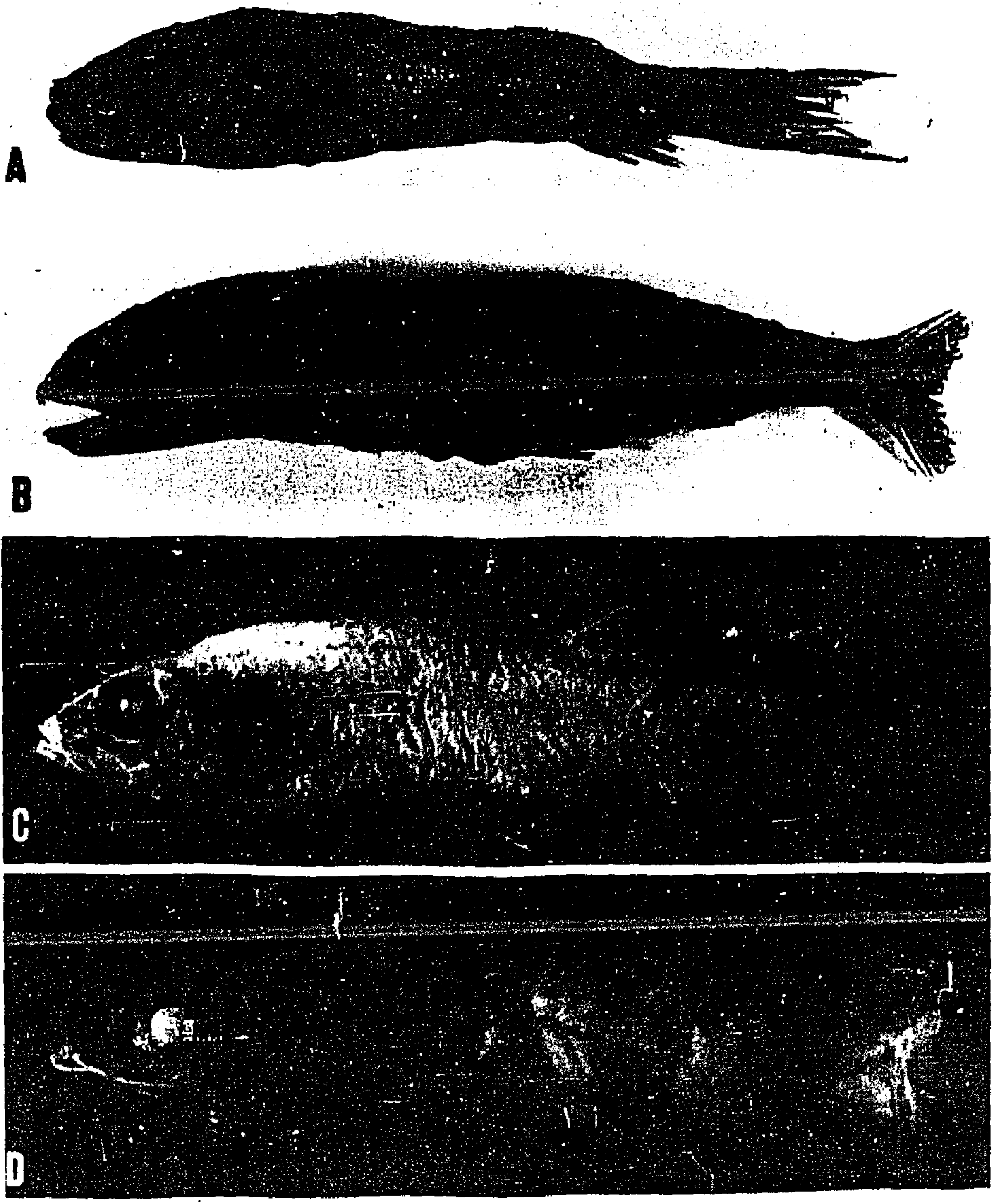

A
B
C
D

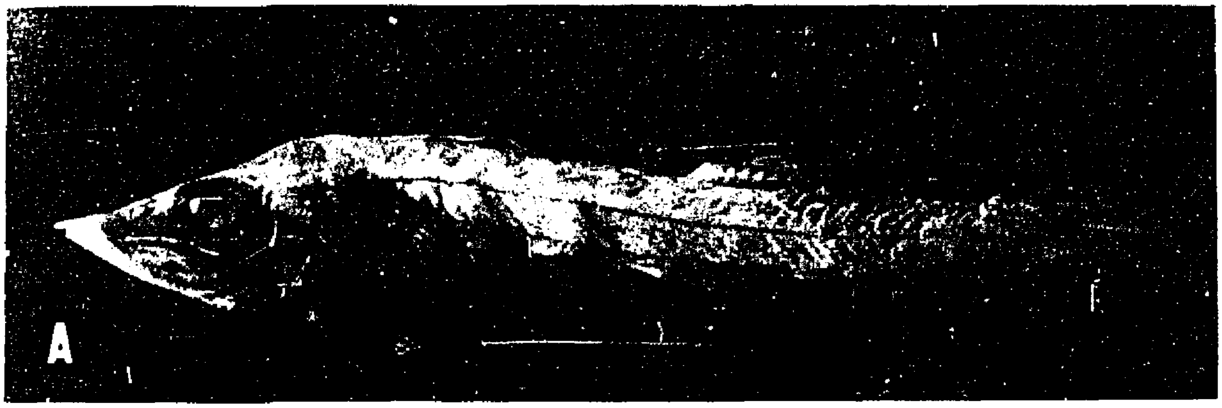
Fig. 39

A. Rinoctes nasutus, USNM 215517, 122 mm SL.

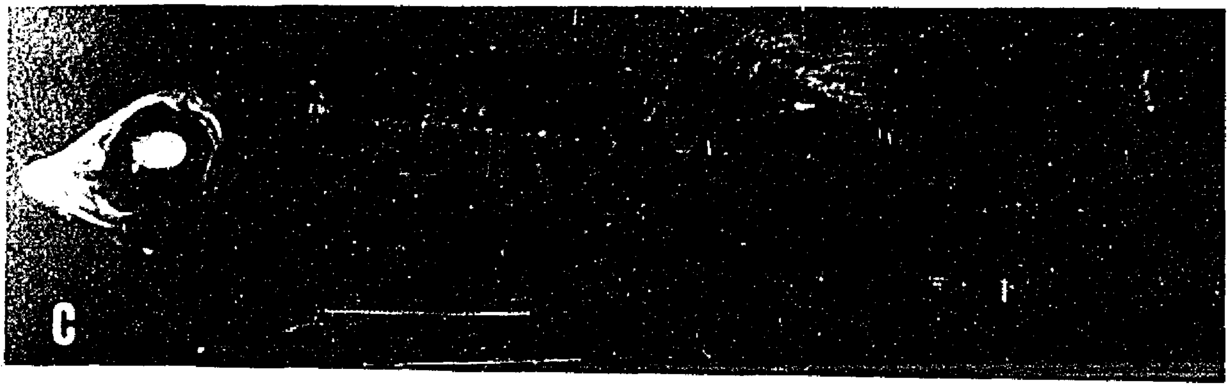
B. Bathyprion danae, ISH 1539/71, 252 mm SL.

