

1984

On the anatomy and phylogeny of the Zoarcidae (teleostei: perciformes)

M. Eric. anderson

College of William and Mary - Virginia Institute of Marine Science

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PERCIFORMES)**

The College of William and Mary in Virginia

Ph.D. 1984

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ON THE ANATOMY AND PHYLOGENY OF THE
ZOARCIDAE (TELEOSTEI: PERCIFORMES)

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

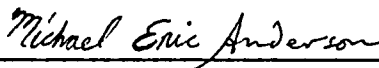
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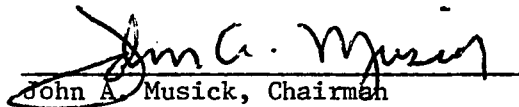
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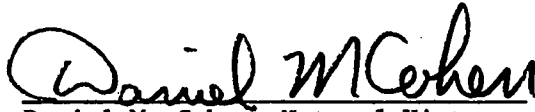


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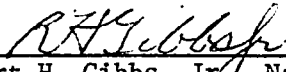
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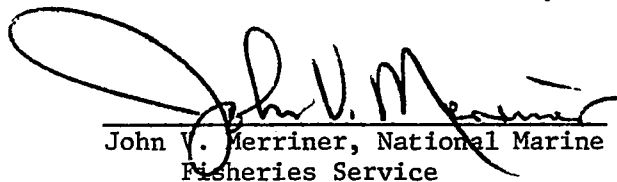
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- I. A) Zoarchias glaber Tanaka, 1908 (Stichaeidae); UMMZ 207710, 100 mm SL. B) Zoarces gillii Jordan and Starks, 1905; CAS 17746, 221 mm SL. C) Davidijordania poecilimon (Jordan and Fowler, 1902); UMMZ 202548, 123 mm SL. D) Krusensterniella multispinosa Soldatov, 1922, USNM 92592, 125 mm SL.
- II. A) Melanostigma atlanticum Koefoed, 1952; VIMS 05646, 108 mm SL. B) Nalbantichthys elongatus Schultz, 1967; USNM 200671, 135 mm SL.
- III. A) Austrolycichthys brachycephalus (Pappenheim, 1912); CAS uncat., 205 mm SL. B) Austrolycichthys conorhynchus (Garman, 1899); UMLL 22862, 211 mm SL. C) Austrolycichthys suspectus (Garman, 1899); SIO 68-106, 216 mm SL.
- IV. A) Austrolycichthys sp. A; USNM 233626, 170 mm SL. B) Head and body of A. C) Pachycara sp. D.; USNM 233627, 161 mm SL.
- V. A) Pachycara obesum Zugmayer, 1911; MCZ 57612, 498 mm SL. B) Pachycara bulbiceps (Garman, 1899); SIO 73-286, 455 mm SL.
- VI. A) Pachycara crassiceps (Roule, 1916). BMNH 1981.6.23:1-2, 512 mm SL. B) Head and body of A. C) Pachycara sp. C; ZMUC P761147, 236 mm SL. D) Head and body of C.
- VII. A) Lycodes concolor Gill and Townsend, 1897; LACM 34164-1, 325 mm SL. B) Lycodes squamiventer (Jensen, 1904); ISH 149/73, 217 mm SL. C) Lyconema barbatum Gilbert, 1895; VIMS 05391, 146 mm SL. D) Eucryphycus californicus (Starks and Mann, 1911); VIMS 05394, 118 mm SL.
- VIII. A) Lycodichthys dearborni (DeWitt, 1962); VIMS 05404, 198 mm SL. B) Lycodichthys antarcticus Pappenheim, 1911; SAMA F353, 181 mm SL. C) Notolycodes schmidti Gosztonyi, 1977; ISH 391/78, 386 mm SL.
- IX. A) Taranetzella lyoderma Andriashev, 1952; CAS 38921, 142 mm SL. B) Lycodonus mirabilis Goode and Bean, 1883; VIMS 05459, 302 mm SL. C) Lycenchelys porifer (Gilbert, 1891); SIO

*Not paginated. Follows page 218.

Plate

- 70-247-61, 257 mm SL. D) Lycenchelys paxilla (Goode and Bean, 1879); VIMS 06545, 248 mm SL.
- X. A) Lycenchelys sp. A; ISH 381/78, 234 mm SL. B) Piedrabuenia ringueleti Gosztanyi, 1977; ISH 389/78, 233 mm SL. C) Lycenchelys bellingshauseni Andriashev and Permitin, 1968; ISH 351/76, 234 mm SL.
- XI. A) Ophthalmolycus bothriocephalus (Pappenheim, 1912); BMNH 1937.7.12:159, 112 mm SL. B) Ophthalmolycus concolor (Roule and Despax, 1911); CAS uncat., 142 mm SL. C) Redirolycus microphthalmus (Norman, 1937); ISH 376/78, 90 mm SL. D) Redirolycus sp. A; ISH 164/78, 147 mm SL.
- XII. A) Bothrocarina microcephala (Shmidt, 1938); HUMZ 34001, 430 mm SL. B) Head and body of A. C) Bothrocara brunneum (Bean, 1890); VIMS 07686, 447 mm SL. D) Lyco-dapus pachysoma Peden and Anderson, 1978; ISH 403/76, 184 mm SL.
- XIII. A) Aiakas kreffti Gosztanyi, 1977; ISH 274/78, 301 mm SL. B) Head and body of A. C) Plesienchelys stehmanni (Gosztanyi, 1977); ISH 377/78, 204 mm SL.
- XIV. A) Iluocoetes fimbriatus Jenyns, 1842; ISH 388/78, 125 mm SL. B) Austrolycus depressiceps Regan, 1913; VIMS 05401, 155 mm SL. C) Crossostomus chilensis (Regan, 1913); MACN 4403, 165 mm SL; anomalously pigmented individual.
- XV. A) Maynea puncta (Jenyns, 1842); LACM 10722-1, 250 mm SL. B) Phucocoetes latitans Jenyns, 1842; VIMS 05399, 109 mm SL. C) Pogonolycus elegans Norman, 1937; ISH 1445/66, 65 mm SL. D) Oidiphorus brevis (Norman, 1937); ISH 380/78, 88 mm SL.

ABSTRACT

The eelpouts, Zoarcidae, are a group of bony fishes, most species of which inhabit continental shelves and slopes of boreal seas. There are about 200 species of eelpouts, most of which are rare in collections, thus they have been only cursorially studied by most workers. As a result, the systematics of the family is in a poor state. This work is a contribution to the improvement of that state.

The anatomy of all nominal genera of Zoarcidae was studied in an attempt to reconstruct phylogeny and establish the limits of genera. From analysis of a matrix of 63 characters, the 43 nominal genera recognized here form two subfamilies. One, Lycozoarcinae, contains only the primitive Lycozoarces regani. The other, Zoarcinae, is divided into three tribes, Zoarcini, Gymnelini and Lycodini. The more primitive zoarcids are characterized by having 4-6 suborbital bones arranged in a circular pattern close to the orbit, and complete cephalic lateralis pore patterns, except some of the few deep-sea forms. The more derived zoarcids are characterized by having 6-11 suborbital bones arranged in an "L-shaped" pattern away from the orbit (except a few which have lost some bones) and the loss of the interorbital pores (except for a few reversals).

An hypothesis is presented for the sister group relationship of Zoarcidae with six zoarceoid families: Ptilichthyidae, Zaproridae, Anarhichantidae, Stichaeidae, Pholididae and Scytalinidae. Bathymasteridae is hypothesized to be the primitive sister group of all the above taxa.

The zoarceoids are probably most closely related to notothenioids and some of the trachinoids than to blennioids, a group recently restricted to six tropical-subtropical families.

Since fully 45% of the genera recognized here are known from less than 15 specimens each, zoogeographic patterns are unsatisfactorily resolved. Considering the known distributions of all zoarcid genera, the highest endemism is found in temperate South America (30%), the northwestern Pacific (23%) and northeastern Pacific (11%). The best known deep-sea genera and species are wide-ranging, this perhaps due to the benthic, precocious larvae of most species.

ON THE ANATOMY AND PHYLOGENY OF THE
ZOARCIDAE (TELEOSTEI: PERCIFORMES)

INTRODUCTION

Fishes of the family Zoarcidae, the eelpouts, primarily inhabit the continental shelves and slopes of boreal seas (Jensen, 1904; Schmidt, 1950; Andriashev, 1954, 1955a; Leim and Scott, 1966; Hart, 1973), though there have been major radiations throughout South America and Antarctica (Norman, 1937a, 1938; Gosztonyi, 1977). A few species are known from tropical-subtropical deep-sea regions (Garman, 1899; Cohen, 1964; Parin, 1977, 1979; Peden and Anderson, 1978; Golovan, 1978; Anderson, 1982a).

There have been 13 family-group names proposed for eelpout groups, and these usually have been treated as subfamilies without comment by authors. Most of these names are not used in this study, being composed of either non-zoarcids (Neozoarcinae, Parabrotulidae), are contained within other monophyletic groups recognized here, or are synonyms (Derepodichthyidae, Gymnelinae, Hadropareinae, Lycodapodidae, Lycodoidea, Lycodidae, Lycogramminae, Melanostigmatidae, Zoarchidae and Zoarceoidae).

Although there have been numerous regional systematic works, many based on good sample sizes, zoarcid systematics has remained in chaos. Many modern collections of earlier, inadequately described or rare species almost defy identification, especially in the genera Bothrocara, Lycenchelys and Lycodes. Other new collections have shown many characters used at the generic level in the past are of question-

able value. Generic affinities remain entangled primarily because there has been no modern cladistic or numerical analysis of character state distributions and discussion of their evolution. The systematics of the family has therefore been constrained within nineteenth century typology. This resulted in the use of many characters now seen to be of lesser value than originally decreed. These include primarily morphometric characters that are sexually dimorphic or allometric, heavy reliance on ecophenotypic characters and those of questionable construction.

The relationships of the Zoarcidae to other fish families have been much discussed in the literature. The family has been allied to the "blennioid" fishes, which most recently have been divided into two groups: the "tropical blennioids," families Blenniidae, Labrisomidae, Tripterygiidae, Clinidae, Chaenopsidae and Dactyloscopidae, and the "northern blennioids," families Bathymasteridae, Ptilichthyidae, Zaproridae, Anarhichantidae, Stichaeidae, Cryptacanthodidae, Pholididae, Cebidichthyidae and Scytalinidae (C. Hubbs, 1952; Gosline, 1968; Springer, 1968; George and Springer, 1980). The "northern blennioids" are usually referred to collectively as superfamily Stichaeoidea (Makushok, 1958; McAllister and Krejsa, 1961; Anderson and Hubbs, 1981). Gill (1893) first used the suprafamilial-group name Zoarceoidea and, as the "northern blennioids" are shown here to be most closely related to zoarcids, all these fish families will be collectively referred to as zoarceoids.

Zoarcids have also been allied to the gadiform and ophidiiform fishes (Greenwood et al., 1966; Rosen and Patterson, 1969; Lauder and Leim, 1983) in recent times, but other authors have convincingly

disputed this (Marshall and Cohen, 1973; Anderson and Hubbs, 1981; Shaklee and Whitt, 1982).

This study was designed to search throughout as many zoarcid species as possible to find reasoned sets of characters. A cladistic analysis of the distribution of character states was performed to resolve monophyletic groups, reconstruct phylogeny, diagnose genera and provide a classification. In addition, I present a discussion of the geographical distribution of the family as a contribution to knowledge of the zoogeography of boreal fishes.

METHODS AND MATERIALS

Measurements were made with ocular micrometer or dial calipers to the nearest 0.1 mm, except standard length (SL, to the nearest mm). Osteological observations were made on alcian blue-alizarin red stained material, or, in specimens preserved in alcohol more than about 20 years, only with alizarin (Dingerkus and Euhler, 1977). A total of 156 of the approximately 200 nominal species of zoarcids were cleared and stained and/or dissected and radiographed for detailed examination. These are listed in Appendix I, as are the non-zoarcids studied, and institutions maintaining specimens. Abbreviations for anatomical terms used in the text figures are given in Appendix II. The zoarcid character matrix used in phylogeny reconstruction is given in Appendix III. Cephalic lateralis pore terminology follows that established by Andriashev and Permitin (1968), with translation of Russian terms that of Gosztonyi (1977) and Anderson (1982b). Jaw and cheek pores are standardized into a preoperculomandibular count even when these canals are separated.

The zoarcid character matrix was analyzed to produce cladograms using J. S. Farris's "Wagner 78" computer program (see Wiley, 1981: 179). Once the limits of all genera were established on anatomical grounds, fifteen separate data entry runs were performed using the program and facilities of the National Museum of Natural History, Washington, D. C. Fifteen runs were arbitrarily chosen because of

slight internal inconsistencies in the program that require the worker to vary data entry to produce a most parsimonious cladogram.

Literature consulted for the study of zoarceoid relationships consisted of Chapman and Townsend (1938), Makushok (1958, 1961a, 1961b, 1961c), Barsukov (1959), McAllister and Krejsa (1961), Kobayashi (1961), Leim and Scott (1966), Gosline (1968), McAllister (1968), Miller and Lea (1972), Hart (1973), Cailliet and Anderson (1975), Lindberg and Krasnyukova (1975) and Richardson and DeHart (1975).

Procedural methodology of phylogeny reconstruction follows that of Hennig (1966), as discussed and modified by Arnold (1981) and Wiley (1981). In any attempt at phylogeny reconstruction or classification of a natural group of organisms, the modern student is faced with, and sometimes bewildered by, philosophies and methods of three schools of evolutionary thought. I reject numerical taxonomy as it was originally proposed (Sneath and Sokal, 1973) on the belief that patristic similarity may often have nothing to do with evolution, is logically contradictory and makes no proviso with respect to homoplasy. The "evolutionary" school (Simpson, 1953; Mayr, 1963; 1981) seems to me to rely too heavily on a taxonomist's intuition and de novo apomorphies in constructing classifications. Hennig's (1966) system groups taxa into series of nested units that reflect the best estimate of ancestry and descent. Taxa are grouped by their possession of shared, derived characters (synapomorphies), the only valid basis of hypotheses of common ancestry. Hypotheses of the phylogeny of a group are based on the principle of parsimony, or the acceptance of the hypothesis requiring the fewest ad hoc assumptions about character transformations.

Character polarity determinations (primitive vs. derived, or plesiomorphy vs. apomorphy) are based on the identification of identical character states in two morphoclines and the comparison of these states in the most closely related third group (the outgroup). States that are identical to those in the outgroup are primitive (plesiomorphous). This is applicable only when the closest related group is recognized, and this is based on the criterion that if one group shares the same derived, unreversed state(s) with another, the two are related--the more states they share, the stronger the evidence of relationship.

Decisions about homology of structure were made on the basis of similarity in location and structure (Wiley, 1976; Arnold, 1981), ontogenetic information on zoarcids being decidedly poor (Anderson, in press). Saether (1983) discussed two sets of criteria for asserting synapomorphy of homologous structures and I have employed that set which allows for secondary reductions and reversals in apomorphic subgroups. The canalized evolutionary potential, through "underlying synapomorphy" (i.e., parallelism as a result of inheritance within monophyletic groups causing incomplete synapomorphy) and parallel selection, allows the recognition of synapomorphy in characters expressing partial reversal, reduction and parallelism.

One strong conclusion from the results of this study requires alterations of the traditional concept of genus as it applies to zoarcids. This taxon has been very differently interpreted by authors, and I have steered away from typological splitting following the discussions of Rosen and Bailey (1963:5-6) and Mayr (1981). Genera are traditionally separated on the degree of morphological difference

but to most workers on zoarcids decisions on the degree have never been well analyzed. The concept of "wide separation" among species groups must be applied within the constructs of the family (Rosen and Bailey, 1963), and there has never been such an analysis of Zoarcidae. Thus, any such review should be expected to alter the interpretation of taxa. The advantages to developing a phylogenetic basis for genus in zoarcids, I think, are three: 1) there is decreased emphasis on parallel reductionism and recognition of the importance of synapomorphy and autapomorphy; 2) the recognition of higher taxa is based on observations of the direction of evolution of specific characters; 3) a phylogenetic concept of genus provides a basis for nomenclatural stability.

Attempts at phylogeny reconstruction and classification have involved some conceptual problems in Zoarcidae. Many genera, as defined herein, are monothetic (Mayr, 1969), i.e., diagnosed almost entirely by autapomorphies, or derived anagenic characters. While this reinforces monophyly in these lineages, autapomorphies do not aid phylogenetic inference. In some large genera, several characters occur in a continuum of states. This raises questions concerning their utility in phylogeny reconstruction. These problems have been noted for ceratioid anglerfishes (Pietsch, 1979), some percoids (D. Johnson, 1980), sebastine scorpaenids (Barsukov, 1981), stomiiforms (Fink and Weitzman, 1982) and aulopiforms (R. Johnson, 1982). Those problems specific to Zoarcidae are discussed in detail in the section on phylogeny.

RESULTS

Relationships among Zoarceoidea

Recent anatomical studies on zoarceoid fishes (Barsukov, 1959; Makushok, 1958, 1961a, 1961b, 1961c; McAllister and Krejsa, 1961; Yarberry, 1965; Anderson and Hubbs, 1981; Anderson, 1982b) strongly suggest that the Zoarcidae are a sister group of the other zoarceoid families listed by Gosline (1968). As a result of this study and others (Peden and Anderson, 1978; Anderson and Hubbs, 1981) I recognize eight zoarceoid families: Bathymasteridae, Ptilichthyidae, Zaproridae, Anarhichantidae (Anarhichadidae of authors), Stichaeidae, Pholididae, Scytalinidae and Zoarcidae. All of these fishes share two derived characters: absence of the basisphenoid bone; loss of the posterior pair of nostrils. These families are at a perciform grade of evolution, as indicated by the following characters that separate them from "Paracanthopterygians" (sensu Rosen and Patterson, 1969; Rosen, 1973):

- 1) 1:1 ratio of vertebrae to unpaired fin pterygiophores; 2) jugular pelvic fins set anterior to pectoral fin base; 3) five or fewer segmented pelvic rays (when present); 4) caudal skeleton with no separate second ural centrum; 5) no beryciform foramen in ceratohyal (McAllister, 1968: 6); 6) branchiostegal rays 4-7, with four external and 1-3 ventral, all acinaciform (McAllister, 1968: 4, 145); 7) insertion of posterior bundle of retractor arcuum brachialium muscle principally on third infrapharyngobranchial bone; 8) reduction of articular surface

of fourth epibranchial and enlargement of second and third epibranchials.

The zoarcids were placed among the gadiform-ophidiiform lineages by Greenwood et al. (1966) and Rosen and Patterson (1969). However, Fraser (1972), Marshall and Cohen (1973) and Anderson and Hubbs (1981) have shown that zoarcids are morphologically distinct from gadiforms and ophidiiforms. Noteworthy zoarcid characters given by these authors separating them from the gadiform-ophidiiform fishes are: 1) 1:1 ratio of vertebrae to unpaired fin pterygiophores; 2) gas bladder absent (bladder absent only in Aphyonidae); 3) a single pair of nostrils; 4) second ural centrum absent; 5) a single-lobed ovary; 6) males of viviparous species without elongate intromittent organ. More recently, Shaklee and Whitt (1981) discovered a genetically derived state in the C4 isozyme of lactate dehydrogenase (LDH) within Zoarcidae and Ophidiiformes which separated them from all Gadiformes. Differential electrophoretic mobility in three LDH homopolymers further separated zoarcids and ophidiiforms.

Nielsen (1968) studied the anatomy of the enigmatic Parabrotula plagiophthalma and Leucobrotula adipata and placed them in Zoarcidae on the basis of their 1:1 ratio of vertebrae to fin pterygiophores, eel shaped body, dorsal and anal fins confluent with the caudal, and lack of spiny rays, scales and ventral fins. Later Nielsen (1973) erected Parabrotulidae for these two fishes and still considered them close to Zoarcidae. However, as a result of this study, only the first of Nielsen's characters may have significance at the family level. Furthermore, parabrotulids cannot be closely related to zoarcids because of their paired nostrils, bilobed ovary and well developed male intromittent organ. Parabrotulids share these characters with

ophidiiforms, and they may be an offshoot of some ophidiiform ancestor, despite their 1:1 ratio of vertebrae to fin pterygiophores. The 1:1 ratio in parabrotulids may be a reduction from the plesiomorphic 2:1 state in ophidiiforms, a derivation in the opposite direction from pterygiophore addition as seen in the gadid Enchelyopus (Fahay and Markle, in press). Much more work is required to assess this question.

Gosline (1968) placed the zoarcids in the perciform suborder Blennioidei, which was a group more restricted than Jordan's (1923) refined Jugulares, or Regan's (1912) polyphyletic Blennioidea. Gosline (1968, fig. 12) has given the clearest distinction to date of the "blennioids," but his expanded concept includes fishes placed in other orders (notothenioids) or suborders (trachinoids, congrogadoids) by some authors (Greenwood et al., 1966; Smith, 1952; Winterbottom, 1982¹). Makushok (1958) and Springer (1968) did not consider the "tropical blennioids" close to the "northern blennioids," based on the absence of the basisphenoid bone in the latter (absent in "tropical blennioids" only in the blenniid tribe Nemophidini), and possession of a single pair of nostrils.

Makushok (1961a) reassigned the cebidichthyid subfamily Neozoarcinae of Okada and Matsubara (1938) as a subfamily within Zoarcidae. This group presently comprises six or seven species placed in Neozoarces Steindachner, 1880 and Zoarchias Jordan and Snyder, 1903. They are known only from the littoral of the Japan Sea and Pacific coast of

¹Winterbottom, R. 1982. The perciform family Congrogadidae-- biogeography and evidence for monophyly. American Society of Ichthyologists and Herpetologists, Abstracts, 62nd annual meeting.

Japan. Makushok believed they were not stichaeids on the basis of the similarity of structure of the caudal fin with zoarcids and other reductional trends, such as a decrease in pectoral fin rays and absence of pelvic fins. The presence of spines in the first half of the dorsal fin, indicating stichaeid relationships, Makushok thought, was the result of evolutionary convergence. However, my analysis of three neozoarcines indicates Neozoarcinae should be expanded to include two enigmatic forms Makushok (1958) placed in Stichaeidae (Azygopterus corallinus Andriashev and Makushok, 1959 and Eulophias tanneri Smith, 1902), and that all four genera compose a distinct subfamily of Stichaeidae. Of the characters given by Makushok (1961a) to place the Neozoarcinae in Zoarcidae, only the elongation of the tail with a concomitant reduction of caudal skeletal features may initially be regarded as potentially synapomorphous in these fishes. But, since this elongation and caudal reduction has occurred repeatedly in fossorial teleosts, and since Anarrhichthys ocellatus (well within the limits of Anarrhichantidae otherwise) exhibits this elongation, and, since the neozoarcines share three other synapomorphies with Stichaeidae neither shares with Zoarcidae (see below), I consider caudal elongation and reduction of elements in the absence of other characters a derived character state homoplasiously distributed.

Thus, the neozoarcines are placed among the "higher stichaeoid" fishes (families Stichaeidae, Pholididae and Scytalinidae) on the basis of the following synapomorphies with either all or most "stichaeoids" that are not shared with Zoarcidae: 1) dorsal fin of all spines (Azygopterus), or pungent spines anteriorly, rays posteriorly ("flexible spines" followed by pungent spines in the zoarcid Krusensterniella

is taken to be autapomorphous for this genus); 2) first anal fin ray element spinous, enlarged; 3) frontal bones long and narrow, their length $\geq 76\%$ skull length, width $\leq 36\%$ their length. The neozoarcines have well developed pleural ribs, a character separating them from the pholidids and Scytalina; thus the inclusion of Neozoarcinae within Stichaeidae. Further, the neozoarcines lack the following important apomorphies that characterize zoarcids: 1) intercalar bone absent; 2) postorbital lateralis canal exits posteriorly through lateral extrascapulars only; 3) branchiostegal membrane attached to isthmus (free in Zoarcidae only in the primitive Lycozoarces and the derived Lycodapus; in the latter this is considered a reversal); 4) caudal fin with one epural (two epurals in zoarcids only in Lycozoarces). Neozoarcinae is accorded subfamilial status within Stichaeidae and diagnosed relative to other Stichaeidae as follows: 1) body and tail elongated, vertebrae 96-130 +; 2) caudal fin greatly reduced, completely confluent with dorsal and anal fins, two epurals present; 3) no anterior ramus of supraoccipital extending under frontals; 4) pectoral fin reduced, 6-10 rays, or absent altogether; 5) lateral line, scales and pelvic fins absent.

Furthermore, the neozoarcines are separable into two groups, one containing Eulophias and Azygopterus, the other Neozoarces and Zoarchias, herein accorded tribal status, Eulophiini Nelson, 1976 and Neozoarcini (Okada and Matsubara, 1938), respectively (table 1). The relationships and taxonomic status of the neozoarcines is not central to the current study except to show that they are not zoarcids, but rather stichaeids, and a more complete description and analysis will be taken up later.

Makushok (1958, 1961c) and most authors recognize four monotypic

TABLE 1. Diagnoses of stichaeid tribes Neozoarcini and Eulophiini.

Character	Neozoarcini	Eulophiini
Number of precaudal vertebrae	17-22	36-45
Sphenotic-parasphenoid articulation	contacting	not contacting*
Parietal-parietal articulation	meeting in midline	not meeting in midline*
Vomerine and palatine teeth	present	absent
Branchiostegal rays	7	6
Pectoral fin rays	9-10	0-6
Pyloric caeca	present	absent

*Observed only in Azygopterus corallinus; after Makushok (1958).

zoarceoid genera as a separate family, Cryptacanthodidae. Jordan and Evermann (1898: 2442) erected this family mostly on superficial characters, the most important of which were 1) elongate, compressed body; 2) oblong, flat head with vertical cheeks; 3) oblique mouth; 4) conspicuous foramina passing the cephalic lateralis system; 5) non-protractile premaxilla; 6) heavy lower jaw; 7) branchiostegal membranes joined to isthmus and 8) no pelvic fins. Though these mostly qualitative characters partially diagnose this group, none by themselves are unique to zoarceoids. Makushok (1961c) has given the clearest osteological description of the cryptacanthodids to date, though this work is incomplete. Makushok listed three characters that are autapomorphic for cryptacanthodids in the phylogenetic scheme I propose (below):

1) extension of the braincase into the anterior myodome; 2) greatly enlarged bone foramina passing the cephalic lateralis canals and 3) greatly elongated pectoral fin actinosts (radials). However, if family Stichaeidae is expanded to include Neozoarcinae, the cryptacanthodids also must be included because they share all stichaeid synapomorphies and do not share the pholidid-scytalinid apomorphy (see below).

Gosline (1968) found Bathymasteridae "a perfectly good zoarceoid family..." (previously placed among the trachinoids) on the basis of its single nostril, pelvic fin with five rays and percoid pattern of the ramus lateralis accessorius nerve (Freihofer, 1963). Anderson and Hubbs (1981) included bathymasterid material in their investigation of the relationships of Derepodichthys alepidotus and did not note distinguishing osteological features that would exclude bathymasterids from a direct genealogy with zoarcids. In fact, they were struck by the close resemblance of bathymasterids to primitive stichaeine and opisthocentrine

stichaeids. Family Bathymasteridae is considered here as the primitive sister group (outgroup) of all other zoarceoid families.

Synapomorphies discovered among zoarceoid groups give evidence relevant to an hypothesis of familial relationships. Some autapomorphies were elucidated, providing a partial diagnosis for those families in which they occurred. More detailed information on the distribution of other derived characters in these fishes should add to the present evidence of monophyly presented for clades discussed below.

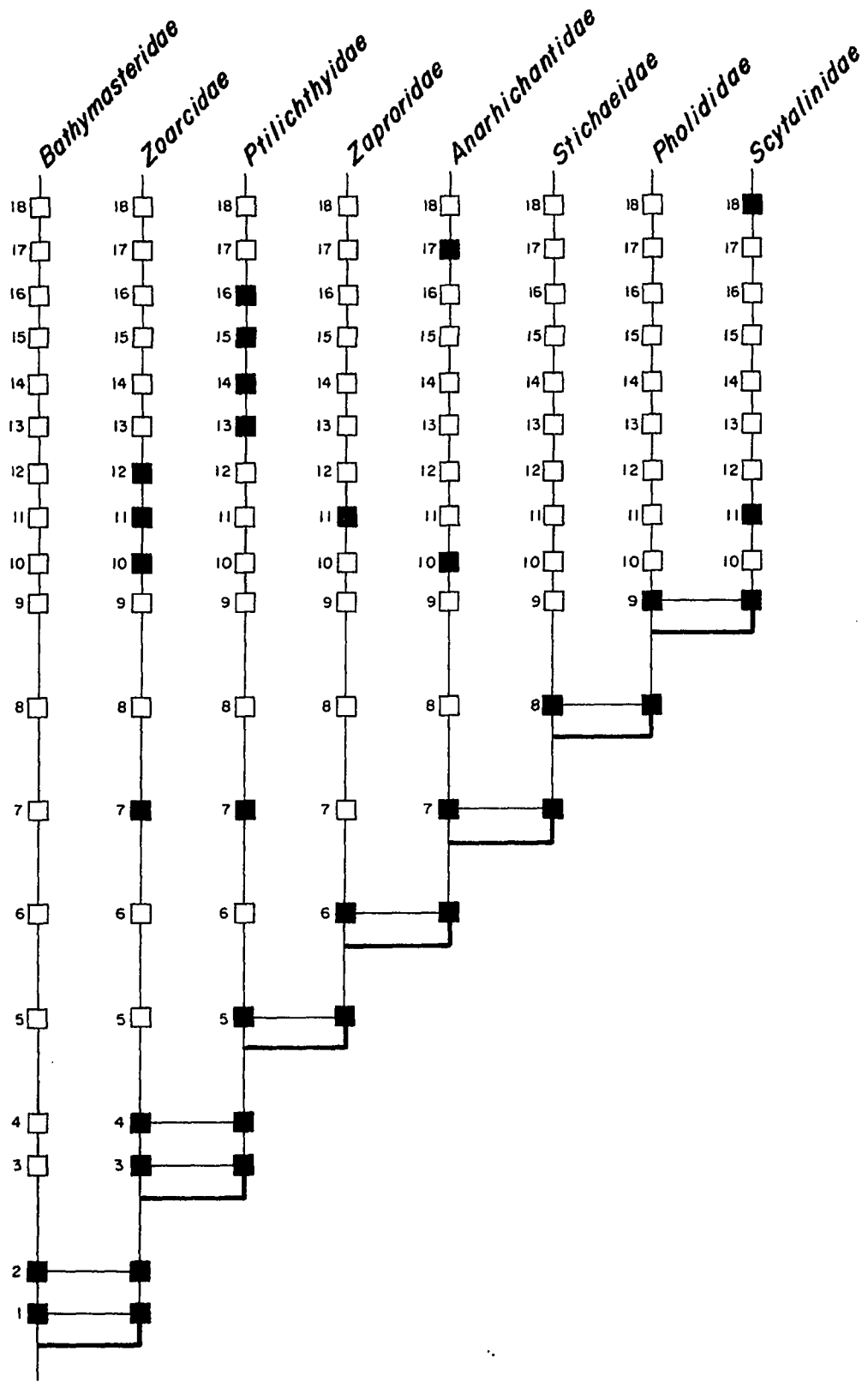
A preliminary character distribution chart, possibly depicting zoarceoid phylogeny, is presented in figure 1. This is based on 18 characters that were selected from about 30 that were verifiable in the literature and in those specimens that I examined for all families (see Appendix I). The distributions and polarities of all 18 characters are given below. Those synapomorphies that distinguish each clade are discussed through decreasing levels of universality and are indicated in a left to right sequence. Thus, the first clade, the eight-family assemblage, would be termed the Bathymasteridae through Scytalinidae clade, the next the Zoarcidae through Scytalinidae clade, and so on. Subsequent to the phylogeny reconstruction, I present a discussion of those derived characters that are autapomorphous in each family, or are seen to be homoplasious with the given hypothesis of relationship.

The Eight-Family Assemblage

All eight families, most likely of boreal origin, are distinguished from all other "blennioids," of tropical or austral distribution, by only two derived characters, taken here as synapomorphies.

- 1) The loss of the basisphenoid bone.
- 2) Reduction of paired nostrils to one on each side by loss of the

Figure 1. Distribution of 18 characters among zoarceoid fishes. Dark boxes, apomorphies, open boxes plesiomorphies. Numbers refer to characters discussed in text.



posteriormost pair.

Zoarcidae Through Scytalinidae Clade

The zoarcids form a sister group with all other "higher" zoarceoid families on the basis of two synapomorphies.

3) The reduction of pelvic fin rays to 2-3 (or loss of the fin) from five rays, with loss or reduction and fusion of the pelvic fin spine.

4) The development of small, imbedded cycloid scales from larger, ctenoid scales. Within some families, scales are lost altogether.

Reports in the literature that bathymasterids have cycloid scales are erroneous.

Ptilichthyidae Through Scytalinidae Clade

The relationship of the highly modified, monotypic Ptilichthyidae to other zoarceoids has never been established with certainty. Most of this family's unusual specializations are seen as autapomorphous and are discussed later. Ptilichthys is united with other "higher" zoarceoids on the basis of one synapomorphy.

5) The presence of 15 or more spines in the anterior portion of the dorsal fin. Zoarcids and bathymasterids have 0-1, rarely two, anterior spines, except the zoarcid Krusensterniella, which has, autapomorphously, 45-57 flexible spines followed by 2-26 pungent spines. Pungent dorsal spines are autapomorphous also for Zoarces and Macrozoarces and this is discussed later.

Zaproridae Through Scytalinidae Clade

The monotypic Zaproridae shares one synapomorphy with the remaining four zoarceoid families.

6) The presence of 1-4 anterior spines in the anal fin. All anal fin elements are divided at the base and have one or more segments in the plesiomorphous state. Scytalina has a completely spinous anal fin, the terminal state in this transformation series.

Anarrhichantidae Through Scytalinidae Clade

This group of four families shares one synapomorphy, though it is an intermediate state that is further derived in some subgroups. Clearly more characters are needed to assess this branching node.

7) The reduction of the caudal skeleton with loss of distinct caudal peduncle, loss of all or most procurrent rays and reduction in number of principal rays. In species exhibiting the more derived state (within Zoarcidae, Ptilichthyidae, Anarrhichthys and neozoarcine stichaeids), the epurals are reduced from the plesiomorphous state of three to one or two, and there is further loss of caudal rays. The homoplasious distribution of this character raises serious doubts about its phylogenetic utility.

Stichaeidae Through Scytalinidae Clade

The littoral fishes of these three families share one synapomorphy.

8) The elongated neurocranium. The derived state uniting this clade is a low, elongated skull; the height is 17.5-45.1% of its length (height measured from the center of the parietals; length along its greatest median axis). The plesiomorphous state is a short, high neurocranium; the height is 53.3-71.1% of the length.

Pholididae Through Scytalinidae Clade

These two specialized families share one synapomorphy.

9) Loss of the pleural ribs.

The remaining nine characters, chosen because of their importance in the literature of zoarceoid systematics, had derived states that were autapomorphous for a given family, or were homoplasiously distributed. The following two characters are homoplasious apomorphies regarded as independently derived in two or more families.

10) Branchiostegal membrane attachment. The branchiostegal membranes are free of the isthmus in most zoarceoids, as in most other of Gosline's (1968) "blennioids." The apomorphic restriction of the gill slits by membrane attachment toward the pectoral fin base (and higher in many zoarcids) is the condition in Zoarcidae, except the primitive Lycozoarces and the derived Lycodapus, and in Anarhichantidae. The free branchiostegal membrane of Lycodapus is considered an evolutionary reversal (see Phylogeny of Zoarcidae, below).

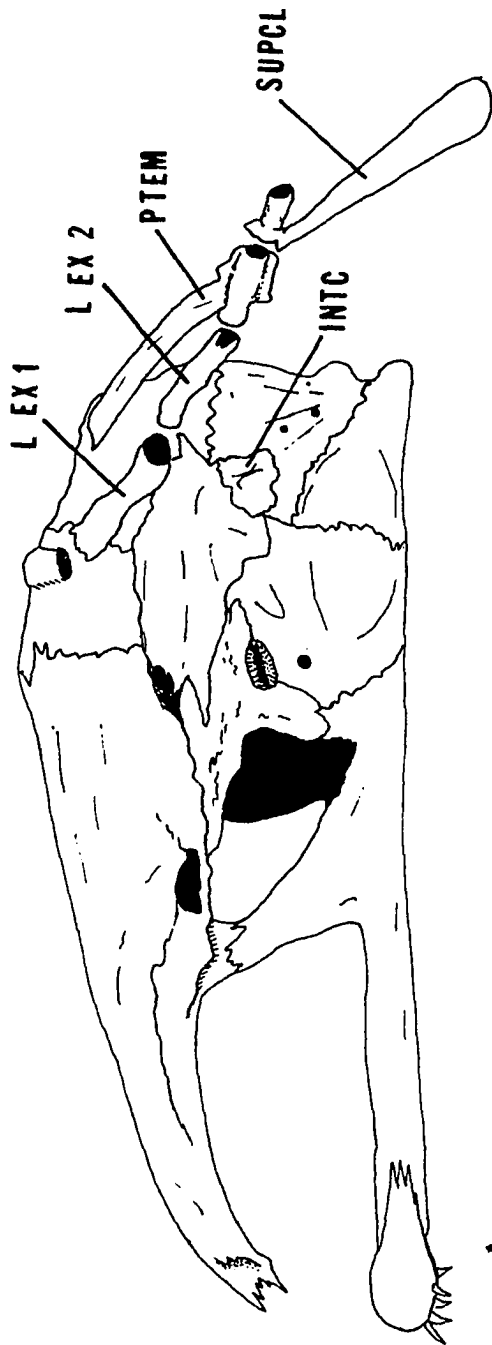
11) Intercalar (opisthotic) bone. The intercalary bone is, primitively, present in perciforms (Gosline, 1968). It has been lost in Zoarcidae, Zaproridae and Scytalinidae.

The next seven characters are autapomorphies, serving to define families.

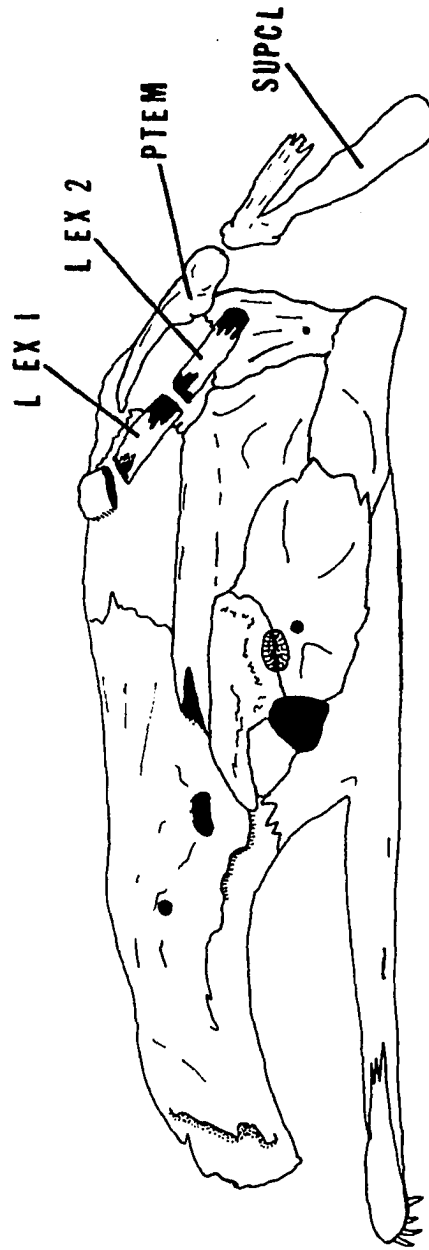
12) Postorbital canal passage. Bony elements that pass the posterior portion of the postorbital lateralis canal represent a transformation series. Primitively, the posterior portion passes through foramina in the posttemporal and supracleithrum, from which exit postorbital pores four and five (fig. 2A). The derived condition exists as an autapomorphy for Zoarcidae, in which the canal separates from the posttemporal and supracleithrum and passes only through the lateral extrascapulars. These lie just anterior to the posttemporal and pass only postorbital pores three and four (five is always absent in

Figure 2. Neurocrania and bones passing the postorbital lateralis canal.

A) Zoarchias veneficus (Stichaeidae), 55 mm SL; fifth post-orbital pore opens from dermal tube between posttemporal and supracleithrum. B) Zoarces viviparus (Zoarcidae), 193 mm SL; tubular structures of posttemporal and supracleithrum lost, no fifth postorbital pore.



A.



B.

Zoarcidae; fig. 2B).

13) Actinost ossification. The pectoral actinosts (radials) are primitively bony in these fishes. Ptilichthys has completely cartilaginous actinosts, an apomorphic state it shares with the zoarcid Lycodapus (see Makushok, 1958, fig. 81).

14) Palatine arch. The bones of the palatine arch are plesiomorphously well developed and fully ossified. Ptilichthys has, apomorphously, lost the endopterygoid and reduced the metapterygoid to a small splint (Makushok, 1958, fig. 38). Reduced palatine arches also exist among some zoarcids, especially Derepodichthys (Anderson and Hubbs, 1981).

15) Upper lip. Plesiomorphously, a groove delimits the snout region from the ensheathed upper jaw bones, with definitive lips formed. No lips are formed in Ptilichthys, an apomorphous condition it shares with the zoarcid Andriashevia.

16) Chin flap. There is no dermal symphyseal projection of the lower jaw in zoarceoids except Ptilichthys. This fish uniquely possesses an enlarged symphyseal flap on the lower jaw (Makushok, 1958, fig. 78).

17) Molariform teeth. Plesiomorphously, the zoarceoids have small simple teeth that reach their greatest diversity in Zoarcidae. Apomorphously, the jaw and palatine teeth have become massive crushing instruments in Anarhichantidae (Barsukov, 1959, pls. I, II) reminiscent of some mammals.

18) Parasphenoid wing. The median parasphenoid wing, apomorphously, has been lost in Scytalina and the bone is a mere strut separated by cartilage from the basioccipital, prootic, pterosphenoid and frontals.

Other apomorphic character states, mostly reductional, used in zoarceoid systematics were found to be homoplasiously distributed

within subgroups and they were not treated in the foregoing analysis. These were: 1) loss of pelvic fins; 2) loss of body lateral line; 3) loss of pyloric caeca; 4) loss of branches of the cephalic lateralis canals; 5) position of the sphenotic relative to the frontal foramen leading to postorbital pore 1; 6) loss of branchiostegal rays. In the latter character Makushok (1958, fig. 9) showed Ptilichthys to possess three branchiostegal rays--a potential autapomorphy if this were correct. However, Kobayashi (1961), McAllister (1968) and Richardson and DeHart (1975) have given 5-6 rays for this species. Makushok's somewhat old, damaged specimen seems to have lost some of its rays either before or during clearing and staining.