C. Talismania antillarum, NIO, Discovery st. 7845, 143 mm SL.

D. Alepocephalus agassizii, USNM 215571, 510 mm SLV (fresh).


A


B


C


D

Fig. 40

A. Genus A. sp. nov., uncatalogued.

B. Genus A (schmidti), uncatalogued.

C, E, and F. Cross sections of body photophores from Genus A, sp. nov. showing position beneath epidermis and gross structure; 5 micron sections, Harris haematoxylin-eosin stain.

D. Cross section of body photophore from Rouleina maderensis; 5 micron sections, Harris haemotoxylin-eosin.

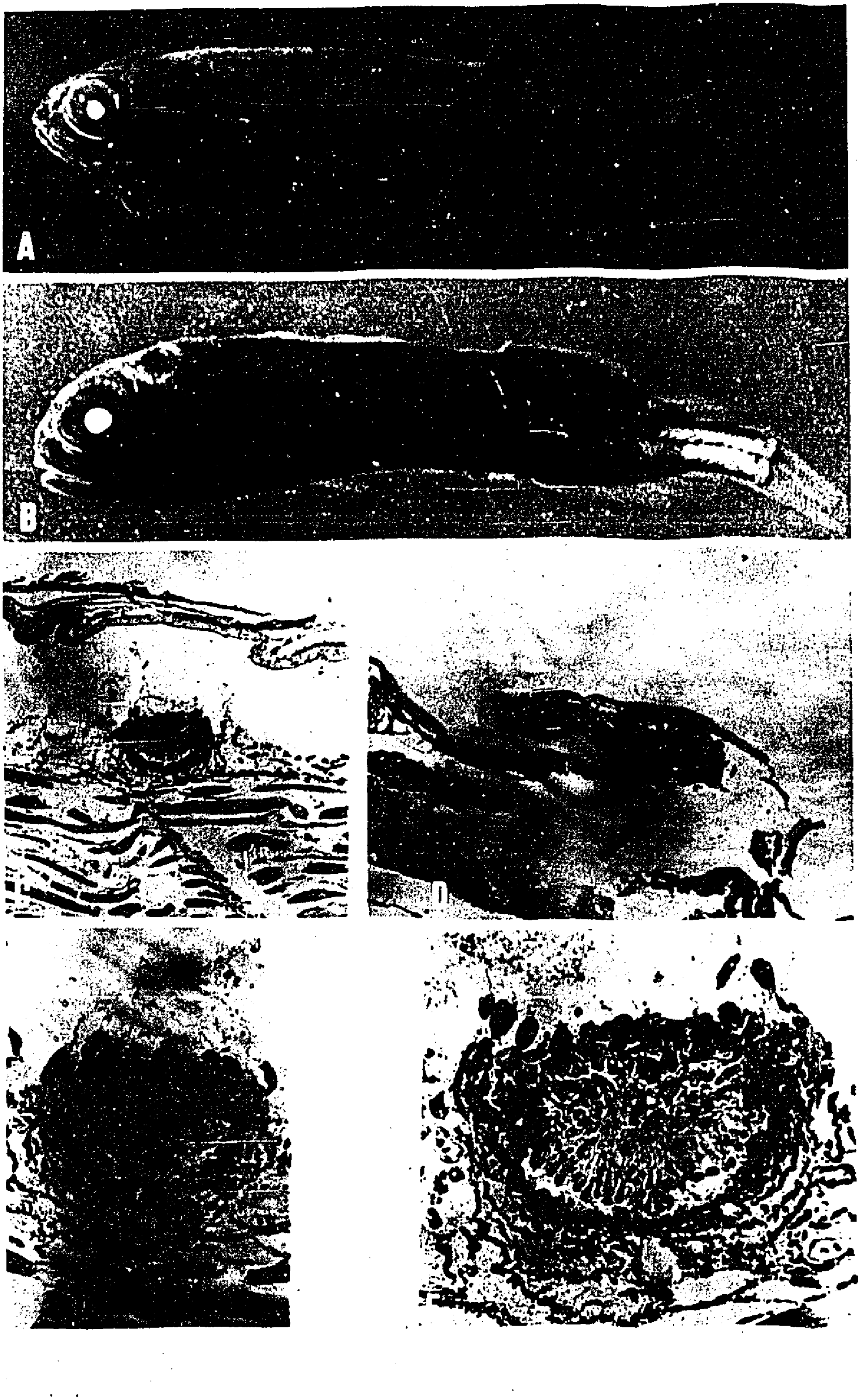

A
B
D

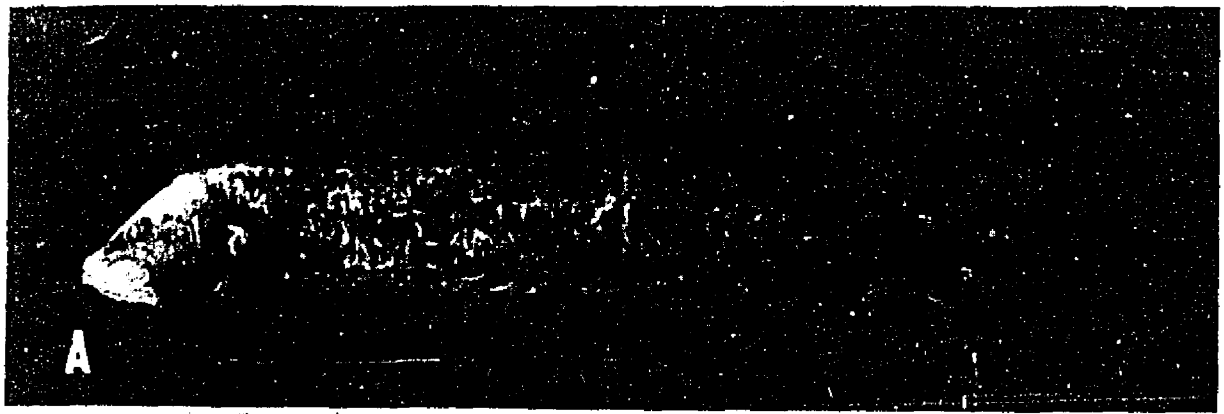
Fig. 41

A. Photostylus pycnopterus, Dana 4007^{VII}, 103 mm SL.

B. Rouleina mollis, USNM 215479, 285 mm SL.

C. Xenodermichthys nodulosus, Dana 3722^{I}, 157 mm SL.

D. Xenodermichthys copei, Dana 4157^{II}, 136 mm SL.


A


B


C


D

ECOLOGY

This section summarizes some rather fragmentary autecological data. The purpose is to try to reach some generalizations about alepocephalid life histories. The major source of most new information presented herein was a trawl survey from 1973 to 1976 on the continental slope off Virginia.

Food and feeding:

The food habits of Alepocephalus agassizii were not intensively studied but some data were obtained. As previously mentioned, the crumenal organ suggests filter feeding, but deep submersible observations made thus far do not support an actively swimming, filter feeding habit and serial sections of crumenal organs reveal only a few diatom tests. Out of many A. agassizii stomachs examined from the continental slope off Virginia, identifiable contents from 20 can be reported. These had mud in 60%, ctenophores in 40%, monogenetic trematodes in 30%, and one stomach each with three planktonic calanoid copepods, a larval form of the macruran crustacean Stereomastis, parts of urchin tests and part of a polychaete. Although mud especially may have been ingested in the trawl, the indication is that A. agassizii is an opportunistic or generalized feeder near the bottom but may frequently feed in the water column on ctenophores and copepods. However, an examination of number of individuals caught over a composite 24 hour period off Virginia does not indicate any regular diel migration off the bottom (Fig. 43A). These results are in basic agreement with food habits of *A. bairdii* reported by Golovan and Pakhorukov (1975).

Among strictly pelagic adults, only one *Bajacalifornia drakei* was found with food, a large caridean shrimp *Acanthephyra purpurea*. Nielsen and Larsen (1968) examined 10 empty stomachs of another bathypelagic form, *Bathylaco nigricans*, and concluded from its morphology that it is a fast swimming predator.

On the basis of the great variation in mouth size and dentition pattern, it is definitely not prudent to make inductive generalizations about an alepocephalid feeding type. Although it would not be surprising if most species were basically generalized, it is apparent that feeding specialization must have occurred at least in the tubular-mouthed forms of *Aulastomatomorpha* and the edentate *Mirognathus*.

Reproduction:

During intensive trawling on the slope off Virginia, 1973-1976, no alepocephalid species could be shown to have a seasonal reproductive cycle. This was primarily due to a lack of material. For example, running ripe males of *Narcetes stomias* were caught in January, April and November and a female with ova up to 4.0 mm was caught in June. Mature *Rouleina mollis* (ova up to 3.2 mm) were only caught in September and November but only 19 fish were caught during the three year survey. A considerable number, 229, of *Alepocephalus agassizii* were caught during the survey but only four were judged mature. These were three males, 473-497 mm SL, caught in January and June and a maturing female (ova up to 2.8 mm), 642 mm SL, caught in September.

Using material from various North Atlantic sources, Markle and Wenner (ms submitted) present evidence which suggests seasonal reproduction in the mesopelagic Xenodermichthys copei. They postulate near-bottom autumn spawning in X. copei.

Part of their reasoning is based on the fact that alepocephalids in general have few, large eggs. In the following the total number in the largest egg size class is given for several species examined in this study and from the literature: 156 mm SL X. copei (151 eggs up to 2.7 mm), 415 mm SL N. stomias (estimated 546 eggs up to 4.0 mm), 268 and 317 mm SL Bathylaco nigricans (estimated 450 and 1000 eggs up to 2.9 mm, Nielsen and Larsen 1968), and a 642 mm SL A. agassizii (estimated 9150 eggs up to 2.8 mm). Golovan and Pakhorukov (1975) reported 115,000-160,000 eggs in A. bairdii but it is not clear whether they refer to all eggs or just the larger (4.0-4.5 mm) eggs. I presume the former. From the foregoing is established that at least some of the bathypelagic and near bottom alepocephalids have large eggs and low fecundity.

Depth distribution:

Alepocephalids inhabit a depth range from 100 m (X. copei, Krefft 1973) possibly to 5850 m Nomoctes koefoedi, MCZ36636). The latter, however, could have been captured in midwater. Most alepocephalids seem to live between 1000 and 2000 m, though some species and genera are exclusively deeper.

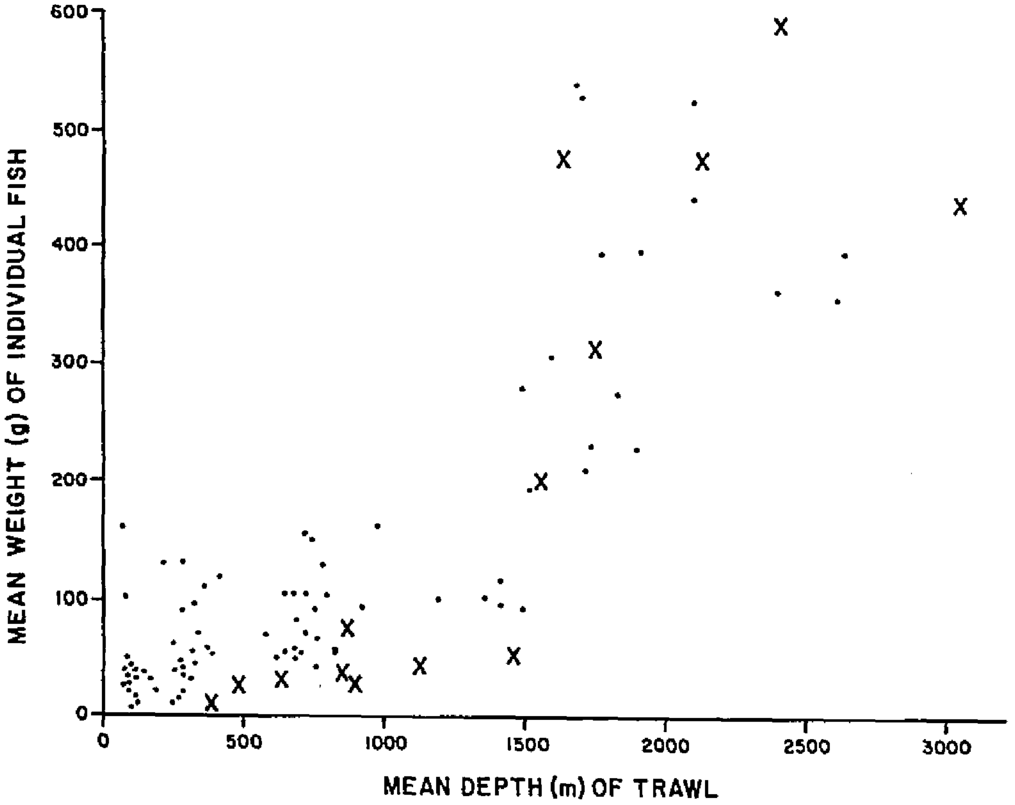
During the intensive trawl survey off Virginia (36°34'-37°10'N) mentioned above, three features of alepocephalid distribution were noted: (1) approximate concordance of minimum depth of capture among different species; (2) suggestions of interspecific and intraspecific size-depth relationships; and (3) universally incomplete length frequency distributions. Each of these is treated separately below.

Minimum depth: Exclusive of presumed midwater captures of _X_. _copei_ and species captured less than twice, all near bottom alepocephalid species showed an inordinate amount of regard for the 1500 m (± 100m) depth contour. The distribution of most began at or near this contour. Thus, thirteen _B_. _microlepis_ were captured at 8 stations with average depths from 1441-1763 m; nineteen _R_. _mollis_ were captured at 5 stations with average depths from 1403-1803 m; ten _N_. _stomias_ were captured at 8 stations with average depths from 1678-2375 m; and 229 _A_. _agassizii_ were caught from 655-2400 m, but all specimens larger than 325 mm and less than 150 mm SL were caught deeper than 1408 m (see Fig. 43B, below).