The hypothesis of relationships among zoarceoid families presented here could be modified if more and better characters could be identified, especially at the tentatively accepted Anarhichantidae-Scytalinidae clade. Future studies should also include other groups that have been traditionally allied with zoarceoids, notably Gosline's (1968) Trachinoidae and Notothenioidae.

Classification of Zoarcidae

The following classification is the result of phylogenetic analysis of the distributions of the 63 characters discussed in the next section. This is a cladistic classification; two subfamilies and three tribes are proposed, but further formal subdivisions are not. This is chiefly due to my inability to examine many characters of rare species and to the high degree of autapomorphy and lack of synapomorphy in some genera, resulting in unresolved multiple branching nodes.

Family Zoarcidae (Cuvier, 1829)

Subfamily Lycozoarcinae Schmidt, 1950

Lycozoarces Popov, 1933

Subfamily Zoarcinae Gill, 1862

Tribe Zoarcini (Gill, 1862)

Macrozoarces Gill, 1864Zoarces Cuvier, 1829

Tribe Gymnelini (Gill, 1864)

Andriashevia Fedorov and Neyelov, 1978Bilabria Schmidt, 1936Davidijordania Popov, 1931Gymnelopsis Soldatov, 1922Gymnelus Reinhardt, 1834Hadropareia Schmidt, 1904Krusensterniella Schmidt, 1904Melanostigma Günther, 1881Nalbantichthys Schultz, 1967Puzanovia Fedorov, 1975

gen. nov. Bond and Stein (ms)

Tribe Lycodini (Gill, 1862)

Aiakas Gosztanyi, 1977Austrolycichthys Regan, 1913Austrolycus Regan, 1913Bothrocarina Bean, 1890Bothrocarina Suvorov, 1935Crossostomus Lahille, 1908Dadyanos Whitley, 1951Derepodichthys Gilbert, 1895Eucryphycus gen. nov.Exechodontes DeWitt, 1977Hadropogonichthys Fedorov, 1982Iluocoetes Jenyns, 1842Lycenchelys Gill, 1884Lycodapus Gilbert, 1891Lycodes Reinhardt, 1831Lycodichthys Pappenheim, 1911Lycodonus Goode and Bean, 1883Lycogrammoides Soldatov and Lindberg, 1929Lycinema Gilbert, 1895Maynea Cunningham, 1871Notolycodes Gosztanyi, 1977Oidiphorus McAllister and Rees, 1964Ophthalmolycus Regan, 1913Pachycara Zugmayer, 1911

Tribe Lycodini (continued)

Phucocoetes Jenyns, 1842
Piedrabuenia Gosztonyi, 1977
Plesienchelys gen. nov.
Pogonolycus Norman, 1937
Redirolycus gen. nov.
Taranetzella Andriashev, 1952

Incertae sedis: "Oidiphorus" laevifasciatus Torno, Tomo and Marschoff, 1977 (see Oidiphorus account).

Some informal names are given to certain generic groups. These names are used for ease of reference and most follow previous supra-generic categories of authors, although many do not have a phylogenetic basis:

- 1) The genera Bilabria, Davidijordania, Gymnelopsis, Gymnelus, Hadropareia and Krusensterniella are referred to as the "gymnelines."
- 2) The genera Puzanovia, Nalbantichthys, Andriashevia and Bond and Stein's new genus are referred to as the "nalbantichthyines."
- 3) The genera Lycodes, Pachycara, Austrolyichthys, Exechodontes, Lycodichthys and Oidiphorus are referred to as the "lycodines."
- 4) The genera Plesienchelys, Ophthalmolycus, Redirolycus, Taranetzella, Lycinema, Eucryphycus, Lycenchelys, Lycodonus, Hadropogonichthys, Piedrabuenia and Derepodichthys are referred to as the "lycenchelyines."
- 5) The genera Bothrocarara, Bothrocarina, Lycogrammoides and Lycodapus are referred to as the "lycodapines."
- 6) The genera Notolycodes, Aiakas, Iluocoetes, Austrolycus, Crossostomus, Dadyanos, Phucocoetes, Pogonolycus and Maynea are referred to as the "mayneines."

Character Matrix

The characters, their states and polarities listed below are those that were recorded for all species, with a few exceptions. Characters found useful in phylogeny reconstruction (characters 1-22) are discussed first, followed by those with derived states that were autapomorphic or had distributions incongruent within my hypothesis of relationship (characters 23-63). Character polarity decisions based on outgroup comparisons were made from observations on specimens listed in Appendix I and literature cited in Methods and Materials. Documentation or illustrations are given where necessary. For each character, the plesiomorphic state is listed first, after "0," followed by the apomorphic states(s). The complete matrix is given in Appendix III.

1) Body height. 0) body relatively high. 1) body low.

Primitively, zoarceoids have a relatively high, robust body (measured from anal fin origin to dorsal fin base; in relation to standard length). Quantification of this state was based on 132 adult specimens in 27 genera. Generic means of body height to SL were calculated and a grand mean obtained from these 18 statistics. Range: 0.083-0.157; \bar{x} = 0.115; SD = 0.013.

The derived state is a lower, slender body. Quantification of this state was based on measurements of 79 adult specimens in 14 genera, calculated as above. Range: 0.023-0.083; \bar{x} = 0.059; SD = 0.019.

The above measurements were made only on adult fish with the exception of Taranetzella lyoderma, of which only one juvenile was available for study. However, its value, 0.065, was within the range of values of its group of genera, identified on the basis of numerous

synapomorphies.

2) Tail length. 0) tail relatively short. 1) tail elongated.

Primitively, zoarcids have a relatively short tail (measured from anal fin origin to end of hypurals; in relation to SL). Quantification was based on measurements of the same 132 specimens as character 1. Range: 0.44-0.63; \bar{x} = 0.567; SD = 0.051.

The derived state is a longer tail and quantification was based on measurements from the same 79 specimens as character 1. Range: 0.63-0.72; \bar{x} = 0.674; SD = 0.0301.

There is very poor correlation between number of vertebrae and this character, thus very little redundancy. Some forms with the primitive state of tail length (a few species of Pachycara and Lycodes) have as many or more vertebrae than some species having the derived state (Redirolycus, Plesienchelys, Ophthalmolycus, Lyconema, Taranetzella). However, the longest tails are found in Lycodonus, Andriashevia, Nalb-antichthys, Puzanovia and some Lycenchelys species, which do possess the greatest number of vertebrae in their groups. Nevertheless, tail elongation in the derived state is considered an underlying synapomorphy of these groups (Saether, 1983). In other words, a structural alteration other than simple addition of vertebrae has produced most of the long-tailed forms.

3) Head pore size. 0) small, rounded. 1) enlarged.

-1) absent.

The cephalic lateralis pores primitively are small, rounded openings. These have become enlarged in the lycenchelyine zoarcids, although Lyconema, Hadropogonichthys and a few species of Lycenchelys exhibit reversal and have secondarily reduced the size of most pores.

Large adult Lycodes usually have their pores closed over, but young stages have pores in the primitive state. Uniquely, lateralis pores never develop in the neotenic Exechodontes.

- 4) Branchiostegal membrane. 0) free of isthmus. 1) attached to isthmus, with gill slit extending to or below ventral edge of pectoral fin base. 2) attached to isthmus, with gill slit extending almost to ventral base of pectoral fin, or well above it.

Primitively, the branchiostegal membrane is free of the isthmus in zoarceoids. Although this condition may itself be derived from a plesiomorphous state of attachment, it can be treated as cladistically primitive at this level of universality (Hennig, 1966). Among zoarcids, the membrane is primitively free of the isthmus only in Lycozoarces. The free membrane in Lycodapus is considered a reversal, on the basis of the most parsimonious distribution of other apomorphic states. In most zoarcids the gill slit extends ventrally to the pectoral base or well below it. In some genera it is much restricted, extending in adults to the mid-pectoral fin base (gymnelines and mayneines), or is a small pore above the fin (nalbantichthyines).

- 5) Tubular facial papillae. 0) absent. 1) present.

Tubular facial papillae (in fresh specimens) have developed, especially anteriorly and between lateralis pores, along both jaws in Crossostomus and Dadyanos (Gosztonyi, 1977, figs. 4, 5, 7). They are absent dorsally in these two genera. Facial papillae or cirri have also developed in Oidiphorus, Hadropogonichthys, Piedrabuenia and Lyconema, but these are non-homologous and only serve as autapomorphies for each genus. The development of each is discussed under character 28.

6) Interorbital pores. 0) present. 1) absent.

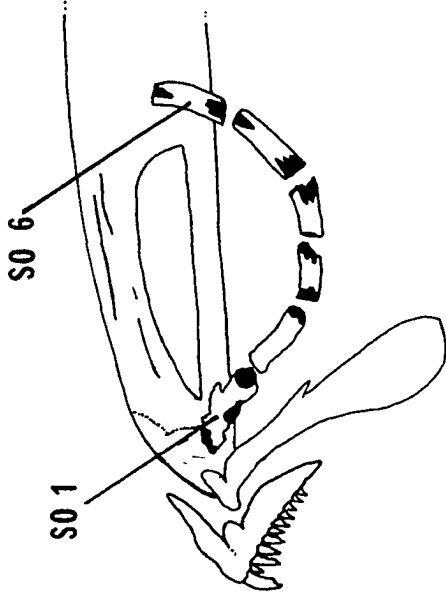
Primitively, an interorbital pore is present in zoarcids. It has been lost in the majority of genera. The interorbital pore is often doubled in some species of Lycodapus (Peden and Anderson, 1978). Within the most parsimonious scheme of relationships, it is apparent that Lycogrammoides, Lycodapus and some species of Bothrocara, Lycodes and Lycenchelys have regained the pore.

7) Suborbital bone configuration. 0) circular pattern, closely joined. 1) L-shaped pattern, separated.

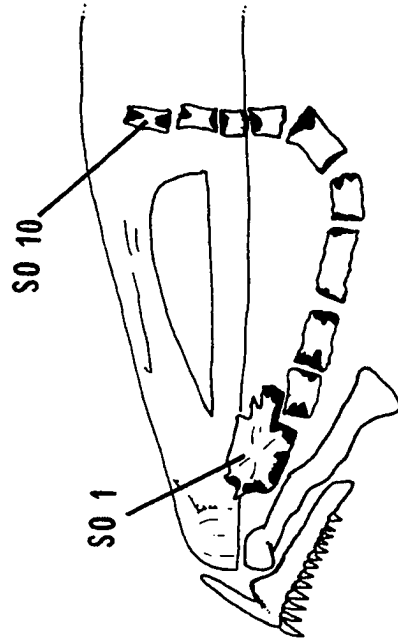
Primitively, five or six suborbital bones form a semicircle immediately below the orbit, and are large and closely spaced (fig. 3A,B). Deep-sea species of the primitive group have the ossified portion of the suborbital chain reduced, but cartilage replacement of bone in these retains the circular pattern.

In the derived condition, there are usually seven or more suborbitals and they have decreased in relative size and moved away from the orbit, forming two branches. The lower branch generally parallels the upper jaw to a point behind it, where it joins an ascending group of bones at a right angle, or nearly so (fig. 3C,D). This shape appears as a reversed "L." Some zoarcids, notably Derepodichthys, Lycodapus and Redirolycus have secondarily reduced the suborbital chain and thus appear to belong to the primitive group. However, the pattern of their pores, and/or possession of other synapomorphies, indicates their membership in the derived group. All Lycodapus have only the first (lacrimal) remaining and no suborbital pores, a condition paralleling that of the stichaeid subfamily Lumpeninae (Makushok, 1958). The number of suborbital pores associated with the bone chain is so highly

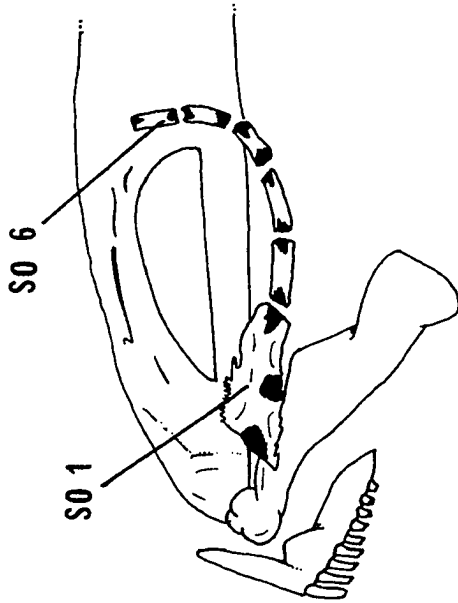
Figure 3. Suborbital bone configuration in four zoarcids. A) Zoarces gillii, 229 mm SL. B) Gymnelus viridis, 156 mm SL. C) Bothrocara tanakai, 323 mm SL. D) Lyconema barbatum, 160 mm SL. A. and B. exhibit primitive, circular pattern; C. and D. exhibit derived, or "L-shaped" pattern.



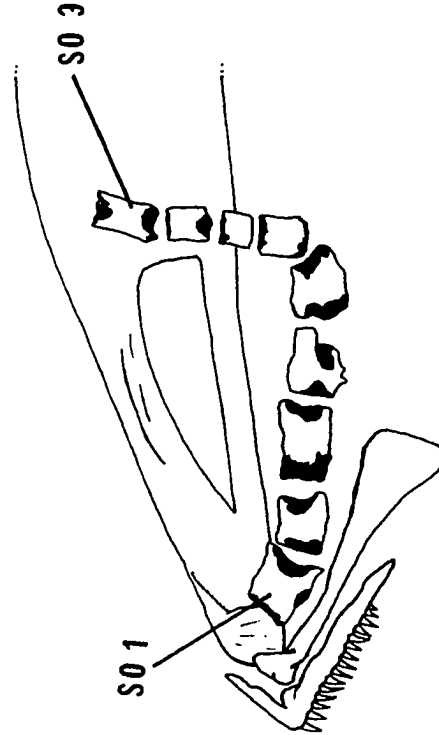
B.



D.



A.



C.

variable, even within a species, that this character has little diagnostic value. Nelson (1969) characterizes the primitive suborbital bone configuration in early teleosts and discusses fusion and loss of elements.

8) Seventh and eighth preopercular foramina. 0) foramen seven at mid-height of preopercle, eighth at dorsal margin.

Primitively, the preopercular foramina leading to pores seven and eight in the preoperculomandibular canals are low, the eighth located just above the seventh on the posterior edge. Zoarces and Macrozoarces share the derived state in which the foramina have moved dorsally (fig. 4A-C).

9) Preopercular and mandibular canals. 0) continuous 1) separated by a septum.

Primitively, the mandibular and preopercular branches of the preoperculomandibular lateralis canals are continuous, thus for simplicity, pore counts are combined for all species. In the derived state, a septum separates the branches posterior to the pore exiting the angulo-articular (pore 5).

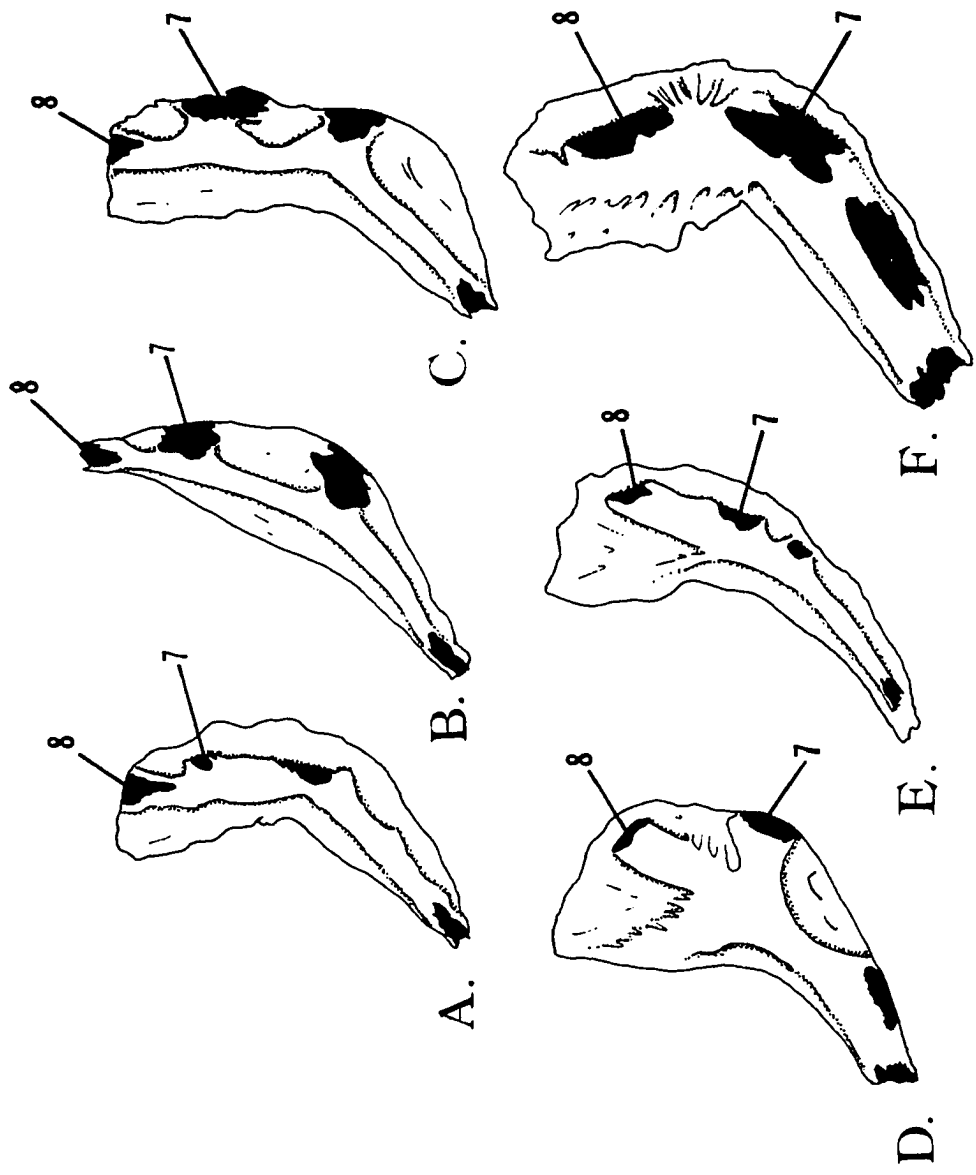
10) Male fang-like dentition. 0) absent. 1) present.

Primitively, zoarcids have small teeth set variously in rows; they are simple and sharp. Females often have more and smaller teeth than males. Males of Melanostigma, Oidiphorus, Lycogrammoides, Lycodapus and both sexes of Derepodichthys have enlarged, curved fangs anteriorly (McAllister and Rees, 1964; Schmidt, 1950; Peden and Anderson, 1978; Anderson and Hubbs, 1981).

11) Palatal arch development. 0) well developed. 1) reduced.

The plesiomorphous state of this character typifies well ossified

Figure 4. Preopercula of six zoarcids; numbers refer to foramina exiting to preoperculomandibular pores seven and eight. A) Zoarces elongatus, 242 mm SL. B) Zoarces viviparus, 193 mm SL. C) Macrozoarces americanus, 261 mm SL. D) Lycodes vahlii, 246 mm SL. E) Gymnelus viridis, 139 mm SL. F) Bothrocara brunneum, 338 mm SL. A.-C. represent derived state; D.-F. represent primitive state.



zoarcids. The ectopterygoid and endopterygoid contact more than half the anterior and dorsal edges of the quadrate (fig. 5A,B; Anderson, 1982b, fig. 4; Gosztonyi, 1977, fig. 5). The endopterygoid and ectopterygoid in the derived state are mere splints, or do not extend along half the anterior and dorsal edges of the quadrate (fig. 5C,D). Primitively, the metapterygoid is equal in size or larger than the quadrate and apomorphously the metapterygoid is smaller than the quadrate.

12) Parasphenoid wing height. 0) well developed. 1) reduced.

Primitively in zoarceoids, the parasphenoid wing is higher than the mid-height of the trigeminofacialis foramen, where it contacts the frontal and pterosphenoid bones (fig. 6A; Makushok, 1958, 1961a). The wing is apomorphously reduced in size in many genera which variously possess either depressed or "normal" neurocrania (fig. 6B), thus the derived state is independent of skull shape.

13) Frontal shape. 0) bones squared off. 1) bones tapering.

In the primitive state, the frontal bones, when viewed dorsally, form a squared-off edge just in front of the foramen leading to the first postorbital pore. The bones are narrow and their mid-orbital width always is less than 15% of the frontal length (fig. 7A,B). In the derived state the frontals taper evenly from the first postorbital foramen to their anterior tips, and the mid-orbital width is always greater than 19% of the frontal length (fig. 7C,D). The derived state was discovered in Iluocoetes, Austrolycus, Crossostomus, Dadyanos, Lycodapus, Lycogrammoides and Bothrocarina.

14) Hyomandibula posterior ramus. 0) normal. 1) elongate.

Primitively, the posterior ramus of the hyomandibula, that which

Figure 5. Palatal arch development in four zoarcids. A) Zoarces viviparus, 193 mm SL. B) Lycodichthys dearborni, 206 mm SL. C) Bothrocarina microcephala, 338 mm SL. D) Derepodichthys alepidotus, 127 mm SL. A. and B. represent primitive state; C. and D. represent derived state.

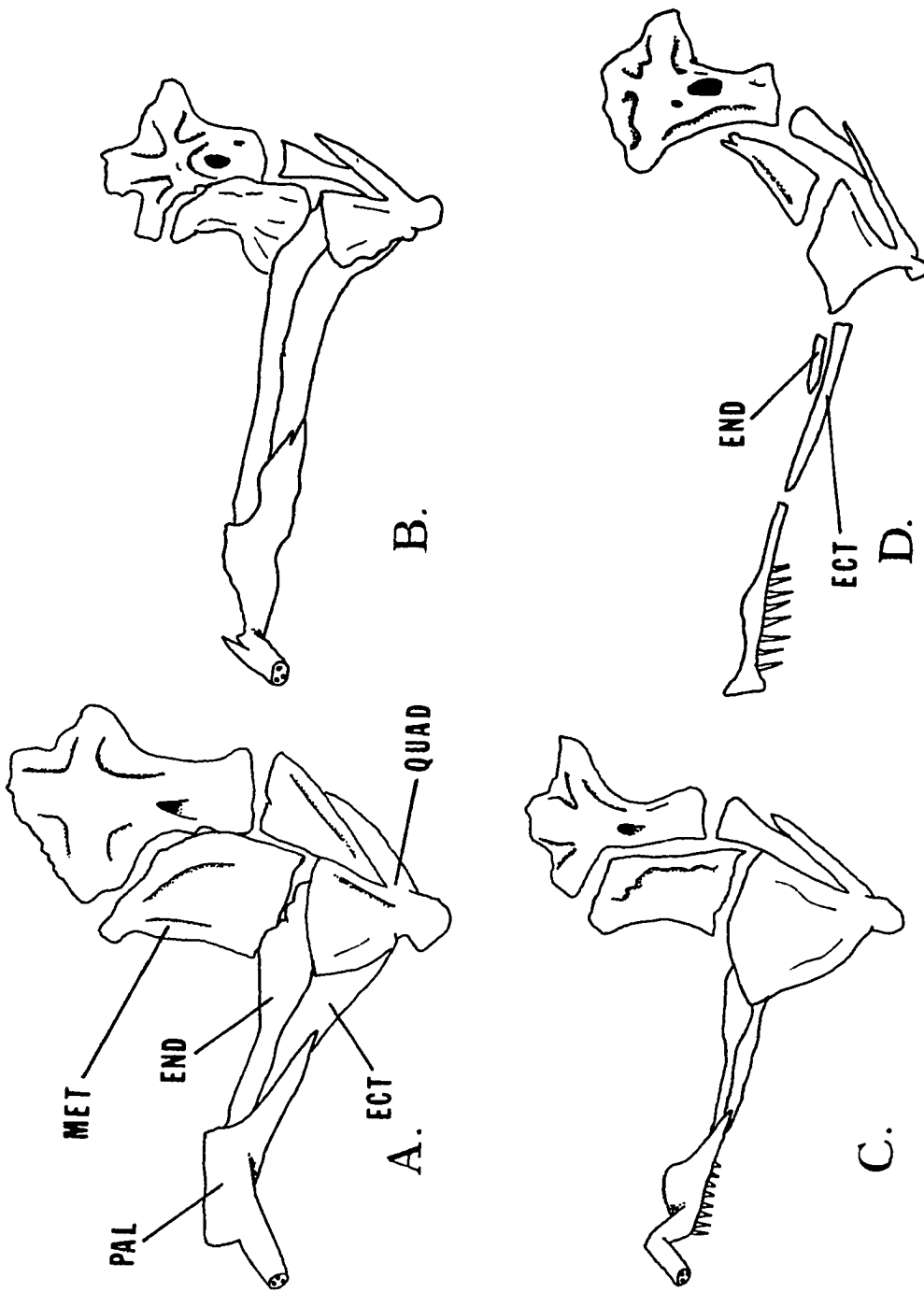


Figure 6. Neurocrania of two zoarcids exhibiting primitive and derived states of parasphenoid wing height. A) Lycodes vahlii, 346 mm SL, exhibiting primitive, high wing. B) Lycenchelys bellingshauseni, 266 mm SL, exhibiting derived, reduced wing.

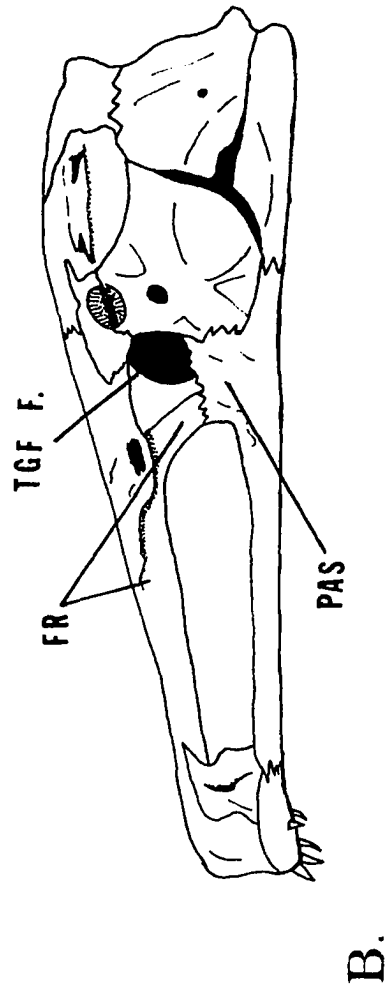
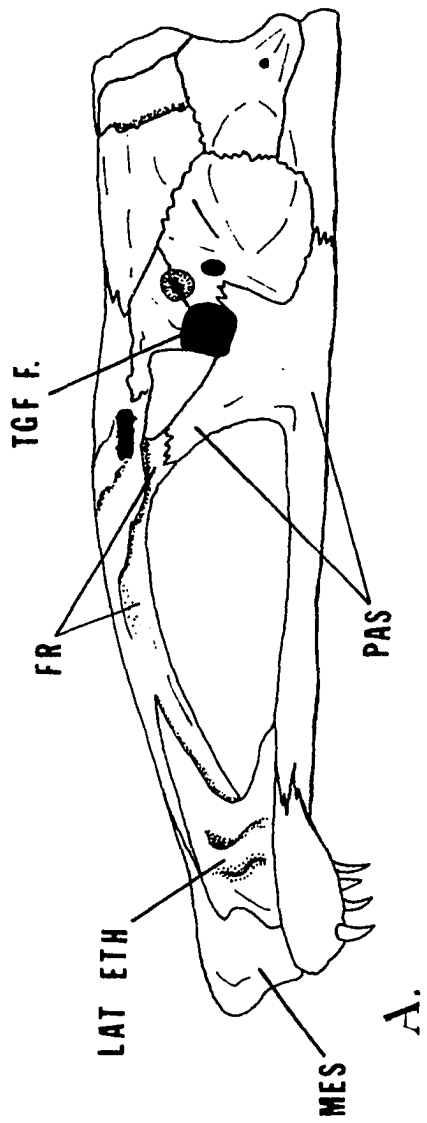
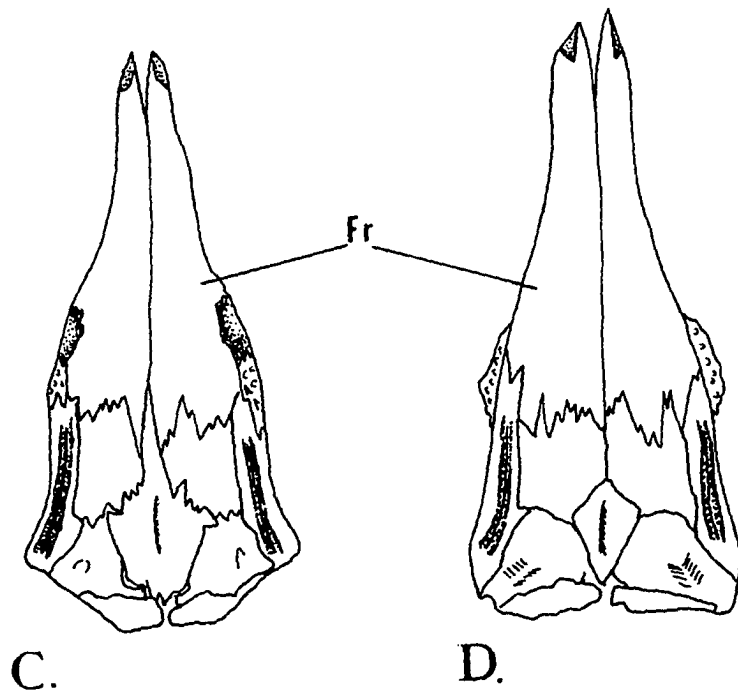
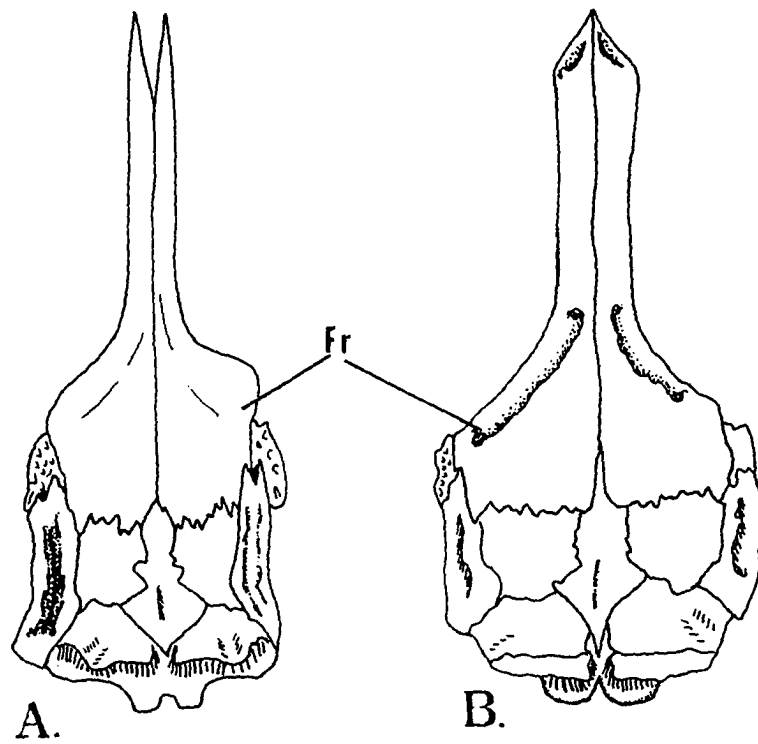


Figure 7. Dorsal views of neurocrania of four zoarcids showing primitive and derived states of frontal bone shape. A) Lycodes vahlii, 346 mm SL. B) Bothrocara pusillum, 145 mm SL. C) Crossostomus fasciatus, 118 mm SL. D) Iluocoetes effusus, 147 mm SL. A. and B. represent primitive state; C. and D. represent derived state.



articulates with the opercle, is not greatly produced and is thus "T-shaped" (fig. 8A-C). The shallow-dwelling zoarcids restricted to temperate South America all possess the character in the derived state (not examined in Pogonolycus, but assumed derived in it) (fig. 8D-F).

15) Ceratohyal-epihyal articulation. 0) smooth. 1) interdigitating.

The juncture of these two hyal bones in zoarceoids is primitively a smooth, cartilage filled space (fig. 9A-C). The shallow-dwelling genera Gymnelus, Gymnelopsis and the mayneines all have a fused, interdigitating articulation (fig. 9D-F; Anderson, 1982b, figs. 5, 15). It was not possible to examine the character in Pogonolycus, Bilabria, Krusensterniella or Hadropareia, but it is presumed to be derived in Pogonolycus and primitive in the latter three genera.

16) Scapular strut. 0) present. 1) absent.

In adult zoarcids the scapula primitively bears a posteriorly directed strut on its dorsal edge that extends to articulate with the upper two or three pectoral fin rays (fig. 10A,B; Yarberry, 1965, fig. 6; Anderson and Hubbs, 1981, fig. 8; Anderson, 1982b, fig. 7A). This strut has been lost with the rounding of the scapula in Lycodapus and Bothrocarina (fig. 10C, D), and is assumed lost also in Lycogramm-oides.

17) Number of pectoral fin rays. 0) (12) 14-24. 1) (5) 6-13.
2) 0-6.

It is hypothesized that the ancestral zoarcids had relatively well developed pectoral fins with more than about 13 rays, the state in bathymasterids. The fin has been reduced in many zoarcids and entirely lost in Andriashevia.

Figure 8. Posterior suspensorium and opercular bones of six zoarcids exhibiting primitive and derived states of hyomandibula posterior ramus. A) Gymnelus viridis, 139 mm SL. B) Lycenchelys camchatica, 145 mm SL. C) Bothrocara pusillum, 145 mm SL. D) Maynea puncta, 149 mm SL. E) Dadyanos insignis, 198 mm SL. F) Austrolycus laticinctus, 194 mm SL. A.-C. represent primitive state; D.-F. represent derived state.

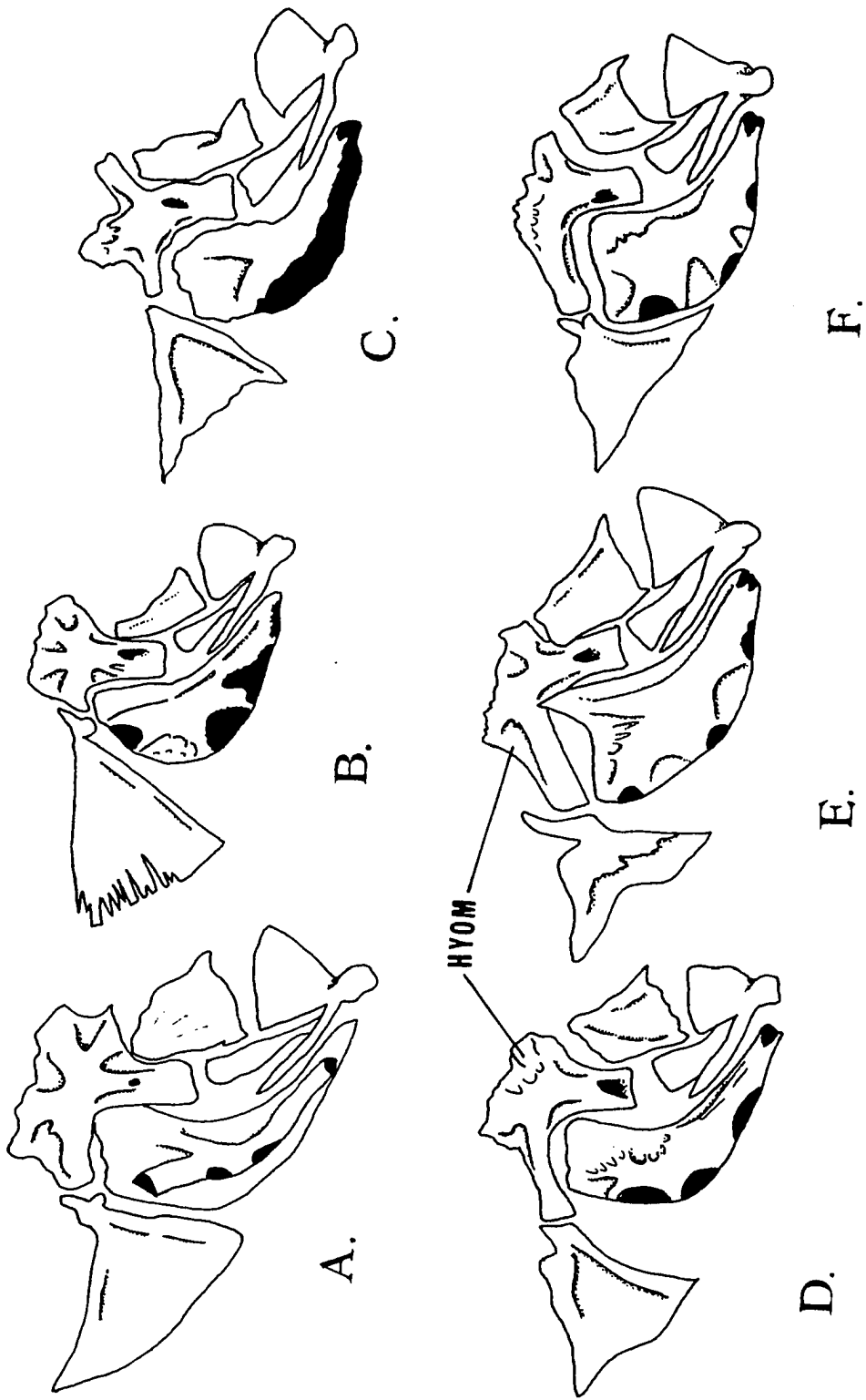


Figure 9. Left hyoid bars of six zoarcids showing primitive and derived states in ceratohyal-epihyal juncture. A) Zoarces viviparus, 193 mm SL. B) Lycodes vahlii, 346 mm SL. C) Bothrocara pusillum, 145 mm SL. D) Austrolycus depressiceps, 209 mm SL. E) Crossostomus fasciatus, 118 mm SL. F) Dadyanos insignis, 198 mm SL. A.-C. represent primitive state; D.-F. represent derived state.

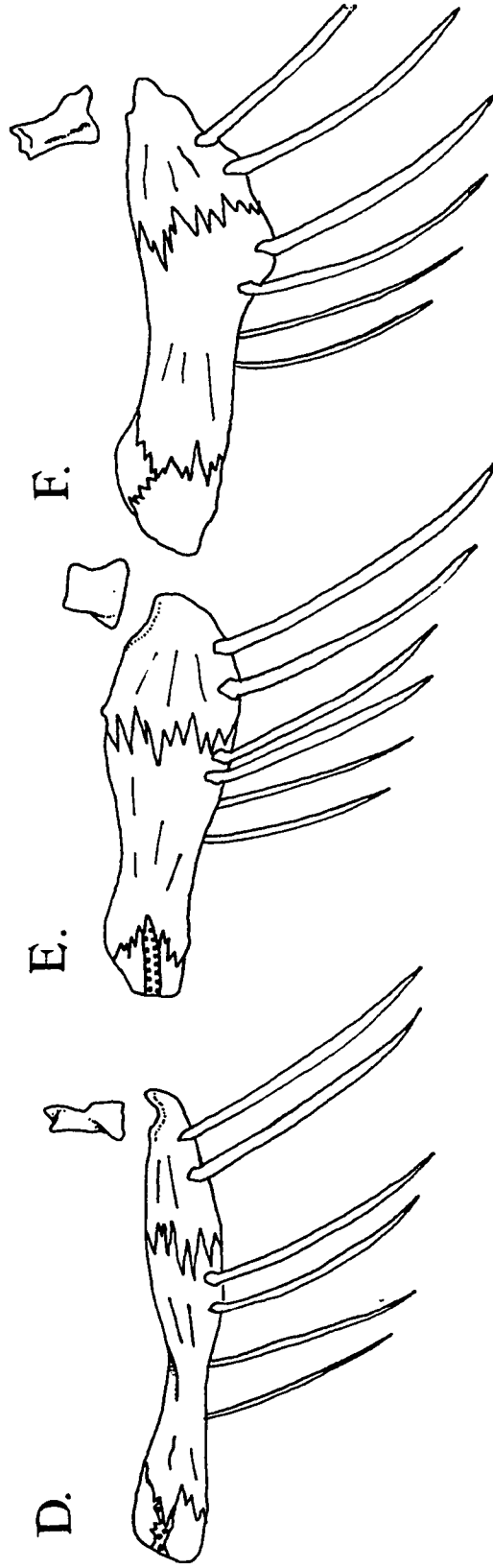
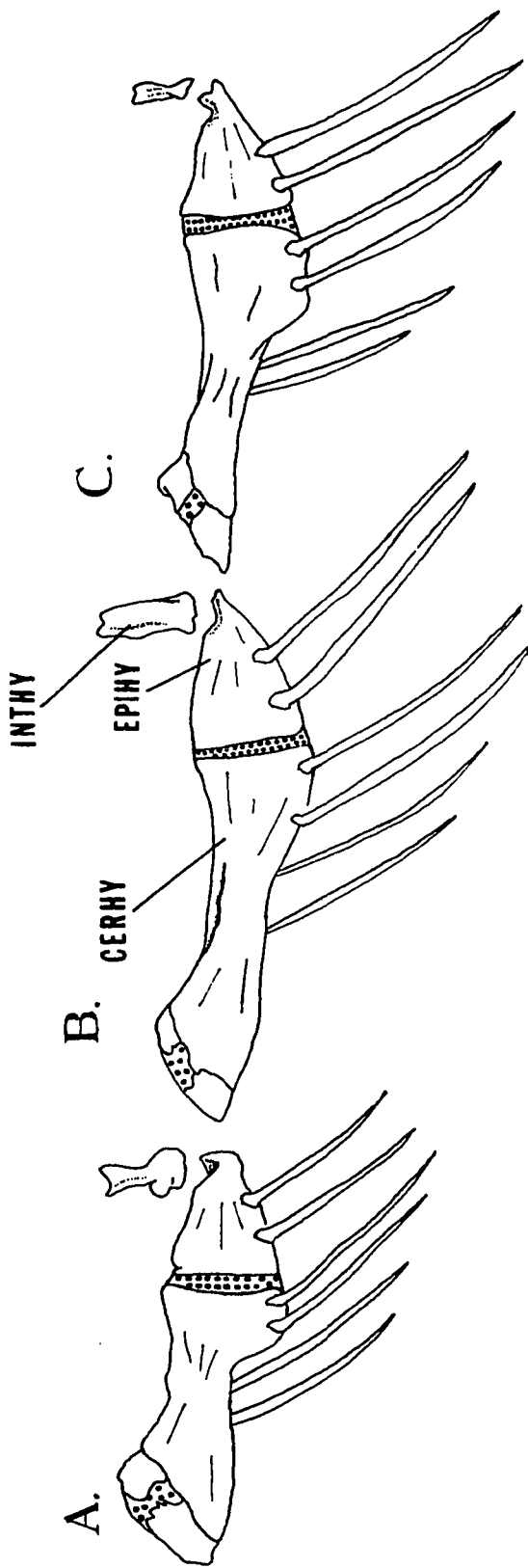
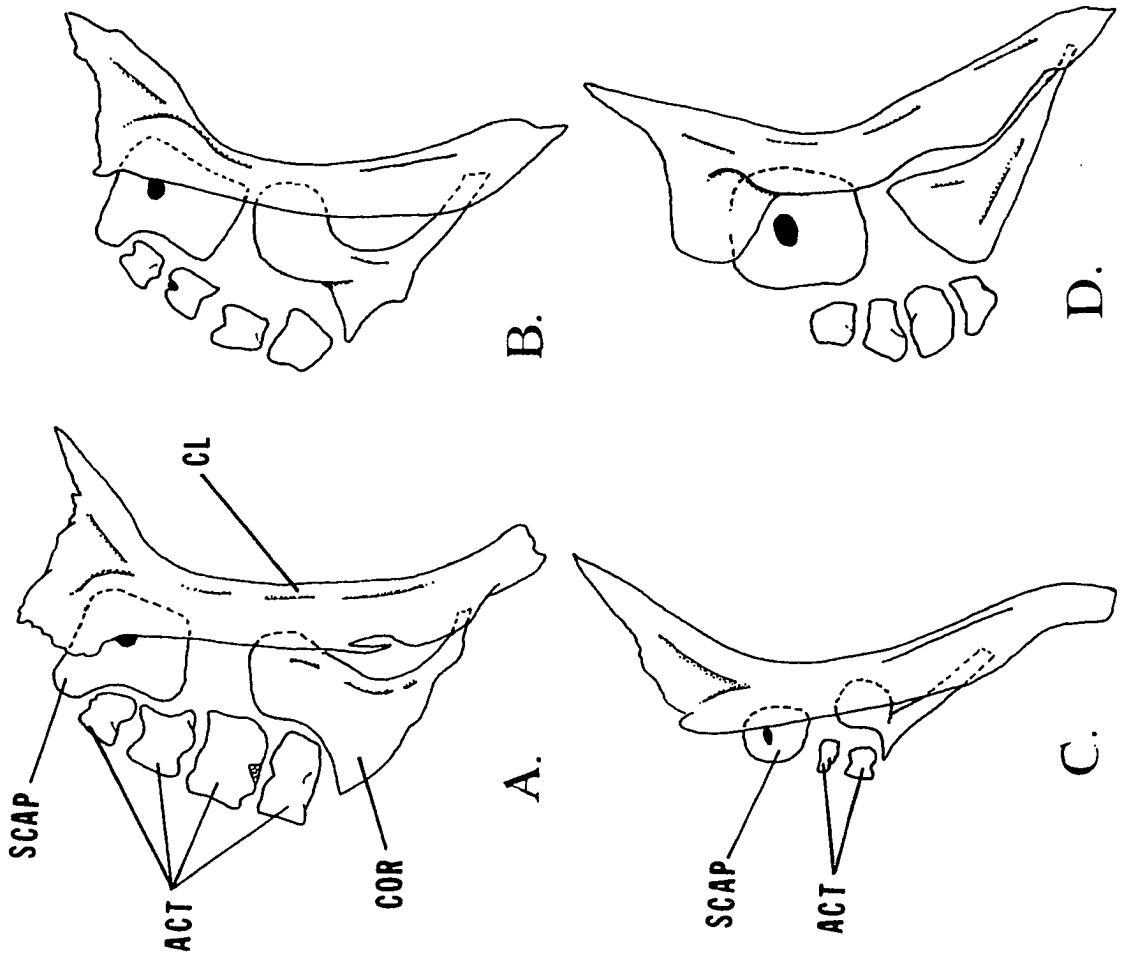


Figure 10. Right pectoral girdle of four zoarcids showing primitive and derived states in scapular shape (pelvic bones, fin rays, postcleithra and supracleithra not shown). A) Zoarces viviparus, 193 mm SL. B) Lycenchelys paxilla, 173 mm SL. C) Lycodapus fierasfer, 99 mm SL. D) Bothrocarina microcephala, 338 mm SL. A. and B. represent primitive state; C. and D. represent derived state.



- 18) Total number of vertebrae. 0) 58-71. 1) 72-104.
 3) 109-134. 4) 134-150.

Great variation and trends toward vertebral addition are seen in several zoarcid lineages. Within the most parsimonious hypothesis of relationships, a vertebral increase from 65-71 in Lycozoarces to more than 84 in all other lineages is synapomorphous. Inside secondary reductions, in the terminology of Saether (1983), occur in the gymnelines and lycodapines, with vertebral loss in Gymnelus (85-105), Gymnelopsis brevifenstrata (89-96), Melanostigma (82-100), Lycogrammoides (67 in one) and Lycodapus (73-104). Oidiphorus brevis, a relatively apomorphic lycodine, also exhibits secondary reduction in this character (vertebrae 58-64).

- 19) Dorsal fin pungent spines. 0) absent. 1) present.

The genera Krusensterniella, Macrozoarces and Zoarces have developed a short series of pungent spines in the posterior section of the dorsal fin (Andriashev, 1938; Taranets, 1937; Lindberg and Krasnyukova, 1975; Bigelow and Schroeder, 1953; Schmidt, 1917). They have apparently evolved from soft rays.

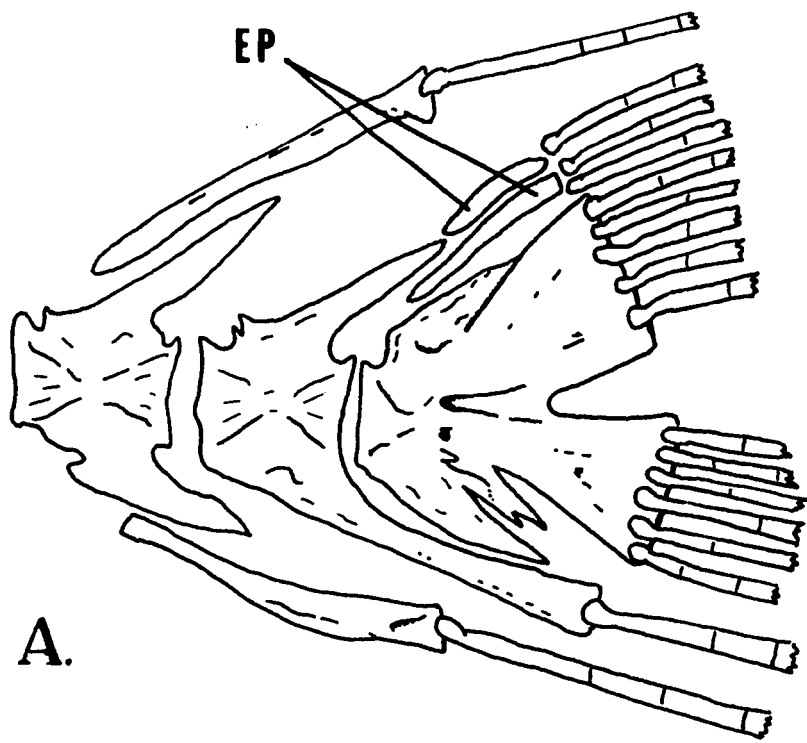
- 20) Number of epurals. 0) 2-3. 1) 0-1.

The zoarceoids primitively possess two or three epurals in the caudal skeleton. Among zoarcids, only Lycozoarces has retained the primitive condition with two epurals (fig. 11A). All other zoarcids have only one epural except Nalbantichthys (known from only two specimens), which has none (fig. 11B,C).

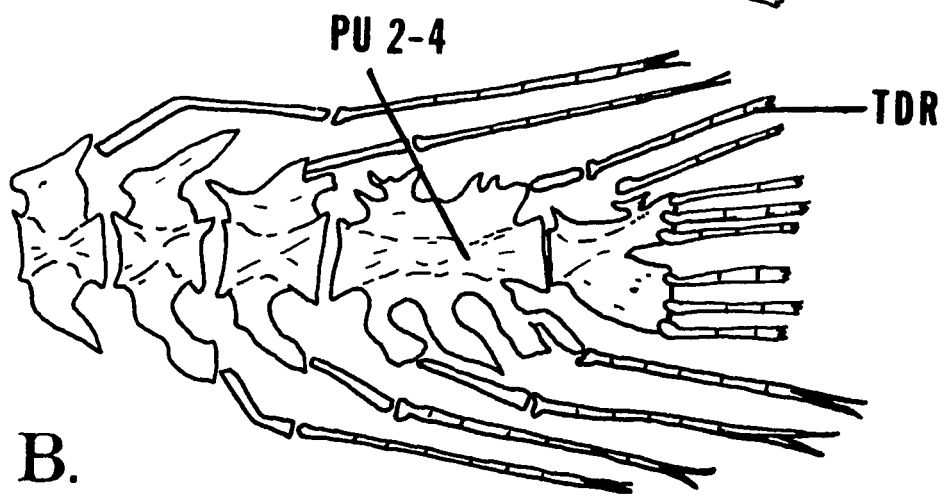
- 21) Palatine membrane. 0) present. 1) absent.

Generally, the more primitive, shallow-dwelling genera have well developed palatine membranes (oral valve). The degree of development of this feature is somewhat arbitrary. Well developed membranes reach,

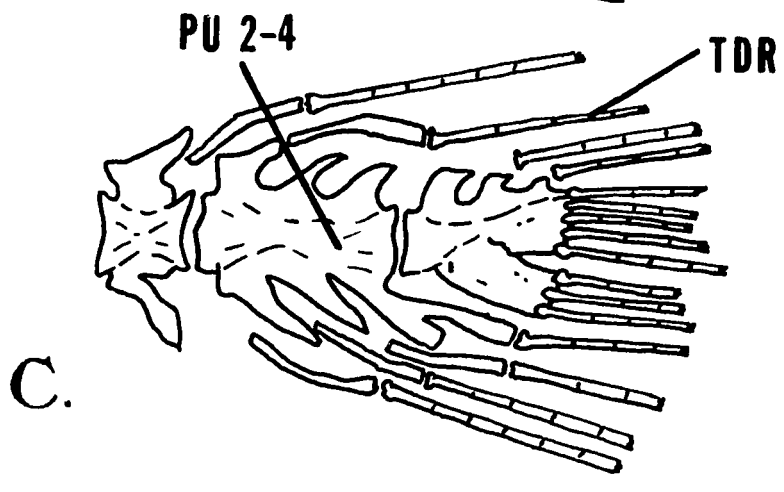
Figure 11. Caudal skeletons of two zoarcids. A) Lycozoarces regani, 152 mm SL, exhibiting primitive state with two epurals. B) Nalbantichthys elongatus, holotype, USNM 200671, 135 mm SL (from radiograph). C) Nalbantichthys elongatus, paratype, Inst. Cerc. Pisc., Bucharest, uncatalogued (from radiograph).



A.



B.



C.

or slightly overlap, the vomer and are well separated from the palate at the edges. Lycodes has a weak membrane; the anterior portion is often fused to the roof of the mouth. Bothrocara, Bothrocarina, Lycogrammoides and Lycodapus have lost the membrane.

22) Postorbital canal passage. 0) through posttemporal and supra-cleithrum. 1) through lateral extrascapulars only.

The posterior section of the postorbital lateralis canal primitively passes over the rear of the cranium into foramina located in the bases of the posttemporal and supra-cleithrum (fig. 2). In zoarcids, the derived condition exists in which the canal exits through one or two lateral extrascapulars set just anterior to the posttemporal bone, and the connection with the posttemporal and supra-cleithrum is lost (see p. 18).

23) Intercalar (opisthotic) bone. 0) present. 1) absent.

The intercalary bone has been lost repeatedly among perciforms (Gosline, 1968). It is absent in all zoarcids (fig. 2), as well as Scytalinidae and Zaproridae.

24) Squamation. 0) present. 1) absent.

Scale loss in zoarcids, as in all other fish groups, is considered apomorphic. Usually a generic character, scales are both present or absent only in Lycodes (absent in L. polaris, L. jugoricus and L. mucosus, present in all others), and in Lycenchelys (absent only in L. platyrhina).

25) Lateral line. 0) present. 1) absent.

Primitively, the body lateral line consists of free neuromasts running along the body midline, sometimes with separate dorsal and/or ventral branches. It has been lost in six deep-sea genera, all of which have gelatinous flesh (Derepodichthys, Exechodontes, Lycodapus,

Melanostigma, Nalbantichthys and Taranetzella).

26) Flesh. 0) firm. 1) gelatinous.

Nine zoarcid genera have a thick layer of lipid between the epithelium and outer body muscles (see Anderson and Hubbs, 1981, fig. 1B). This is considered derived from a firmer condition. All genera with the derived state are deep-sea fishes, yet not all deep-sea genera have gelatinous flesh. The derived condition is thought to be an adaptation for energy storage and/or increased buoyancy, found also in some cottids, liparidids, ophidiids and carapids (Cohen, 1963; Peden and Anderson, 1978; Markle et al., 1983). Genera with the derived state, in addition to the six named in character 25, include Andriashevia, Lycogrammoides and Oidiphorus.

27) Lips. 0) normal. 1) developed.

The lips are primitively well delimited from the jaws in zoarcids, with the upper free of the snout and lower attached to the dentary symphysis. Five different, non-homologous derived states exist among zoarcids and each is autapomorphous for the genus in which it occurs. The lips have deep grooves in Crossostomus; the grooves may be scalloped or smooth (Gosztonyi, 1977, fig. 5). The lips have become greatly enlarged in adult Macrozoarces (Olsen and Merriman, 1946, fig. 8). The upper lip is adnate to the snout in Bilabria (Shmidt, 1950, fig. 9). The lower lip is free of the dentary symphysis in Aiakas. Lips are absent in Andriashevia (Fedorov and Neyelov, 1978).

28) Facial papillae or cirri. 0) absent. 1) present.

As mentioned under character 5, seven zoarcid species have evolved papillae or cirri on the head, especially anteriorly and ventrally. On the jaws they occur between lateralis pores and are uniquely tubular in Crossostomus and Dadyanos. The five other zoarcids have differently

developed, non-homologous cirri or papillae. In Oidiphorus the papillae are low, triangular and present on the head and cheeks dorsally, as well as ventrally. The papillae are also triangular in Piedrabuenia, but form a double row on the lower jaw. Branched cirri occur on the jaws of Pogonolycus, and they are absent posteriorly. In Hadropogonichthys, in which the cirri reach an extreme in development, they are present posteriorly. Lyconema possesses long, simple cirri that are absent on the upper jaw. Illustrations are found in Jordan and Evermann (1896-1900, fig. 863), Norman (1937, fig. 57), Gosztanyi (1977, figs. 20, 21) and Fedorov (1982, fig. 2).

29) Chin pad. 0) absent. 1) present.

The monotypic Notolycodes possesses a coarse, thickened pad of skin at the symphysis of the lower jaw that is unique among zoarcids (Gosztanyi, 1977, fig. 13).

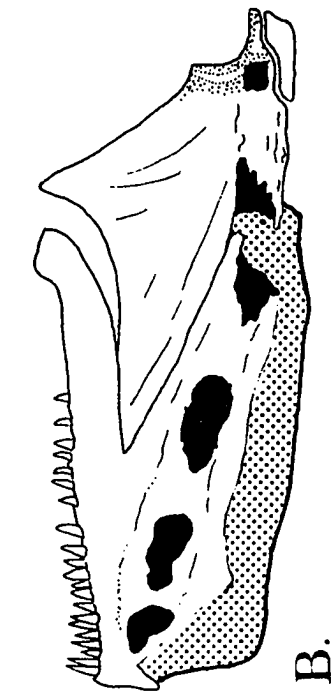
30) Mental crests. 0) absent. 1) present.

The ventral surface of the dentary in the large genus Lycodes has a broad sheath of cartilage enveloping it, producing characteristic ridges, or "mental crests" (Andriashev, 1954). Figure 12A,B shows this development on the bones; external illustrations are found in Jensen (1904), Popov (1931a), Taranets and Andriashev (1935a), Andriashev (1954, 1955b, 1959a), Matsubara (1955) and McAllister (1975). This character is autapomorphic for Lycodes.

31) Number of lateral extrascapulars. 0) two. 1) one or none.

Primitively, there are two lateral extrascapulars developed joining the postorbital and occipital (supratemporal) canals. The first lateral extrascapular usually lies above the pterotic-epioccipital juncture, and pieces of it, or the entire bone, often fuse with the skull, though it remains distinct. The second lateral extrascapular lies imbedded in

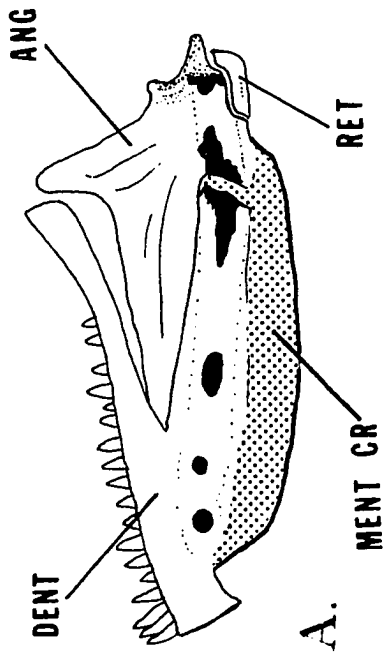
Figure 12. Left lower jaw bones of four zoarcids showing derived and primitive states of mental crest development. A) Lycodes vahlii, 346 mm SL. B) Lycodes toyamensis, 317 mm SL. C) Pachycara crassiceps, 445 mm SL. D) Ophthalmolycus concolor, 215 mm SL. A. and B. represent derived state; unique to Lycodes; C. and D. represent primitive state found in all other zoarcids.



B.



D.



A.



C.

tissue distally, just anterior to the supracleithrum; it is often lost.

- 32) Parietal commissure and occipital pores. 0) present, with one,
two or three pores. 1) absent, no pores.

The parietal commissure, opening in one medial, two lateral or both lateral and medial pores has been lost repeatedly in zoarcids. Loss of the commissure and pores does not uniquely characterize any genus, and the character has systematic significance at the species level.

- 33) Postorbital pores. 0) present. 1) absent.

Primitively, all four, or the first three postorbital pores are present in zoarcids. In some species only the first pore is present. The apomorphic loss of these pores occurs in some species of Melanostigma.

- 34) Posterior nasal pores. 0) single. 1) doubled. -1) lost.

The supraorbital canal is divided into two sections: the anterior portion opens through nasal pores, located immediately anterior and posterior to the nostrils, and the interorbital pore(s) opens between the eyes or slightly behind them. Primitively in zoarcids, both nasal pores are present and single. Apomorphously, the posterior nasal pore is lost in Melanostigma, some specimens of Plesienchelys and some species of Lycenchelys, or a doubling of it occurs in Nalbantichthys and some Lycodes.

- 35) Dentary foramina and position. 0) foramina for preoperculo-
mandibular pores 1-4 present. 1) any foramen absent, or all
replaced with shallow groove.

Primitively, there are three closely spaced anterior foramina and one posterior foramen in the dentary exiting to preoperculomandibular pores 1-4 in zoarcids (Anderson, 1982b). One or two foramina, variously placed, have been lost in Gymnelus pauciporus, Gymnelopsis, Krusensterniella, Lycodapus and occasionally Lycozoarces. A shallow, open groove

replaces the foramina in Piedrabuenia, Plesienchelys, Exechodontes and Derepodichthys, except in the latter the first pore opens from a very small foramen.

- 36) Ventralmost preopercular foramen. 0) foramen exiting to external pore. 1) foramen not exiting to external pore.

The ventralmost preopercular foramen in zoarcids generally does not open to an external pore, although primitively it does so in bathymasterids and most other zoarceoids. The occurrence of a pore at this position in Lycodapus and four species of Lycenchelys (Anderson, 1982a), is considered an evolutionary reversal. Its occasional expression in Lycenchelys antarctica is apparently atavistic.

- 37) Incisiform dentition. 0) absent. 1) present.

The monotypic Dadyanos uniquely possesses incisiform, or "blade-like" teeth (Gosztonyi, 1977, fig. 7). Both sexes have these teeth and they develop from simple, conical teeth.

- 38) Palatine teeth. 0) present. 1) absent.

Palatine teeth have been variously lost in many zoarceoids. Specimens of Gymnelus viridis, Lycodapus derjugini and Lycenchelys monstrosa, species which may normally possess palatine teeth, have been found to lack them. Because of this and the loss of teeth in some species that otherwise comprise monophyletic genera (Gymnelus, Crossostomus, Zoarces, Lycenchelys, Lycodes and Lycodapus), this character is valued at the species level in zoarcids.

- 39) Vomerine teeth. 0) present. 1) absent.

The apomorphic loss of vomerine teeth is usually correlated with palatine tooth loss and this character is treated similarly at the species level.

- 40) Frontal-parasphenoid articulation. 0) not separated by pterosphenoid. 1) separated by pterosphenoid.

Primitively, the frontals contact the parasphenoid at the posterior border of the orbit, where they are joined by the pterosphenoid. The pterosphenoid is enlarged and separates the frontals and parasphenoid in Lyconema, Exechodontes, Melanostigma, Lycodapus and Derepodichthys; the frontals and parasphenoid meet in all other zoarcids. The difficulty in using this character for phylogeny reconstruction has been the inability to observe it in many zoarcids.

- 41) Sphenotic-parietal articulation. 0) separated by frontals. 1) in contact with one another.

The sphenotics and parietals are separated from each other in most zoarcids and all zoarceoids observed to date. The apomorphic state occurs in four deep-sea zoarcid genera (Derepodichthys, Exechodontes, Lycodapus and Melanostigma) and is apparently due to the expansion of the sphenotic and retreat of the posterolateral edge of the frontals from the parietal area.

- 42) Parietal-parietal articulation. 0) separated from midline. 1) meeting in midline.

The parietals are primitively small and separated from the cranial midline in zoarceoids. They are enlarged and meet in the midline, apparently independently, in many other zoarceoids. No, or little, correlation between skull height, width or length and parietal articulation was found.

- 43) Supraoccipital blade. 0) present. 1) absent or reduced.

The supraoccipital bone has an anterior ramus, or blade, projecting under the frontals (see Anderson, 1982b, figs. 10, 11). The blade is apomorphously lost in Dadyanos and is a mere thorn-like projection in

Derepodichthys (Anderson and Hubbs, 1981, fig. 4).

- 44) Supraoccipital-exoccipital articulation. 0) broadly contacting.
1) narrowly contacting or excluded by epioccipitals.

The primitive state of this character is typified by wide, high exoccipitals broadly articulating with the supraoccipital (see Makushok, 1958; Anderson, 1982b, figs. 2, 10). The primitive state is present in zoarcids, as far as currently known, only in Lycozoarces, Gymnelus and Gymnelopsis. The state of the character was not observed due to specimen scarcity in Krusensterniella, Bilabria and Hadropareia.

- 45) Number of branchiostegal rays. 0) 6-7. 1) 4-5.

Primitively, six or seven branchiostegal rays are present in zoarcids. Ray formula presented in the generic accounts are those attached to the ceratohyal plus those on the epihyal. The formula 4 + 2 is typical of most zoarcids, except Lycodapus, which has the formula 3 + 3. Normal branchiostegal ray variation occurs within these genera: Gymnelopsis (4 + 2 or 3 + 2), Iluocoetes (4 + 2 or 3 + 2), Lycenchelys (4 + 2 or 3 + 2), Lycodonus (3 + 2 or 2 + 2) and Melanostigma (5 + 2, 4 + 2 or 3 + 2). Individuals of the following species have been found with variation in branchiostegal ray number: Gymnelus hemifasciatus (5 + 2, 4 + 2 or 3 + 2), G. pauciporus (4 + 2 or 3 + 2), G. popovi (5 + 2, 4 + 2 or 3 + 2), G. retrodorsalis (4 + 2 or 3 + 2), G. viridis (5 + 2, 4 + 2 or 3 + 2), Hadropareia middendorffi (5 + 2 or 6 + 2), ² Lycodichthys dearborni (5 + 2 or 4 + 2), Melanostigma bathium (4 + 2 or 3 + 2) and M. pammelae (5 + 2 or 4 + 2). Large series of all the above species have

²I have examined only five specimens of Hadropareia. All possessed seven rays on both sides except one which had eight on one side. This is probably an individual atavism, as no zoarceoid known has more than seven branchiostegal rays (see McAllister, 1968: 145).

been examined, except M. bathium and H. middendorffi, and probably more species will be found to exhibit individual variation of this character. Thus, the character is diagnostic for some genera or species, while not so for others.

46) Fifth ceratobranchial teeth. 0) present. 1) absent.

Primitively, the fifth ceratobranchials are toothed in zoarceoids. Apomorphous loss of these teeth in zoarcids occurs in Exechodontes, Melanostigma and Oidiphorus.

47) Pairs of infrapharyngobranchials. 0) three. 1) two.

Primitively, there are three pairs of infrapharyngobranchials in zoarceoids; all bear tooth plates. These bones are associated with gill arches two, three and four (the first infrapharyngobranchial has been lost or is cartilaginous). Zoarcids with only two pairs of infrapharyngobranchials have lost the one associated with gill arch four, and this state is correlated with the derived state of character 46 except in Derepodichthys, which has retained the ceratobranchial teeth (Anderson and Hubbs, 1981, fig. 7).

48) Number of gill rakers. 0) 12-14. 1) 15 or more. -1) 11 or fewer.

The number of gill rakers is primitively about 12-14 in zoarceoids, but a mid-range for a decision on how much loss or addition needed to show derivation in this character is somewhat arbitrary. Both addition and loss of gill rakers occurs distally on both the ceratobranchial and epibranchial.

49) Posttemporal strut. 0) well developed. 1) weak or absent.

The posttemporal bone has a ventral ramus which ligamentously connects the bone to the neurocranium. Primitively it is well developed

in zoarceoids (fig. 13). The length of this strut is variable among genera. Generally, the most weakly ossified fishes have poorly developed posttemporal struts, such as in Scytalina, neozoarcines, Ptilichthys and deep-sea zoarcids (fig. 13; Makushok, 1958, 1961a).

50) Cleithrum ramus. 0) absent. 1) present.

Primitively, the cleithrum in zoarceoids bears no elongate ramus, and the pelvic bones insert distally just slightly anteroventrally to the pectoral fin base (see Yarberry, 1965, fig. 6; Anderson, 1982b, fig. 7). Derepodichthys bears a greatly elongated, anteriorly directed ventral ramus, with the pelvic bones inserting at its end under the eye (Anderson and Hubbs, 1981, fig. 8). This condition curiously parallels that of most ophidiines.

51) Scapular foramen. 0) enclosed by bone. 1) open.

There is a large foramen passing nerves and blood vessels in the scapula of many teleosts. In zoarceoids it is primitively completely enclosed by bone (Starks, 1930; Anderson, 1982b). In zoarcids the derived condition is present only in Derepodichthys (Anderson and Hubbs, 1981, fig. 8).

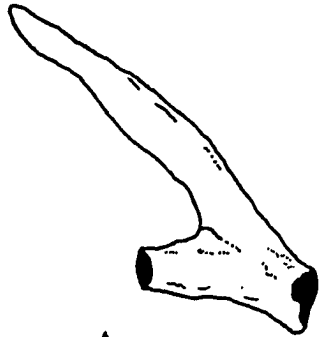
52) Number of pectoral actinosts (radials). 0) four. 1) 0-3.

Primitively, there are four pectoral actinosts in zoarceoids, as in most higher teleosts. These are reduced (not fused) to two or three in Derepodichthys, Lycodapus and most Melanostigma species. Andriashevia has lost the pectoral fin and all supporting actinosts.

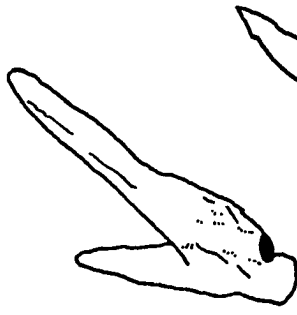
53) Number of pelvic fin rays. 0) 2-3. 1) fin absent.

Zoarcids, except Derepodichthys, have rudimentary pelvic fins. Most species that have the fins have three rays. Two rays are always present in Lyconema, Crossostomus, Ophthalmolycus bothriocephalus,

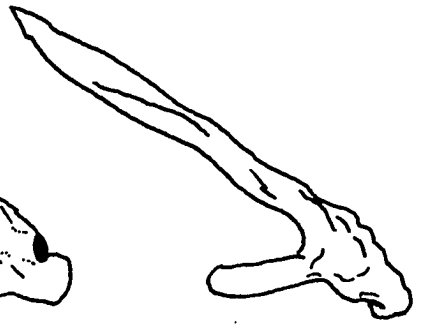
Figure 13. Left posttemporal bones of zoarceoids. A) Bathymaster signatus, 189 mm SL. B) Anoplarchus purpurescens, 136 mm SL. C) Lycodes diapterus, 234 mm SL. D) Ptilichthys goodei, (after Makushok, 1958, fig. 81). E) Scytalina cerdale, 79 mm SL. F) Pachycara obesum, 332 mm SL. A.-C. show the plesiomorphous state, with well developed ventral ramus; D.-F. show derived state, with ventral ramus reduction.



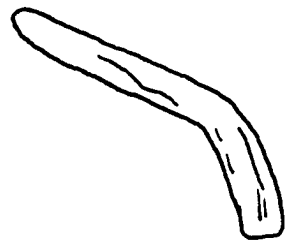
A.



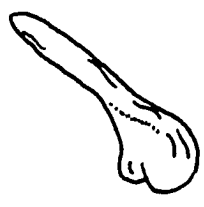
B.



C.



D.



E.



F.

Pogonolycus, Lycenchelys platyrhina and Piedrabuenia. Two or three rays are present in some species of Lycenchelys, in Exechodontes and Ophthalmolycus macrops. The fin is present or absent in these genera: Austrolycichthys, Crossostomus, Lycenchelys, Lycodichthys and Pachycara. The widespread reduction of this already rudimentary feature has resulted in many unnatural species assemblages to be accorded generic rank, whereas the absence of pelvic fins is diagnostic at the species level only. Pelvic fins are always absent in 17 genera, eight of which are monotypic.

54) Number of precaudal vertebrae. 0) less than 19. 1) 19-33.

This character, like total number of vertebrae, seems to correlate with increasing trunk length. Total number of vertebrae seems to reflect relationships better and number of precaudal vertebrae is considered redundant in that regard. However, it is valuable in diagnosing most genera.

55) Dorsal fin origin. 0) associated with vertebrae 1 or 2.

1) associated with vertebrae 3-17.

In some genera (Gymnelus, Gymnelopsis, Lycodes, Lycodonus and Lycenchelys) there is a continuum of vertebrae up to 17, with which the dorsal fin originates (Anderson, 1982b). In other genera it is constant, thus the derived state may diagnose some genera or species, but not others.

56) Free dorsal fin pterygiophores. 0) 0-2. 1) 3-14.

In most zoarcids there are no, or rarely 1-2, free dorsal fin pterygiophores (Anderson, 1982b). The number of free pterygiophores in the derived state is individually variable and diagnostic in some species of Gymnelus, Gymnelopsis, Lycenchelys and Lycodonus.

57) Dorsal and anal fin scutes. 0) absent. 1) present.

The genus Lycodonus is partly defined by the development of broadened bases of the dorsal and anal fin pterygiophores (fig. 14). This autapomorphy seems to give support to the fins in these very elongated fishes.

58) Number of epural caudal fin rays. 0) three. 1) 1-2.

Loss of caudal fin rays associated with the epurals is apomorphic in zoarceoids. Two or three rays are found in Lycozoarces and one to three in Gymnelus. In all other zoarcids there are one or two rays, but the degree of individual variation in the character could not be studied with the present rarity of most species.

59) Total caudal fin rays. 0) 13-15. 1) 9-12. 2) less than 9.

Lycozoarces is partly diagnosed by its high caudal fin ray count, the highest and most primitive in the family. Most zoarcids have 9-12 rays, with a few specimens of Lycodes possessing 13. Sharp reduction is seen in many genera whether they are deep-sea or shallow-dwelling forms.

60) Pyloric caeca development. 0) nubs. 1) elongate.

-1) absent.

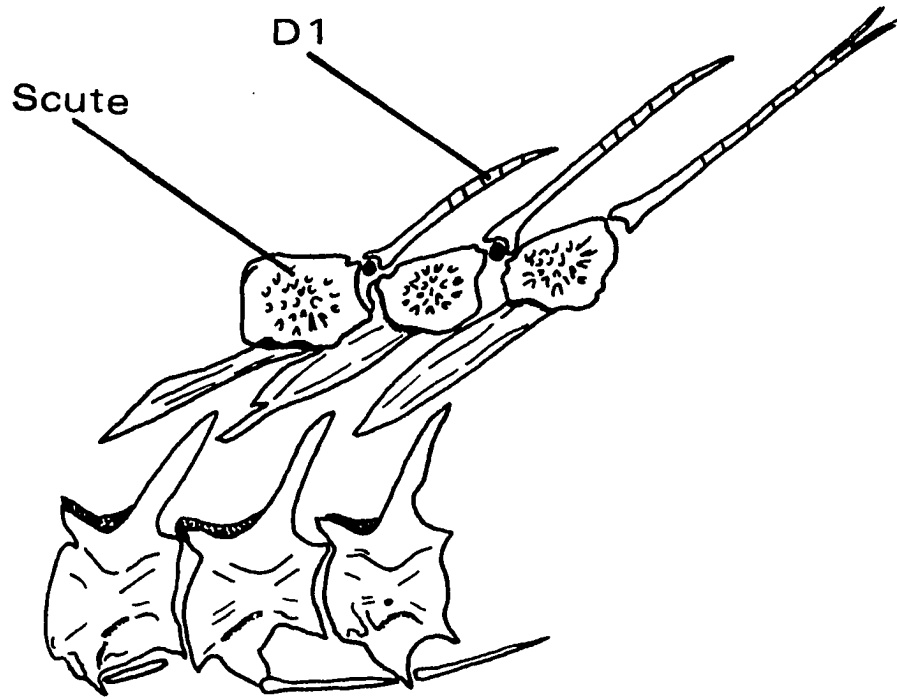
The rudimentary pyloric caeca of zoarcids are primitively small nubbins set on either side of the entrance to the intestine. Apomorphically they are lengthened, becoming finger-like, in Krusensterniella multispinosa, Ophthalmolycus concolor, O. bothriocephalus, Aiakas, Lycogrammoides and Bothrocarina. Pyloric caeca are always absent in Iluocoetes fimbriatus, Nalbantichthys and Hadropogonichthys.

61) Peritoneum color. 0) light. 1) black.

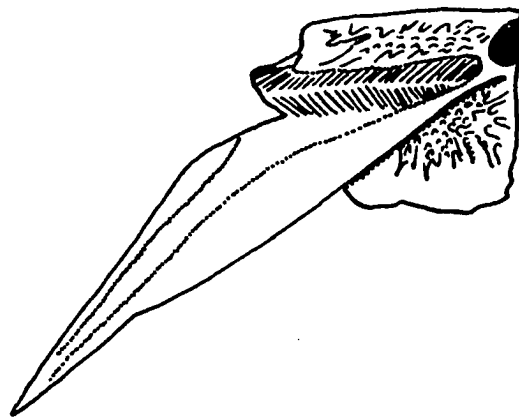
The peritoneum is primitively light or dusky in shade in zoarceoids.

Figure 14. Dorsal fin elements of Lycodonus mirabilis, 278 mm SL.

A) Vertebrae 15-17, pterygiophores showing dorsal scutes and first three dorsal fin rays. B) Posteroventral 2/3 view of a dorsal fin pterygiophore.



A.



B.

As part of a general trend in deep-sea fishes, many zoarcids have also evolved black peritonea in diverse lineages, presumably preventing luminescent prey from shining through the body wall (McAllister, 1961).

62) Number of pseudobranchial filaments. 0) 5-13. 1) 0-4.

Primitively, zoarcids possess about five or more feathery pseudo-branchial filaments. A trend toward reduction in the number of filaments is seen among deep-sea genera, which represent diverse lineages. Thus, the character is diagnostic for some genera or species, but not so for others.

63) Reproductive mode. 0) oviparous. 1) viviparous.

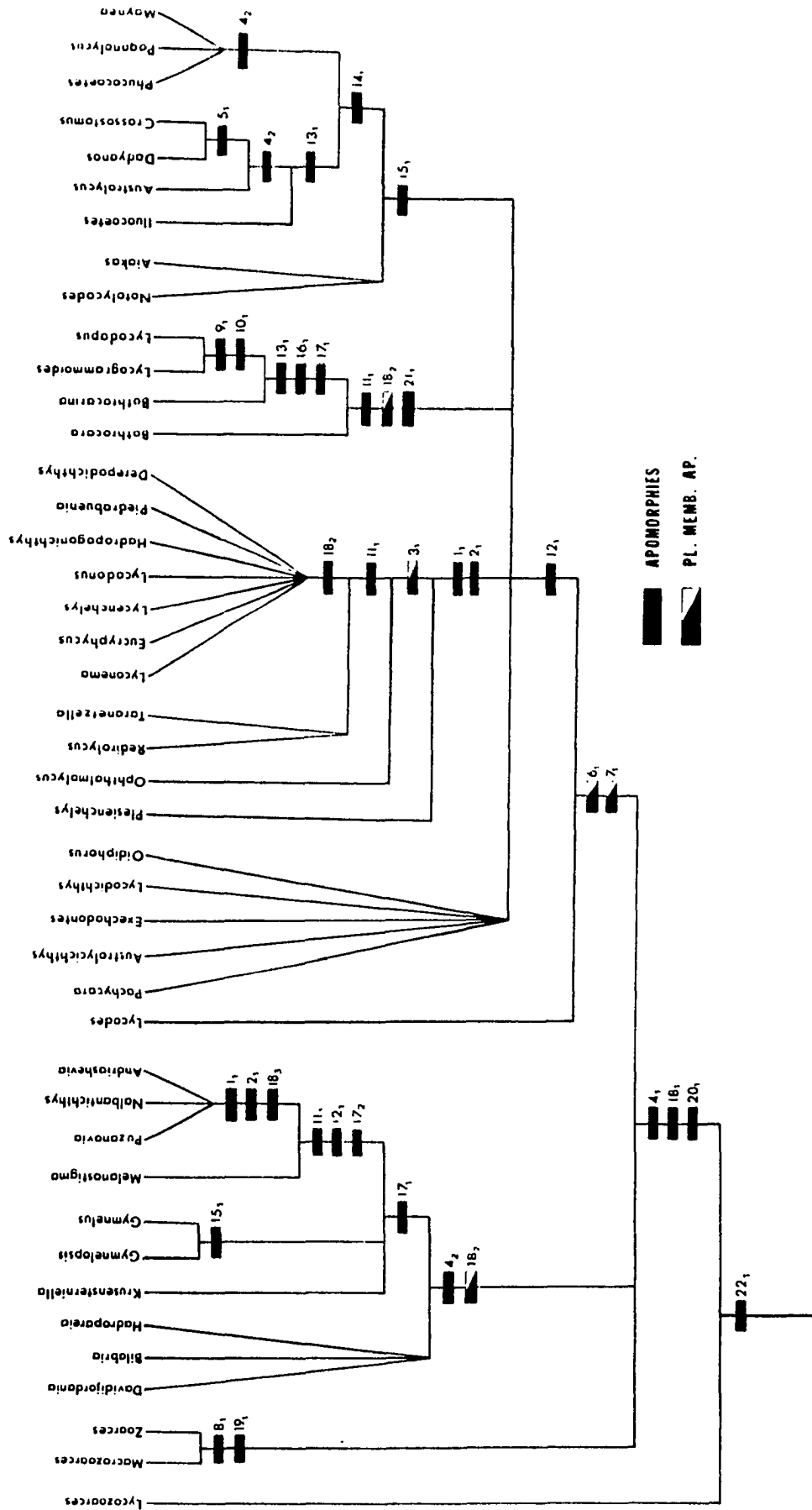
Viviparity has developed only once in zoarceoids--in Zoarces. This, then is autapomorphic for the genus.

Phylogeny of Zoarcidae

Cladistic analysis of the zoarcid character matrix presented in the previous section provided relevant information for constructing hypotheses of relationship among these fishes. The following discussion details the synapomorphies that distinguish each clade within each of the recognized subfamilies and tribes. Subsequently, homoplasies requiring assumptions of the most parsimonious model of relationships are discussed.

The most parsimonious phylogenetic hypothesis is presented in figure 15. The discussion of each clade within subfamilies and tribes is ordered left to right from figure 15. As shown earlier (figs. 1, 2), the zoarcids are distinguished from all other zoarceoids by the apomorphic loss of the postorbital canal passage through the posttemporal and supracleithrum (character 22).

Figure 15. Cladogram illustrating hypothesized relationships of zoarcid genera. One type of trend (characters 3, 6, 7 and 18) satisfies the criteria of Saether (1983) as secondary reductions, or reversals, in some apomorphic taxa. Abbreviation: pl. memb. ap. = plesiomorphic members have the apomorphous character state. Footnoted numbers refer to character number in text; footnote is its state.



Lycozoarcinae

The monotypic Lycozoarces possesses no derived characters within the analyzed zoarcid anatomical systems. As its phylogenetic position cannot be determined on the basis of character states it lacks, it is hypothesized to be the primitive sister group of all other zoarcids. To place Lycozoarces anywhere else would require three character reversals (see below; fig. 15).

Zoarcinae clade

Three important derived characters define all zoarcids except Lycozoarces. These are the attachment of the branchiostegal membrane to the isthmus (character 4), an increase in the number of vertebrae (character 18) and loss of one or more epurals (character 20). A basal, unresolved node divides the Zoarcinae into three groups, herein designated tribes Zoarcini, Gymnelini and Lycodini.

Zoarcini clade

Zoarces and Macrozoarces are structurally very similar and only the unique development of viviparity in Zoarces and enlarged lips in Macrozoarces caused recognition of these forms at the generic level. They share two derived characters: the elevation of the preopercular foramina of pores seven and eight (character 8) and possession of pungent spines in the dorsal fin (character 19). Dorsal fin pungent spines are also possessed by Krusensterniella (four species). However, to hypothesize this one character as synapomorphous for Zoarces, Macrozoarces and Krusensterniella requires the assumption of parallelism in branchiostegal membrane restriction (character 4) and pectoral fin ray reduction (character 17) in Krusensterniella and other Gymnelini.