An obvious feature of the trawl data during the survey was a tendency for large animals to be caught in deeper water. In preliminary analyses of data from two of the cruises (June 1973 and November 1974 with a 45' otter trawl and a July 1975 cruise with a 30' otter trawl) Wenner (ms, and Figure 42) has found a break near 1500 m in the average weight of fish trawled. Even at these depths, 1400-1600 m, it is difficult to maintain a relatively constant depth during the trawl. Seven of the 8 trawls in this depth range in Figure 42 exceeded 50 m of depth variation during the 30 minute trawl and five of the trawls had a range of depth variation from 120-335 m! Thus, this break in average weight must be considered about as sharp a break as the sampling technique and the local physiography can discern. If, for convenience, the slope from 1500 to 3000 m is referred to as the big fish habitat, it is clear that the four most frequently encountered alepocephalids are members of this habitat.

Fig. 42

Relationship between mean weight, in gm, of individual fish and mean depth of trawl on continental slope off Virginia. Dots (.) indicate stations made with a 45' otter trawl and X's indicate stations made with a 30' otter trawl.



MEAN WEIGHT (g) OF INDIVIDUAL FISH
0
100
200
300
400
500
600
MEAN DEPTH (m) OF TRAWL
0
500
1000
1500
2000
2500
3000

Size-depth: A suggestion of an interspecific, intrageneric size-depth relationship was obtained from all examined specimens of western North Atlantic Rouleina. The smaller of the two species, R. maderensis, has been caught between 595 and 1460 m in the western North Atlantic. Seven of eight captures were in depths less than 1070 m. The larger species, R. mollis, has been caught from 1020 to 1960 m. Fifteen of sixteen captures were in depths greater than 1100 m. Since these data were from a large area of the western North Atlantic and since it cannot be stated at this time whether or not the minimum depth of the big fish habitat changes or whether or not it even exists everywhere, it cannot be positively stated that one of these is a big fish habitat species and one is not. However, off Virginia R. mollis is in the big fish habitat and the single captured specimen of R. maderensis was not.

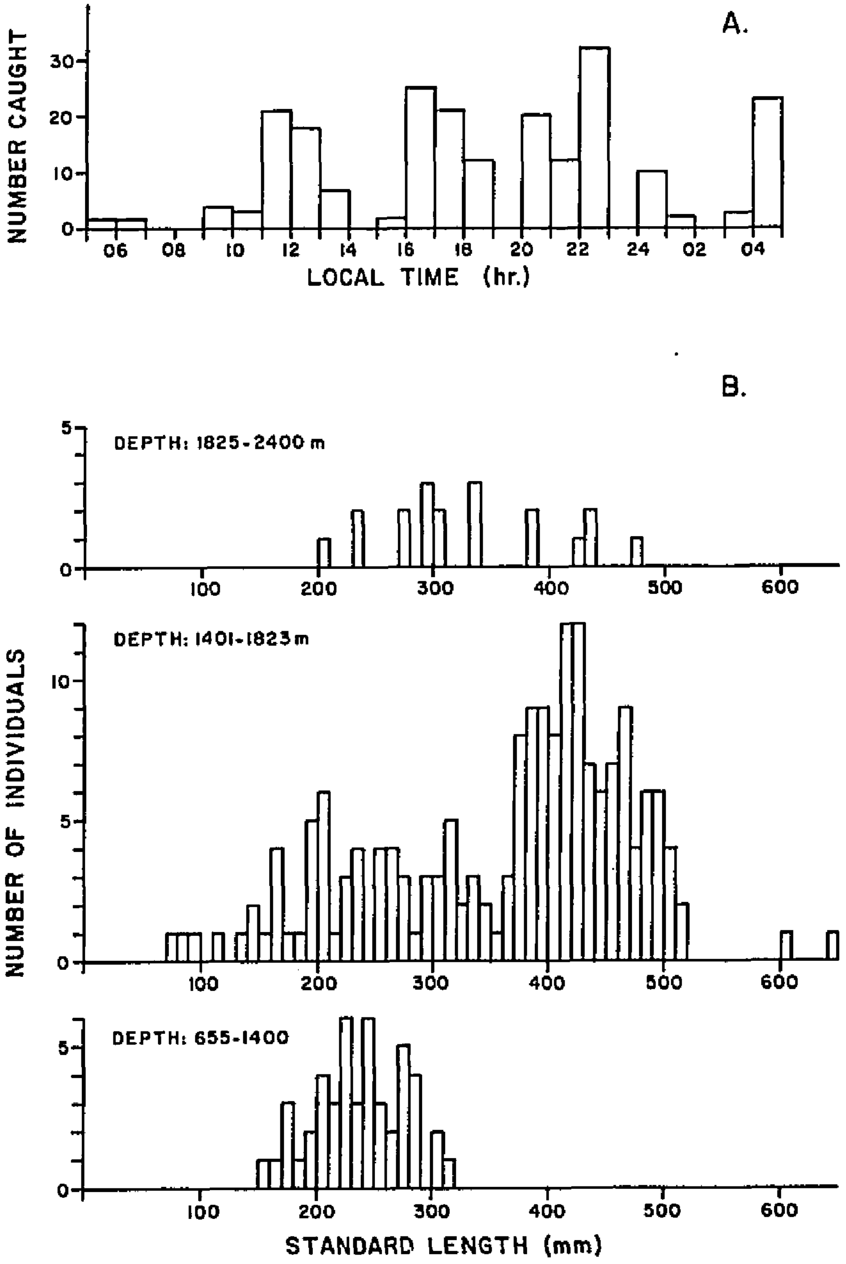
Only Alepocephalus agassizii was present in sufficient quantities to determine intraspecific size-depth relationships off Virginia. No seasonal differences in size-depth relationships were discerned. Figure 43B is a composite of four seasonal cruises in June 1973, November 1974, September 1975 and January 1976.

During this survey no identifiable alepocephalid larvae were caught. The smallest specimens of A. agassizii (75 to 150 mm SL) were caught fairly deep, 1488 to 1823 m, while intermediate sized specimens (150 to 300 mm SL) were caught over the species depth range, 655 to 2400 m (Fig. 43B). Individuals larger than 300 mm SL were caught between 1408 and 2100 m. There was no simple relationship between size and depth of capture. Figure 43B suggests that juveniles first appear in relatively deep water, then disperse over the total bathymetric range before becoming relatively stenobathyal when over 300 mm SL.

Fig. 43

A. Relationship between number of <u>Alepocephalus agassizii</u> caught over a composite 24 hour period from four seasonal cruises on the continental slope off Virginia.

B. Relationship between number of <u>Alepocephalus agassizii</u> caught and the depth range of the trawl from four seasonal cruises on the continental slope off Virginia.


A.
NUMBER CAUGHT
0
10
20
30
06
08
10
12
14
16
18
20
22
24
02
04
LOCAL TIME (hr.)
B.
DEPTH: 1825-2400 m
DEPTH: 1401-1823 m
DEPTH: 655-1400
NUMBER OF INDIVIDUALS
0
5
10
100
200
300
400
500
600
STANDARD LENGTH (mm)

Bullis and Struhsaker (1970) found a positive linear correlation between mean size and depth in fifteen upper slope fishes. That relationship can also be seen in the A. agassizii data in Figure 43B. It is somewhat misleading because all of the smallest juveniles were caught at the deep end of the depth range, intermediate sized (150-300 mm SL) individuals were caught throughout the depth range, and 43% of the intermediates were caught outside the depth range of larger individuals.