Gymnelini clade

Davidijordania through Andriashevia clade

The 10 genera of Gymnelini possess two synapomorphies. First is a further fusion of the branchiostegal membrane to the isthmus producing a reduced gill slit (character 4), a parallelism with six genera of Lycodini and some of the mayneines. Secondly, there is further increase in the number of vertebrae (character 18), with inside secondary reduction occurring in Gymnelus, Melanostigma and one species of Gymnelopsis. No apomorphies were found among the characters used here in Davidijordania, Bilabria and Hadropareia, primarily because they are so imperfectly known.

Krusensterniella through Andriashevia clade

The seven genera of this clade share one derived character, the reduction of the pectoral fin (character 17).

Gymnelopsis-Gymnelus clade

These two genera possess one synapomorphy, the interdigitating ceratohyal-epihyal juncture (character 15), a parallelism shared with the mayneines.

Melanostigma through Andriashevia clade

The deep-sea fishes of these four genera share three derived characters: 1) the reduction of the bones of the palatal arch (character 11), a parallelism shared with the lycodapines and most of the lycenchelyines; 2) the reduction in size of the parasphenoid wing (character 12), a parallelism shared with most Lycodini; 3) reduction of the pectoral fin (character 17) further. The pectoral fin and supporting actinosts have been lost autapomorphously in Andriashevia.

Puzanovia through Andriashevia clade

These three, poorly known monotypic genera, the nalbantichthyines, possess three synapomorphies: 1) the body is slender (character 1); 2) the tail is elongated (character 2) (both these are parallelisms shared with the lycenchelyines); 3) there is further increase in the number of vertebrae (character 18) to the highest values in the family (to 150 in Nalbantichthys).

Lycodini clade

All the remaining zoarcids share two synapomorphies: loss of the interorbital pore (character 6) and possession of the L-shaped suborbital bone pattern (character 7). A few reversals of these states are postulated; these are discussed below in the clades in which they occur. Lycodes lacks other synapomorphies of this clade and is hypothesized to be the primitive sister group of all other lycodines. An hypothesis otherwise requires a reversal of parasphenoid wing height (character 12). A few species of Lycodes exhibit reversal in character 6 and have redeveloped the interorbital pore.

Pachycara through Maynea clade

The 29 genera of this clade share one derived feature, the reduced parasphenoid wing (character 12). Zoarcids of this clade include both deep-sea and littoral forms. This multiple branching node includes five genera that have no synapomorphies within the clade and are hypothesized to be the primitive sister group (Pachycara, Austrolycichthys, Exechodontes, Lycodichthys and Oidiphorus), and three furcations that do possess synapomorphies (fig. 15).

Plesienchelys through Derepodichthys clade

The 11 genera of this clade share two derived characters: the thinning of the body (character 1) and elongation of the tail (character

1) and elongation of the tail (character 2). These are the lycenchelyine zoarcids.

Ophthalmolycus through Derepodichthys clade

All the zoarcids of this clade possess one synapomorphy, the enlargement of the cephalic lateralis pores, especially the suborbitals and preoperculomandibulars (character 3). Inside secondary reductions in pore size are hypothesized to have occurred in Lyconema, Hadropogonichthys and a few species of Lycenchelys.

Redirolycus through Derepodichthys clade

This trifurcating node contains those nine lycenchelyines with reduced palatal arches (character 11), a parallelism shared with four genera of Gymnelini. Redirolycus (southern hemisphere) and Taranetzella (northern hemisphere) share no additional derived characters. Both Redirolycus and Derepodichthys exhibit inside secondary reduction in character 7 in losing the suborbital bones of the ascending ramus.

Lyconema through Derepodichthys clade

The seven genera of this clade, five of them monotypic, are characterized by autapomorphies and share only one derived character, an increase in the number of vertebrae to a higher state (character 18), a parallelism shared with Gymnelini and the lycodapines. A few species of Lycenchelys exhibit reversal in character 6 and have redeveloped the interorbital pore. These are some of the upper slope dwelling species; the deep living Lycenchelys species have reduced the lateralis pore systems (Andriashev, 1955, 1958; Anderson, 1982a).

Bothrocara through Lycodapus clade

The four genera of this clade, the lycodapines, possess three synapomorphies: 1) the reduction of the palatal arch (character 11),

a parallelism shared with some of the Gymnelini and most lycenchelyines; 2) increase in the number of vertebrae to a higher state (character 18), also a parallelism shared with Gymnelini and some lycenchelyines; 3) loss of the palatine membrane (character 21). Lycogrammoides, Lycodapus and a few species of Bothrocarina exhibit reversal in character 6 and have redeveloped the interorbital pore. Lycodapus exhibits inside secondary reduction in character 7 in losing all but the first suborbital bone (lacrimal). Lycodapus also exhibits reversal in character 4 in having the branchiostegal membrane free of the isthmus.

Bothrocarina through Lycodapus clade

The three genera of this clade possess three synapomorphies: 1) wide, tapering frontal bones (character 13), a parallelism shared with four mayneine genera; 2) absence of the posterior scapular strut (character 16) and reduction in the number of pectoral fin rays (character 17), a parallelism shared with most Gymnelini.

Lycogrammoides-Lycodapus clade

These two deep-sea genera possess two synapomorphies: the mandibular and preopercular canals are separated by a septum (character 9) and males exhibit canine teeth (character 10), a parallelism shared with Oidiphorus and Melanostigma.

Notolycodes through Maynea clade

The twelve species of this clade, the mayneines, possess one synapomorphy, the interdigitating ceratohyal-epihyal juncture (character 15), a parallelism shared with Gymnelus and Gymnelopsis. The trifurcating node includes the very imperfectly known Notolycodes and Aiakas, which share no other uniquely derived features.

Iluocoetes through Maynea clade

The seven shallow-dwelling genera of this clade possess one synapomorphy, the elongation of the posterior ramus of the hyomandibula (character 14).

Iluocoetes through Crossostomus clade

These three genera possess one synapomorphy, the broadened, tapering frontal bones (character 13), a parallelism shared with most of the lycodapines.

Austrolycus through Crossostomus clade

The zoarcids of this clade possess one synapomorphy, the further fusion of the branchiostegal membrane to the isthmus producing a restricted gill slit (character 4), a parallelism shared with three other mayneines and Gymnelini.

Dadyanos-Crossostomus clade

The three species of this clade possess uniquely evolved, tubular papillae between lateralis pores on both jaws (character 5).

Phucocoetes-Maynea clade

These three monotypic genera possess branchiostegal membranes producing a restricted gill slit (character 4), a parallelism shared with other mayneines and Gymnelini. Although these are relatively apomorphic fishes, no other synapomorphies were found relating these three genera.

Reduction in the number of vertebrae in Oidiphorus, Lycogrammoides and Lycodapus is perhaps explained by the concept of pleomerism, the widespread tendency for maximum body size to be correlated with vertebral number (Lindsey, 1975). These three genera are dwarfed compared to their hypothesized nearest sister groups. For example, Bothrocara

and Bothrocarina, reaching up to about 450 mm, have 113-132 vertebrae, whereas the dwarves Lycodapus and Lycogrammoides, reaching about 220 mm, have 67-104 vertebrae. The same seems to be true of the diminutive Oidiphorus (to 110 mm; 58-64 vertebrae). Its nearest sister genera, Pachycara, Austrolycichthys, Exechodontes, and Lycodichthys have 92-122 vertebrae and all are larger (300-500 mm), except Exechodontes (115 mm) which does not exhibit pleomerism. The small adult size, along with gelatinous flesh and, in Lycogrammoides and Lycodapus, lack of body pigment, are hypothesized to have evolved paedomorphically. This is a process that produces a descendant with adult morphology similar to the juvenile morphology of an ancestor (see Gould, 1977).

The apparent evolutionary reversal of regaining the interorbital pore in Lycogrammoides, Lycodapus and some species of Bothrocarina, Lycenchelys and Lycodes, and reduction in size of the pores of Lycinema, Hadropogonichthys and some species of Lycenchelys is more difficult to explain. Perhaps this relates to shifting areas for different kinds of sensory reception.

The detachment of the branchiostegal membrane from the isthmus in Lycodapus, also an apparent reversal, is also difficult to explain. Lycodapus is a deep-pelagic genus (Peden and Anderson, 1978, 1981; Anderson, 1981) most, if not all, species of which seem to occupy oxygen minimum layers. Perhaps the detached membrane is an adaptation for more efficient respiration and/or feeding mechanics.

The foregoing analysis reveals that most derived states found in Zoarcidae have been evolved convergently, and well expressed synapomorphy is infrequent. The rarity of synapomorphy was seen by Eldridge

and Cracraft (1980) as a common feature of adaptive radiation: "There should be a high percentage of species marked with a number of autapomorphies, with synapomorphies among subgroups of species less common." Carroll (1982) stated that adaptive radiation, "...by its very nature is based on differences in structure, physiology and behavior..." and if "...each (group) has evolved separately from a single, distinct adaptive pattern...specializations will have evolved separately in each advanced group and will obviously have had no effect on or relationship to those evolving in other groups." These statements characterize zoarcid subgroups, in that de novo apomorphies have arisen throughout the family, such as the non-homologous development of the lips and facial papillae in several lineages, viviparity in Zoarces, loss of pectoral fins in Andriashevia, mental crests in Lycodes, dorsal and anal fin scutes in Lycodonus, branchiostegal rays 3 + 3 in Lycodapus, the pectoral-pelvic girdle of Derepodichthys, to name a few.

Zoarcidae (Cuvier, 1829)

Type genus: Zoarces Cuvier, 1829, by subsequent designation of Gill (1893).

Remarks. Decisions on the proper family group name for the eelpouts have been various, especially in the older literature. Confusion stems from placing eelpouts with fishes having spineless fins, reduced, thoracic pelvics and six branchiostegal rays. The earliest known eelpouts were often placed in different suprafamilial groups or broadly expanded polyphyletic families, e.g., ophidioids (Reinhardt, 1838; Yarrell, 1841, 1859; Müller, 1846; Kaup, 1856), gobioids (Richardson, 1836, 1855;

Reinhardt, 1838; DeKay, 1842; Storer, 1846; Carpenter and Westwood, 1863; Yarrell, 1886), anguilloids (DeKay, 1842; Fitzinger, 1873), or blennioids (Linnaeus, 1758; Schneider, 1801; Cuvier, 1829; Müller, 1846; Owen, 1846; Günther, 1861; Gill, 1862; Cope, 1873). A full literature synonymy of Zoarcidae is given in Bayliff (1954) and is not repeated here.

Norman (1966) and Gosline (1968) pointed out that the first Latinized generic name for an eelpout was Zoarcaeus Nilsson, 1832, based on the vernacular "Les Zoarcés" of Cuvier (1829). These two names applied only to Blennius viviparus Linnaeus, 1758. Despite the fact that Zoarcaeus and Zoarces are junior objective synonyms of Enchelyopus Gronovius, 1760, in the interests of nomenclatural stability, I follow Cohen and Russo's (1979) argument in considering Gronovius' (1760) names as unavailable for the purposes of zoological nomenclature. Cuvier's "Zoarcés" is based on a Greek word meaning "life-supporting," or "live bearing," spelled zōarkēs, or zōarchēs, in the Roman alphabet. Nilsson (1832) and Swainson (1839), in attempting to recognize this spelling, seem to have "hardened" their suffices, namely -caeus and -chus, respectively. Thus Gosline (1968) proposed Zoarceoidae as the correct spelling for Nilsson's generic name and Swainson proposed Zoarchidae for his. Gill (1893) gave the spelling Zoarcidae for Cuvier's vernacular and pointed out that Lycodidae Günther, 1862, was a junior synonym. Gill may have proposed Zoarcidae after consultation with D. S. Jordan, as Jordan and Gilbert (1883) gave the family name Zoarcidae in their key (p. 79), yet listed all species in Lycodidae in their family accounts. Lycodidae has rarely appeared in faunal works since 1893, thus according to Article 11 (e) (iii) of

the International Code of Zoological Nomenclature, XV Congress, Zoarcidae (Cuvier, 1829) should be considered the correct family group name, as Zoarceoidae and Zoarchidae are based on subsequent improper generic emendations.

Diagnosis. Of the eight zoarceoid families recognized in this study, Zoarcidae is diagnosed by only one apomorphous character state not shared with another group: the loss of passage of the posterior section of the postorbital canal through the posttemporal and supracleithrum (character 22).

Description. The following summary description is provided for the benefit of the reader attempting to identify unknown specimens as possibly belonging to Zoarcidae. Some characters much discussed in the literature are only briefly mentioned. For exceptions to general characters and more elaboration, the reader is referred to the appropriate generic accounts.

Body and tail elongate (generally eel-shaped), laterally compressed, tapering posteriorly. Head ovoid or dorsoventrally flattened. Dorsal and anal fins confluent with caudal fin. Dorsal and anal fin pterygiophores in 1:1 relationship with successive vertebral centra. Dorsal fin usually with no spines anteriorly (first and/or second elements sometimes "flexible spines"), except in Krusensterniella. Pungent spines in posterior section of dorsal fin only in Krusensterniella, Macrozoarces and Zoarces. Anal fin with no spines. Pelvic fin rays 2-3 or absent; inserted under gill slit or eye (Derepodichthys). Gill slit united to isthmus except in Lycodapus and Lycozoarces, or is a small pore above pectoral fin base (Melanostigma, Andriashevia and Nalbant-

ichthys). Scales cycloid, minute, generally not contacting one another, or absent. Nostrils single. Septal bones, orbitosphenoid, basisphenoid and intercalar (opisthotic) absent. Lateral line of free lateralis organs (Springer and Freihofer, 1976; Peden and Anderson, 1978), or absent. Preoperculomandibular canal not connected to postorbital canal. Premaxilla with ascending and articular processes, toothed in all species; maxilla without teeth. No supramaxilla. Branchiostegal rays 4-7. Gill arches four, with slit behind last; 2-3 pairs infrapharyngo-branchials, associated with arches 2-4 (that associated with arch four lost in Exechodontes, Oidiphorus, Melanostigma and Derepodichthys); unciniate processes on epibranchials 3, 4. First three basibranchials ossified, fourth cartilaginous, with no tooth patches. Pectoral actinosts usually four (2-4 in Melanostigma, 2-3 in Lycodapus, absent in Andriashevia). Vertebrae amphicoelus, constriction shifted anteriorly in shallow dwelling genera or species. Pleural ribs originating on vertebrae 1-3, usually extending to ultimate or penultimate precaudal vertebra; epipleural ribs originating on vertebrae 1-3, extending posteriorly variously. Caudal skeleton much reduced, with one epural (two in Lycozoarces), with 1-2 rays attached (2-3 rays in Lycozoarces). Gas bladder absent. Ovary single-lobed; only one genus viviparous (Zoarces), males without elongate intromittent organ. Pyloric caeca usually two small nubs, sometimes both absent or both elongated. Pseudobranchs usually present (absent in some specimens of some species of Lycodapus, Exechodontes, Lycenchelys and Pachycara).

Artificial Key to Genera of Adult and Late Juvenile Zoarcidae.

- 1A. Branchiostegal membrane free of isthmus, at least posteriorly.....2
- 1B. Branchiostegal membrane attached to isthmus, gill slit either
a small pore above pectoral fin or extending ventrally well below
pectoral fin base.....3
- 2A. Suborbital pores present; flesh firm; C 13-15.....Lycozoarces Popov
- 2B. Suborbital pores absent; flesh gelatinous (fresh specimens only);
C 10.....Lycodapus Gilbert
- 3A. Mental crests present, prominent (character 30).....
.....Lycodes Reinhardt
- 3B. Mental crests absent.....4
- 4A. Scales absent.....5
- 4B. Scales present (except in Lycenchelys platyrhina).....12
- 5A. Pelvic fins present.....6
- 5B. Pelvic fins absent.....8
- 6A. Pelvic fins long, inserted under eye on common, erectile base;
teeth fang-like.....Derepodichthys Gilbert
- 6B. Pelvic fins normal, inserted slightly in advance of gill slit;
teeth small.....7
- 7A. No cephalic lateralis pores; known only from off Cuba and Florida..
.....Exechodontes DeWitt
- 7B. Cephalic lateralis pores present; known only from Okhotsk Sea.....
.....Hadropareia Schmidt
- 8A. Gill slit a small pore above pectoral fin.....9
- 8B. Gill slit broader, extending to opposite second pectoral fin ray or
ventral edge of pectoral base.....11
- 9A. Pectoral fin absent.....Andriashevia Fedorov and Neyelov
- 9B. Pectoral fin present.....10
- 10A. Vomerine and palantine teeth present; one pair of nasal pores;
lower pharyngeal teeth absent; vertebrae 82-100.....
.....Melanostigma Günther

- 10B. Vomerine and palatine teeth absent; three pairs of nasal pores; lower pharyngeal teeth present; vertebrae 144-150.....Nalbantichthys Schultz
- 11A. Head, above eyes, on cheeks and jaws, with low tuberculate papillae; vertebrae 58-64; outer shelf, upper slope of temperate South America.....Oidiphorus McAllister and Rees
- 11B. No papillae on head, vertebrae 85-105; high Arctic and boreal seas.....Gymnelus Reinhardt
- 12A. Papillae or cirri present around jaws.....13
- 12B. Papillae or cirri absent.....18
- 13A. Cirri simple, long, in two rows restricted to lower jaw; coasts of Oregon to Baja California.....Lyconema Gilbert
- 13B. Papillae or cirri on both jaws.....14
- 14A. Six branchiostegal rays.....15
- 14B. Five branchiostegal rays.....17
- 15A. Lips with deep grooves; papillae long, simple, tubular anteriorly; teeth simple; nostril extending beyond upper lip margin.....Crossostomus Lahille
- 15B. Lips without grooves.....16
- 16A. Papillae short, tubular anteriorly, never branched; teeth incisiform (character 37); vertebrae 107-116.....Dadyanos Whitley
- 16B. Papillae fringed, especially anteriorly; teeth small, simple; vertebrae 132-134.....Hadropogonichthys Fedorov
- 17A. Cirri on both jaws and lips fringed; vertebrae 91-93.....Pogonolycus Norman
- 17B. Papillae on both jaws simple, tuberculate; vertebrae 120-126.....Piedrabuenia Gosztanyi
- 18A. Lower lip continuous (no adnate section at symphysis); nostrils elongate, extending over upper lip; pyloric caeca greatly enlarged, finger-like.....Aiakas Gosztanyi
- 18B. Lower lip adnate at symphysis.....19
- 19A. Upper lip adnate at symphysis; Okhotsk Sea.....Bilabria Shmidt
- 19B. Upper lip continuous at symphysis.....20

- 20A. Dorsal fin with short series of pungent spines in posterior section.....21
- 20B. Dorsal fin without pungent spines.....23
- 21A. Vomerine and palatine teeth present; gill slit restricted, extending ventrally to mid-pectoral base; pelvic fins absent; P 11-12.....Krusensterniella Schmidt
- 21B. Vomerine and palatine teeth absent; gill slit extending below ventral edge of pectoral fin base; pelvic fins present; P 16-21..22
- 22A. Vertebrae 129-146; gill rakers on lower limb of first arch 12-14; lips in largest adults enormous; oviparous; eastern coast of North America.....Macrozoarces Gill
- 22B. Vertebrae 101-132; gill rakers on lower limb of first arch 9-12; lips normal; vivparous; seas of northern Europe and the Okhotsk, Japan and East China seas.....Zoarces Cuvier
- 23A. Scales restricted to posterior section of tail, or, if present on body to nape, with a large black blotch on pale pectoral fin....24
- 23B. Scales cover entire body, never a black blotch on pectoral fin..26
- 24A. Pelvic fin present; flesh gelatinous; anterior lateralis pores enlarged, surrounded by loose skin.....Taranetzella Andriashev
- 24B. Pelvic fin absent; flesh firm; anterior lateralis pores small....25
- 25A. Vomerine teeth absent; gill slit extending to pectoral fin base or just above it; vertebrae 134-147; C 9.....Puzanovia Fedorov
- 25B. Vomerine teeth present; gill slit extending to mid-pectoral base or above it; vertebrae 89-115; C 5-8.....Gymnelopsis Soldatov
- 26A. Gill slit restricted, usually extending ventrally only to mid-pectoral base, occasionally almost to its lower margin.....27
- 26B. Gill slit normal to broad, extending ventrally to at least lower margin of pectoral base or well anteroventrally to it.....32
- 27A. Vomerine and palatine teeth absent; vertebrae 90-93; suborbital bones 5.....Lycodichthys Pappenheim
- 27B. Vomerine and palatine teeth present; vertebrae 93-128; suborbital bones (5) 6-7.....28
- 28A. Pelvic fins present.....29
- 28B. Pelvic fins absent.....31
- 29A. Total gill rakers on first arch 14-18; head greatly depressed.....

-Austrolycus Regan
- 29B. Total gill rakers on first arch 10-11; head normal.....30
- 30A. Cephalic lateralis pores enlarged; pelvic fin rays 2; seas of Antarctica.....Ophthalmolycus bothriocephalus (Pappenheim)
- 30B. Cephalic lateralis pores small; pelvic fin rays 3; littoral areas of temperate South America.....Phucocoetes Jenyns
- 31A. Branchiostegal rays 5; total gill rakers 13-14; vertebrae 119-128; suborbital bones 8.....Maynea Cunningham
- 31B. Branchiostegal rays 6; total gill rakers 8-10; vertebrae 93-99; suborbital bones 4.....Redirolycus microphthalmus (Norman)
- 32A. Body height at anal fin origin low, 2.3-8.3% SL (all species have anterior suborbital pores paralleling upper jaw)(character 7)....33
- 32B. Body height at anal fin origin high, 7.4-15.7% SL (specimens with values below 8.3% have closely spaced suborbital pores forming a circle around eye).....35
- 33A. Dorsal and anal fin bases with enlarged scutes (character 57).....Lycodonus Goode and Bean
- 33B. Dorsal and anal fin bases without scutes.....34
- 34A. (Triplet) Vertebrae 102-144; suborbital and anterior preoperculo-mandibular pores enlarged, or if small, flesh around pores flaccid; endopterygoid and ectopterygoid weakly overlapping quadrate (character 11).....Lycenchelys Gill
- 34B. Vertebrae 94-104; suborbital and anterior preoperculo-mandibular pores enlarged; endopterygoid and ectopterygoid broadly overlapping quadrate (character 11).....Ophthalmolycus Regan (macrops, concolor)
- 34C. Vertebrae 86-93; suborbital and anterior preoperculo-mandibular pores small, flesh firm; endopterygoid and ectopterygoid broadly overlapping quadrate (restricted to upper slope waters of temperate South America).....Plesienchelys gen. nov.
- 35A. Suborbital pores closely spaced, forming a circle around eye (character 7); pelvic fins present; precaudal vertebrae 20-23; Okhotsk and Japan seas.....Davidijordania Popov
- 35B. Suborbital pores moderately separated from one another, not circling eye, but more or less paralleling upper jaw anteriorly (character 7).....36

- 36A. Chin pad present (character 29); scales covering nape of interorbital region and cheeks, becoming ovoid; pelvic fins one eye diameter in length.....Notolycodes Gosztonyi
- 36B. Chin pad absent; no scales at interorbital region or on cheeks; pelvic fins, when present, much smaller than one eye diameter...37
- 37A. Precaudal vertebrae 14-24 (25).....38
- 37B. Precaudal vertebrae (25) 26-32.....42
- 38A. Palatine membrane absent.....39
- 38B. Palatine membrane present.....41
- 39A. Pectoral fin rays 13-17; pseudobranchial filaments 6-8; suborbital bones 7-9.....Bothrocarina Bean
- 39B. Pectoral fin rays 9-11; pseudobranchial filaments 10; suborbital bones 6.....40
- 40A. No scales on nape; head length 19-20% SL; interorbital pore present; mandibular and preopercular canals separated by septum; gill rakers 11-12; P 9; C 8.....Lycogrammoides Soldatov and Lindberg
- 40B. Scales present on nape; head length 14-15% SL; interorbital pore absent; mandibular and preopercular canals connected; gill rakers about 15; P 10-11; C 11.....Bothrocarina Suvorov
- 41A. Peritoneum pale; pseudobranchial filaments 6-7; total vertebrae 82-99; littoral and outer shelf regions of temperate South America.....Iluocoetes Jenyns
- 41B. Peritoneum black; pseudobranchial filaments 2-3; total vertebrae 92-110; not present in temperate South America.....Austrolycichthys Regan
- 42A. Supratemporal commissure and occipital pore(s) present.....43
- 42B. Supratemporal commissure and occipital pores absent; suborbital pores 6-7; gill rakers 11-19; C 10-12; worldwide at lower slope and abyssal depths.....Pachycara Zugmayer
- 43A. One (median) occipital pore; suborbital pores 5-6; gill rakers 9; C 7; southwestern Atlantic slope.....Rediolyucus sp. A
- 43B. Three occipital pores; suborbital pores 7-8; gill rakers 14-15; C 10; coast of California.....Eucryphycus gen. nov.

Generic Accounts

A diagnosis and brief, mostly osteological, description for each of the 43 recognized genera is given below. Synonymies include only those works pertaining to the composition and/or nomenclature of the genus. Those works giving descriptions, illustrations or other important contributions are given at the end of each account. The scheme of presentation is phylogenetic and follows the classification (p. 20).

Subfamily Lycozoarcinae Schmidt, 1950

Diagnosis. Branchiostegal membrane entirely free of isthmus; two epurals; C 13-15; vertebrae 15-17 + 50-55 = 65-71; suborbital bones 5-6, forming a circle around eye; P 13-15; pelvic fins long, equal to one eye diameter in length or longer; parasphenoid wing extending well above mid-height of trigeminofacialis foramen; interorbital pore present; palatal arch well developed; three pair of infrapharyngo-branchials.

Lycozoarces Popov, 1933

(fig. 11A)

Lycozoarces Popov, 1933: 151, fig. 5 (type species: Lycozoarces regani, by monotypy); Popov, 1935: 303, fig. 1; Schmidt, 1950: 109, pl. X, fig. 2; Toyoshima, 1981a: 296-300, figs. 1, 2; Anderson, 1982b: 19-25.

Remarks. Two nominal species were recognized in this genus, L. regani and L. hubbsi, until Toyoshima (1981a) redescribed the genus and showed that L. hubbsi was based only on males and is thus a junior synonym of L. regani. Anderson (1982b) compared the osteology of Lycozoarces to some of the Gymnelini and this is expanded here.

Diagnosis. As for subfamily.

Description. Scales absent. Flesh firm. Lateral line complete, mediolateral. Body relatively short; tail short, robust.

Neurocranium truncated, deep. Parasphenoid wing extending above mid-height of trigeminofacialis foramen; frontal and parasphenoid not separated by pterosphenoid. Sphenotic separated from parietal by frontal. Parietals separated from dorsal mid-line. Supraoccipital and exoccipital broadly contacting posteriorly.

Cephalic lateralis pore system complete; pores small and rounded. Two lateral extrascapulars present. All four postorbital pores present. Two nasal pores. One interorbital pore. Three occipital pores. Six or seven suborbital pores exiting from five or six tubular suborbital bones. Eight preoperculomandibular pores (pore three absent in two specimens; this may be anomalous). Mandibular and preopercular branches joined.

Teeth simple, those in outer row on upper jaw largest, conical. Teeth present on vomer and palatine bones. Endopterygoid and ectopterygoid broadly contacting quadrate. Posterior ramus of hyomandibula normal. Branchiostegal rays 4 + 2. Ceratohyal-epihyal juncture smooth. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2-3 + 11-12 = 13-15.

Posttemporal ventral ramus well developed. Scapular foramen enclosed; scapula with well developed posterior strut. Four actinosts bearing 13-15 pectoral fin rays. Pelvic fins long, with three fin rays.

Epipleural ribs extending from second to ultimate precaudal vertebra. Dorsal fin origin associated with first or second vertebra, or with one pterygiophore anterior to first vertebra. Dorsal fin very high anteriorly in males; rays longer than posteriormost. Fringed

cirri developed on tips of anteriormost dorsal rays in largest males. Dorsal rays low, all of equal length in females (Toyoshima, 1981a, fig. 1). No cirri in females. Dorsal fin elements 64-69, first two flexible spines. Zero to two anal pterygiophores anterior to haemal spine of first caudal vertebra. Two epurals with 2-3 caudal rays, hypurals with 10-12 rays, thus total caudal rays 13-15 in my material (fig. 11A). Both Schmidt (1950) and Toyoshima (1981a) reported one specimen each with 11 caudal rays. I re-examined Schmidt's material and his count is incorrect--he apparently counted epural rays as dorsal rays; Toyoshima seems to have done the same. Last dorsal ray associated with fourth preural vertebra; last anal ray associated with second preural vertebra.

Palatal membrane well developed, overlapping anterior edge of vomer. Pseudobranchial filaments 9-13. Two nub-like pyloric caeca. Peritoneum pale. Reproductive mode unknown, probably oviparous. Vertebrae asymmetrical.

Distribution and species. Lycozoarces regani Popov, 1933 is known from only 11 specimens taken on the outer shelf of the Okhotsk Sea between 70 and 200 m.

Additional references. Taranets (1937: 166); Matsubara (1955: 283); Lindberg (1974: 205, fig. 793); Lindberg and Krasnyukova (1975: 124, fig. 102).

Subfamily Zoarcinae Gill, 1862

Diagnosis. Branchiostegal membrane attached to isthmus, except in Lycodapus; one epural; C 5-13.

Tribe Zoarcini (Gill, 1862)

Diagnosis. Preopercular foramen leading to pore 7 above mid-height of preopercle, foramen leading to pore 8 at top of preopercle (character 8); posterior portion of dorsal fin with short series of pungent spines; five suborbital bones, forming circle around eye.

Macrozoarces Gill, 1864

(fig. 16)

Macrozoarces Gill, 1864: 256 (type species: Blennius anguillaris Peck, 1804 = Blennius americanus Schneider, 1801; by original designation); Olsen and Merriman, 1946: 47-48.

Diagnosis. A very large eelpout, with 16-24 pungent spines in posterior portion of dorsal fin; oviparous; upper lip in large adults becoming greatly enlarged; vertebrae 25-28 + 103-118 = 129-146; scales and pelvic fins present.

Description. Scales present, complete. Flesh firm. Lateral line mediolateral, complete. Upper jaw longer in males than in females. Upper lip in largest adults of both sexes greatly expanded, thicker at symphysis (Olsen and Merriman, 1946, fig. 8).

Neurocranium deep. Parasphenoid wing above mid-height of trigeminofacialis foramen. Frontal and parasphenoid wings articulate anteriorly, not separated by pterosphenoid. Sphenotic separated from parietal by frontals. Parietals separated from dorsal midline. Supraoccipital and exoccipital narrowly contacting.

Cephalic lateralis pores minute, system complete. Two lateral extrascapulars present; all four postorbital pores usually present (one or two closed over in some of the largest fish); two nasal pores; one interorbital pore; three occipital pores; six or seven suborbital pores;

five or six suborbital bones present forming closely spaced circle around eye; eight preoperculo-mandibular pores; preopercular and mandibular branches joined.

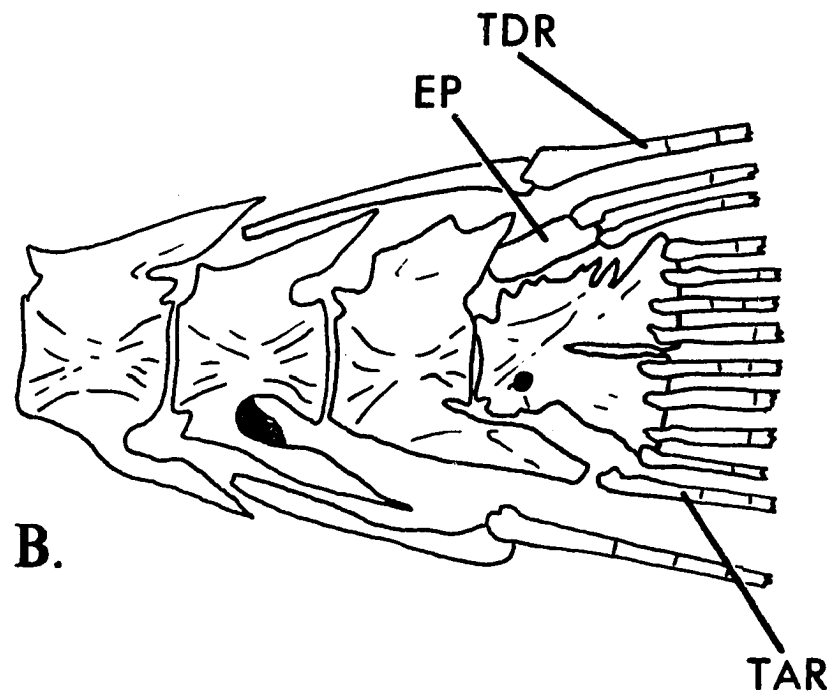
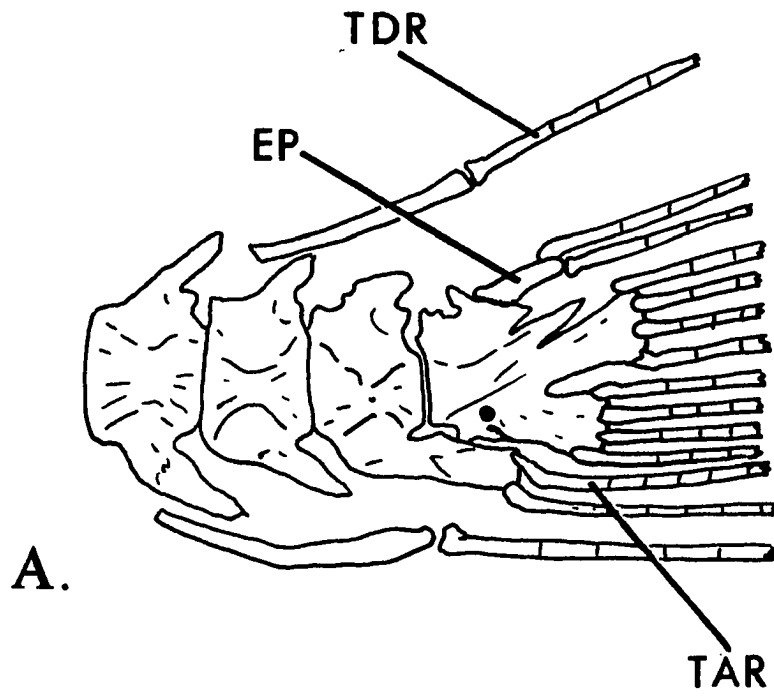
Teeth simple, outer row largest, broad-based and flattened; often stained emerald green (probably due to its predation on a detritivorous echinoid, Echinarachnius sp.). No teeth on vomer or palatine bones. Endopterygoid and ectopterygoid broadly articulate with quadrate. Posterior ramus of hyomandibula normal. Branchiostegal rays 4 + 2. Ceratohyal-epihyal juncture smooth. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials with tooth plates. Gill rakers 4-5 + 12-14 = 16-19.

Posttemporal ventral ramus poorly developed. Scapular foramen enclosed; scapula with well developed posterior strut. Four actinosts, with 17-20 pectoral fin rays. Pelvic fin rays 3.

Epipleural ribs on vertebrae 1-17 or 18. Dorsal fin origin in advance of first vertebra, with 2-4 ray-bearing pterygiophores. D 92-103, XVI-XXIV, 16-30. Four to six anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two caudal rays, hypurals with 7-8 rays, thus total caudal rays, 9-10. In all specimens examined there were two fin rays attached to the haemal spine of the second preural centrum, where in most other zoarcids there is one (fig. 16). Apparently the ventralmost hypural ray has become detached and is associated with the second preural vertebra. Last dorsal ray associated with second or third preural vertebra; last anal ray associated with third through fifth preural vertebrae.

Palatal membrane well developed. Pseudobranchial filaments 9-11. Two nub-like pyloric caeca. Reproductive mode oviparous. Peritoneum

Figure 16. Caudal skeletons of two zoarcids. A) Macrozoarces americanus, 200 mm SL, with two anal fin rays associated with haemal spine of second preural centrum. B) Eucryphycus californicus, 196 mm SL, with typical zoarcid fin ray configuration.



pale. Vertebrae asymmetrical.

Distribution and species. A single species, Macrozoarces americanus (Schneider, 1801), is found along the eastern coast of North America from off Battle Harbour, Labrador ($52^{\circ}15'N$, $55^{\circ}40'W$) south to off Virginia ($37^{\circ}03'N$, $74^{\circ}05'W$) (Orach-Meza, 1975). Adults move into shallow water to spawn in late summer to fall; larvae have been taken in zooplankton nets in February. Intertidal zone to 300 m (Orach-Meza, 1975).

Comments. A specimen of M. americanus I collected off Nantucket Shoals in 1980 is apparently the largest eelpout recorded at 1180 mm SL. Olsen and Merriman (1946) and Bigelow and Schroeder (1953) reported specimens over 750 mm were rare, but this was during a time of intensive commercial harvesting. In 1980 I measured hundreds of specimens over 1 m during a one week period at sea. Reports on the fishery and edibility are given by Olsen and Merriman (1946), Orach-Meza (1975) and Sheehy et al. (1977).

Additional references. Schneider (1801: 171); Peck (1804: 46, fig. 3); Mitchill (1815: 374-375, pl. I); Storer (1846: 123); Clemens and Clemens (1921: 69-83, pl I); Leim and Scott (1966: 326-328).

Zoarces Cuvier, 1829

(figs. 2-5, 9, 10, 17; pl. I)

Zoarces Cuvier, 1829: 240 (type species: Blennius viviparus Linnaeus, 1758, by original designation); Valenciennes, in, Cuvier and Valenciennes, 1836: 450-471; Günther, 1861: 295; Regan, 1912: 275-276, figs. 2C, 3.3, 4.

Zoarcaeus Nilsson, 1832: 105 (new spelling; takes same type as Zoarces).

Zoarchus Swainson, 1839: 184 (new spelling; takes same type as Zoarces).

Diagnosis. A genus of large eelpouts (Smitt, 1895 reports specimens to 610 mm) with up to 19 pungent spines in posterior section of dorsal fin (very rarely without spines); viviparous; upper lip normal in all stages; vertebrae 21-26 + 80-106 = 101-132.

Description. Scales present. Flesh firm. Lateral line complete, mediolateral. Upper jaw in males longer than in females.

Neurocranium deep. Parasphenoid wing well above mid-height of trigeminofacialis foramen. Frontal and parasphenoid wings articulate anteriorly. Sphenotic excluded from parietal by frontal. Parietals separated from mid-line except in Z. gillii (fig. 17). Supraoccipital and exoccipital narrowly contacting.

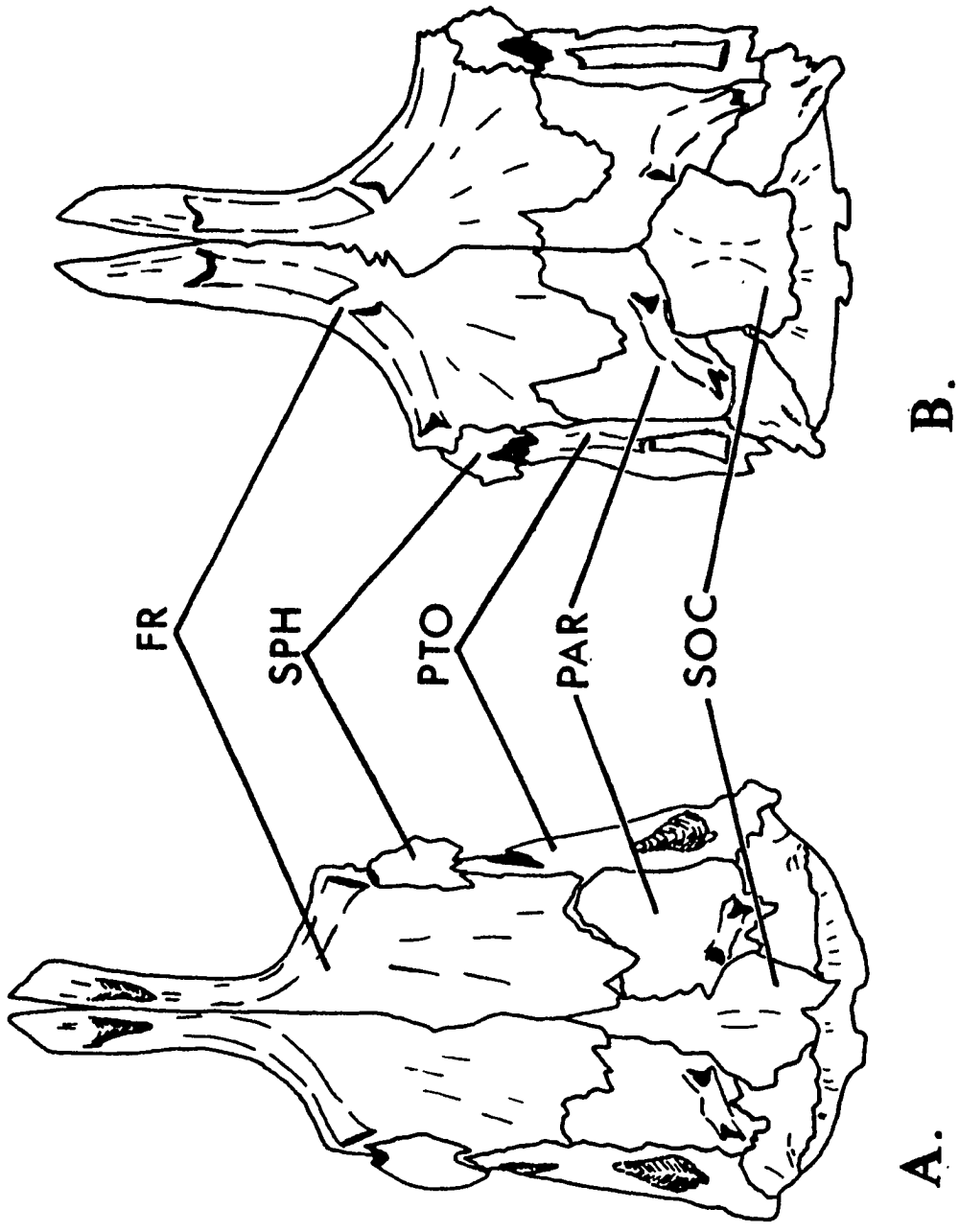
Cephalic lateralis pore system complete. Two lateral extrascapulars present; all four postorbital pores present; two nasal pores; one interorbital pore; three occipital pores; six or seven suborbital pores; five or six suborbital bones; eight preoperculomandibular pores; preopercular and mandibular branches joined.

Teeth simple, conical, not noticeably flattened or with broad bases. Teeth absent on vomer and palatine bones. Endopterygoid and ectopterygoid broadly articulate with quadrate. Posterior ramus of hyomandibula normal. Branchiostegal rays 4 + 2. Ceratohyal-epihyal juncture smooth. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 5-6 + 9-12 = 14-18.

Posttemporal ventral ramus very weak or absent. Scapular foramen enclosed; scapula with well developed posterior strut. Four actinosts; pectoral fin rays 16-21. Pelvic fin rays 3.

Epipleural ribs extend from first to 14th or 15th vertebrae. Dorsal fin origin associated with first vertebra--no pterygiophores in

Figure 17. Dorsal view of neurocrania of Zoarces. A) Z. elongatus, 242 mm SL, parietals not meeting in midline. B) Z. gillii, 229 mm SL, parietals meeting in midline. Lateral extra-scapulars and ethmoid region removed.



A.

B.

advance of first neural spine. D 72-94, 0-XIX, 14-27. Two to four anal fin pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two caudal rays, hypurals with 7-9 rays, thus total caudal rays 9-11. Last dorsal ray associated with second or third preural vertebra; last anal ray associated with fourth preural vertebra.

Palatal membrane well developed. Pseudobranchial filaments 9-10. Two nub-like pyloric caeca. All species are viviparous. Vertebrae asymmetrical.

Distribution and species. Zoarces viviparus (Linnaeus, 1758): English Channel northward to White Sea, including Faeroe Islands and Baltic Sea (Andriashev, 1954). Steindachner (1868) recorded specimens from near Cadiz, Spain. Zoarces gillii Jordan and Starks, 1905: Foochow, China (about 26° N) north to Japan Sea coast of Hokkaido (Wu, 1930; Lindberg and Krasnyukova, 1975). Zoarces tangwangi Wu, 1930 is a junior synonym of Z. gillii. Zoarces elongatus Kner, 1868: Gulf of Chihli (Pohai), China to northern Okhotsk Sea (Lindberg and Krasnyukova, 1975). All species inhabit the continental shelf and littoral regions and occasionally enter brackish or fresh water.

Comments. The European eelpout, Zoarces viviparus, has been harvested for perhaps the last thousand years or more; indeed, the vernacular stems from the Anglo-Saxon "aelepute." The first renaissance reference seems to be that of Schonevelde (1624) who reported it to birth all eels, a commonly held view then, due to its viviparity. At present I am not aware of any reference actually documenting viviparity in Z. gillii or Z. elongatus, though specimens of Z. gillii with ovaries bearing embryos are present in the Zoological Institute, Leningrad. The first detailed description of embryonic development in Z. viviparus is that of

Forchhammer (1819) and since then Soin (1968) has given a modern description. Detailed studies on the genetics of Z. viviparus populations have been published by a group at the University of Aarhus, Denmark (Christiansen et al., 1981 and papers within). Regan's (1912) illustration of the skull of Z. viviparus bearing the intercalar (opisthotic) bone is in error.

Additional references. Schmidt (1917a, 1917b); Smitt (1895: 603).

Tribe Gymnelini (Gill, 1864)

Diagnosis. Branchiostegal membrane broadly fused to isthmus, with gill slit extending just to or well above lower edge of pectoral base, or a small pore well above pectoral fin; 4-8 suborbital bones forming a circle around eye.

Andriashevia Fedorov and Neyelov, 1978

Andriashevia Fedorov and Neyelov, 1978: 952-955, figs. 1-2 (type species: Andriashevia aptera, by original designation).

Diagnosis. Suborbital bones 4, with five pores forming a circle under eye; pectoral fins and actinosts absent; vertebrae 22 + 125 = 147. Scales absent, lateral line mediolateral; vomerine teeth absent, palatine teeth present; lips absent; gill slit a small pore above pectoral fin base; body short and low, tail greatly elongated (characters 1 and 2).

Description. Only the holotype of this species is known. The original description is rather complete and I can add only a few comments. What follows paraphrases the original description in part.

Body robust, short and low. Tail very long with high number of caudal vertebrae. Skin moderately firm; thin, gelatinous layer present, but not nearly as flaccid as Melanostigma or Lycodapus. Scales absent.

Mouth large, terminal. No lips formed around premaxilla and maxilla; upper jaw extending posteriorly well beyond orbit. Body lateral line present, complete to tail tip, mediolateral. Gill slit a small pore, above mid-section of cleithrum and directly behind eye. Color a uniform pinkish-orange in life, abdomen dark. Nostril tubular, short, not reaching to upper margin of jaw.

Cephalic lateralis pores very small, rounded. Postorbital pores 1, 3, 4 present. Probably two lateral extrascapulars. Two nasal pores. One interorbital pore. Parietal (supratemporal) commissure complete, with three pores. Five suborbital pores, with four suborbital bones. Preoperculomandibular pores eight, pores six and seven exit preoperculum on a very low level. Eighth preopercular pore very high on cheek.

Teeth on jaws small, outer row at symphysis enlarged. Vomerine teeth absent. Palatine teeth present, in single series, 9 on one side, 11 on the other. Details of bones of suspensorium not seen in radiographs. Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed. Gill rakers 4 + 12.

Posttemporal ventral ramus weak, a mere nubbin. No pectoral actinosts, pectoral fins or pelvic fins.

Dorsal fin origin associated with second vertebra, no free pterygiophores. Dorsal, anal and caudal rays all soft, anteriormost dorsal ray not segmented. Dorsal and anal rays covered with skin. Two anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one ray, hypurals with eight rays, thus total caudal rays 9.

Palatine membrane well developed. Pseudobranch present. Status of pyloric caeca unknown. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae asymmetrical anteriorly, more symmetrical

on tail.

Distribution and species. The only known specimen of Andriashevia aptera was taken by otter trawl off the Pacific coast of Japan (37°29'N, 142°25'E) in 1025 m.

Comments. Andriashevia may be benthic and associated with hydrocorals. The only evidence for this supposition is the species' reddish coloration (similar to that of Puzanovia--see that account below and Fedorov, 1975) and loss of pectoral fins, perhaps a further result of reduction due to a fossorial life, as in muraenids.

Bilabria Shmidt, 1936

Bilabria Shmidt, 1936: 93-96, fig. 1 (type species: Lycenchelys ornatus Soldatov, 1922, by original designation); Anderson, 1982b: 19-25.

Remarks. This genus, containing a single species, is very close to Davidijordania Popov, and may be included within it when more is known. At present, only four specimens have been collected and detailed observations have not been possible. The curious upper lip of Bilabria, completely adnate to the symphysis, is similar to that of some specimens of Gymnelus viridis and G. hemifasciatus (Anderson, 1982b). However, the anterior portion of the lip is very different in B. ornata than in these aberrant Gymnelus in having a high, free anterior lobe and the genus is retained.

Diagnosis. Suborbital bones 5, forming close circle around eye; upper lips discontinuous, forming wide interspace, with high anterior lobes; dorsal fin with 1-2 ray-bearing pterygiophores anterior to first vertebra; vertebrae 23 + 95-96 = 118-119; C 9-10; pelvic fins present; vomerine teeth present; palatine teeth absent; gill slit restricted,

extending ventrally to mid-pectoral base.

Description. Scales present, very small. Flesh firm. Lateral line mediolateral, complete. Upper edge of operculum with well developed, posteriorly directed siphonal fold.

Neurocranium truncated, moderately deep. Osteological observations limited; restricted to those obtained from radiographs at present. Parietal separated from midline by supraoccipital.

Cephalic lateralis pore system complete. Two lateral extrascapulars present; all four postorbital pores present; two nasal pores; one interorbital pore; three occipital pores; six suborbital pores; five suborbital bones; eight preoperculomandibular pores; mandibular and preopercular branches joined.

Teeth simple, conical, outer row on both jaws larger. One adult male (219 mm SL) with 11-12 teeth on premaxilla, 10-12 teeth on dentaries. Teeth absent on palatines, 3-4 teeth on vomer. Posterior ramus of hyomandibula normal. Branchiostegal rays 4 + 2, except one aberrant individual with 4 + 2 on one side and 2 + 2 on the other. Ceratohyal-epihyal juncture smooth. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials with tooth plates. Gill rakers 2 + 11 (in two).

Posttemporal ventral ramus moderate. Scapular foramen probably enclosed. Four actinosts bearing 15-16 pectoral fin rays. Pelvic fin rays 3.

Epipleural ribs extend from first to 12th or 13th vertebrae. Pleural ribs on vertebrae 2-23. Dorsal fin origin well in advance of pectoral base. All dorsal rays bilaterally divided, segmented. Five anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two rays, hypurals with eight rays, thus total caudal

rays 10. Last anal ray associated with second preural vertebra, last dorsal ray associated with fourth preural vertebra.

Palatine membrane well developed. Pseudobranchial filaments 4, very long. Peritoneum pale. Reproductive mode unknown, probably oviparous. Vertebrae asymmetrical.

Distribution and species. A single species in the genus, Bilabria ornata (Soldatov, 1922) is known only from the southern Okhotsk Sea in Aniva Bay, Sakhalin Island, and Tatar Strait, Japan Sea, on the continental shelf. Probably widely distributed in the Okhotsk Sea.

Additional references. Soldatov (1922a: 162-163, fig. 2); Soldatov and Lindberg (1930: 500, fig. 72); Taranets (1937: 164); Shmidt (1950: 113-114, fig. 9); Norman (1966: 475); Lindberg and Krasnyukova (1975: 169-170, figs. 133, 134).

Davidijordania Popov, 1931

(pl. I)

Davidijordania Popov, 1931a: 210-215 (type species: Lycenchelys lacertinus Pavlenko, 1910, by original designation); Popov, 1931b: 136; DeWitt, 1977: 789-790; Anderson, 1982b: 19-25.

Davidojordania Popov, 1931. Shmidt, 1936: 97-100; Taranets, 1937: 164; Shmidt, 1950: 111-113, figs. 6-8; Lindberg and Krasnyukova, 1975: 171-177, figs. 135-140.

Remarks. Shmidt (1936) improperly emended Davidijordania to Davidojordania, a fact first noted by DeWitt (1977).

Diagnosis. Suborbital bones 6-8, forming close circle around eye; upper lips continuous; dorsal fin with no pterygiophores anterior to first vertebra; Vertebrae 20-23 + 77-97 = 98-120; C 10; exoccipital separated from supraoccipital; pelvic fins present; vomerine and palatine teeth present; gill slit extending ventrally to mid-pectoral base or just to

its ventral edge.

Description. Scales present. Flesh firm. Lateral line mediolateral, incomplete, running from above gill opening to vertical through middle of pectoral fin or just before anus. Lateral line difficult to detect and may be more extensive (or absent) in some species (material examined by me collected between 1901 and 1929). Gill slit extending ventrally to mid-pectoral base or slightly beyond.

Osteological observations based on D. poecilimon only (UMMZ 202551 and 202552). Neurocranium truncated, moderately deep. Parasphenoid wing very high, extending to near ventral surface of frontal, not separated from frontal by pterosphenoid. Sphenotic and parietal separated by frontal. Parietals meeting in midline. Exoccipital separated from supra-occipital by wide expanse of epioccipitals.

Cephalic lateralis pore system complete. Two lateral extrascapulars present; all four postorbital pores present; two nasal pores; one inter-orbital pore; one postocular pore in D. poecilimon; three occipital pores; six to nine suborbital pores, six to eight suborbital bones; eight preoperculo-mandibular pores; mandibular and preopercular branches joined.

Teeth simple, moderately enlarged, sharp, few on both jaws of both sexes. Teeth on palatines and vomer of males larger than females, recurved. Posterior ramus of hyomandibula normal. Branchiostegal rays 4 + 2. Endopterygoid and ectopterygoid broadly articulate with quadrate. Ceratohyal-epihyal juncture smooth. Ceratobranchial 5 toothed. Three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2 + 10-11.

Posttemporal ventral ramus moderate. Scapular foramen enclosed, scapula with well developed posterior strut. Four actinosts bearing 12-17 pectoral fin rays. Pelvic fin rays 3.

Epipleural ribs extend from first to tenth vertebrae. Pleural ribs on third to ultimate precaudal vertebrae. Dorsal fin origin associated with fourth vertebrae (in four fish). D 97-118, all soft rays, first not segmented, but divided. Two or three anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two rays, hypurals with eight rays, thus total caudal rays 10. Last anal ray associated with second preural vertebra, last dorsal ray associated with fourth preural vertebra.

Palatine membrane moderately developed. Pseudobranchial filaments 4, very long. Two nub-like pyloric caeca. Peritoneum pale. Reproductive mode unknown, probably oviparous. Vertebrae asymmetrical.

Distribution and species. Davidijordania jordaniana Popov, 1936: northern Japan Sea. Davidijordania poecilimon (Jordan and Fowler, 1903): east and west coasts of Japan Sea, Pacific coast of Japan from Hokkaido to Matsushima Bay. Lycenchelys spilotus Fowler, 1943 is a junior synonym of D. poecilimon. Davidijordania lacertina (Pavlenko, 1910): Peter the Great Bay and vicinity, Japan Sea. Davidijordania brachyrhyncha (Shmidt, 1904): Tatar Strait, Japan Sea to northwestern Okhotsk Sea. The genus inhabits the continental shelf.

Comments. The species of Davidijordania are in great need of modern systematic review, and there may be one or more undescribed species in present collections, particularly in Leningrad.

Additional references. Jordan and Fowler (1903: 748-749, fig. 2); Shmidt (1904: 201-202, pl. VI, fig. 2); Pavlenko (1910: 53, fig. 10-11); Jordan, Tanaka and Snyder (1913: 399, 400, fig. 371); Soldatov and Lindberg (1930: 497-500, ex. L. fasciatus); Fowler (1943: 89-90, fig. 24).

Gymnelopsis Soldatov, 1922

Gymnelopsis Soldatov, 1922a: 160-161, fig. 1 (type species: Gymnelopsis ocellatus, by original designation); Shmidt, 1950: 123-126, tab. 26, 27; Lindberg and Krasnyukova, 1975: 178-180, figs. 141, 142; Anderson, 1982b: 27, 49-55, figs. 13-15, 31-34, tabs. 1, 3.

Derjuginia Popov, 1931b: 137-138 tab. 1, fig. 1 (type species: Derjuginia ochotensis, by monotypy); Shmidt, 1950: 126; Toyoshima, 1981b: 254-258, figs. 1, 2, tab. 1.

Gengea Katayama, 1943: 101-104, fig. 1 (type species: Gengea japonica, by original designation).

Remarks. A generic revision and thorough descriptions are given in Anderson (1982b), thus only the major characters are described here. While my revision was in press, Toyoshima (1981b) reported on 16 specimens of Gymnelopsis ochotensis, dividing them into two species (ochotensis and japonica) and recognizing Derjuginia. The major basis for recognizing two species was in different positions of the dorsal fin origin, which Anderson (1982b) showed could not be used to identify two species groups. I mistakenly reported the gender of Gymnelopsis to be masculine, but it is feminine (Bull. Int. Comm. Zool. Nomencl. 29 (4): 177). My original reference to Katayama's Gengea japonica for 1941 is in error (Anderson, 1982b: 51), that reference being for Petroschmidtia toyamensis.

Diagnosis. Suborbital bones 5-6, forming close circle around eye; upper lips continuous; ceratohyal-epihyal juncture with bone interdigitating; dorsal fin origin associated with vertebrae 1-17; vertebrae 16-23 + 73-95 = 89-115; scales present, restricted to posterior portion of tail in all but one species; exoccipital broadly contacting supra-occipital; pelvic fins absent; C 5-8; gill slit extending ventrally to mid-pectoral fin base, or above it.

Description. Scales present, in wedge-shaped pattern on posterior portion of tail except in G. ochotensis, in which scales extend to pectoral axil. Flesh firm. Lateral line mediolateral, extending from above gill slit to about mid-body. Gill slit extending ventrally to mid-pectoral base or above it.

Neurocranium truncated, moderately deep. Parasphenoid wing extending well above mid-height of trigeminofacialis foramen, not excluded from frontal by pterosphenoid. Sphenotic and parietal excluded by frontal and pterotic. Parietals not meeting in mid-line. Exoccipital broadly contacting supraoccipital posteriorly (Anderson, 1982b, fig. 10).

Cephalic lateralis pore pattern variable, species-specific. Two lateral extrascapulars, posteriormost reduced, trough-like; postorbital pores present are 1, 2, 3, 4; 1, 3, 4 or 1 and 4. Two nasal pores in all species. One interorbital pore. Zero to three occipital pores. Suborbital pores usually 6-7; absent in G. ocellata; five or six suborbital bones. Preoperculomandibular pores 5-7; mandibular and preopercular branches joined.

Teeth simple, small, few on both jaws of both sexes. Teeth on vomer and palatines not noticeably larger in males than in females, individually variable. Posterior ramus of hyomandibula normal. Branchiostegal rays 3 + 2, except in G. ocellata (4 + 2). Endopterygoid and ectopterygoid broadly articulating with quadrate. Ceratohyal-epihyal juncture strongly interdigitating, bones thickened (Anderson, 1982b, fig. 15). Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2-3 + 7-11 = 9-14.

Posttemporal ventral ramus well developed or moderate. Scapular foramen enclosed; scapula with well developed posterior strut in adults.

Four actinosts bearing 9-12 pectoral fin rays. Pelvic fins absent, pelvic bone greatly reduced.

Epipleural ribs on vertebrae 1-10 or 15. Pleural ribs on vertebrae 2-3 to antepenultimate or ultimate precaudal vertebrae. Dorsal fin origin on vertical through pectoral base, posterior margin of pectoral fin, or on anal fin origin in G. ochotensis (this species has 7-12 free dorsal pterygiophores; others have 0-5). Dorsal fin elements 80-113, first a flexible spine in all known specimens. Zero to four anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural bearing one fin ray, hypurals with 4-7 rays, thus total caudal rays, 5-8. Last anal ray associated with second preural vertebra, last dorsal ray associated with fourth preural vertebra.

Palatine membrane well developed. Pseudobranchial filaments 4-6, very long. Two nub-like pyloric caeca. Peritoneum pale. This genus is oviparous, spawning in late summer or fall. Vertebrae asymmetrical.

Distribution and species. There are four species of Gymnelopsis: G. bra-shnikovii Soldatov, 1922, G. brevifenestrata Anderson, 1982, G. ocellata Soldatov, 1922 and G. ochotensis (Popov, 1931). The genus is imperfectly known (only 46 specimens have been collected) and the first three species may not be restricted to the Okhotsk Sea, as present collections indicate. G. ochotensis is known from the northern Okhotsk Sea to southern Japan, on both east and west coasts of the Japan Sea (Anderson, 1982b, fig. 31). Depths of capture for Gymnelopsis range between 70 and 783 meters.

Gymnelus Reinhardt, 1834

Gymnelus Reinhardt, 1834: 4 (type species: Ophidium viride Fabricius, 1780, by original designation); Andriashev, 1973: 540-541; Anderson,

1982b: 1-48, figs. 1-12, 16-30, tabs. 1, 2.

Gymnelis Reinhardt, 1837: 37, 49; Krøyer, 1862: 258-266; Collett, 1880: 123-125; Andriashev, 1937: 71.

Cepolophis Kaup, 1856: 96 (type species: Ophidium viride, by original designation).

Gymnelichthys Fischer, 1885: 60, pl. 2, fig. 9 (type species: Gymnelichthys antarcticus, by original designation).

Nemalycodes Herzenstein, 1896: 14 (type species: Nemalycodes grigorjewi, by monotypy).

Commandorella Taranets and Andriashev, 1935b: 267-270, fig. 1 (type species: Commandorella popovi, by original designation).

Remarks. As with Gymnelopsis, Anderson (1982b) gave a generic revision, thus only the salient characters are described below.

Diagnosis. Suborbital bones 5-6 (7), forming close circle around eye; upper lips continuous except in aberrant specimens; ceratohyal-epihyal juncture with bone interdigitating; dorsal fin origin associated with vertebrae 17-26 + 65-84 = 85-105; scales absent; exoccipital broadly contacting supraoccipital; pelvic fins absent; C 9-12; gill slit extending ventrally to mid-pectoral base or just below it in very young fish.

Description. Scales always absent. Flesh firm. Lateral line medio-lateral, complete. Gill slit extending to mid-pectoral base or above it in adults, usually slightly beyond mid-pectoral base in young juveniles, but never to lower margin of fin.

Neurocranium truncated, not deep. Parasphenoid wing extending dorsally to mid-height of trigeminofacialis foramen or slightly above it, not separated from frontal by pterosphenoid. Sphenotic and parietal separated by frontal and pterotic. Parietals meeting in midline. Exoccipital broadly contacting supraoccipital posteriorly (Anderson,

1982b, fig. 2).

Cephalic lateralis pore pattern quite variable, species-specific or even population specific (Anderson, 1982b: 38). Two lateral extrascapulars, distalmost sometimes lost in specimens with reduced pore patterns. All four postorbital pores usually present, though much variation occurs. Two nasal pores. One interorbital pore in G. popovi and some G. viridis, absent in others. Zero to three occipital pores, this pattern individually variable in most species. Suborbital pores 0-11, normally six, except in G. pauciporus in which they are always absent (absent in a few G. retrodorsalis from the Kara and Barents seas as well). Usually five suborbital bones, fragmentation produces up to seven. Preoperculo-mandibular pores 5-9; 5-6 in G. pauciporus, usually eight in all other species.

Teeth simple, small, few in both jaws of both sexes. Teeth on vomer and palatines not noticeably larger in males than in females, individually variable; no vomer and palatine teeth in G. popovi. Posterior ramus of hyomandibula normal. Branchiostegal rays 4 + 2 except 5 + 2 or 3 + 2 in a few aberrant specimens. Endopterygoid and ectopterygoid broadly articulating with quadrate. Ceratohyal-epihyal juncture strongly interdigitating, bones thickened (Anderson, 1982b, fig. 5). Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates (Anderson, 1982b, fig. 6). Gill rakers 2-6 + 7-15 = 10-20.

Posttemporal ventral ramus usually well developed (absent in G. hemifasciatus). Scapular foramen enclosed; scapula with well developed or moderate posterior strut in adults. Four actinosts bearing 9-14 pectoral fin rays. Pelvic fins absent, pelvic bone greatly reduced (Anderson, 1982b, fig. 7).

Epipleural ribs on vertebrae 1-7 or to 15. Pleural ribs on vertebrae 3 to antepenultimate or ultimate precaudal vertebrae. Dorsal fin origin on vertical through pectoral base to vertical passing about one half pectoral fin length posterior to rear margin of pectoral fin. Zero to two free dorsal fin pterygiophores except in G. retrodorsalis which has 3-14. Dorsal fin elements 77-102, first always a flexible spine. One to five anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural bearing 1-2 fin rays, hypurals with 8-10 rays, thus total caudal rays 9-12. Last anal ray associated with second through fourth preural vertebrae, last dorsal ray associated with fourth preural vertebra.

Palatine membrane well developed. Pseudobranchial filaments 4-12, very long. Two nub-like pyloric caeca, slightly longer in juveniles than in adults. Peritoneum pale. This genus is oviparous, spawning in late summer or fall. Vertebrae asymmetrical.

Distribution and species. There are five species of Gymnelus: G. hemifasciatus Andriashev, 1937, G. retrodorsalis LeDanois, 1913 and G. viridis (Fabricius, 1780) are high Arctic to subarctic and semi-circumglobal (Anderson, 1982b, figs. 20, 21). G. popovi (Taranets and Andriashev, 1935) is intertidal at Kodiak, the Aleutian and Kuril islands and probably adjacent mainlands with suitable habitat (Anderson, 1982b, fig. 28). G. pauciporus Anderson, 1982 is known only from the Okhotsk Sea and eastern Kamchatka coast. Maximum depth for the genus is 481 m for a specimen of G. retrodorsalis in the Arctic Atlantic

Additional references. Fabricius (1780: 141-142); Lacépède (1800: 280, 282); Lay and Bennett (1839: 64, tab. 20); Richardson (1855: 21-26);

Jordan and Evermann (1898: 2477, figs. 864a-c); Knipovich (1908: 1-16); Andriashev (1954: 260-262, fig. 135); Leim and Scott (1966: 317); Lindberg (1974: 207, fig. 799).

Hadropareia Schmidt, 1904

Hadropareia Schmidt, 1904: 204-206, fig. 14 (type species: Hadropareia middendorffi, by original designation); Anderson, 1982b: 19-25.

Remarks. This genus, based on a single species, is one of the most poorly known eelpouts. Hadropareia is close to Bilabria and Davidijordania and is distinguished mainly by the absence of scales. Specimens labelled Hadropareia sp. reported by Anderson (1982b) possessed partial squamation and may be referable to Davidijordania.

Diagnosis. Suborbital bones 5, forming close circle around eye; upper lip continuous; dorsal fin origin on vertical through pectoral base; vertebrae 24-28 + 83-89 = 108-114; scales absent; pelvic fins present; C 7-8; branchiostegal rays 5 + 2; ceratohyal-epihyal juncture smooth; gill slit extending ventrally to mid-pectoral base.

Description. Scales always absent. Flesh firm, greenish, abdomen reddish-orange. Lateral line mediolateral, complete. Gill slit extending ventrally to mid-pectoral base.

Head small, not deep. Adductor mandibulae well developed in males, giving head triangular shape when viewed dorsally, as in Gymnelus (Anderson, 1982b).

My observations on cephalic lateralis pore pattern were limited. Two lateral extrascapulars seen in radiographs of one specimen, postorbital pore pattern probably complete. Two nasal pores, six suborbital and eight preoperculo-mandibular pores present. Mandibular and preoperc-

ular branches joined.

Teeth simple, outer row enlarged, somewhat larger in males than females. Few teeth on both jaws of both sexes, but more teeth than Gymnelopsis. Jaw teeth of males may be statistically fewer in number than females. Palatine teeth absent in all specimens seen; teeth on vomer rather stout and blunt. Bones rather massive in suspensorium--endopterygoid and ectopterygoid probably broadly articulate with quadrate. Ceratohyal-epihyal juncture smooth. Posterior ramus of hyomandibula normal. Branchiostegal rays 5 + 2 except in one specimen which had 5 + 2 on one side and 6 + 2 on the other (a probable atavism; see discussion under character 45). Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2 + 12 (in one).

Posttemporal ventral ramus well developed. Scapula not seen in radiographs, but probably like all others, with enclosed foramen. Four actinosts bearing 13-15 pectoral fin rays. Pelvic fins rather small, with three rays each.

Epipleural ribs on vertebrae 1-14 or 16. Pleural ribs on vertebrae 3 through ultimate precaudal. Dorsal fin origin associated with vertebra 1 or 2, with no free pterygiophores. D 106-113, of all soft rays; first divided to tip. Five or six anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural bearing one or two fin rays, hypurals with six rays, thus total caudal rays 7-8. Last anal fin ray associated with second preural vertebra, last dorsal ray associated with fourth preural vertebra.

Palatine membrane well developed. Two nub-like pyloric caeca. Peritoneum pale. Reproductive mode unknown, probably oviparous. Vertebrae asymmetrical.

Distribution and species. Hadropareia middendorffi Schmidt, 1904 is known only from the Okhotsk Sea; from Penzhinskaya Bay in the far north to the Shantar Islands (Schmidt, 1950). Intertidal and shallow subtidal.

Additional references. Soldatov and Lindberg (1930: 492, fig. 69); Popov (1931b: 136); Taranets (1937: 159, 164); Matsubara (1955: 771, 778, 779); Norman (1966: 475, 478); Lindberg (1974: 207, fig. 797); Lindberg and Krasnyukova (1975: 169).

Krusensterniella Schmidt, 1904

(pl. I)

Krusensterniella Schmidt, 1904: 197-199, fig. 12 (type species: Krusensterniella notabilis, by original designation); Soldatov, 1922b: 157-159, fig.; Andriashev, 1938: 117-121; Andriashev, 1955b: 393-394, fig. 1; Lindberg and Krasnyukova, 1975: 126-131, figs. 103-105; Anderson, 1982b: 19-25.

Diagnosis. Suborbital bones 5-6, forming close circle around eye; upper lip continuous; dorsal fin with series of pungent spines posteriorly preceded by flexible spines; dorsal fin origin associated with vertebrae 1-2; vertebrae 19-25 + 80-97 = 100-121; scales present; pelvic fins absent; C 5-7; branchiostegal rays 5; gill slit extending ventrally to mid-pectoral base.

Description. Scales present, sparse anterior to anus except in K. maculata, the most scaly species, absent anterior to anus in K. multispinosa. Flesh firm. Lateral line mediolateral, incomplete, extending from above gill slit to about $2\frac{1}{2}$ head lengths behind anus in K. notabilis to just before anus in K. pavlovskii. Gill slit extending ventrally to mid-pectoral base or slightly above.

Osteological observations based on radiographs and superficial

dissections of K. notabilis and K. multispinosa only (Anderson, 1982b). Neurocranium truncated, not deep, similar to Gymnelus and Gymnelopsis. Parietals separated from midline, relatively small.

Cephalic lateralis pore pattern complete, with little variation among species. Two lateral extrascapulars, distalmost often quite reduced, trough-like; all four postorbital pores present. Two nasal pores. One interorbital pore. Three occipital pores. Six or seven suborbital pores; five or six suborbital bones. Preoperculomandibular pores seven, first one absent in K. notabilis, K. multispinosa and K. maculata. Status of first pore unknown in K. pavlovskii, if also absent, this condition (and status of first dentary foramen) would be diagnostic for genus. Mandibular and preopercular branches joined.

Teeth simple, small, conical, few in both jaws of both sexes. Teeth on vomer and palatines not noticeably larger in males than in females, individually variable. Hyomandibular posterior ramus normal. Branchiostegal rays 3 + 2. Ceratohyal-epihyal juncture smooth. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2 + 10 (in two fish).

Posttemporal ventral ramus weakly developed. Scapular foramen enclosed; scapula with weak posterior strut (seen in one juvenile--probably stronger in adults). Four actinosts bearing 11-12 pectoral fin rays. No pelvic fins, pelvic bone greatly reduced, even more so than in Gymnelus.

Epipleural ribs on vertebrae 2 to penultimate precaudal vertebra. Pleural ribs on vertebrae 3 to ultimate precaudal vertebra. Dorsal fin origin on vertical through pectoral fin base or just slightly behind. Dorsal fin higher anteriorly in males than in females. All dorsal fin

elements flexible spines anterior to pungent spines, the latter located far more anteriorly and relatively much longer than pungent spines in Macrozoarces and Zoarces. D XLV-LVII, II-XXVI, 37-64. Three anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural bearing one fin ray, hypurals with 4-6 rays, thus total caudal rays 5-7. Last anal ray associated with second preural vertebra, last dorsal ray associated with fourth preural vertebra.

Palatine membrane well developed. Pseudobranchial filaments 4, reduced in length relative to Gymnelopsis. Two nub-like pyloric caeca, except K. multispinosa, in which they are long and finger-like. Peritoneum pale. Reproductive mode unknown, probably oviparous (see Andriashev, 1955b). Vertebrae asymmetrical.

Distribution and species. Krusensterniella maculata Andriashev, 1938: Japan Sea from Tatar Strait to Peter the Great Bay in 53-150 m. Krusensterniella multispinosa Soldatov, 1922: Okhotsk Sea from the Shantar Islands to southeastern Sakhalin Island in 87-160 m. Krusensterniella notabilis Schmidt, 1904: Okhotsk Sea, off northeastern Sakhalin Island in 55-90 m. Krusensterniella pavlovskii Andriashev, 1955: one collection off southeastern Kamchatka in 105 m.

Additional references. Soldatov and Lindberg (1930: 490-492, fig. 68); Taranets (1937: 159, 161, fig. 99); Schmidt (1950: 83-84); Matsubara (1955: 770-773); Norman (1966: 474, 477).

Melanostigma Günther, 1881

(pl. II)

Melanostigma Günther, 1881: 20 (type species: Melanostigma gelatinosum, by monotypy); Gilbert, 1895: 472, pl. 35; Goode and Bean, 1896: 314, pl. 82; Koefoed, 1952: 19-20, pl. II, fig. D; McAllister and Rees, 1964: 85-109, figs. 1-9; Yarberry, 1965: 442-462, figs. 1-9;

Bussing, 1965: 219-222, figs. 14-16; Tominaga, 1971: 151-156, fig. 1; Parin, 1977: 63-67, figs. 1, 2; Parin, 1979: 167-170, figs. 1, 2; Anderson and Hubbs, 1981: 345, 349, fig. 5.

Remarks. Gosline (1968) following Yarberry's (1965) erroneous figure of the skull of Melanostigma pammelas bearing a basisphenoid bone suggested the removal of Melanostigma from Zoarcidae, a not unreasonable assumption if the bone was present. Andriashev (1973), Gosztonyi (1977) and Parin (1977, 1979) followed this idea, but only Gosztonyi provided characters to base such a decision. Anderson and Hubbs (1981) showed the basisphenoid is always absent in zoarceoids and that Melanostigma has no significant characters to warrant its exclusion from Zoarcidae.

Diagnosis. Suborbital bones 4-5, with 3-6 pores, forming circle, or nearly so, around eye; endopterygoid and ectopterygoid weakly articulating with quadrate; gill slit a small pore entirely above pectoral fin; preopercular canal and pores absent (preopercular pore 6 rarely developed in M. atlanticum); frontal excluded from parasphenoid wing by pterosphenoid; sphenotic and parietal articulating; one pair of nasal pores (set anterior to nostril tubes); ceratobranchial 5 without teeth; two pairs of infrapharyngobranchials and tooth plates; vertebrae 18-23 + 62-81 = 82-100; pectoral actinosts 2-4; flesh gelatinous; scales, pelvic fins and lateral line absent.

Description. Head very small, rounded, mouth terminal. Scales and lateral line absent. Flesh gelatinous, thin and delicate. Eye large, rounded. Gill slit a small pore above pectoral fin.

Neurocranium truncated, not deep, bones thin and overlying thick cartilaginous capsules. Parasphenoid wing low, extending dorsally just to lower margin of trigeminofacialis foramen. Frontal without descending

wing; parasphenoid and frontal separated by pterosphenoid. Sphenotics enlarged, contacting parietals. Parietals separated from midline. Supraoccipital without pronounced anterior ramus, but rather large, narrowly contacting exoccipital and without medial crest (Yarberry, 1965, fig. 2; Anderson and Hubbs, 1981, fig. 5).

Cephalic lateralis pore system greatly reduced, pore patterns species- or individually-specific. Two lateral extrascapulars present, even in species without posterior postorbital pores. One pair of nasal pores. No interorbital pore except in M. gelatinosum, which only occasionally possesses one. Supratemporal commissure present or absent, but no occipital pores ever develop. Three to six suborbital pores, loss occurs to dorsalmost pores. Four or five suborbital bones. Dentary with foramina for all four pores, but occasionally some pores not developed. No preopercular foramina, instead a shallow, open groove running along posterior margin present. Preoperculomandibular pores 2-6, when 6, ventralmost preopercular foramen opens to sixth pore, with no septum separating pores five and six.

Teeth of adult males caniniform; small and more numerous on jaws and palate in females (see McAllister and Rees, 1964, fig. 7). Vomerine and palatine teeth present in all species. Endopterygoid and ectopterygoid weakly articulating with quadrate. Metapterygoid greatly reduced. Hyomandibula posterior ramus normal. Opercular bones greatly deossified, thin. Ceratohyal-epihyal juncture smooth. Branchiostegal ray number variably 5 + 2 or 4 + 2 in M. pammelae and 4 + 2 or 3 + 2 in M. bathium; branchiostegals 4 + 2 in all other specimens seen. No teeth on ceratobranchial 5; infrapharyngobranchials of gill arches 2 and 3 present only. Gill rakers 1-2 + 6-14 = 8-16. Posttemporal ventral strut absent.

Cleithrum reduced, posterior ramus mostly cartilaginous. Scapular foramen enclosed, with well developed posterior strut. Usually four actinosts bearing 6-9 pectoral fin rays (M. atlanticum with 2-4 actinosts, M. pammelas with three actinosts). Pelvic fins absent, pelvic bone greatly reduced (Yarberry, 1965, fig. 6).

Epipleural ribs reduced, on vertebrae 1-4 or to 8. Pleural ribs on vertebrae 2-7 or 8. Dorsal fin origin associated with vertebra 3 or 4, with no free pterygiophores. Dorsal fin elements all soft rays, first or second not segmented, but bilaterally divided. One to three anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural bearing one fin ray, hypurals bearing 7-9 rays, thus total caudal rays 8-10. Last anal ray associated with second or third preural vertebra, last dorsal ray associated with second to fourth preural vertebra.

Palatine membrane well developed. Two or three weak pseudobranchial filaments. Two nub-like pyloric caeca. Peritoneum black. This genus is oviparous; at least one species probably has demersal spawning (Markle and Wenner, 1979). Vertebrae asymmetrical.

Distribution and species. Melanostigma contains seven species, all of which are undoubtedly mesopelagic, despite most published accounts which consider the genus benthic. All species live close to continental margins or mid-ocean ridges. Melanostigma atlanticum Koefoed, 1952: western North Atlantic from Grand Banks to Virginia, eastern North Atlantic from Faeroe-Iceland Ridge to Cap Blanc, Mauritania including Mediterranean Sea and Mid-Atlantic Ridge (Anderson and Almeida (ms); Gushchin and Kukuev, 1980). Melanostigma bathium Bussing, 1965: eastern South Pacific from off the Galapagos Islands to southern Chile and

southeast of South Georgia Island. Melanostigma gelatinosum Günther, 1881: off Valpariso Chile to Scotia Sea, off South Africa, Kerguelen and Heard islands in the Indian Ocean and off New Zealand. Melanostigma flaccidum Waite, 1914 is a junior synonym of M. gelatinosum. Melanostigma pammelas Gilbert, 1895: eastern North Pacific from central British Columbia to central Mexico (Hart, 1973; Brewer, 1973). Melanostigma orientale Tominaga, 1971: known only from three specimens from Sagami and Suruga bays, Japan. Melanostigma inexpectatum Parin, 1977: known only from the holotype taken just north of New Guinea (01°15'S, 142°46'E). Melanostigma vitiazi Parin, 1979: known only from the holotype taken in the Banda Sea (06°39'S, 126°37'E).

Additional references. Leim and Scott (1966: 328, fig.); Hart (1973: 247-248, fig.); Lindberg (1974: 207, fig. 798); McCosker and Anderson (1976: 214, 215, 217, fig. 2); Belman and Anderson (1979: 366-369); Belman and Gordon (1979: 275-281).

Nalbantichthys Schultz, 1967

(fig. 11B,C; pl. II)

Nalbantichthys Schultz, 1967: 1-5, figs. 1-3 (type species: Nalbantichthys elongatus, by original designation); Fedorov, 1975: 587, 588; Fedorov and Neyelov, 1978: 952.

Remarks. The penultimate vertebral element in both known specimens is a fusion of the second, third and fourth preural vertebrae. Schultz (1967) did not consider this abnormal for the genus since both specimens were alike. I think this is faulty reasoning since fusion of terminal caudal vertebrae and the rearrangement of pterygiophres and fin rays is variable and widespread in Zoarcidae, despite Schultz's inability to see it in the zoarcids he radiographed. In fact, the number and

association of pterygiophores is not alike in both specimens of Nalbantichthys (see description below, fig. 11B,C), thus this unusual condition is removed from the generic diagnosis.

Diagnosis. Suborbital bones 4, with five pores forming a circle under eye; body very long and slender, vertebrae 25 + 119-125 = 144-150; epural absent; three pairs of nasal pores; palate with two membranes; preoperculomandibular pore 7 absent; branchiostegal rays 5 + 2; pectoral fin very small, of six rays; scales, lateral line, pyloric caeca, pelvic fins, vomerine and palatine teeth absent; nostril tubes long, overhanging dorsal margin of upper jaw; gill slit a small pore above pectoral fin base.

Description. Body very slender, compressed at tail, head rounded. Skin scaleless, rather thin and delicate, but without gelatinous mass enveloping body. Fin membranes weak. No body lateral line seen even in recently preserved specimens (Schultz, 1967). Pectoral fin extremely small, only 2% of total length. Gill slit a tear drop-shaped opening entirely above pectoral fin. Nostril tubes very long, extending forward to over upper jaw margin.

Teeth on jaws very small, few. No teeth on vomer or palatines of both type specimens. Mouth terminal, rather large, lower jaw thickened, high. No details of cranial anatomy could be seen.

Cephalic lateralis pores small and rounded. Postorbital pores 1, 3 and 4 present, probably two lateral extrascapulars. Supraorbital canal with three pairs of nasal pores and an interorbital pore. Supratemporal commissure complete, with three occipital pores. Five suborbital pores formed from four suborbital bones in circle. Preoperculomandibular

pores and foramina in primitive condition, but pore seven absent. Preopercular and mandibular canals joined (Schultz, 1967, fig. 2).

Observations on bones of suspensorium minimal. Palatal arch appears reduced. Hyomandibula posterior ramus normal. Branchiostegal rays 5 + 2 in both type specimens. Ceratobranchial 5 with teeth, three pairs of infrapharyngobranchials and tooth plates. Gill rakers 4 + 13, with two on hypobranchials of holotype.

Posttemporal ventral ramus very weak. Scapula not seen in radiographs. Four ossified actinosts bearing only six pectoral fin rays. Pelvic bone not seen in radiographs, but very small if present; no pelvic rays.

Epipleural ribs on vertebrae 3-11. Pleural ribs on vertebrae 3-14. Dorsal fin origin associated with first or second vertebra, with zero or one free pterygiophore. Dorsal and anal fin composed of soft rays; first dorsal element bilaterally divided and segmented. Two anal pterygiophores anterior to haemal spine of first caudal vertebra.

Caudal skeleton variable in type specimens. Schultz (1967, fig. 3) has inaccurately depicted the skeleton of the paratype and the bones of both specimens are redrawn from a series of radiographs (fig. 11B,C). The ural neural arch is not developed in the holotype, but is well developed in the paratype. There is no epural in either specimen, but the holotype possesses one fin ray above the uroneural remnant and the paratype has two. There are six hypural rays in the holotype and eight in the paratype, thus total rays are, paratype: 1 + 6, holotype: 2 + 8. The last dorsal fin ray is associated with fused section of the second preural vertebra in the holotype and fourth preural in the paratype. The last anal fin ray is associated with the fused section of

of the second preural vertebra in both specimens and is attached to a spur of bone on its haemal spine which probably originated as the last anal pterygiophore and not the haemal spine of a "fourth vertebra" as Schultz (1967) contended. No anal pterygiophore and fin ray associated with third preural vertebra in holotype, but there is one in paratype.

Palate with well developed anterior membrane overhanging vomer and a weaker membrane just posteriorly. Pseudobranchial filaments 3, rather short. Pyloric caeca absent. Peritoneum black. Reproductive mode unknown, probably oviparious. Vertebrae asymmetrical.