Beebe's (1933b) larval distribution data on the bathypelagic Bajacalifornia drakei has led to the reasonable, albeit inductive, conclusions that alepocephalid larvae are bathypelagic (Mead, et al 1964) and develop directly (Gosline 1969). The present data on A. agassizii do not provide good evidence for or against a bathypelagic larval or juvenile stage. The juveniles 75-150 mm, for example, if pelagic, would have been expected as incidental captures in all areas below a certain minimum depth. This is because the bottom trawl fishes obliquely through midwater during descent and retrieval and, thus, would spend about the same amount of time in any midwater zone above the bottom. Instead smaller juveniles were encountered in a relatively narrow zone, 1488 to 1823 m.

Study of the numerous Dana collections of midwater alepocephalid larvae shows that almost all identifiable larvae are of meso- and bathypelagic genera and species (Xenodermichthys, Bathylaco, Photostylus, Bajacalifornia drakei, Einara edentulus, Talismania antillarum, and genus A). Only two specimens of Conocara, a benthic genus, have been identified in these midwater collections. This lack of larval forms of bottom fish is also characteristic of macrourids (Marshall 1973) and the abundant morid, Antimora (Cohen, personal communication). Marshall (1973) further notes that larval development is rapid in some bottom forms and this presumably prevents their expatriation from the narrow slope habitat.

Length frequencies: The four frequently encountered species off Virginia were generally restricted in their size ranges. The thirteen B. microlepis were all between 227 and 296 mm SL, the nineteen R. mollis were between 220 and 378 mm SL, and the ten N. stomias were between 389 and 490 mm SL. The length frequency distribution of A. agassizii is shown in Figure 44A for four cruises. Again no seasonal differences were apparent, possibly because of the small sample size.

These data indicate that either the gear is selecting larger specimens, that juveniles of these species are not present in the sampling area or that juvenile growth rate is very rapid. Since some small alepocephalids, R. maderensis and X. copei, and other smaller fishes were captured by the gear, the second explanation is more probable.

A generalized alepocephalid life history:

Only a few of the slope fishes off Virginia have a length frequency distribution which, within the limits of the gear selectivity, includes more juveniles than adults. The macrourid, Coelorhynchus c. carminatus (Fig. 44B) is one such species. In November 1974 it was caught between 169 and 864 m and showed a fairly normal length frequency distribution with 3 or 4 different size classes. With the exception of the class around 47 mm head length, each size class was progressively less numerous than its predecessor. Thus, one can reasonably assume, since the maximum known size is 73 mm HL (Marshall and Iwamoto 1973), that most, if not all, of the species' life history can take place within the confines of a relatively small area of its total geographic range.

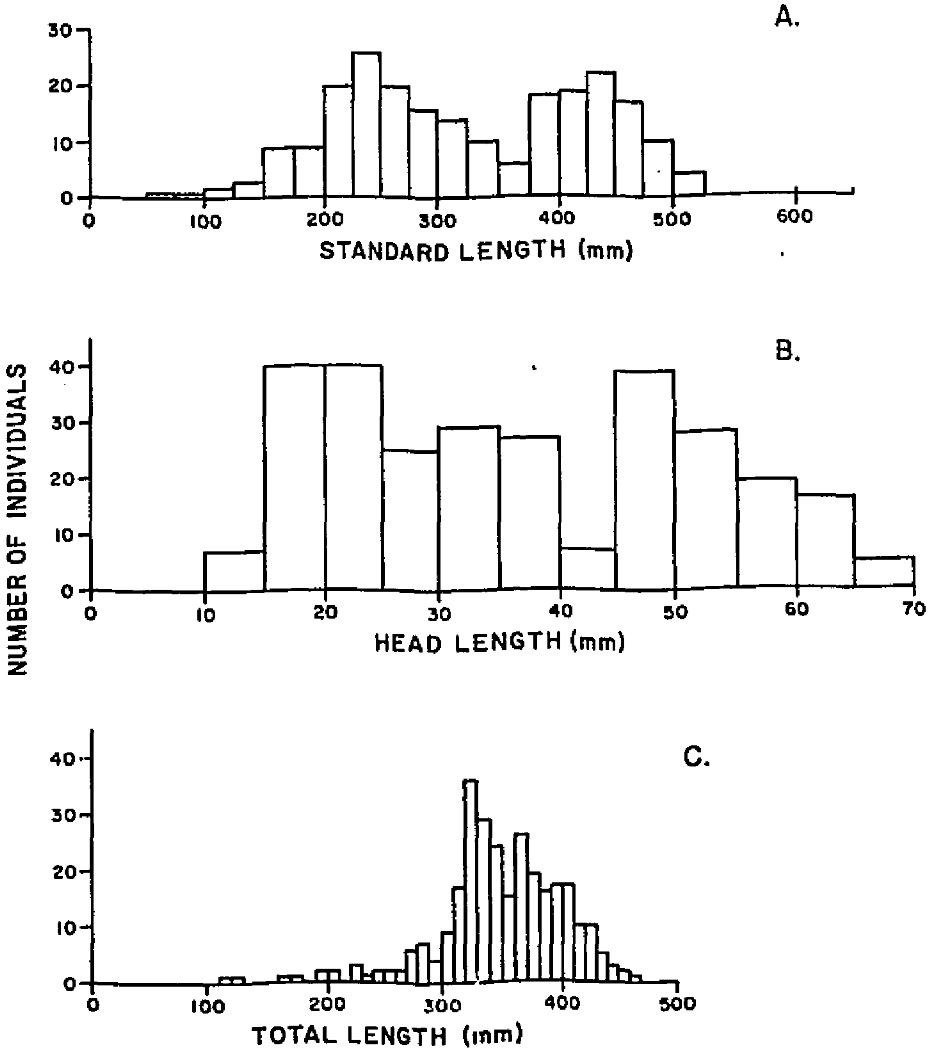
Most other species on the slope, even those within the depth range of C. c. carminatus, such as the hogfish, Myxine glutinosa (Fig. 44C), have

Fig. 44

A.. Length frequency distribution of Alepocephalus agassizii caught during four seasonal cruises on the continental slope off Virginia.

B. Length frequency distribution of Coelorhynchus c. carminatus from the continental slope off Virginia, November 1974.

C. Length frequency distribution of Myxine glutinosa from the continental slope off Virginia, November 1974.


A.
30
20
10
0
0
100
200
300
400
500
600
STANDARD LENGTH (mm)
NUMBER OF INDIVIDUALS
B.
40
30
20
10
0
0
10
20
30
40
50
60
70
HEAD LENGTH (mm)
C.
40
30
20
10
0
0
100
200
300
400
500
TOTAL LENGTH (mm)

a completely different length frequency distribution. These specimens, also from the November 1974 cruise, were caught between 195 and 675 m. Although adults of M. glutinosa, including ovigerous females, were quite common, post-metamorphic juveniles and subadults less than 30 cm were virtually non-existent in the samples. The possibility of escape by smaller individuals is minimal in view of captures of small eels, Synaphobranchus affinis elvers 72-105 mm total length (Wenner 1975) and Pisodonophis cruentifer 19-40 cm total length (Wenner 1976) in the same or smaller gear with identical, 0.5 inch stretched mesh cod end liners.