Distribution and species. A monotypic genus, Nalbantichthys elongatus was first collected in the south central Bering Sea in 1964. Since then another specimen has been taken from the Bering Sea, by Soviet scientists, and is in the collection of fishes at the Zoological Institute in Leningrad. An upper slope dwelling species.

Puzanovia Fedorov, 1975

Puzanovia Fedorov, 1973: 19, 23 (nomen nudum).

Puzanovia Fedorov, 1975: 587-591, figs. 1, 2 (type species: Puzanovia rubra, by original designation); Amaoka et al., 1977: 93-96, fig. 3, tab. 2; Fedorov, 1982: 77-84.

Diagnosis. Suborbital bones 5, with six pores forming a circle under eye. Scales present, on tail only; vertebrae 22-24 + 110-125 = 134-147; vomerine teeth absent; palatine teeth present or absent; gill slit extending ventrally to lower edge of pectoral base or slightly above it; P 9-12.

Description. The original description of this genus is rather complete and I can add only a few osteological observations. What follows para-

phrases the original description in part.

Body short, robust. Head rounded, moderately high. Tail extremely long due to high number of caudal vertebrae. Scales present only on tail, extending anteriorly only to about one head length behind anal fin origin. Lateral line present, complete, mediolateral. Skin firm and moderately thick. Gill slit extending to pectoral fin base or just above it, but well separated from throat region as in other nalbant-ichthyines due to high placement of reduced pectoral fin. Nostril tubes rather small, not reaching upper lip. Both lips well formed, continuous.

Cephalic lateralis pore pattern complete. All four postorbital pores present, with probably two lateral extrascapulars. Two pair of nasal pores. One interorbital pore. Supratemporal commissure well formed, with three occipital pores. Suborbital pores 6, with five suborbital bones forming a circle around eye. Preoperculo-mandibular system with four dentary, one angulo-articular and three preopercular foramina and pores. Mandibular and preopercular branches joined.

Teeth moderately developed, outer row of jaw teeth enlarged. Teeth on palatine bones, which are usually present, large, recurved. No teeth on vomer in any specimen, although original description incorrectly reports vomerine teeth present (V. Fedorov, pers. comm.). Palatal arch reduced. Hyomandibula posterior ramus normal. Opercle and subopercle relatively well ossified. Ceratohyal-epihyal juncture smooth. Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed, three pairs of infrapharyngobranchials and tooth plates. Gill rakers 3-5 + 10-13 = 13-17.

Posttemporal ventral strut weak. Scapula not observed. Four

actinosts bearing 9-12 short pectoral rays. Pelvic bones reduced to small splints, no pelvic fins.

Epipleural ribs on vertebrae 1-16. Pleural ribs on second through ultimate precaudal vertebrae. Dorsal fin origin associated with first vertebra, with no free dorsal pterygiophores. Dorsal and anal fins of all soft rays. One to three anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one fin ray, hypurals with eight rays, thus total caudal rays 9. Last dorsal ray associated with fourth preural vertebra, last anal ray associated with second preural vertebra.

Palatine membrane well developed. Pseudobranchial filaments 6-7, rather long. Two nub-like pyloric caeca. Peritoneum black. This genus is oviparous. Vertebrae asymmetrical.

Distribution and species. Puzanovia rubra Fedorov, 1975: Bering Sea from Bower's Bank to Shirshov Ridge, off the Kuril Islands and Cape Erimo, Japan and northwestern Okhotsk Sea, in 200-610 m. Undoubtedly widely distributed along eastern Bering Sea slope and possibly the Pacific coast of Japan. Puzanovia virgata Fedorov, 1982: one collection off the northern Kuril Islands ($48^{\circ}24.5'N$, $153^{\circ}49.2'E$) in 480-505 m. Puzanovia rubra was always taken in association with the hydrocoral Primnoa resedaeformis, which has the same reddish color as Puzanovia. This fact and the similar color and slope domain of Andriashevia and Nalbantichthys suggests that all nalbantichthyines lurk about in the branches of these corals, reminiscent of the behavior of Eucryphycus in benthic drift kelp (see below).

Additional reference. Toyoshima (1983).

Tribe Lycodini (Gill, 1862)

Diagnosis. Suborbital bones and/or pores forming L-shaped configuration under and behind orbit (character 7); interorbital pore absent except in Lycodapus, Lycogrammoides and a few species of Bothrocarra, Lycodes and Lycenchelys.

Aiakas Gosztonyi, 1977

(pl. XIII)

Aiakas Gosztonyi, 1977: 198-200, fig. 2 (type species: Aiakas kreffti Gosztonyi, 1977, by original designation).

Diagnosis. Body robust, tail relatively short; frontal bones squared-off (character 13); hyomandibula posterior ramus normal (character 14); ceratohyal-epihyal articulation interdigitating (character 15); lower lip continuous at symphysis; nostril tubes extremely long, overhanging upper lip; gill slit extending to mid-pectoral base; pelvic fins, vomerine and palatine teeth absent; six suborbital bones, with six small pores; three occipital pores; palatine membrane absent; palatal arch well developed (?); pyloric caeca greatly enlarged; P 18-19; scales present; vertebrae 26 + 65-66 = 91-92.

Description. Scales present, relatively small, extending forward to near vertical through pectoral base; head and pectoral fins scaleless. Lateral line mediolateral, complete. Flesh firm. Gill slit restricted, extending ventrally to mid-pectoral base. Nostril tubes elongated, overhanging upper lip and produced beyond it. Both upper and lower lips continuous at symphysis, narrow, no fleshy lobes at sides.

Details of neurocranium not observed, except through radiographs. Head rather short and high. Bony elements of suspensorium appear well

ossified, as do those of gill arches.

Cephalic lateralis pore system moderately complete, pores small and rounded. Postorbital pores 1, 3 and 4 present. Two nasal pores. No interorbital pore. Three occipital pores. Suborbital bones 6, with five pores on ventral branch and one on ascending branch. Preoperculomandibular pores in primitive state, with four dentary, one anguloarticular and three preopercular pores. Mandibular and preopercular branches joined.

Teeth moderate, conical. No vomerine or palatine teeth. Palatal arch appears well developed. Hyomandibula posterior ramus normal. Ceratohyal-epihyal juncture with bone interdigitating dorsally, closely fused ventrally. Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth paltes. Gill rakers 4 + 11.

Posttemporal ventral ramus very weak. Scapular foramen probably enclosed. Four actinosts bearing 18-19 pectoral fin rays. Pelvic fins absent, pelvic bones of average size.

Epipleural ribs on first to ultimate precaudal vertebra. Pleural ribs on third through ultimate precaudal vertebra. Dorsal fin origin associated with second vertebra, with no free pterygiophores. All dorsal fin elements soft rays. Three anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with eight rays, thus total caudal rays 10. Last dorsal ray associated with fourth preural vertebra; last anal ray associated with second preural vertebra.

Palatine membrane absent. Two pseudobranchial filaments. Two very long pyloric caeca. Peritoneum black. Reproductive mode unknown,

probably oviparous. Vertebrae asymmetrical.

Distribution and species. A single species in the genus, Aiakas krefftii Gosztonyi, 1977 is known from two specimens taken on the Patagonian slope in 640-800 m. In addition, there is one specimen from the same area in the Zoological Institute, Leningrad.

Austrolycichthys Regan, 1913

(figs. 18, 19; pls. III, IV)

Austrolycichthys Regan, 1913: 244, 245, fig. 2 (type species: Lycodes brachycephalus Pappenheim, 1912, by subsequent designation of Jordan, 1920: 550); Norman, 1938: 81, 83, 84.

Remarks. This genus has traditionally contained two species allocated to it in addition to the type, namely Pappenheim's (1912) Lycodes bothriocephalus by Regan (1913) and Roule and Despax's (1911) Lycodes concolor by Norman (1938). These two species are here removed to the genus Ophthalmolycus Regan, 1913, and Austrolycichthys is expanded to include three rare species: Garman's (1899) Phucocoetes suspectus and Gymnelis conorhynchus and one undescribed species.

Diagnosis. Body robust, tail short; mental crests not developed; parasphenoid wing below margin of trigeminofacialis foramen; palatal arch well developed; vertebrae 20-24 (25) + 72-87 = 92-110; suborbital bones 7-8; scales present, absent on nape and cheeks; pelvic fins very small or absent; gill slit extending almost to ventral edge of pectoral base or just below it.

Description. Scales small, present on body and tail only. Lateral line mediolateral or mediolateral and ventrolateral. Flesh firm. Gill slit extending ventrally to just above lower edge of pectoral base or just

to it in A. brachycephalus, or well below it in other species.

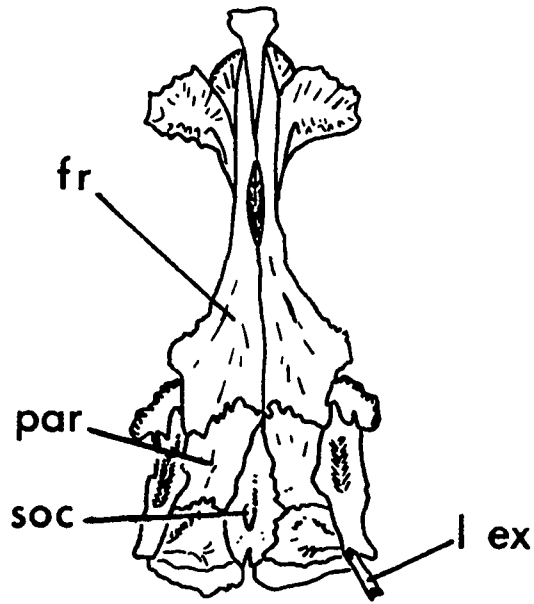
Detailed osteological observations made only on A. brachycephalus and A. suspectus. Parasphenoid wing below mid-height of trigeminofacialis foramen (fig. 18); frontal and parasphenoid not excluded by pterosphenoid. Sphenotic and parietal separated by frontal. Parietals not meeting in midline. Supraoccipital crest small; anterior ramus extending well under frontals. Supraoccipital and exoccipital narrowly contacting posteriorly (fig. 18).

Cephalic lateralis pores reduced, relatively small, rounded. Postorbital pores present are 1, 3, 4; 1, 4 or 4 only. One lateral extrascapular. Two pair of nasal pores. No interorbital pore. Supratemporal commissure absent and no occipital pores. Suborbital pores 5-6 on ventral segment, 0-2 on ascending segment, thus total pores 5-8. Seven suborbital bones except some individuals of A. suspectus with eight. Preoperculomandibular system in primitive condition, with four dentary, one anguloarticular and three preopercular foramina and pores (fig. 19). Preopercular and mandibular branches joined.

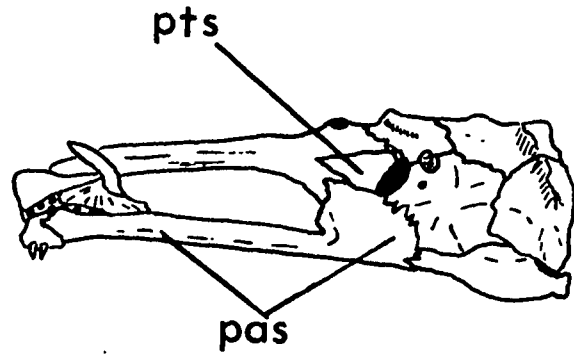
Teeth in jaws small, stout, sharp. Vomerine and palatine teeth present, sharp. Endopterygoid and ectopterygoid broadly articulating with quadrate (fig. 19). Hyomandibula posterior ramus normal. Opercle and subopercle well ossified. Ceratohyal-epihyal juncture smooth; these bones well ossified. Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed; three pair of infrapharyngobranchials and tooth plates. Gill rakers 1-3 + 9-15 = 10-16. One to three gill rakers on first hypobranchial bone.

Posttemporal ventral strut moderate to well developed. Scapular foramen enclosed; scapula with well developed posterior strut. Four actinosts bearing 15-19 pectoral rays. Pelvic fins with three short

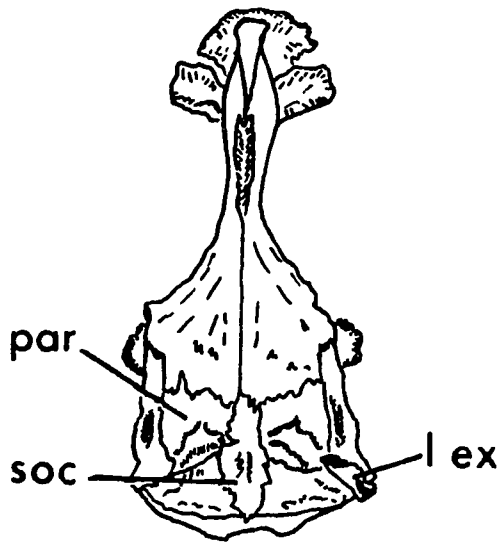
Figure 18. Neurocrania of Austrolycichthys. A) and B) Dorsal and lateral views, respectively, of A. brachycephalus, 263 mm SL. C) and D) Dorsal and lateral views, respectively, of A. suspectus, 280 mm SL. B. and D. rotated to show 3/4 lateral view. Left lateral extrascapular removed in both species.



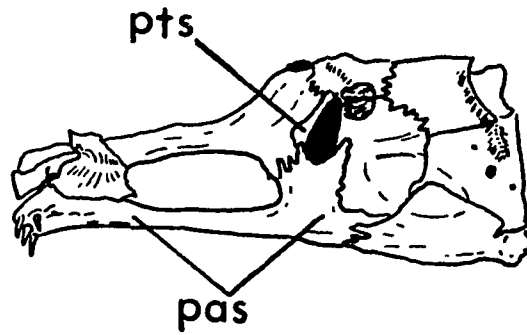
A.



B.

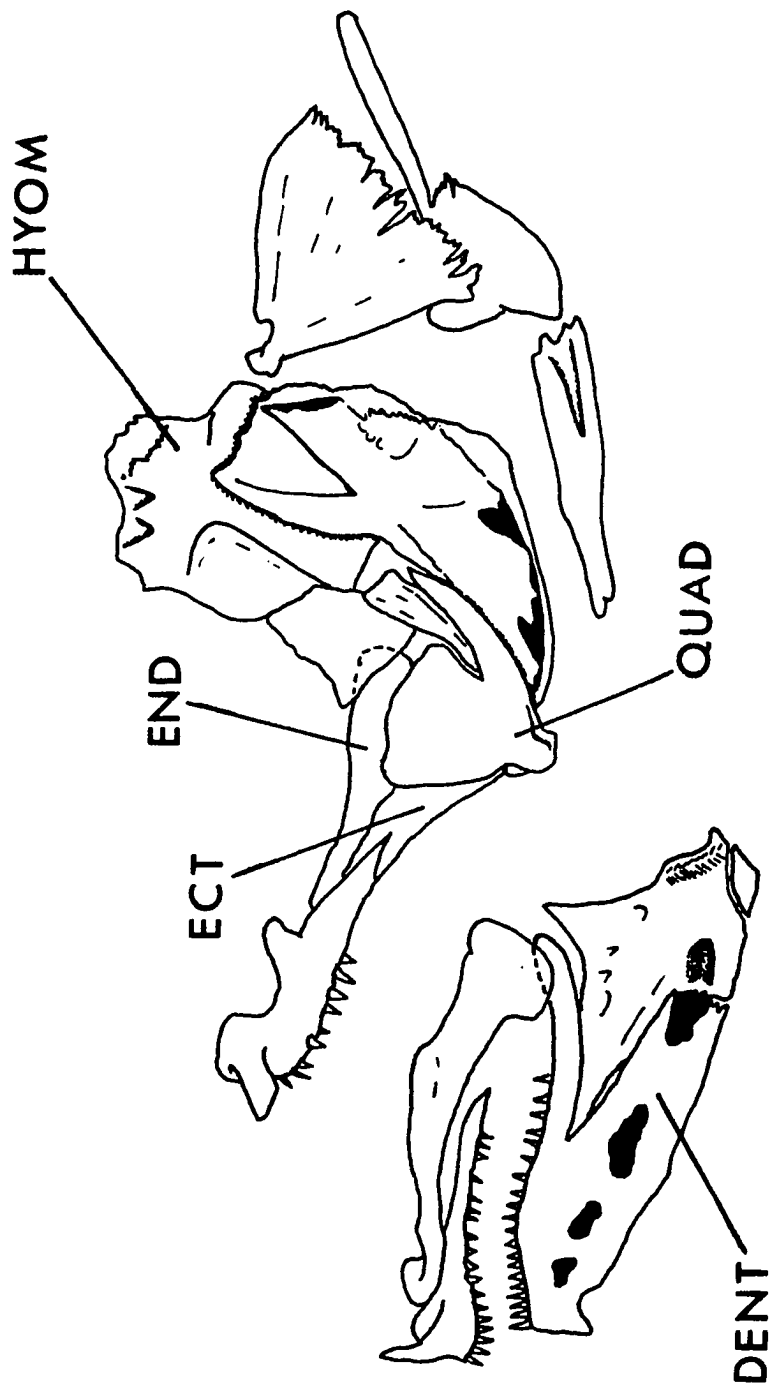


C.



D.

Figure 19. Jaws, suspensorium and opercular bones of Austrolycichthys suspectus, 280 mm SL. Jaw bones moved anteroventrad of their position in situ.



rays, except in A. conorhynchus in which they are absent.

Epipleural ribs on vertebrae 1 to 13-22. Pleural ribs on third to ultimate or penultimate precaudal vertebrae. Dorsal fin origin associated with vertebrae 2-6, with no free pterygiophores. Dorsal fin of all soft rays, or anterior first or second are flexible spines. Two to four anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural bearing one or two rays, hypurals with eight rays, thus total caudal rays 9-10. Last dorsal ray associated with third or fourth preural vertebra, last anal ray associated with second preural vertebra.

Palatine membrane weak. Pseudobranchial filaments 2-3. Two nub-like pyloric caeca. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae symmetrical only on tail.

Distribution and species. Austrolycichthys brachycephalus (Pappenheim, 1912): Antarctica, from Wilkes Land to Antarctic Peninsula in 200-600 m; probably circumpolar in coastal Antarctica. Austrolycichthys conorhynchus (Garman, 1899): Gulf of Panama in 3193-3280 m. Austrolycichthys suspectus (Garman, 1899): Coast of Peru to Gulf of California in 860-1280 m. Austrolycichthys sp. A: Straits of Florida in 867 m.

Additional references. Garman (1899: 131, 137, pls. 30, 31); Pappenheim (1912: 179, pl. 10, fig. 3); Waite (1916: 15, pl. 1, text figs. 2, 2A); Nybelin (1947: 55, 65); Andriashev (1959: 7); McAllister and Rees (1964: 106-107); Andriashev (1965: 513); Permitin (1969: 174).

Austrolycus Regan, 1913
(figs. 8F, 9D, 20; pl. XIV)

Austrolycus Regan, 1913: 245, 246 (type species: Austrolycus depressiceps Regan, 1913, by subsequent designation of Jordan, 1920); Norman,

1937a: 103, fig. 52; Gosztonyi, 1977: 200-204, fig. 3.

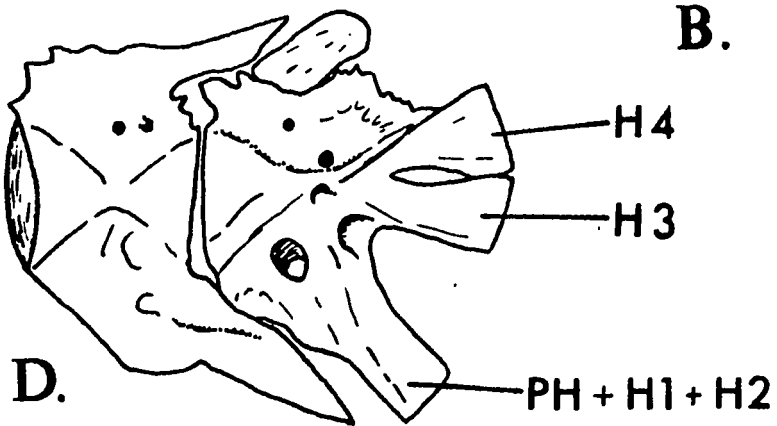
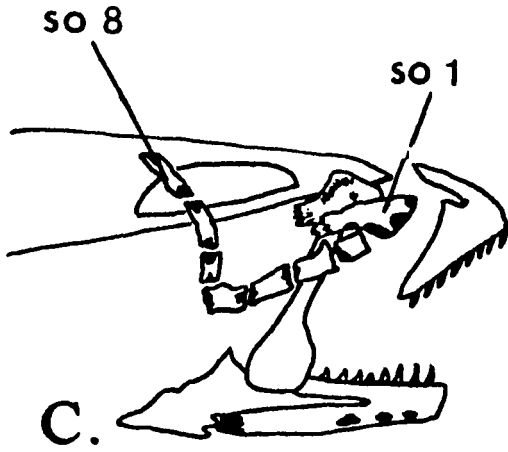
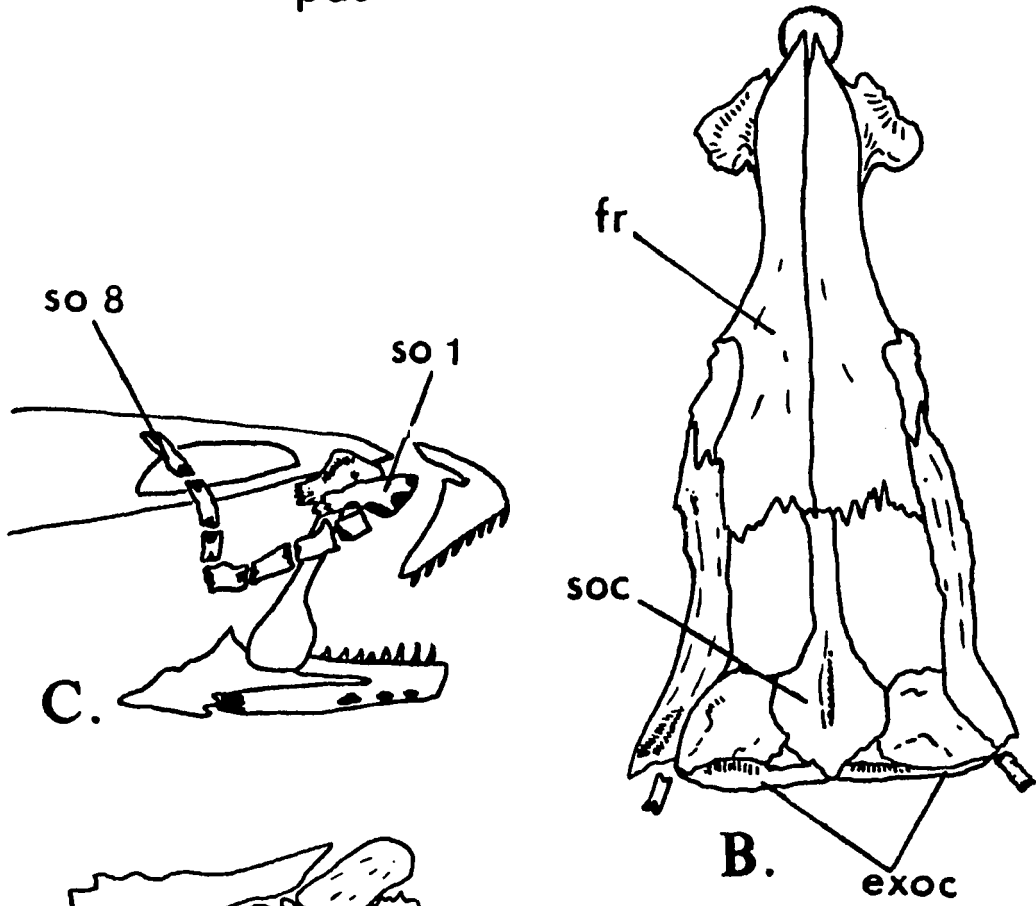
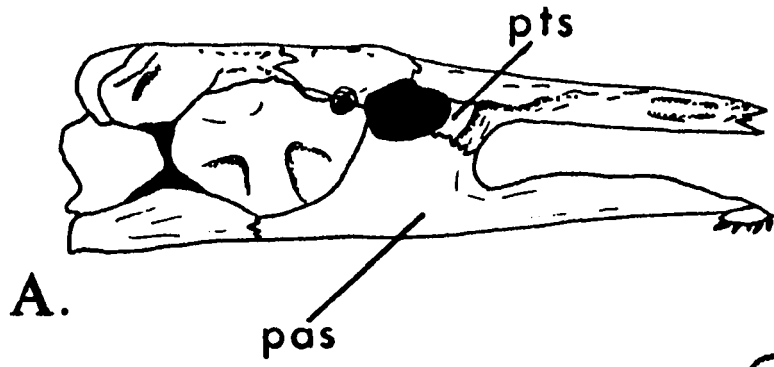
Diagnosis. Body robust, tail relatively long; frontal bones tapering (character 13); hyomandibula posterior ramus elongate (character 14); ceratohyal-epihyal juncture interdigitating (character 15); head strongly depressed, interorbital space flat; postorbital canal opening through pore 4 only; suborbital bones 7-8, with 6-7 pores; palatal arch well developed; no pyloric caeca; vomerine and palatine teeth present; scales and pelvic fins present; vertebrae 27-33 + 73-88 = 106-116.

Description. Scales present, very small. Lateral line mediolateral, complete. Flesh firm, not greatly thickened. Gill slit extending ventrally to mid-pectoral base or just slightly below it.

Parasphenoid wing broad, but no rami formed; dorsal edge more or less parallel with ventral surface, forming floor of trigeminofacialis foramen (fig. 20A). Pterosphenoid reduced, not excluding frontal and parasphenoid. Sphenotic moderate, excluded from parietal by frontal and pterotic. Parietals not meeting in midline. Supraoccipital rather large, anterior ramus extending well under frontals; mesial crest well developed. Posterior portion of neurocranium squared-off, steeply slanting; supraoccipital and exoccipital narrowly contacting (fig. 20B).

Cephalic lateralis pore system reduced in number, pores very small. One small lateral extrascapular present. Only postorbital pore 4 present. Two nasal pores. No interorbital or occipital pores, no supratemporal commissure and no remnants of bony supports on parietals. Suborbital bones 7-8, with six or seven pores on ventral branch and none on ascending branch (fig. 20C). Preoperculomandibular system in primitive condition, with four dentary, one anguloarticular and three preopercular pores. Mandibular and preopercular branches joined.

Figure 20. Some osteological features of Austrolycus. A) Lateral view of neurocranium of A. depressiceps, 191 mm SL. B) Dorsal view of neurocranium of A. depressiceps, 209 mm SL. C) Suborbital bones and jaws of A. laticinctus, 194 mm SL. D) First preural, ural vertebrae and hypural complex of A. depressiceps, 268 mm SL.



Teeth small, conical, anterior few slightly enlarged. Teeth present on vomer and palatine bones. Endopterygoid and ectopterygoid broadly articulating with quadrate. Hyomandibula posterior ramus elongate (fig. 8F). Opercle and subopercle well ossified. Ceratohyal-epihyal juncture strongly interdigitating (fig. 9D). Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers rather numerous: 2-5 + 11-15 = 14-18.

Posttemporal ventral strut absent. Scapular foramen enclosed; scapular posterior strut well developed. Four actinosts bearing 15-20 pectoral fin rays. Pelvic fins small, with three rays each.

Epipleural and pleural ribs on second through ultimate precaudal vertebrae. Dorsal fin origin associated with second vertebra, with no free pterygiophores. All dorsal fin elements soft rays. Two anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with eight rays, thus total caudal rays 10. Some individual variation expressed in shape of caudal elements, including one apparently atavistic specimen which had a separated parhypural-hypurals 1-2 complex (fig. 20D). Last dorsal fin ray associated with third or fourth preural vertebra; last anal ray associated with second preural vertebra.

Palatine membrane well developed. Seven pseudobranchial filaments. No pyloric caeca. Peritoneum light. This genus is oviparous, laying and guarding egg masses in the intertidal zone (A. E. Gosztonyi, pers. comm.). Vertebrae asymmetrical.

Distribution and species. Both Austrolycus depressiceps Regan, 1913 and A. laticinctus (Berg, 1895) spawn throughout the intertidal-shallow subtidal regions of temperate South America in appropriate habitats.

When not spawning, they may be found on the outer shelf to about 80 m. Rather abundant species, most collections are from the Patagonian-Falkland-Fuegian coasts, but both may be expected to occur throughout southern Chile.

Additional references. Günther (1862: 321, 322); Vaillant (1888: 21, pl. 3, fig. 1); Berg (1895: 71, pl. I, fig. 2); Steindachner (1898: 318-320, pl. XIX, fig. 8); Smitt (1898: 55 (partim), pl. V, fig. 35); Lahille (1908: 413-423, 428, 429, figs. 4-6).

Bothrocara Bean, 1891

(figs. 3C, 4F, 7B, 8C, 9C, 21; pl. XII)

Bothrocara Bean, 1891: 38, 39 (type species: Bothrocara mollis Bean, 1891, by monotypy); Bayliff, 1954: 82-108.

Bothrocaropsis Garman, 1899: 127-129, pl. XXXII, fig. 2, pl. XXXIII, figs. 1, 2 (type species: Bothrocaropsis alalonga Garman, 1899, by subsequent designation of Jordan, 1920).

Lycogramma Gilbert, 1915: 364-366, pl. XX, fig. 18 (type species: Maynea brunnea Bean, 1891, by original designation); Jordan and Hubbs, 1925: 320, 321; Schmidt, 1950: 114-117, pl. XI, figs. 1, 2.

Zesticthys Jordan and Hubbs, 1925: 321, 322, pl. XII, fig. 1 (type species: Zesticthys tanakae Jordan and Hubbs, 1925, by original designation).

Allolepis Jordan and Hubbs, 1925: 322, 323, pl. XII, fig. 2 (type species: Allolepis hollandi Jordan and Hubbs, 1925, by original designation); Schmidt, 1950: 120-122, pl. XII, figs. 1-3.

Remarks. Bothrocara is in great need of revision. The genus has been inordinately split on the basis of minor differences in dentition, allometry of the head, extent of the body lateral line branches and extent of squamation and scale shape. Allolepis was created on the basis of its possessing elongate scales set at right angles--the "basket-weave" pattern seen in some eels and ophidiids. In fact, most of the scales

of this species (Bothrocara hollandi) posteriorly are cycloid and rounded, as in other zoarcids. The anterior body scales of B. pusillum approach the "basket-weave" pattern as well.

Diagnosis. Body robust, tail relatively short; suborbital bones 7-9 (fig. 3C), with 8-10 very small pores; scapula with well developed posterior strut; palatal arch weakly developed; palatine membrane absent; branchiostegal membrane narrowly attached to isthmus; P 13-17; total vertebrae 114-132; two nub-like pyloric caeca; pelvic fins absent; scales present.

Description. Squamation fairly extensive, body, tail and abdomen scaled, nape with scales except in B. pusillum. Lateral line mediolateral, or mediolateral and dorsolateral (anteriorly). Flesh firm, rather delicate and transparent in juveniles and adult B. pusillum, especially on head. Gill slit extending ventrally to throat region, isthmus very narrow.

Parasphenoid wing very small, reaching base of trigeminofacialis foramen or slightly above it; well below its mid-height. Frontal and parasphenoid not separated by pterosphenoid. Sphenotic small, separated from parietal by pterotic and frontal (fig. 7B). Parietals moderate, not meeting in midline. Supraoccipital large, with well developed anterior ramus extending under frontals. Supraoccipital and exoccipital narrowly contacting posteriorly, or separated entirely by epioccipitals (fig. 7B).

Cephalic lateralis pore system relatively complete, pores very small. One or two lateral extrascapulars. Postorbital pores 1-4 or 1 and 4 present. Two nasal pores. One or no interorbital pore. One or no postocular pore in supraorbital canal. One mesial, two lateral or

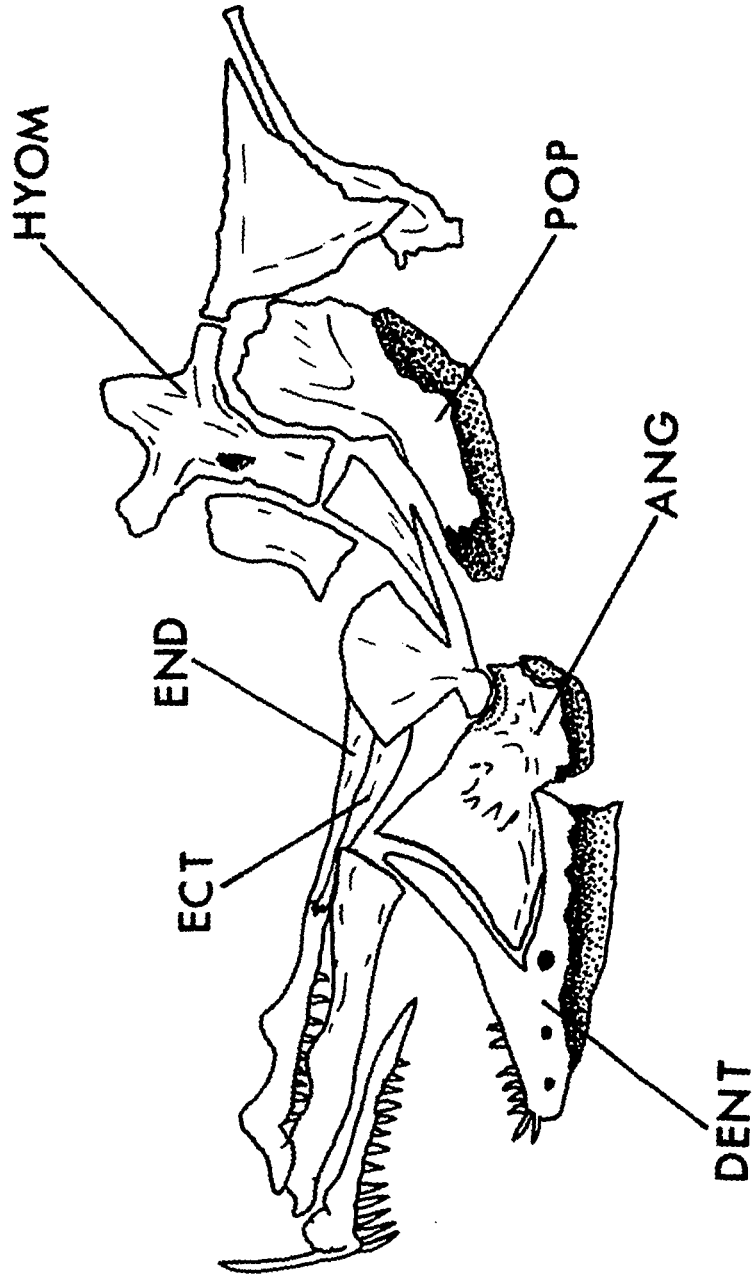
no occipital pores; those species with pores present have no bony supports on parietals for supratemporal commissure. Suborbital bones 7-9, rather truncated; suborbital pores 6-7 on ventral branch, 2-3 on ascending branch, total suborbital pores 8-10 (fig. 3C). Preoperculo-mandibular pores exiting from cavernous foramina in bones, or from deep trough (fig. 21). Four dentary, one anguloarticular and three preopercular pores, all in primitive state. Mandibular and preopercular branches joined.

Teeth small, numerous, no produced canines, multiserial anteriorly; teeth longer in males than females. Vomerine and palatine teeth present. Endopterygoid and ectopterygoid weakly articulating with quadrate (fig. 21). Hyomandibula posterior ramus normal. Opercle moderately well developed, subopercle mostly cartilage. Ceratohyal-epihyal juncture smooth (fig. 9C). Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed; three pair of infrapharyngobranchials and tooth plates. Gill rakers 2-6 + 11-18 = 13-23, rather numerous for eelpouts.

Posttemporal ventral strut very weak. Scapular foramen enclosed; scapula with well developed posterior strut. Four actinosts bearing 13-17 pectoral fin rays. Pelvic fins absent, pelvic bone a mere splint.

Epipleural ribs on vertebrae 1-10 or to 16. Pleural ribs extending from third to ultimate or penultimate precaudal vertebra. Dorsal fin origin associated with vertebrae 2-4, with no free pterygiophores. All dorsal fin elements soft rays. Zero to three anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with 8-12 rays, thus total caudal rays 10-13. Last dorsal fin ray associated with third or fourth preural vertebra; last anal ray associated with second or third preural vertebra.

Figure 21. Jaws, suspensorium and opercular bones of Bothrocara pusillum, 145 mm SL. Preoperculo-mandibular canal passes through open trough in dentary, anguloarticular and preopercle.



Palatine membrane absent; no vestige remains. Pseudobranchial filaments 7-8, rather long. Two nub-like pyloric caeca, never elongate. Peritoneum black. Reproductive mode oviparous (Kendall et al., 1983). Vertebrae symmetrical.

Distribution and species. Bothrocara alalongum (Garman, 1899): Gulf of California to Peru in about 1200-1900 m. Bothrocaropsis rictolata Garman, 1899 is probably a junior synonym of B. alalongum. Bothrocara brunneum (Bean, 1891): Okhotsk Sea to Baja California in 294-1752 m. Lycogramma soldatovi Shmidt, 1950 is probably a junior synonym of B. brunneum. Bothrocara elongatum (Garman, 1899): reliably known only from the holotype taken in the Gulf of Panama in 1271 m. Bothrocara hollandi (Jordan and Hubbs, 1925): throughout the Japan Sea and eastern Yellow Sea in about 200-1800 m. Allolepis nazumi Mori, 1956 is a junior synonym of B. hollandi. Bothrocara molle Bean, 1891: Kamchatka coast to northern Baja California (at least) in 577-2688 m. Bothrocara remigera Gilbert, 1915 is a junior synonym of B. molle. Bothrocara pusillum (Bean, 1891): eastern Bering Sea to off southern British Columbia in 221-2189 m. Bothrocara tanakai (Jordan and Hubbs, 1925): Pacific coast of Japan and central Japan Sea north to southern Okhotsk Sea in about 300-900 m and probably deeper. Bothrocara zestum Jordan and Fowler, 1903: Pacific coast of Japan and Japan Sea in about 600-1200 m.

Comments. Oshima (1957) described Lycogramma japonica from the Japan Sea. The description is very poor and short. The specimen is said to have no lateral line and four branchiostegal rays, in which case it could not belong in Bothrocara. In addition, such strange statements as "eye large, ...nearer to tip of snout than to eye..." indicate the

carelessness of this description, and others in the paper (see Lycodonus account herein and Anderson, 1982b: 30). The specimen was not figured nor a museum number indicated. It is probably a specimen of a previously described species of Bothrocarina as recognized here.

Additional references. Goode and Bean (1896: 527, 528); Jordan and Fowler (1903: 749, 750, fig. 3); Evermann and Goldsborough (1907: 344, pl. XXI, fig. 2); Starks and Mann (1911: 16, 17); Jordan, Tanaka and Snyder (1913: 400); Gilbert (1915: 366, 367, pl. XX, fig. 19); Soldatov and Lindberg (1930: 501, 502); Barnhart (1936: 90, 91, figs. 274, 276); Andriashev (1937: 343); Taranets (1937: 160, 165, 166); Hubbs and Schultz (1941: 16, 17); Matsubara (1955: 772, 782, 783, fig. 30); Bayliff (1959: 78, 79); Fedorov (1973: 19, 24); Hart (1973: 235-237, figs.); Lindberg (1974: 205, 206, figs. 788, 800); Lindberg and Krasnyukova (1975: 181-184, figs. 144-146); Peden (1979: 183, 184, figs. 1, 2).

Bothrocarina Suvorov, 1935

(figs. 5C, 10D, 22, 23; pl. XII)

Bothrocarina Suvorov, 1935: 435-437, 439, 440, fig. 1 (type species: Bothrocarina nigrocaudata Suvorov, 1935, by original designation); Schmidt, 1950: 118-120, fig. 10, pl. III, fig. 1.

Bothrocarichthys Schmidt, 1938: 653, 654 (type species: Bothrocarichthys microcephalus Schmidt, 1938, by monotypy); Taranets, 1937: 160, 165 (nomen nudum).

Diagnosis. Body robust, tail relatively short; six suborbital bones, with seven moderate pores; scapula without posterior strut; P 10-11; total vertebrae 113 (one fish); pyloric caeca enormous, two eye diameters in length; pterospheoid entirely cartilaginous; parhypural not fused to hypurals or ural centra (?; see below); frontal bones wide and truncated, their width >19% their length (character 13); branchiostegal

membrane narrowly attached to isthmus; palatal arch weakly developed; palatine membrane and pelvic fins absent; scales present.

Description. Squamation extensive, covering body, tail, vertical fins, nape to interorbital region and cheeks. Lateral line mediolateral, complete. Flesh firm. Gill slit extending ventrally to throat region, isthmus very narrow.