As with the four alepocephalids, juveniles of M. glutinosa and many other dominant slope fishes (Antimora rostrata, Coryphaenoides armatus and Halosauropsis macrochir, for example) are not found at all or not in quantities sufficiently large enough to account for the numbers in the larger size classes. Recruitment from other areas is probably involved.

It is interesting to note that Grassle and Sanders (1973) surveyed length frequency data in many deep-sea invertebrates and found a high proportion of adults also. Their conclusions were largely negative since they discussed what the data didn't show. But more recently (Turekian et al 1975), they have found evidence of extremely slow growth rates (8 mm per 100 years) and long delayed sexual maturity (gonadal development beginning at age 50 to 60 years) in the small bivalve, Tindaria callistiformis.

Among deep-sea fishes slow growth rate and longevity may also explain the lack of juveniles. Species with large eggs and low fecundity, such as alepocephalids, are usually considered to be making an evolutionary response to achieve a relatively large size early in life (Calow 1973), presumably to avoid predation and increase the range of size of potential prey. If growth rate is slow, a large size at hatching is the only way to achieve some size early in life.

Relatively large body size, as exemplified by alepocephalids and their associates in the big fish habitat, has several advantages and disadvantages (Southwood et al 1974, Thiel 1975). Among the disadvantages is a metabolic rate usually equal to $W^{0.7}$, where W is body weight (Bourliere 1957, Hughes 1965). This rate may be lower in deep sea fishes, such as alepocephalids, in which a higher percentage of body weight is due to water (Childress and Nygaard 1973). Thus, large size may have been achieved while one of its disadvantages in a nutrient-poor habitat has been minimized. At the same time, large animals are usually able to move faster and cover a larger area, thus able to take advantage of large food falls and clumped prey (Dayton and Hessler 1972). Finally, large animals usually live longer, those with low fecundity are sometimes iteroparous (breed more than once) and all are able to undertake relatively long reproductive migrations, virtually impossible in smaller animals (Calow 1973, Southwood et al 1974).

A recent theory on avian diversity in the tropics (Klopfer et al 1974) suggested that in stable environments with an essentially uniform yearly food supply, the adults of all species would expand to the upper limits of available resources. Without the temporal increase in daily productivity in the spring and early summer characteristic of temperate areas, tropical birds would be required to have a prolonged developmental period for their young, as is apparently commonly observed. As a consequence, migratory birds, present in the tropics only when food resources were seasonally reduced in temperate areas, would be unable to breed in the tropics due to their more rapid developmental rates adapted to the seasonally richer temperate productivity. Further, they showed that without predation the young of the most common species (the best competitor) would get most of the available resources and a disproportionately larger portion would be recruited to the adult population. They then stipulated that if predation removed a disproportionate number of young of the dominant species there would be an increase in recruitment rate of competitor species and an increase in community species diversity.

Some of these ideas, which have been developed through numerous studies of birds (Thompson 1975) are worthy of consideration with respect to fishes, which, like birds are motile inhabitants of three-dimensional space. For example, in the big fish habitat below 1500 m the food supply is generally believed to be low and relatively constant on a seasonal time scale. One can assume that the adults of all species have expanded (numerically) to the limits of available resources. Deep-sea baited camera photographs suggest that motility is advantageous in locating widely separated falls of large food items (Dayton and Hessler 1972) and food habit studies (Pearcy and Ambler 1974, Haedrich and Henderson 1974) suggest that large generalized feeders, capable of wide ranging feeding movements off the bottom, are major resource exploiters in the deep sea.

Under these conditions the big fish habitat offers little comfort to eggs or larvae. Although big fish tend to eat big food items (Pearcy and Ambler 1974), in a food-poor environment being able to take the largest possible meal doesn't negate eating copepods (Marshall 1960). The bird scenario of Klofper <u>et al</u> (1974) offers two possibilities: alteration of larval development and reproductive migration. Little is known of larval development in deep sea fishes, but in the big fish habitat immediate large size would seem to be necessary to compete for food and avoid predation. Large egg size and rapid larval development would be predicted. Marshall (1973) noted that newly hatched macrourids were larger than nearly all gadids (both groups in the Gadiformes) and that in one species, *Macrourus berglax*, newly hatched larvae must be around 10 mm. In both macrourids and alepocephalids large eggs are apparently universal. Marshall (1973) further noted fast development of pelagic larvae of some engybenthic but not bathypelagic macrourids.

Evidence for reproductive migrations is essentially absent for deep-sea fishes. Although running ripe male alepocephalids have been found in the survey off Virginia, no ripe females are known. Reproductive migrations will be difficult to prove in deep sea fishes. If the prupose of migrations is to get eggs and larvae out of the big fish habitat, migrations could be into shallower water, into deeper water, into mid-water, to a geographical site such as the Sargasso Sea, or merely to the center of a deep bottom current moving out of the habitat. Before migrations can be investigated, the somatic distribution must be determined. Verified captures of reproductive specimens outside the somatic habitat will then offer minimal evidence of migration.

The above indicates the potential pitfalls of life history studies of alepocephalids when based on only a local or moderately extensive sampling program. Quite probably the life history of an individual involves large geographic areas and the insidious effects of currents as well as the reproductive strategy of the species. The possibility of large-scale reproductive migrations in alepocephalids, an advantage of large size, must be considered especially since minor vertical reproductive migrations are suspected in a relatively small member of the family, *X. copei* (Markle and Wenner, ms submitted).

There is little more available data relevant to alepocephalid life histories. The most valuable information, on life tables and reproduction at least, will come from analysis of world-wide or ocean-wide data sources. Information on ageing must come from methods independent of seasonal assumptions such as the preliminary work by Turekian _et_ _al_ (1975). Finally, although it was only touched upon, there is probably much to gain from avian ecology. The hypotheses, tautologies and analogies are as applicable, if not more so, to fishes than those of benthic invertebrate ecology. The perplexing problems of three-dimensional motility, virtually ignored in benthic ecology, are paramount in avian and fish ecology and much better understood in the former.

APPENDIX

List of Material Examined:

The following list of material gives only museum or other collection numbers and the number of specimens in parentheses. Locality data are in the hands of the author and the appropriate museums. Specimens subjected to muscle dissection and skeletal preparation are indicated with an asterisk. Museum and collection abbreviations are as follows:

Alpha Helix spring 1975 cruise (AH),
American Museum of Natural History (AMNH), New York City,
British Museum (Natural History) (BMNH), London,
California Academy of Sciences (CAS), San Francisco,
Dana Oceanographic Collections (DANA), Copenhagen,
Field Museum of Natural History (FMNH), Chicago,
Institutfur Seefischerei Hamburg (ISH), Hamburg,
Museum of Comparative Zoology, (MCZ), Harvard,
Museu Municipal do Funchal (MMF), Madeira,
Museum National d'Histoire Naturelle (MNHN), Paris
National Institute of Oceanography, (NIO), England,
Peabody Museum of Natural History, collection of Bingham Oceanographic Collection (BOC), Yale,
United States Museum of Natural History (USNM), Washington D. C.,
University of Miami Marine Laboratory (UMML), Miami

Virginia Institute of Marine Science (VIMS), Gloucester Pt.,

Woods Hole Oceanographic Institution (WHOI), Woods Hole,

Scripps Institution of Oceanography (SIO), LaJolla.