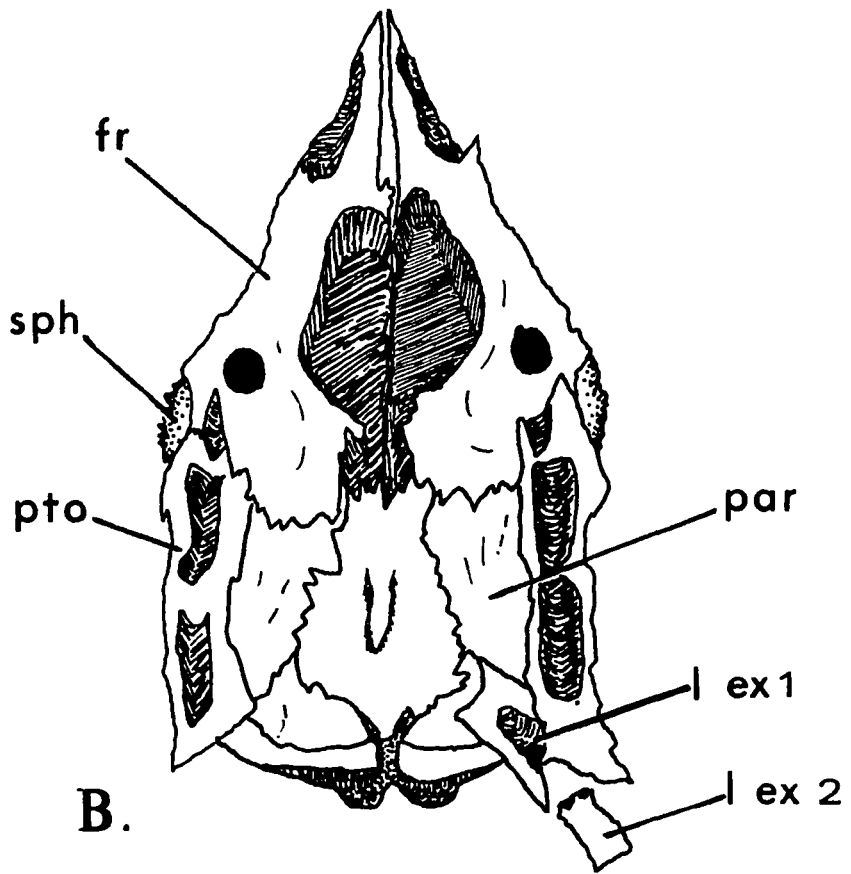
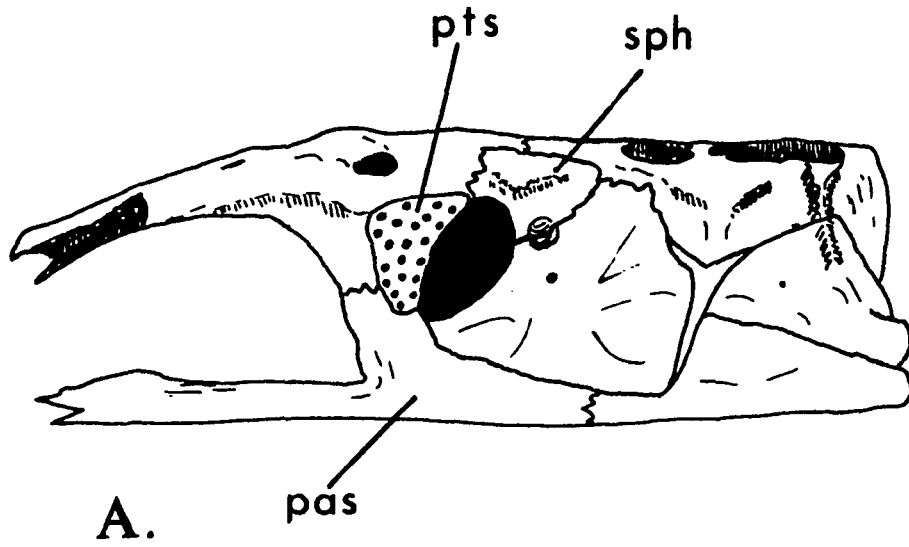
Parasphenoid wing low, not extending to mid-height of trigemino-facialis foramen; frontal and parasphenoid wing not excluded by pterosphenoid; pterosphenoid entirely cartilaginous (fig. 22A). Sphenotic very small, separated from parietal by pterotic and frontal. Parietal with two slender rami extending anteriorly well under frontal. Dorsal surface of frontals with deep cavernous trough (fig. 22B), through which passes the supraorbital commissure. Parietals reduced, well separated from midline. No anterior ramus of supraoccipital; supraoccipital narrowly contacting exoccipital.

Cephalic lateralis pore system moderately reduced. Foramina in bones very large, pores enlarged somewhat. Two lateral extrascapulars, proximalmost rather wide and flattened (fig. 22B). Postorbital pores 1-4 present. Two nasal pores. No interorbital pores; supratemporal commissure absent, with no bony supports or occipital pores. Suborbital bones six, with five pores on ventral branch and two on ascending branch. Preoperculo-mandibular system in primitive condition, with four dentary pores and foramina, one anguloarticular pore and three preopercular pores; preopercular pores open from shallow trough in preopercle. Mandibular and preopercular branches joined.

Teeth on jaw and palate small, needle-like. Endopterygoid and ectopterygoid weakly articulating with quadrate (fig. 5C). Hyomand-

Figure 22. Neurocranium of Bothrocarina microcephala, 338 mm SL.

A) Lateral view of left side. B) Dorsal view. Ethmoid region and left lateral extrascapulars not shown.



ibula posterior ramus normal. Opercle and subopercle almost entirely cartilage. Ceratohyal-epihyal juncture smooth (fig. 23A). Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed, with three rows of villiform teeth anteriorly; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 5 + 10 in one fish.

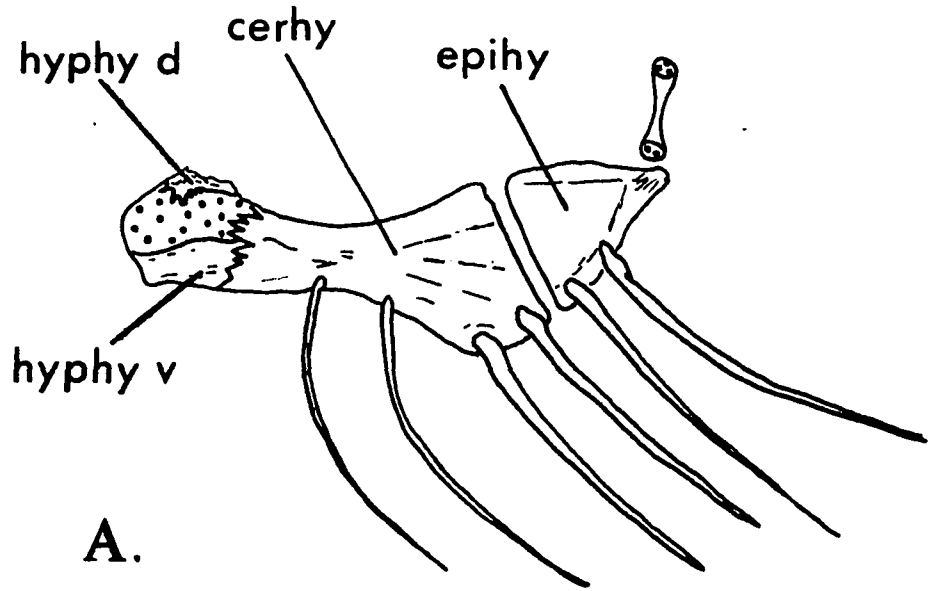
Posttemporal ventral ramus very weak. Scapula rounded, with no posteriorly directed strut supporting fin rays; scapular foramen enclosed (fig. 10D). Four actinosts, all entirely cartilaginous, bearing 10 or 11 pectoral fin rays. Pelvic fins absent, pelvic bones of average size, but almost entirely cartilage.

Epipleural ribs on vertebrae 1-11. Pleural ribs on vertebrae 3-19. Dorsal fin origin associated with vertebra 5, with no free pterygiophores. First dorsal fin element a flexible spine. One epural with two fin rays, hypurals with nine rays, thus total caudal rays 11 (in one fish). Bony remnant, apparently the parhypural, completely detached from caudal skeleton and associated with ventralmost caudal fin ray (fig. 23B). The significance of this unique occurrence may be questionable, due to the varied structures of the caudal skeleton in deossified zoarcids and because only two fish have been observed. The condition is provisionally accepted as diagnostic for Bothrocarina. Penultimate vertebra without neural arch. Last dorsal and anal fin rays associated with second preural vertebra.

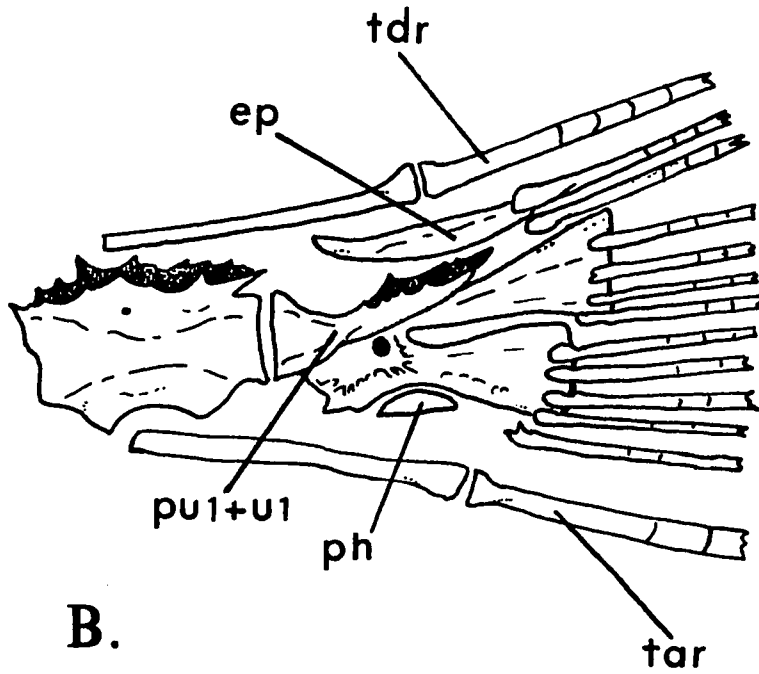
Palatine membrane absent. Pseudobranchial filaments 10, very long. Two greatly elongated pyloric caeca, their length about two eye diameters; caeca longer than those of any other zoarcid. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae symmetrical.

Distribution and species. Bothrocarina microcephala (Shmidt, 1938);

Figure 23. Bothrocarina microcephala, 338 mm SL. A) Left hyoid bar.
B) Bones of the caudal skeleton showing free parhypural
remnant.



A.



B.

Okhotsk Sea, from Tauiskaya Bay south to Hokkaido, Japan in 70-190 m and undoubtedly deeper. Bothrocarina nigrocaudata Suvorov, 1935: known only from the holotype taken off the east coast of Kamchatka (Ozernoy Bay) in 134-235 m.

Additional references. Matsubara (1955: 772, 782); Toyoshima (1983).

Crossostomus Lahille, 1908

(figs. 7C, 9E, 24, 25; pl. XIV)

Crossostomus Lahille, 1908: 408, 410, fig. 2 (type species: Lycodes (Iluocoetes) fimbriatus (non Jenyns, 1842) Steindachner, 1898, by original designation, = Crossolycus chilensis Regan, 1913); Norman, 1937a: 105, 106; Gosztonyi, 1977: 204-210, figs. 4-6.

Crossolycus Regan, 1913: 247 (type species: Crossolycus chilensis Regan, 1913, by subsequent designation of Jordan, 1920).

Diagnosis. Body robust, tail relatively short; frontal bones tapering (character 13); hyomandibula posterior ramus elongate (character 14); ceratohyal-epihyal juncture interdigitating (character 15); lips thickened, with deep grooves, which may be smooth-edged or scalloped; short tubular papillae between anterior suborbital and mandibular pores; gill slit extending ventrally to mid-pectoral fin base; palatal arch well developed; suborbital bones six, with five small pores; pelvic fin rays two or absent; vomerine and palatine teeth present or absent; vertebrae 28-32 + 67-70 = 95-106.

Description. Scales present, very small. Lateral line mediolateral, complete. Flesh firm, barred or monotone. Gill slit extending ventrally only to mid-pectoral base or slightly beyond it in very young fish. Mouth terminal, lips fleshy, with deep parallel grooves, edges of which may be smooth (C. fasciatus) or scalloped (C. chilensis).

Papillae between jaw pores longer in C. fasciatus, anteriormost almost tubular. Nostril tube very long in C. fasciatus, overhanging upper lip; shorter in C. chilensis, not reaching lip.

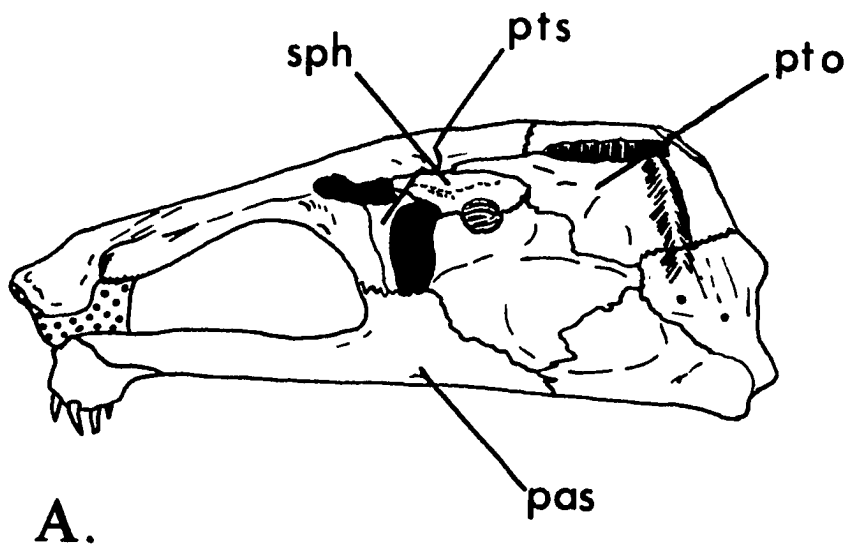
Parasphenoid wing moderately well developed, with no upward projecting ramus (fig. 24A). Frontal and parasphenoid not separated by pterosphenoid. Sphenotic reduced, separated from parietal by frontal and pterotic. Parietals moderate, not meeting in midline. Supraoccipital large, anterior ramus extending well under frontals, with moderate crest. Supraoccipital and exoccipital narrowly contacting posteriorly.

Cephalic lateralis pore system relatively reduced in number, pores small, rounded. One lateral extrascapular present. Postorbital pores 1 and 4 present. Two nasal pores. No interorbital or occipital pores; no supratemporal commissure or its bony supports across parietals. Six suborbital bones, first one (lacrima) massive, with broad cartilaginous border (fig. 24B). Five suborbital pores on ventral branch and none on upper branch. Preoperculo-mandibular system in primitive state, with four dentary, one angulo-articular and three preopercular pores and bone foramina. Mandibular and preopercular branches joined.

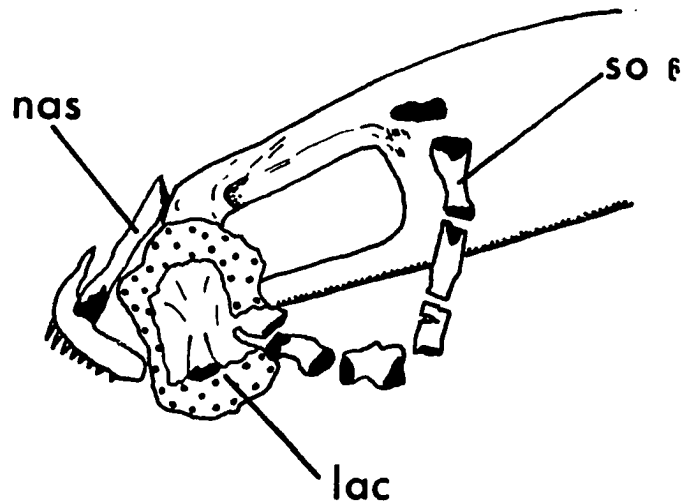
Teeth moderate, conical. Teeth present on vomer and palatine bones (C. fasciatus) or absent (C. chilensis). Bones of suspensorium and jaws massive; endopterygoid and ectopterygoid broadly articulating with quadrate (fig. 25A; Gosztonyi, 1977, fig. 5). Hyomandibula posterior ramus elongate. Opercle and subopercle well ossified at edges. Ceratohyal-epihyal juncture strongly interdigitating (fig. 9E). Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2 + 5-9 = 7-11.

Posttemporal ventral strut weak (fig. 25B). Scapular foramen

Figure 24. Crossostomus fasciatus, 118 mm SL. A) Left lateral view of neurocranium. B) Left lateral view of skull and suborbital bones.

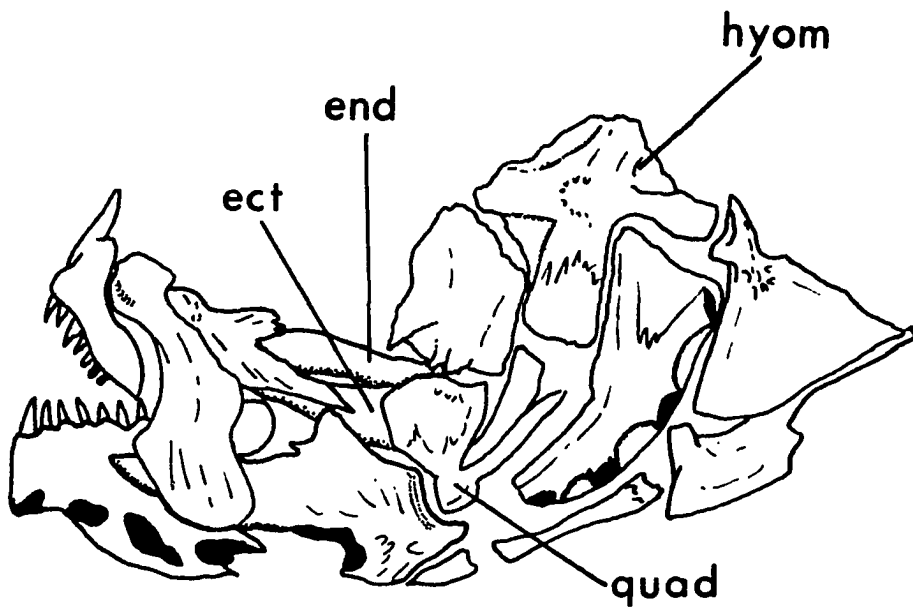


A.

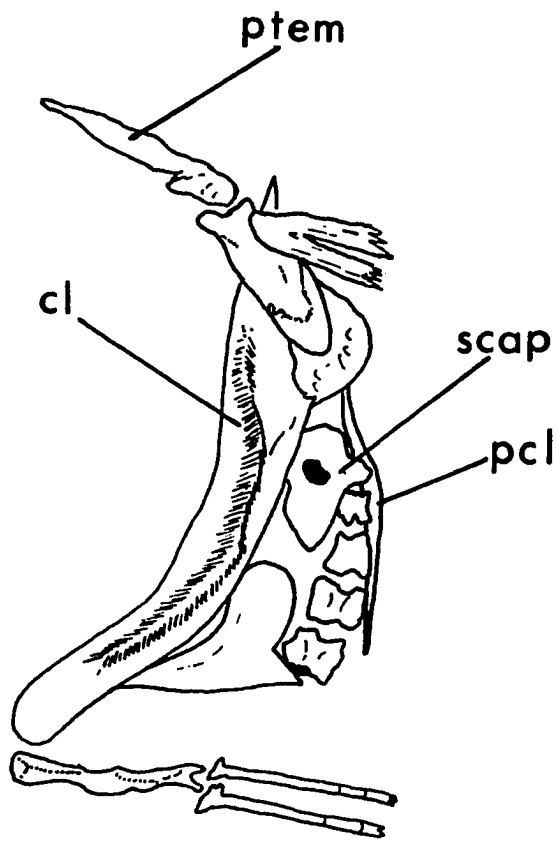


B.

Figure 25. Crossostomus fasciatus, 118 mm SL. A) Left lateral view of jaws, suspensorium and opercular bones. B) Left lateral view of pectoral girdle.



A.



B.

enclosed; scapula with well developed posterior strut. Four actinosts bearing 16-17 pectoral fin rays. Pelvic bones rather large, bearing two fin rays in most known specimens. Crossostomus chilensis occasionally lacks pelvic fins (Gosztonyi, 1977).

Epipleural ribs on vertebrae 2-24. Pleural ribs on third to ultimate precaudal vertebra. Dorsal fin origin associated with first vertebra, with no free pterygiophores. All dorsal fin elements soft rays. One or two anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with eight rays, thus total caudal rays 10. Last dorsal ray associated with fourth preural vertebra; last anal ray associated with second preural vertebra.

Palatine membrane well developed, covered with sensory papillae. Six pseudobranchial filaments. Two nub-like pyloric caeca. Peritoneum light. Both species of Crossostomus are oviparous, laying and guarding egg masses in the intertidal zone (A. E. Gosztonyi, pers. comm.). Vertebrae asymmetrical.

Distribution and species. Both Crossostomus chilensis (Regan, 1913) and C. fasciatus (Lönnberg, 1905) live in the Patagonian-Falkland-Fuegan region but may be expected to occur in the poorly collected southern Chile. Young and adults have been taken in subtidal kelp stands and the rocky intertidal zone.

Additional references. Steindachner (1898: 322, pl. XX, fig. 10); Lönnberg (1905: 20-22).

Dadyanos Whitley, 1951
(figs. 8E, 9F, 26, 27)

Platea Steindachner, 1898: 323, pl. XXII, fig. 12 (type species: Platea

insignis Steindachner, 1898, by original designation. Preoccupied by Platea Brisson, 1760, in Aves).

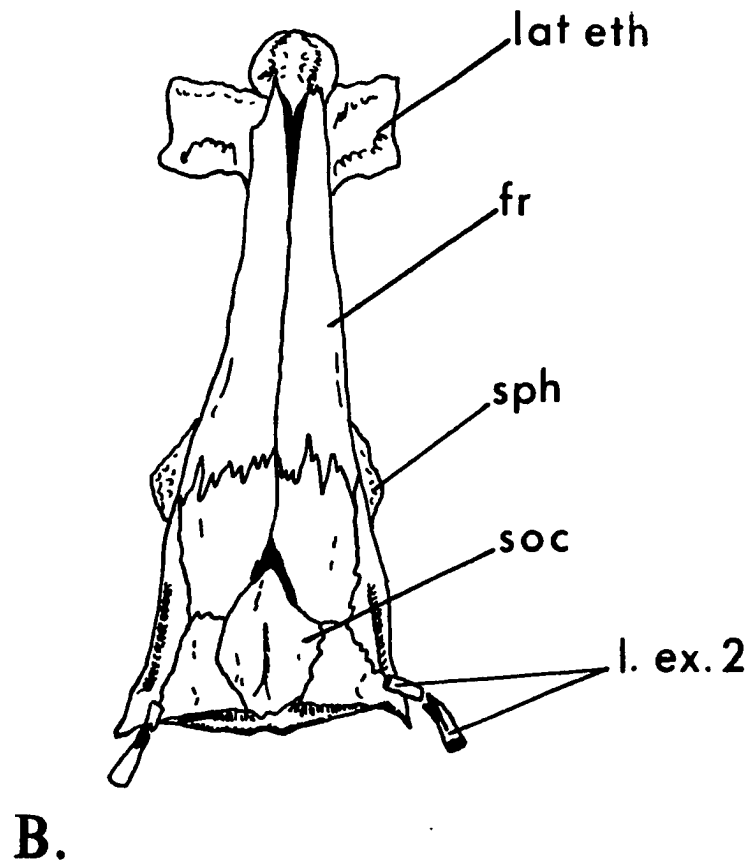
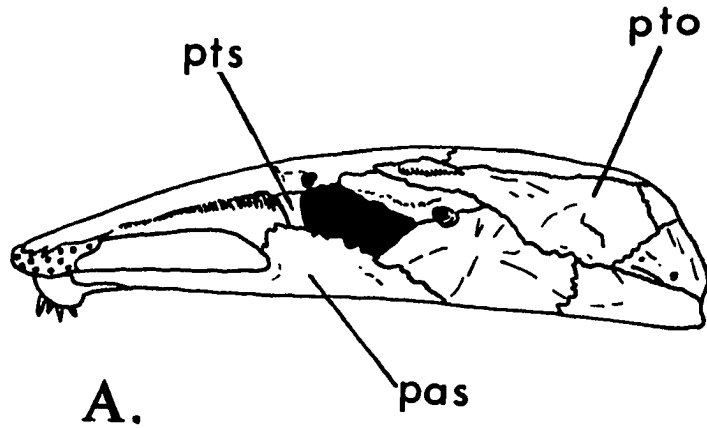
Dadyanos Whitley, 1951: 68 (new combination, takes same type species); Gosztonyi, 1977: 210-212, figs. 6, 7.

Diagnosis. Body robust, tail relatively short; frontal bones tapering (character 13); hyomandibula posterior ramus elongate (character 14); ceratohyal-epihyal juncture interdigitating (character 15); teeth in adults incisiform (character 37); scales present only in small area on tail in largest adults; gill slit extending ventrally to mid-pectoral base; tubular dermal papillae between anterior jaw pores; palatal arch well developed; suborbital bones seven, with six pores; vomerine and palatine teeth absent; pelvic fins present; only postorbital pore 4 present; parietals meeting in midline; no supraoccipital anterior ramus; vertebrae 21-24 + 84-93 = 107-116.

Description. Scales develop only in posterior patch on tail of fish over about 170 mm; this patch larger in some specimens than others. Gosztonyi (1977) first noted delayed scale development in Dadyanos; it had been reported previously as scaleless, as did Fedorov (1982). Lateral line mediolateral, complete. Flesh firm, but not thickened. Gill slit extending ventrally to mid-pectoral base in all specimens; pectoral base moderately high on body. Dermal papillae between anteriormost suborbital and mandibular pores; more triangular and broader-based on lower jaw, but tubular anteriorly on face.

Parasphenoid wing rather large, but broader than high; not extending above mid-height of trigeminofacialis foramen; frontal and parasphenoid not separated by pterosphenoid (fig. 26A). Sphenotic small, separated from parietal by pterptic and frontal. Frontals tapering,

Figure 26. Neurocranium of Dadyanos insignis, 198 mm SL. A) Left lateral view. B) Dorsal view.



mid-orbital width scarcely narrower than widest point posteriorly (fig. 26B). Parietals enlarged, meeting broadly in midline. Supraoccipital ovoid, moderate, with no anterior ramus; mesial crest moderate; supraoccipital and exoccipital narrowly contacting posteriorly.

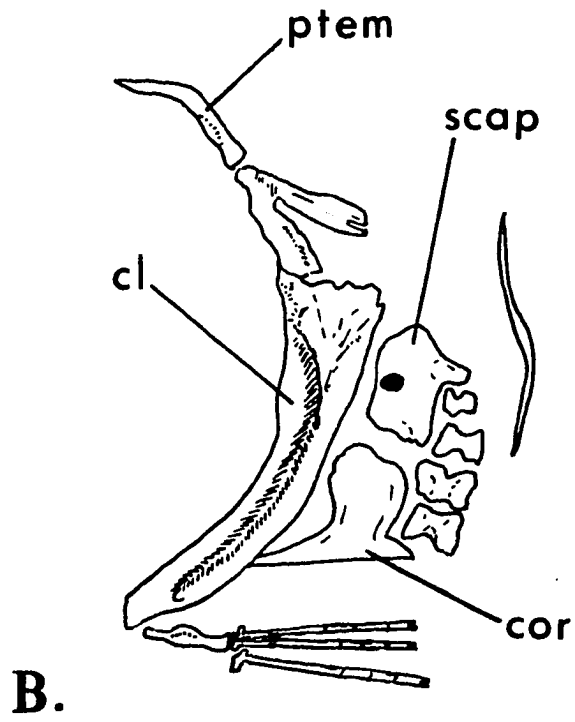
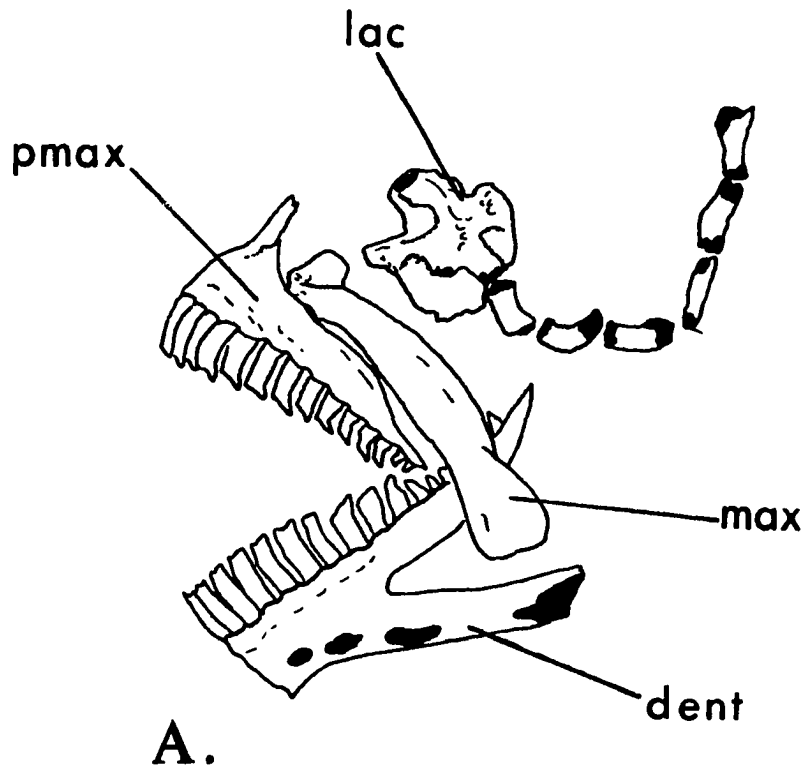
Cephalic lateralis pore system reduced in number, pores small and rounded. One lateral extrascapular (distalmost) present, but fragmented into two ossifications in one specimen (fig. 26B). Postorbital pore 4 present only in this canal, as in Austrolycus and Iluocoetes effusus. Two nasal pores. No interorbital or occipital pores. No supratemporal commissure or bony supports across parietals. Seven suborbital bones, first rather large, with six pores on ventral branch and none on ascending branch (fig. 27A). Preoperculomandibular system in primitive state, with four dentary, one anguloarticular and three preopercular pores and bone foramina. Mandibular and preopercular branches joined.

Teeth on jaws of juveniles rather long and stout. These develop into evenly spaced, uniserial incisors in adults of both sexes (fig. 27A; Gosztanyi, 1977, fig. 7). No teeth on vomer or palatine bones. Endopterygoid and ectopterygoid broadly articulating with quadrate. Hyomandibula posterior ramus elongate (fig. 8E). Metapterygoid large. Opercle and subopercle well ossified, but opercle reduced in size. Ceratohyal-epihyal juncture strongly interdigitating (fig. 9F). Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed; three pairs of infra-pharyngobranchials and tooth plates. Gill rakers 1-2 + 8-10 = 9-12.

Posttemporal ventral strut very weak (fig. 27B). Scapular foramen enclosed; scapular posterior ramus well developed. Four actinosts bearing 16-17 pectoral fin rays. Pelvic fins present, with three rays each, pelvic bones not enlarged (fig. 27B).

Figure 27. Some osteological features of Dadyanos insignis, 198 mm SL.

A) Jaws and suborbital bones; jaws moved anteroventrad to their position in situ. B) Left lateral view of pectoral girdle.



Epipleural ribs on vertebrae 2-17 or 22. Pleural ribs on third through ultimate precaudal vertebra. Dorsal fin origin associated with second vertebra, with no free pterygiophores. All dorsal elements soft rays. Two anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with eight rays, thus total caudal rays 10. Last dorsal fin ray associated with fourth preural vertebra; last anal ray associated with second preural vertebra.

Palatine membrane well developed, covered with small sensory papillae. Six pseudobranchial filaments, rather long. Two nub-like pyloric caeca. Peritoneum light. This species is oviparous, laying and guarding egg masses in the intertidal zone (A. E. Gosztonyi, pers. comm.). Vertebrae asymmetrical.

Distribution and species. A single species in the genus, Dadyanos insignis (Steindachner, 1898) is known from Patagonia and Tierra del Fuego intertidal zone (when spawning) and subtidal regions to about 40 m (Gosztonyi, 1977). Probably also occurs in the poorly collected but similar habitats of southern Chile.

Additional references. Lahille (1908: 407, 408, fig. 3); Regan (1913: 247, 248); Hussakof (1914: 91); Thompson (1916: 417); Norman (1937a: 107, 108, fig. 56).

Derepodichthys Gilbert, 1895
(figs. 5D, 28)

Derepodichthys Gilbert, 1895: 456 (type species: Derepodichthys alepidotus Gilbert, 1895, by original designation); Clemens and Wilby, 1949: 196, 197, fig. 134; Hart, 1973: 248, 249, fig.; Anderson and Hubbs, 1981: 341-352, figs. 1-10, tab. 1.

Remarks. This monotypic genus was known in the literature from only

the holotype, and placed in a separate family, Derepodichthyidae, until Anderson and Hubbs (1981) redescribed it, showing its relationships within Zoarcidae.

Diagnosis. Body low, tail elongate; cleithrum extended far forward, pelvic fins inserted under eye, each of three joined rays emanating from a common, erectile base; pelvic bones enlarged; teeth on jaws very long, recurved; sphenotic and parietal articulating; two pair of infra-pharyngobranchials; four suborbital bones; palatal arch greatly reduced; scales and lateral line absent; flesh gelatinous; vertebrae 22-26 + 92-98 = 114-122.

Description. Scales and lateral line absent. Flesh delicate, with thick gelatinous layer (Anderson and Hubbs, 1981, fig. 1B). Gill slit restricted, extending ventrally to lower edge of pectoral base, but well away from isthmus due to small, high-placed pectoral fin (Anderson and Hubbs, 1981, fig. 2).

Bones of neurocranium thin, extensive areas of cartilaginous capsules not covered by bone. Parasphenoid wing low; frontal and parasphenoid separated by pterosphenoid; trigeminofacialis foramen minute. Sphenotic enlarged, broadly contacting parietal along its lateral edge. Parietals not meeting in midline. No supraoccipital anterior ramus. Supraoccipital and exoccipital separated by epioccipital (Anderson and Hubbs, 1981, figs. 4, 5).

Cephalic lateralis pore system reduced, but pores enlarged (Anderson and Hubbs, 1981, fig. 2). Lateral extrascapulars absent. Only postorbital pore 1 present. Two nasal pores. No interorbital or occipital pores. Supratemporal commissure absent and no bony supports remain

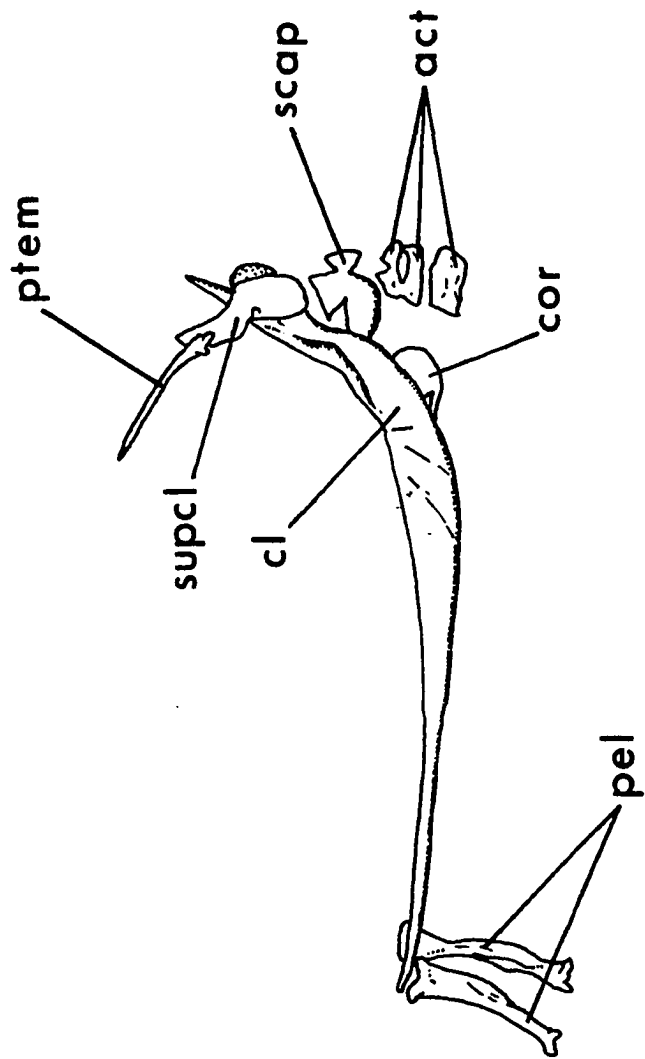
on parietal. Four suborbital bones, all these on ventral branch, greatly reduced. Five suborbital pores, all these also ventral. Dentary with minute foramen at symphysis, but preoperculomandibular pore 1 never formed; preoperculomandibular pores 2-4 open from shallow groove in dentary. Anguloarticular pore present; three preopercular pores and bone foramina in primitive condition (Anderson and Hubbs, 1981, fig. 6). Mandibular and preopercular branches joined.

Teeth on jaws, vomer and palatine bones extremely long; more numerous and smaller in females than males (Anderson and Hubbs, 1981, fig. 3). Palatine teeth rarely absent. Endopterygoid and ectopterygoid very weak, separated from quadrate and palatine by thin cartilaginous pads. Hyomandibula posterior ramus normal. Ceratohyal-epihyal juncture smooth. Branchiostegal rays 4 + 2 (Anderson and Hubbs, 1981, fig. 6). Ceratobranchial 5 with single row of teeth; two pairs of infrapharyngo-branchials with tooth plates, corresponding to gill arches two and three (Anderson and Hubbs, 1981, fig. 7). Gill rakers few, 0-1 + 11-12 = 11-13.

Posttemporal ventral strut absent. Cleithrum with anteriorly extended ventral ramus supporting enlarged pelvic bones and fin rays (fig. 28). Postcleithrum absent. Scapular foramen a small, anterior, open slit; scapular posterior strut well developed. Three actinosts bearing 10-11 small pectoral fin rays. Pelvic fin rays three, moderately long, joined, on a fleshy, erectile base (Anderson and Hubbs, 1981, fig. 1).

Epipleural ribs absent. Pleural ribs beginning on vertebrae 3-4, extending to vertebrae 6-8. Dorsal fin origin associated with vertebrae 6-9, with no free pterygiophores. All dorsal fin elements soft rays.

Figure 28. Left lateral view of pectoral girdle of Derepodichthys
alepidotus, 127 mm SL; redrawn from Anderson and Hubbs
(1981).



One or two anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one fin ray, hypurals with 7-8 rays, thus total caudal rays 8-9. Last dorsal fin ray associated with third preural vertebra in all specimens; last anal fin ray associated with second preural vertebra (Anderson and Hubbs, 1981, fig. 10).

Palatine membrane weak. Pseudobranchial filaments 2-4, very short. Two nub-like pyloric caeca. Peritoneum black. This species is oviparous. Vertebrae symmetrical.

Distribution and species. A single species, Derepodichthys alepidotus Gilbert, 1895, is known from thirteen specimens from off the Queen Charlotte Islands, British Columbia, the deep basins of southern California and in the Gulf of California in ca. 1000-2904 m. All but two captures are from below 1600 m.

Eucryphycus gen. nov.

(figs. 16B, 29; pl. VII)

Maynea (non Cunningham, 1871). Starks and Mann, 1911: 16-18; Gilbert, 1915: 362-364, pl. XIX, fig. 17; McAllister and Rees, 1964: 106, 107.

Type species. Maynea californica Starks and Mann, 1911; herein designated.

Remarks. This genus contains a single species which has been allied to the South American Maynea puncta (Jenyns, 1842), entirely on the basis of the absence of pelvic fins, small mouth and some unstated characters. In fact, E. californicus and M. puncta are quite different, being separated mostly on the basis of synapomorphies unique to Maynea and its close relatives (see Phylogeny of Zoarcidae).

Etymology. From the Greek εὐκρυφίος (well-hidden) and φύκος (seaweed),

alluding to its habit of hiding in masses of benthic drift-kelp (Cailliet and Lea, 1977).

Diagnosis. Suborbital bones 8-9, in L-shaped pattern around orbit; upper lips continuous; dorsal fin origin associated with vertebrae 4-6; vertebrae 27-28 + 79-84 = 106-114; C 10; exoccipital separated from supraoccipital; pelvic fins absent; vomerine and palatine teeth present; parietals meeting in midline.

Description. Scales present. Flesh firm, reddish orange. Lateral line mediolateral, incomplete, extending from above gill opening to just before anus. Gill slit extending below pectoral fin base.

Neurocranium truncated, moderately deep. Parasphenoid wing extending to mid-height of trigeminofacialis foramen or slightly above, not separated from frontal by pterosphenoid. Sphenotic and parietal separated by frontal. Parietals very large, meeting in midline; with well developed supratemporal commissure at posterior margin (fig. 29A). Exoccipital separated from supraoccipital by epioccipitals.

Cephalic lateralis pore system nearly complete. Two lateral extrascapulars, first sometimes fragmenting into two pieces (fig. 29A). All four postorbital pores present. Two nasal pores. No interorbital pore. Three occipital pores. Preoperculomandibular system in primitive condition, with four dentary, one anguloarticular and three preopercular pores. Eight suborbital pores; eight or nine suborbital bones (this high number probably represents fragmentations of the third and sixth suborbitals--seven bones would be true condition; fig. 29B). Mandibular and preopercular branches joined.

Teeth simple, moderate, sharp. Teeth on palatines and vomer of

Figure 29. Eucryphycus californicus, 173 mm SL. A) Dorsal view of neurocranium; ethmoid region not shown. B) Left lateral view of jaws, suspensorium and opercular bones.

males larger than females, stout. Posterior ramus of hyomandibula normal (fig. 29B). Branchiostegal rays 4 + 2. Endopterygoid and ectopterygoid weak, not extending along half of quadrate upper and anterior surfaces (fig. 29B). Metapterygoid weakly developed. Ceratohyal-epihyal juncture smooth. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2-3 + 12-13 in adults, juveniles have fewer (1 + 7 in smallest).

Posttemporal ventral ramus well developed. Scapular foramen enclosed, scapula with well developed posterior strut. Four actinosts bearing 13-14 pectoral rays. No pelvic fins.

Epipleural ribs extend from first to 13th or 14th vertebrae. Pleural ribs on first to ultimate precaudal vertebrae. Dorsal fin origin above middle of pectoral fin, associated with vertebrae 4-6. D 97-107, all soft rays, first not segmented, but divided. Two to four anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with eight rays, thus total caudal rays 10. Last dorsal ray associated with third to fifth preural vertebrae; last anal ray associated with second preural vertebra; occasionally two anal rays attached to haemal spine of second preural vertebra, as in Macrozoarces (fig. 16B).

Palatine membrane very weak. Pseudobranchial filaments 4, very long. Two nub-like pyloric caeca. Peritoneum black. Eucryphycus is oviparous, spawning year-round, with peak activity in winter months (Kliever, 1976). Vertebrae symmetrical.

Distribution and species. A monotypic genus, Eucryphycus californicus (Starks and Mann, 1911) is known only along the coast of California, from off San Diego to Monterey Bay in 73-545 m. Habitat is drifting masses

of seaweed, or similar refugia, which attracts its major prey, gammarid amphipods. Chiefly known from over 1200 individuals captured in the Monterey Submarine Canyon between 1972 and 1976 (Cailliet and Lea, 1977).

Additional references. Hubbs (1916: 166); Eschmeyer and Herald (1983: 106, pl. 11).

Exechodontes DeWitt, 1977

(figs. 30, 31)

Exechodontes DeWitt, 1977: 789-793, figs. 1-3 (type species: Exechodontes daidaleus DeWitt, 1977; by original designation); Anderson and Hubbs, 1981: 348; Anderson, 1982b: 19, 20.

Remarks. DeWitt (1977) placed Exechodontes in undiagnosed subfamily Hadropareinae of Schmidt (1950), but I place it among the Lycodini on the basis of its L-shaped suborbital bone configuration.

Diagnosis. Body robust, tail short; cephalic lateralis pores absent; suborbital bones six, in L-shaped pattern; body lateral line and scales absent; sphenotic and parietal articulating; frontal and parasphenoid separated by pterosphenoid; two pair of infrapharyngobranchials and tooth plates; ceratobranchial 5 without teeth; pseudobranch absent; palatal arch well developed; vomerine teeth present or absent; palatine teeth absent; flesh gelatinous; vertebrae 19-21 + 72-78 = 92-97; dorsal fin origin associated with vertebrae 9-11; pelvic fins present.