Alepocephalidae

Alepocephalus agassizii - western North Atlantic, more than 300 specimens, including USNM 215571 (1), USNM 215572 (8), USNM 215573 (2), USNM 215574 (1), USNM 215575 (2), USNM 215576 (3), USNM 215577 (1), USNM 215578 (10), USNM 215579 (1)*, VIMS uncatalogued (2)*, MNHN 1976-11 (7), AMNH 35399 (9), BMNH uncat. (6), FMNH 80468 (2). eastern North Atlantic, ISH 186/73 (2), NIO uncat. (1).

Alepocephalus australis - western North Atlantic, USNM 215583 (1), USNM 215584 (1), USNM 215585 (1), USNM 215586 (1), USNM 215587 (2), USNM 215588 (2), WHOI uncat. (1), UMML 21680 (2), FMNH 66650 (1).

Alepocephalus bairdii - North Atlantic, USNM 22468 (1, holotype), USNM 215590 (4), USNM 215589 (1)*, ISH 838/64.

Alepocephalus bicolor - Indian Ocean, USNM 215607 (1)*, USNM 215608 (12), USNM 215609 (2).

Alepocephalus productus - western North Atlantic, USNM 33341 (1, holotype), FMNH 64069 (1), FMNH 64070 (1).

Alepocephalus owstoni? - eastern Pacific, USNM 215592 (1), USNM 215593 (1), USNM 215594 (2), USNM 215595 (19).

Alepocephalus rostratus - eastern North Atlantic, NIO uncat. (5), NIO uncat. (2)*.

Alepocephalus tenebrosus - eastern Pacific, USNM 125331 (1, holotype), USNM 215580 (1), USNM 215581 (1), USNM 215582 (8), MCZ 51960 (1).

Anomalopterus megalops - western North Atlantic, USNM 170957 (1, holotype).

Asquamiceps longmani - Indo-Pacific, USNM 92325 (1).

Asquamiceps hjorti - eastern North Atlantic, ISH 486/71.

Asquamiceps sp. - western North Atlantic, USNM 214938.

Bajacalifornia burregei - eastern Pacific, USNM 87553 (1, holotype), USNM 215610 (2).

Bajacalifornia drakei - North Atlantic, USNM 215504 (1), USNM ? (1, holotype), MCZ 40654 (1), BOC 3722 (1), NIO uncat. (4, 7, 6, 7), DANA 4402^{VII} (1), DANA 1208^{XIII} (1), DANA 3978^{VII} (1), eastern Pacific, USNM 215504 (1), MCZ 49352 (1), MCZ 49356 (2).

Bajacalifornia calcaratus - eastern North Atlantic, USNM 215505 (1), USNM 215506 (2), USNM 215507 (1), UMML 15157 (9)*. Indo-Pacific, USNM 137612 (1), MCZ 45299.

Bathylaco nigricans - Indo Pacific, USNM 206693 (1)*, USNM 206694 (1), USNM 200468 (1), USNM 215519 (1).

Bathylaco "specimen" - eastern Pacific, DANA 1206^{I} (1).

Bathytroctes microlepis - western North Atlantic, USNM 159331 (1, holotype of *G. bullisi*), FMNH 64073 (3, paratypes of *G. bullisi*), USNM 33325 (1), USNM 215491 (1),USNM 215492 (2), USNM 215493 (1)*, USNM 215494 (2),USNM 215495 (1), USNM 215496 (1),USNM 215497 (3), VIMS 3537 (3), CAS uncat. (2), BMNH uncat. (1),UMML uncat. (1). eastern Noeth Atlantic, MCZ 40599 (1). eastern Pacific, USNM 215498 (1).

Bathytroctes squamosus - Indo Pacific, USNM 137753 (1). western North Atlantic, UMML 30879 (1), UMML 30957 (1), UMML 30894 (2), UMML 30927 (1), USNM 215499 (1), USNM 215500 (1), UMML uncat. (2, 1, 2, 1, 1, 1 2, 3, 1, 1, 1, 1, 1)*.

Bathytroctes oligolepis - North Atlantic, ISH 2482/71 (2)*.

Bathyprion danae - Atlantic, MMF 22053 (1), ISH 1539/71 (1)*.

Conocara macroptera - eastern North Atlantic, NIO uncat. (1).

Conocara mcdonaldi - western North Atlantic, USNM 215596 (1), USNM 215597 (6), USNM 215598 (11), USNM 215599 (1)*, USNM 215600 (9), USNM 39482 (1, holotype), FMNH 80469 (3), MCZ 49351 (1), MCZ 39351 (1), UMML 27058 (1), UMML 26713 (1), UMML 27059 (1).

Conocara murrayi - North Atlantic, FMNH 64071 (1), NIO uncat. (1), DANA 1186^{II} (1).

Einara edentulus - Atlantic, DANA 4201^{XVIII} (1), NIO uncat. (1), MCZ 49348 (1). Indian, USNM 200522 (1), MCZ 45300 (1).

Einara macrolepis - eastern North Atlantic, NIO uncat. (1).

Einara sp. - Indian, USNM 200465.

Ericara microlepis - Indian, USNM 215601 (1).

Ericara salmonea - eastern Pacific, USNM 48769 (1, holotype), USNM 75826 (1, holotype of *X. profundorum*). western Atlantic, UMML 32360 (3), UMML 31749 (1), UMML 32354 (1)*, UMML 31750 (1).

Ericara werneri - Atlantic, radiograph of holotype.

Leptoderma lubricum - complex, North Atlantic, NIO uncat. (2, 2)*. eastern Pacific, USNM 215602 (1), USNM 215603 (1).

Leptoderma macrops - North Atlantic, USNM 163280 (1, holotype of *L. springeri*), BMNH 1890-6-16-44 (1, paratype), MNHN 85-233-235 (3, paratypes, radiographs only), USNM 215604 (35), USNM 215605 (2)* , USNM 186069 (3), USNM 189013 (1), USNM 215606 (4), FMNH 65730 (2), FMNH 65735 (7), FMNH 65731 (6), FMNH 66143 (2), ISH 1896/68 a-c (3).

Mirognathus normani - eastern North Atlantic, ISH 917/73 (1)*.

Narcetes alveatus - eastern Pacific, MCZ 28477 (1, holotype).

Narcetes lloydi - Indo-Pacific, USNM 92335 (1, holotype), USNM 161457 (1), USNM 215508 (1), FMNH 75809 (1).

Narcetes stomias - eastern Pacific, USNM 43081 (1, holotype), MCZ 28474 (1, holotype of *N. pluriserialis*), USNM 215516 (1). western North Atlantic, USNM 215515 (1)*, USNM 215514 (2), USNM 215513 (2), USNM 215512 (1), USNM 215509 (6), USNM 215510 (1), USNM 215511 (2), UMML 27049 (1), FMNH 64073 (2), CAS 36300 (1), VIMS 3538 (1).

Nomoctes alvifrons - eastern Pacific, MCZ 28478 (1, holotype).

Nomoctes inspector - eastern Pacific, MCZ 28475 (1, syntype).

Nomoctes koefoedi - North Atlantic, USNM 215502 (1), MCZ 36636 (1).

Nomoctes michaelsarsi - North Atlantic, USNM 215501 (1), UMML 21628 (1), NIO uncat. (1).

Nomoctes pappenheimi - western Pacific, USNM 92336 (1, holotype).

Photostylus pycnopterus - North Atlantic, NIO uncat. (1), FMNH 65651 (1), FMNH 71740 (1), UMML 27429 (1), DANA 4007^{VII} (1), DANA 1370^{XI}. eastern Pacific, DANA 1208^{XIII} (2). Indo-Pacific, USNM 215518 (1), DANA 3917^{I} (1), DANA 3917^{II} (1), DANA 3656^{II}(1).

Rinoctes nasutus - western North Atlantic, USNM 189010 (1), USNM 215517 (1).

Rouleina harperi - Indo-Pacific, USNM 92333 (1, holotype).

Rouleina funebris - Indo Pacific, USNM 99534 (1, holotype).

Rouleina maderensis - western North Atlantic, USNM 215478 (1), USNM 215474 (5), USNM 215475 (1), USNM 215473 (1)*, USNM 215472 (1), USNM 215471 (6), USNM 215476 (10), MCZ 39349 (2), DANA 1183^{I} (1), VIMS 3541 (2). eastern North Atlantic, MMF 50 (1, paratype), MMF 2395 (1, paratype), MMF 2396 (1, paratype), MMF 2933 (1), NIO uncat. (1, 1, 1).

Rouleina mollis - western North Atlantic, USNM 44085 (1, holotype of Bathytroctes aequatoris) USNM 215484 (2), USNM 215481 (3), USNM 215482 (4), USNM 215479 (9). USNM 215483 (1), USNM 215485 (3), USNM 215486 (2), USNM 215480 (1)*, VIMS 3542 (1), VIMS 3540 (1), UMML 22353 (2), FMNH 65711 (1), VIMS 3539 (1), CAS uncat. (2), MCZ 40609 (1). eastern North Atlantic, NIO uncat. (1), southeastern Pacific, USNM 215487 (1), USNM 215488 (1), USNM 4085 (1). Indian, USNM 215489 (1).

Talismania antillarum - western North Atlantic, USNM 43739 (1, holotype), BOC 3724 (1, holotype of B. microphos), USNM 21558 (1), USNM 215555 (1), USNM 215552 (1), USNM 215557 (4), USNM 215554 (1), USNM 215553 (3), USNM 215556 (10), USNM 215560 (1)*, MNHN 1976-10 (2), MCZ 51957 (3), MCZ 51958 (1). eastern North Atlantic, NIO uncat. (2), USNM 215551 (1), USNM 215550 (1). Indo-Pacific, USNM 201160 (1), USNM 200521 (1), USNM 215559 (1). USNM 92331, 93390 and 93389 (syntypes of B. hataii).

Talismania aphos - southeast Pacific, USNM 215540 (12), USNM 215541 (15), USNM 215542 (18), USNM 215543 (7), USNM 215544 (4), USNM 215545 (2), USNM 215546 (3), USNM 215547 (4), USNM 215548 (1), USNM 215549 (1)*, CAS 36294 (8), CAS 36295 (13), CAS 36296 (13), FMNH 80465 (2), FMNH 80466 (2), BMNH 1976-5-10-5 (1), MCZ 51939 (5), MCZ 49350 (2).

Talismania bifurcata - eastern Pacific, USNM 215570 (1)

Talismania longifilis - eastern Atlantic, UMML 31256 (1).

Talismania mekistonema - western North Atlantic, UMML 15544 (1). eastern North Atlantic, NIO uncat. (1).

Talismania oregoni - western North Atlantic, USNM 160482 (1, holotype), USNM 215561 (1, paratype), USNM 215562 (2), USNM 215563 (1), USNM 215564 (8), USNM 215565 (1), USNM 215566 (3), USNM 215567 (9), USNM 215568 (5), USNM 215569 (2), FMNH 71744 (1), FMNH 65727 (2), FMNH 66650 (1), FMNH 47910 (2), BMNH 1976.5.10.6-10 (5), CAS 36298 (2), CAS 36299 (1), MCZ 51959 (6), AMNH 35398 (15), UMML 22613 (1), USNM uncat. (1)*.

Xenodermichthys copei - western North Atlantic, USNM 33551 (1. holotype). USNM 215523 (75), USNM 215522 (43), USNM 215524 (10), USNM 215525 (9), USNM 215526 (8), USNM 215527 (8), USNM 215528 (17), USNM 215529 (2), USNM 215530 (1), USNM 215531 (1), USNM 215532 (1), USNM 215533 (1), USNM 215534 (1), USNM 215535 (1), USNM 215536 (3), USNM 215537 (1), USNM 215538 (1)*, USNM 215539 (1)*, VIMS uncat. (3), AMNH 35397 (1), CAS 36293 (1), CAS 36292 (1), CAS 36291 (1), FMNH 65733 (2), FMNH 45340 (1), FMNH 65736 (1), MNHN 1976-9 (2), MCZ 51938 (3), BMNH 1976.5.10.1-4 (4), DANA 1296^{I} (1), DANA 1257^{I} (1), DANA 1293^{I} (2) DANA 1270^{VII} (1), DANA 1198^{I} (1), DANA 1274^{II} (1), DANA 1281^{I} (1), DANA 6691^{VI} (1), DANA 1217^{V} (1), DANA 1239^{XIV} (1), DANA 1183^{XII} (1), DANA 1196^{I} (1), eastern North Atlantic, DANA 4014^{I} (5), DANA 4157^{I} (4), DANA 4158^{VII} (2), DANA 4157^{II} (1), DANA 4158^{VI} (1), DANA 4206^{I} (1), DANA 4158^{XV} (1), DANA 1386^{I} (1) DANA (Thor 234 (1)), DANA Thor 36 (1)), USNM 215521 (2), NIO uncat. (2). Indo Pacific, MCZ 45287 (1), DANA 3630^{II} (1).

Xenodermichthys nodulosus - Philippine Sea, DANA 3722[I] (1).

Genus A spp. - Indo-Pacific, AH 26, MWT 11 (1), AH 142 (1).

Leptochilichthyidae

Leptochilichthys agassizii - eastern North Atlantic, ISH 916/73 (1)*. Pacific, MCZ 28479 (1, holotype), SIO 66-55 (1).

Searsidae

Mentodus rostratus - western North Atlantic, USNM 215612 (1)*, VIMS 3472 (1).

Argentinidae

Argentina striata - western North Atlantic, Vims 1747 (1)*.

Bathylagidae

Bathylagus berycoides - western North Atlantic, Vims 4087 (1)*.

Esocidae

Umbra pygmaea - Virginia, VIMS 500 (1)*.

Osmeridae

Mallotus villosus - western North Atlantic, VIMS 1231 (1)*.

Salmonidae

Salvelinus fontinalis - Virginia, VIMS 633 (1)*.

Oncorhynchus kisutch - western North Atlantic, VIMS 2473 (1).

Engraulidae

Anchoa hepsetus - western North Atlantic, VIMS 2516 (98).

Bathysauridae

Bathysaurus agassizii - western North Atlantic, VIMS uncat. (1).

Synodontidae

Saurida brasiliensis - western North Atlantic, VIMS 2557 (1).

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