Description. Body and tail moderately elongated, but vertebral counts low (see above). Head rounded. Flesh gelatinous, delicate, without scales or lateral line neuromasts on body or head. Gill slit extending ventrally to pectoral base lower margin, but away from throat region, due to reduction of pectoral fin.

Parasphenoid wing well below mid-height of trigeminofacialis foramen. Frontal separated from small parasphenoid wing by rather large, triangular pterosphenoid; frontal wing not extensive. Sphenotic enlarged, overlapping frontal and contacting parietal posteriorly (fig. 30A). Pterotic smooth, without groove for postorbital commissure. One greatly reduced lateral extrascapular. Parietals meeting in midline. Supraoccipital extending well anteriorly under frontal, with very low mesial crest. Supraoccipital and exoccipital narrowly contacting posteriorly.

No cephalic lateralis pores in any specimen, all of which are adult or subadult. Area of passage of canals through dentary and preopercle an open trough (fig. 30B). No supraorbital, postorbital or supratemporal commissures or grooves in bones to pass these, except shallow trough in anterior part of frontals. Suborbital bones greatly deossified, but forming typical L-shaped configuration of all "higher" zoarcids (fig. 30C).

Teeth on jaws very small, slightly enlarged anteriorly. No teeth on palatine bones. Teeth on vomer 1-4, except in two individuals which had no teeth (both adults). Endopterygoid and ectopterygoid strongly articulating with quadrate. Hyomandibula posterior ramus normal. Opercle and subopercle poorly ossified. Ceratohyal-epihyal juncture smooth (fig. 31A). Gill rakers 4 + 2. Pharyngeal dentition reduced; none on ceratobranchial 5, only two pairs of infrapharyngobranchials, corresponding to gill arches 2 and 3, teeth few and small. Gill rakers 0 + 9-12.

Posttemporal ventral ramus very weak. Scapular foramen enclosed, with well developed posterior strut. Four actinosts bearing 13-15 short pectoral fin rays (fig. 31B). Pelvic fins present, with two or three rays, distalmost unsegmented or absent (fig. 31C).

Figure 30. Exechodontes daidaleus, 92 mm SL. A) Dorsal view of neurocranium. B) Left lateral view of jaws, suspensorium and opercular bones. C) Head and jaws with suborbital bones.

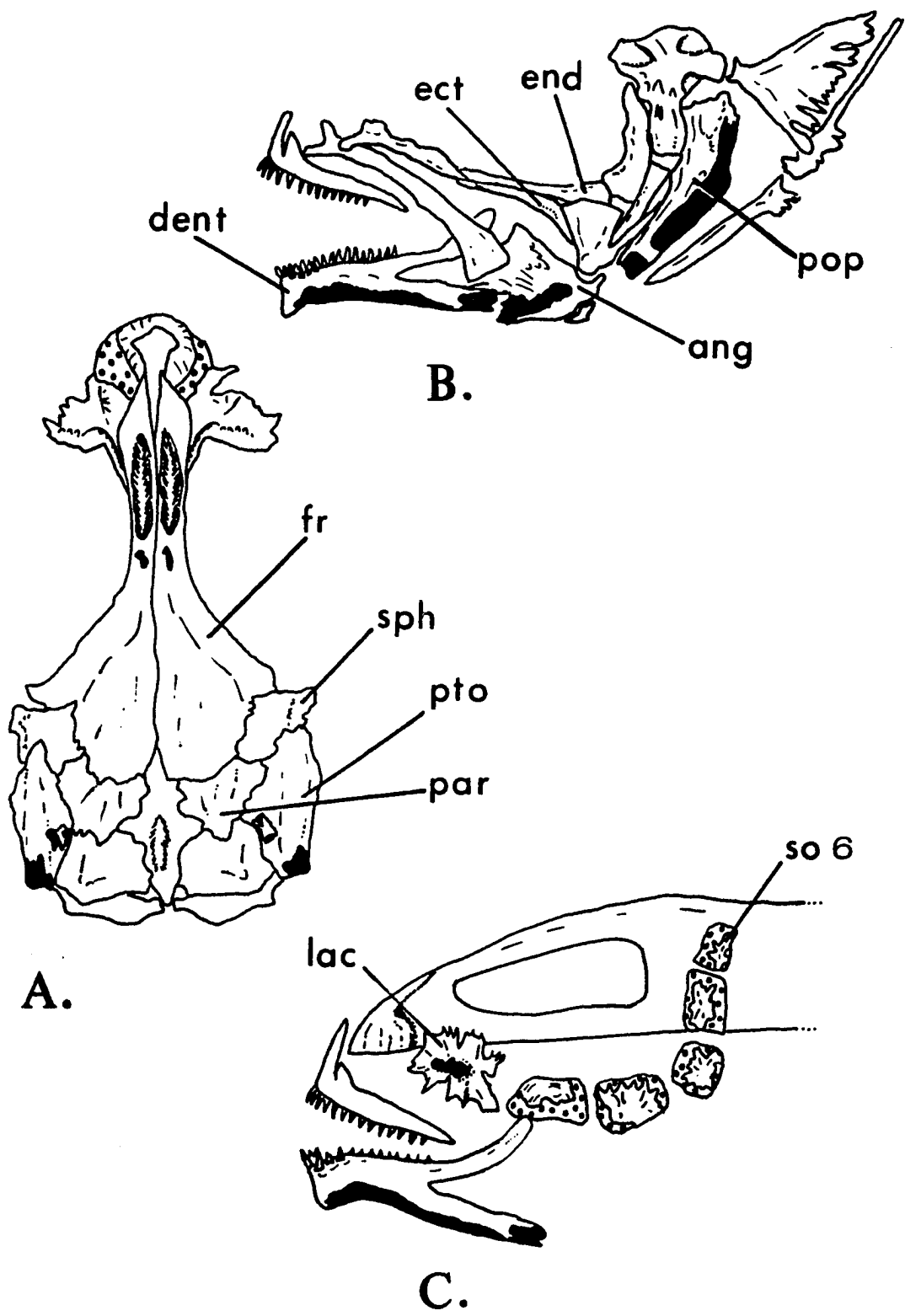
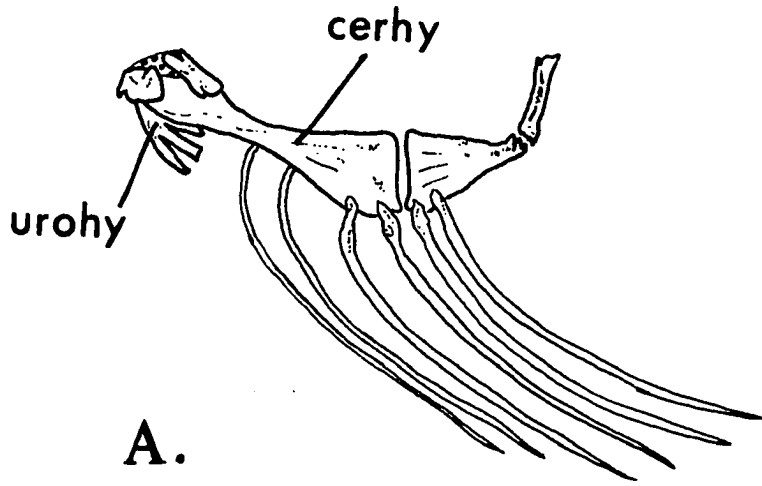
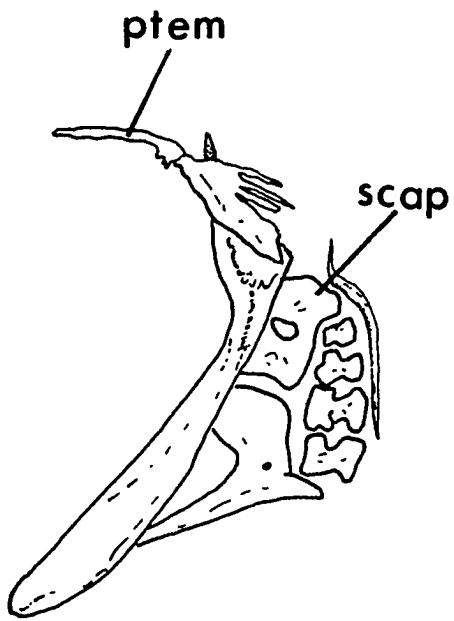


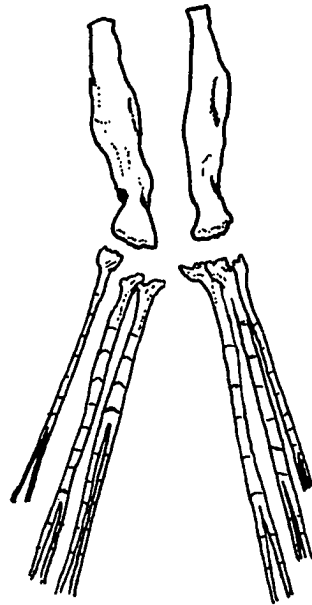
Figure 31. Exechodontes daidaleus, 92 mm SL. A) Left lateral view of
hyoid bar. B) Left lateral view of pectoral girdle.
C) Dorsal view of pelvic bones and pelvic fin rays.



A.



B.



C.

Epipleural ribs on vertebrae 3-14. Pleural ribs on vertebrae 1-18. Dorsal fin origin well posterior to pectoral base, associated with vertebrae 9-11, but with no free pterygiophores. D 80-86, of all soft rays. Zero to three anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with eight rays, thus total caudal rays 10. Last dorsal fin ray associated with third or fourth preural vertebra, last anal ray associated with second preural vertebra.

Palatine membrane weak. Pseudobranch absent in all 14 specimens. Two nub-like pyloric caeca. Peritoneum black. Reproductive mode probably oviparous; one 93 mm SL female contained about 25 eggs 2.9-4.0 mm in diameter and was obviously close to spawning (UMML 3818). Vertebrae symmetrical.

Distribution and species. Exechodontes daidaleus DeWitt, 1977, the only species in the genus, is known from off Florida and Cuba in 219-1004 m. This fish inhabits hard bottom areas under the Florida Current among jagged limestone and hydrocoral peaks (Bullis and Rathjen, 1959: 8), which undoubtedly accounts for its rarity in collections.

Comments. DeWitt (1977) suggested there might be a number of undescribed zoarcids in the tropical western Atlantic. My discoveries of one undescribed Austrolycichthys from the same habitat as Exechodontes, one undescribed Pachycara from the Caribbean Sea abyss and one unknown zoarcid (now lost) from the Caribbean slope of Panama verify DeWitt's prediction.

Additional references. Bullis and Thompson (1965: 58); Staiger (1970: 48). Both references as Melanostigma sp.

Hadropogonichthys Fedorov, 1982

Hadropogonichthys Fedorov, 1982: 16-23, figs. 1, 2 (type species: Hadropogonichthys lindbergi Fedorov, 1982, by original designation).

Remarks. This genus was described on the basis of two specimens, neither of which have been examined by me. The original description is rather complete, except for detailed osteological observations, and is mostly repeated here.

Diagnosis. Body slender, tail elongate; upper and lower jaws and lips and branchiostegal membranes with numerous simple or branched cirri; pelvic fins enveloped in thickened, distally divided tissue; pyloric caeca absent; cephalic lateralis pores reduced in size; preoperculum and mandibular pores 9; palatal arch weakly developed; scales, lateral line, vomerine and palatine teeth present; suborbital bones 9-10; vertebrae 23-24 + 109-110 = 132-134.

Description. Scales present, complete, small. Lateral line ventrolateral, complete. Flesh firm. Gill slit extending ventrally to pelvic fin base. Lower jaw, upper and lower lip and branchiostegal membrane with clusters of simple, short cirri. Upper jaw with unique row of extended, distally divided cirri.

Osteological features unknown except those obtained from radiographs and some dissection. I predict Hadropogonichthys has a reduced parasphenoid wing, frontal and parasphenoid not separated by pterosphenoid, sphenotic and parietal separated by frontal, parietals separated from midline and supraoccipital separated or narrowly contacting exoccipital.

Cephalic lateralis pores small, this apparently a reversal to the plesiomorphic state (see Phylogeny of Zoarcidae). Postorbital pores 1-4

present; probably two lateral extrascapulars. Two nasal pores. No interorbital pores. Supratemporal commissure present, with two (lateral) occipital pores. Suborbital bones probably 9-10, with 7-8 pores on ventral branch and two pores on ascending branch. Preoperculo-mandibular system with four dentary, one angulo-articular and four preopercular pores and bone foramina (ventralmost preopercular foramen leading to a pore). Mandibular and preopercular branches probably joined.

Teeth on jaws small, conical. Teeth present on vomer and palatine bones. Endopterygoid and ectopterygoid probably reduced, metapterygoid probably equal in size to, or smaller than, quadrate. Hyomandibula posterior ramus probably normal. Ceratohyal-epihyal juncture probably smooth. Branchiostegal rays 4 + 2. Ceratobranchial 5 probably toothed; probably three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2 + 12.

Osteological details of pectoral girdle unknown. I predict posttemporal ventral ramus weak or absent, scapular foramen enclosed, with well developed posterior strut, and four actinosts present. Pectoral fin rays 19. Pelvic fin rays 2 (?), with unique, thickened, branched cutaneous layer enveloping rays.

Epipleural ribs on vertebrae 3-22. Dorsal fin rays associated with vertebrae 5-6, with no free pterygiophores. Dorsal fin rays 126-128, apparently all soft, though this requires confirmation. Five anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with four upper and five lower rays, thus total caudal rays 11.

Palatine membrane present. Pseudobranchial filaments 4-6. Pyloric caeca absent. Fedorov (1982) reports no distinct stomach developed, but

this is probably due to its emptiness rather than an anatomical feature.

Peritoneum light. Reproductive mode unknown, probably oviparous.

Vertebrae symmetrical.

Distribution and species. The only species in this genus, Hadropogon-ichthys lindbergi Fedorov, 1982, is known from only two specimens taken by bottom trawl off the northern Kuril Islands, USSR, in 600-615 m.

Iluocoetes Jenyns, 1842

(figs. 7D, 32, 33; pl. XIV)

Iluocoetes Jenyns, 1842: 165-167, pl. XXIX, fig. 2 (type species: Iluocoetes fimbriatus Jenyns, 1842, by monotypy); Lönnberg, 1905: 8; Regan, 1913: 243, 244; Norman, 1937a: 94-102, figs. 50, 51; Gosztonyi, 1977: 212-217, figs. 8, 9.

Paralycodes Bleeker, 1874: 369 (type species: Lycodes variegatus Günther, 1862 (= Iluocoetes fimbriatus Jenyns), by original designation).

Phucocoetes (non Jenyns, 1842). Smitt, 1898: 43-55, figs. 32-34, 36; Lahille, 1908: 424-427, fig. 7.

Caneolepis Lahille, 1908: 431-437, pl. 7.

Remarks. This genus contains two species, Jenyns (1842) I. fimbriatus and another, known in the literature until now as I. elongatus (Smitt, 1898). Smitt named four subspecies of his Phucocoetes variegatus, only the third of which (P. v. elongatus) was thought to represent a distinct species by Regan (1913) and Norman (1937a), the others being placed in synonymy by them with Iluocoetes fimbriatus. Gosztonyi (1977) re-examined all Smitt's types in Stockholm and discovered only P. v. macropus was identical with I. fimbriatus. The other three names refer to the other species, of which effusus is prior, not elongatus. Curiously, Gosztonyi, although noting this, continued to improperly refer to the species by its junior synonym, elongatus.

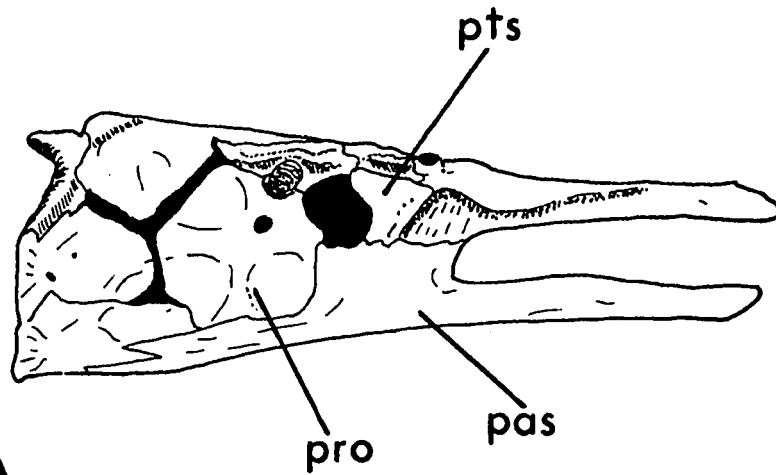
Diagnosis. Body robust, tail relatively short; frontal bones tapering (character 13); hyomandibula posterior ramus elongate (character 14); ceratohyal-epihyal juncture interdigitating (character 15); gill slit extending ventrally to or just anterior to pectoral base; parietals meeting in midline; dentary teeth of adult males present only anteriorly; suborbital bones 7-8, with 6-7 small pores; palatal arch well developed; C 7-9; scales, vomerine and palatine teeth present; branchiostegal rays 5-6; vertebrae 19-24 + 62-79 = 82-99.

Description. Scales present, complete, on pectoral base and proximal part of fin in adults. Lateral line complete, mediolateral. Flesh firm. Gill slit broad, extending ventrally to lower edge of pectoral fin or below it, almost reaching pelvic fins. Lips thickened, no grooves.

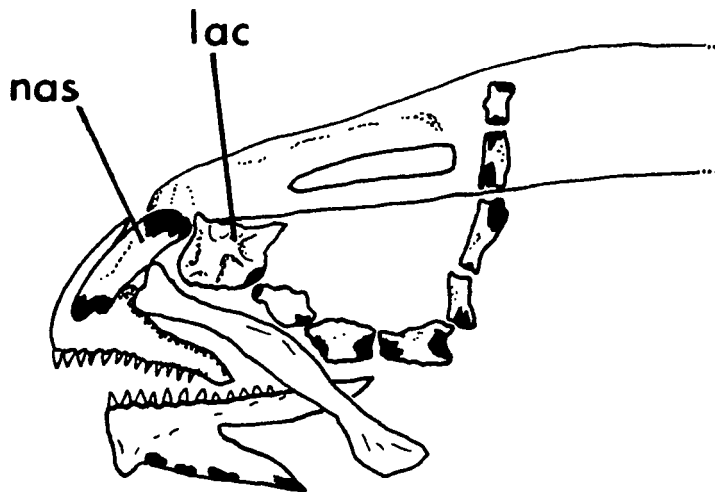
Parasphenoid wing rather large, but with no anterior ramus, and dorsal surface parallel with ventral surface. Frontal and parasphenoid wing not separated by relatively large pterosphenoid (fig. 32A). Frontal bones tapering, thickened (fig. 7D). Sphenotic separated from parietal by pterotic and frontal. Parietals large, meeting in midline. Supraoccipital small, but with anterior ramus extending anteriorly under frontals. Supraoccipital narrowly contacting exoccipital posteriorly (fig. 7D).

Cephalic lateralis pore system reduced in number, pores very small and rounded. One lateral extrascapular, may be fragmented. Postorbital pores 1 and 4 or 4 only (*I. effusus*) present. Two nasal pores. No interorbital or occipital pores. No supratemporal commissure and no bony supports remain across parietals. Eight suborbital bones, with seven pores on ventral branch and none on ascending branch (fig. 32B). Preoperculo-mandibular system in primitive state, with four dentary, one

Figure 32. Iluocoetes effusus, 147 mm SL. A) Right lateral view of neurocranium, ethmoid region and vomer not shown.
B) Head and jaws with suborbital bones.



A.



B.

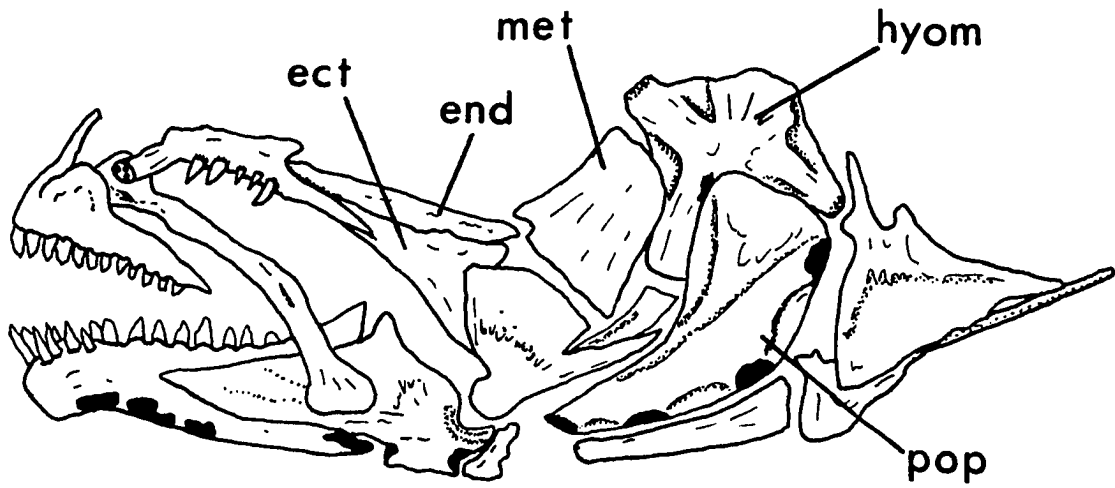
anguloarticular and three preopercular pores and bone foramina, at least in young. Oldest adults have some pores of this system closed over, as in Lycodes. Mandibular and preopercular branches joined.

Teeth small, extending posteriorly in both jaws more than half the length of jaw bones in females (fig. 33A). Teeth of adult males restricted to anterior half of jaw bones, lateral teeth strongly caniniform (Gosztanyi, 1977, fig. 8). Teeth present on vomer and palatine bones, more numerous and smaller in females than males. Endopterygoid and ectopterygoid broadly articulating with quadrate. Hyomandibula posterior ramus elongate (fig. 33A). Metapterygoid relatively large. Opercle and subopercle well ossified. Ceratohyal-epihyal juncture interdigitating dorsally. Branchiostegal rays 4 + 2 in I. effusus, 3 + 2 in I. fimbriatus. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2-3 + 9-14 = 12-16.

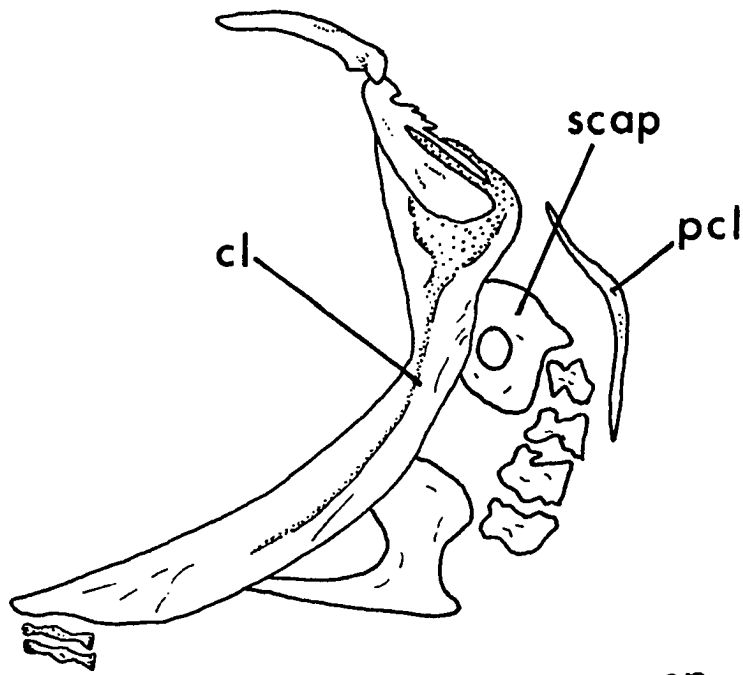
Posttemporal ventral strut absent. Scapular foramen enclosed; scapular posterior strut well developed (fig. 33B). Four actinosts bearing 15-19 fin rays. Pelvic fin rays three, pelvic bones not enlarged.

Epipleural ribs on vertebrae 2-13 or to ultimate precaudal vertebra. Pleural ribs on vertebrae 3-4 to ultimate precaudal vertebra. Dorsal fin origin associated with second or third vertebra, with no free pterygiophores. All dorsal fin elements soft rays. Anterior dorsal rays very high, and much higher than posterior rays in male I. fimbriatus than females; all dorsal rays about the same height in I. effusus (Lahille, 1908, pl. 7; Norman, 1937a, fig. 50). One epural with one fin ray, hypurals with 6-8 rays, thus total caudal rays 7-9 (fig. 33C). Last dorsal ray associated with second or third preural vertebra, last anal ray associated with second preural vertebra.

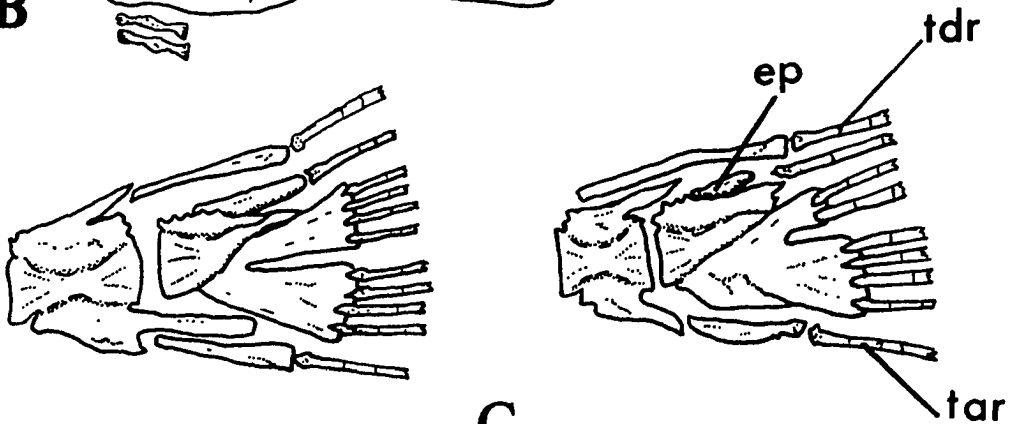
Figure 33. Iluocoetes effusus, 147 mm SL. A) Left lateral view of jaws, suspensorium and opercular bones. B) Left lateral view of pectoral girdle, fin rays not shown. C) Caudal skeleton of 147 mm specimen (left) and 131 mm specimen (right), showing variation in fin ray number.



A



B



C

Palatine membrane well developed, covered with small sensory papillae. Pseudobranchial filaments 6-7, rather long. Two nub-like pyloric caeca, or caeca absent. Peritoneum light. Both species of Iluocoetes are oviparous, spawning in the intertidal zone (Gosztonyi, 1977).
Vertebrae asymmetrical.

Distribution and species. Iluocoetes fimbriatus Jenyns, 1842: widely distributed in temperate South America, from about 41°S in Chile to the mouth of the Rio Paraná, Argentina, from the intertidal zone and brackish areas to about 600 m. Iluocoetes effusus (Smitt, 1898): Patagonia and Tierra del Fuego, including Straits of Magellan, in the intertidal zone to depths of about 40 m.

Additonal references. Günther (1862: 322, 323); Vaillant (1888: 21); Steindachner (1898: 321). All as Lycodes.

Lycenchelys Gill, 1884

(figs. 6B, 8B, 10B, 34; pls. IX, X)

Lycenchelys Gill, 1884: 180 (type species: Lycodes muraena Collett, 1878, by subsequent designation of Jordan, 1887); Goode and Bean, 1896: 309-312, figs. 277, 279, 282; Jensen, 1904: 78-89, figs. 15-28, pl. X, figs. 2, 3; Regan, 1913: 242, pl. IX, fig. 3; Norman, 1937a: 81-82, fig. 52; Andriashev, 1955a: 349-378, figs. 1-20; Andriashev, 1958: 171-180, figs. 1-4; Andriashev and Permitin, 1968: 611-618, figs. 1-4; Peden, 1973: 116-120, fig. 1, tab. 1; Fedorov, 1976: 3-18; Gosztonyi, 1977: 217-220, figs. 10, 11; DeWitt and Hureau, 1979: 812-817, figs. 8-10; tab. XI; Anderson, 1982a: 207-212, figs. 1, 2.

Lycodophis Vaillant, 1888: 311 (type species: Lycodes albus Vaillant, 1888, by original designation).

Embryx Jordan and Evermann, 1898: 2458-2459 (type species: Lycodopsis crotalinus Gilbert, 1891, by original designation); Andriashev, 1955a: 378, 379; Peden, 1973: 119, 120, fig. 1D; Fedorov, 1976: 12-17, tabs. 8, 9.

Lyciscus Evermann and Goldsborough, 1907: 342 (type species: Lycodopsis crotalinus Gilbert, 1891, by original designation).

Apodolycus Andriashev, 1979: 29-32, figs. 1, 2 (type species: Apodolycus hureaui Andriashev, 1979, by original designation).

Remarks. Among zoarcids, the degree of splitting in Lycenchelys has been rivaled only by that in Bothrocara and Lycodes (for example, three generic names were proposed for two Lycenchelys species differing only in their lack of vomerine and palatine teeth). The keystone paper on this genus is that of Andriashev (1955a) who cogently diagnosed Lycenchelys on the basis of three characters that separate it and close relatives from Lycodes : 1) cephalic lateralis pores enlarged; 2) body greatly elongated, 3) mental crests absent. However, Andriashev included four characters that, on close examination of extensive material, are not different, or are insignificant: 1) mouth inferior; 2) teeth on jaws, vomer and palatine bones; 3) no canine teeth anteriorly; 4) palatine membrane present. The latter character, though somewhat difficult to characterize, quantitatively, is present as a low fold, sometimes completely coalesced anteriorly in some adult Lycodes, but is as well expressed in other Lycodes as in some adult Lycenchelys (e.g., L. verrillii, L. paxilla, L. porifer). For purposes of differentiating the palatine membrane in Lycodini, as opposed to the primitive state in Lycozoarces, Zoarcini and Gymnelini, I consider the reduction in the palatine membrane equal in Lycodes and Lycenchelys, although the membrane is generally poorer in Lycodes. Quantification of the difference between Lycodes and Lycenchelys shows trivial results.

Diagnosis. Body low, tail elongate; pseudobranchial filaments 0-5; vertebrae 20-30 + 77-118 = 102-144; dorsal fin origin associated with vertebrae 7-13, with 0-7 free pterygiophores; scales, pelvic fins and vomerine and palatine teeth present or absent; palatal arch weakly developed;

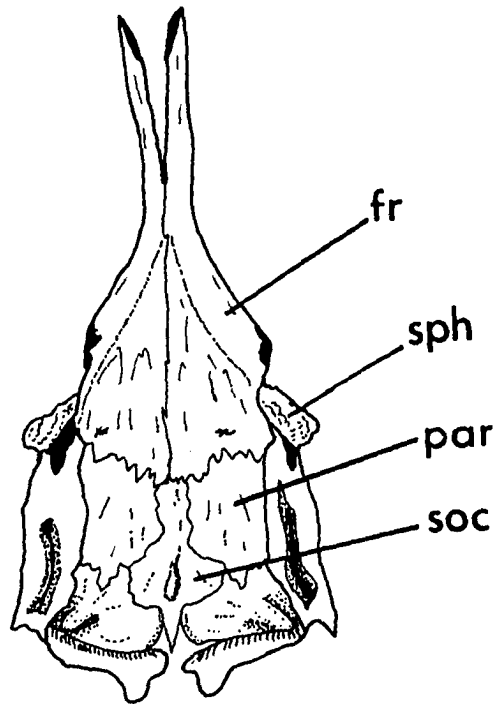
palatine membrane weak; C 9-12 (14); suborbital bones 6-10.

Description. Scales present, complete, small; scales absent in Lycenchelys platyrhina, but, as this species is known only from a single juvenile male, the possibility exists that scales are present in the adult. Lateral line variably mediolateral, ventrolateral or both; either branch complete or incomplete. Flesh firm, slightly thickened on body in shallow dwelling species; flesh about head somewhat gelatinous in most deep living forms. Gill slit extending ventrally to slightly above lower edge of pectoral fin base or almost to pelvic base.

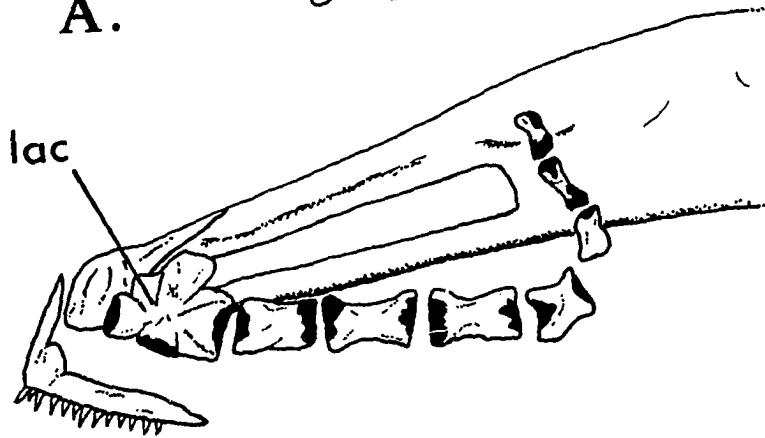
Parasphenoid wing well below mid-height of trigeminofacialis foramen; frontal and parasphenoid not separated by pterosphenoid, which is relatively small in this genus (fig. 6B). Sphenotic small, separated from parietal by frontal or frontal and pterotic together (fig. 34A). Parietals not meeting in midline. Supraoccipital moderate, anterior ramus extending well under frontals; mesial crest low; supraoccipital completely separated from exoccipital by epioccipitals, or narrowly contacting posteriorly (fig. 34A).

Cephalic lateralis pore system variable. Pore patterns species-specific, with great individual variation in suborbital, supraorbital and postorbital canals. Pores usually enlarged, especially anterior suborbitals and preoperculomandibulars. Greatest number of these pores in upper slope species; species living on continental rises and trenches lose most pores (Andriashev, 1955a, 1958; Anderson, 1982a). Two lateral extrascapulars, or both lost in L. antarcticus and probably other deep living forms without posterior postorbital pores. Two nasal pores, except in L. nigripalatium, which has only one pair anterior to nostril tube. Zero or one interorbital pore. Supratemporal commissure present

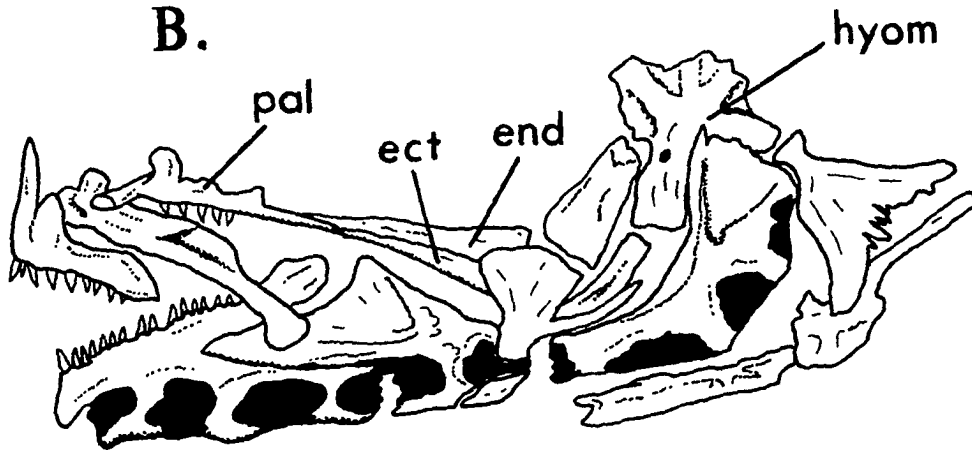
Figure 34. Lycenchelys bellingshauseni, 266 mm SL. A) Dorsal view of neurocranium, ethmoid region and extrascapulars not shown. B) Head and suborbital bones. C) Left lateral view of jaws, suspensorium and opercular bones.



A.



B.



C.

with 2-4 pores, or absent and without occipital pores. Suborbital bones 6-10, with 6-10 pores; from 6 to 9 pores on ventral branch (one side of holotype of L. tristichodon with 5 pores), and 0-2 pores on ascending branch (fig. 34B). Preoperculo-mandibular system in primitive condition, with four dentary, one angulo-articular and three preopercular pores and bone foramina (fig. 34C). Some deep living species with sixth preoperculo-mandibular pore exiting from ventralmost foramen in preopercle, in which case there are nine pores in this system (Anderson, 1982a). Mandibular and preopercular branches usually joined, separated by septum in some deep living species.

Teeth on jaws small, conical. Teeth present on vomer and palatine bones, except in L. crotalina and L. scaura. Endopterygoid and ectopterygoid weakly articulating with quadrate (fig. 34C). Hyomandibula posterior ramus normal. Opercle and subopercle poorly ossified. Ceratohyal-epihyal juncture smooth. Branchiostegal rays 4 + 2, except in L. bachmanni and one undescribed species, both of which have 3 + 2. Ceratobranchial 5 toothed; three pair of infrapharyngobranchials and tooth plates. Gill rakers 0-4 + 8-17 = 10-19, with 0-2 on hypobranchial.

Posttemporal ventral ramus absent or weak. Scapular foramen enclosed; scapula with well developed posterior strut (fig. 10B). Four actinosts bearing 13-21 pectoral rays. Pelvic fins present, with two (L. platyrhina, L. antarctica) or three rays, or pelvics absent (L. hureaui, most L. monstrosa).

Epipleural ribs on first to seventh or seventeenth precaudal vertebrae. Pleural ribs on third to penultimate precaudal vertebrae. Dorsal fin origin posterior to vertical through pectoral base, associated with vertebrae 7-13; free dorsal pterygiophores 0-7, usually less than two.

First dorsal fin element usually a soft ray; 1-2 flexible spines in some species. Three to eight anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one or two fin rays, hypurals with 8-12 rays, thus total caudal rays 9-14 (one specimen of L. scaura had 14 rays; others with 11-12). Last dorsal ray associated with third or fourth preural vertebra, last anal ray associated with second preural vertebra.

Palatal membrane weak, barely developed in some species. Pseudo-branchial filaments usually 2-5, none in some species (e.g., L. paxilla, L. alba). Two nub-like pyloric caeca always present; reference to three in the literature is erroneous (e.g., Gosztonyi, 1977). Peritoneum black. Reproductive mode oviparous, gravid females with less than 100 ova. Vertebrae symmetrical; some species with symmetrical vertebrae in tail, as well as trunk.

Distribution and species. There are 40-41 known species of Lycenchelys, with 16-17 species distributed in the North Pacific between the Gulf of California and the Okhotsk Sea; five species known in the eastern tropical Pacific; nine species known in the North Atlantic, five of which reach the high Arctic; two species in the South Atlantic on the Patagonian slope; eight species in the Antarctic and subantarctic, including Kerguelen Plateau in the Indian Ocean (L. hureaui). The distribution of this genus is instructive in understanding the biogeography of boreal, deep-sea benthic fishes. Present distributions indicate the potential for as yet undiscovered species in the Kermadec Trench and Peru-Chile Trench, as well as basins of the temperate Indian Ocean.

Additional references. Collett (1871:62, pl. I; 1878: 15; 1880: 116,

pl. IV, fig. 1); Goode and Bean (1877: 474; 1879: 44); Vaillant (1888: 309-311, pl. XXVI, fig. 1); Gilbert (1891: 104); Garman (1899: 133-136, pls. XXX, figs. 1, 2, XXXI, fig. 1); Toyoshima (1983).

Lycodapus Gilbert, 1891

(figs. 10C, 35, 36, 37; pl. XII)

Lycodapus Gilbert, 1891: 107, 108 (type species: Lycodapus fierasfer Gilbert, 1891, by monotypy); Gilbert, 1895: 455, pl. 32; Garman, 1899: 138; Gilbert, 1915: 369-373, pl. 20; Andriashev, 1937: 346; Norman, 1937a: 110-111, fig. 59; Schmidt, 1950: 108; Peden and Anderson, 1978: 1925-1961, figs. 1-25; Peden and Anderson, 1981: 667-678, figs. 1-7.

Diagnosis. Body robust to thin, tail relatively short; scales and pelvic fins absent; gill slit entirely free of isthmus posteriorly; frontal and parasphenoid separated by pterosphenoid; sphenotic and parietal articulating; no suborbital pores; only first suborbital bone (lacrimal) present; first preoperculo-mandibular pore and dentary foramen absent; branchiostegal rays 3 + 3; two or three cartilaginous actinosts; P 5-9; vertebrae 13-19 + 59-85 = 73-104; frontal width >19% their length (character 13); palatal arch weakly developed; palatine membrane absent; flesh gelatinous; anterior teeth of adult males caniniform; mandibular and preopercular canals separated by septum.

Description. Scales absent, flesh gelatinous, lateral line mediolateral when present (not observable in most specimens in ethanol). Gill slit not directed forward dorsally in most species, not extending above pectoral fin in L. parviceps; free of isthmus posteriorly, connected anteriorly by small strip of tissue.

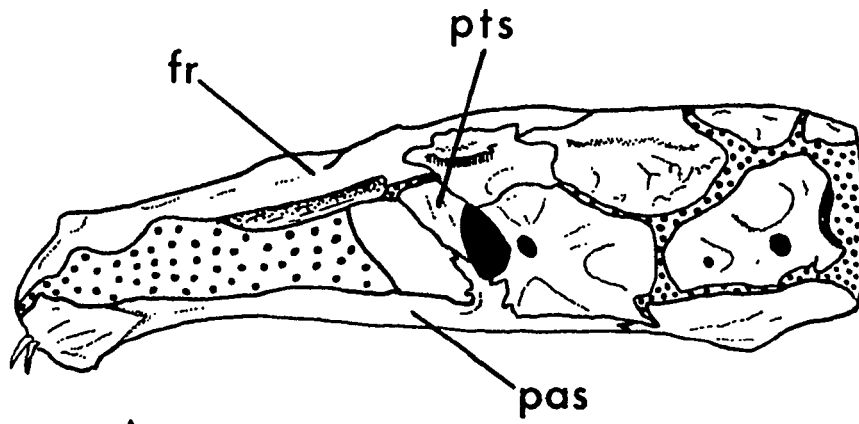
Ethmoid cartilage very extensive, almost reaching pterosphenoid (fig. 35). Parasphenoid wing weak; no frontal wing; pterosphenoid large,

separating frontal and parasphenoid (fig. 35A). Sphenotic very large, articulating with parietal. Parietals reduced, not meeting in midline. No anterior ramus of supraoccipital, or ramus present but not extending under frontals; mesial crest very low; supraoccipital separated from exoccipital by epioccipital.

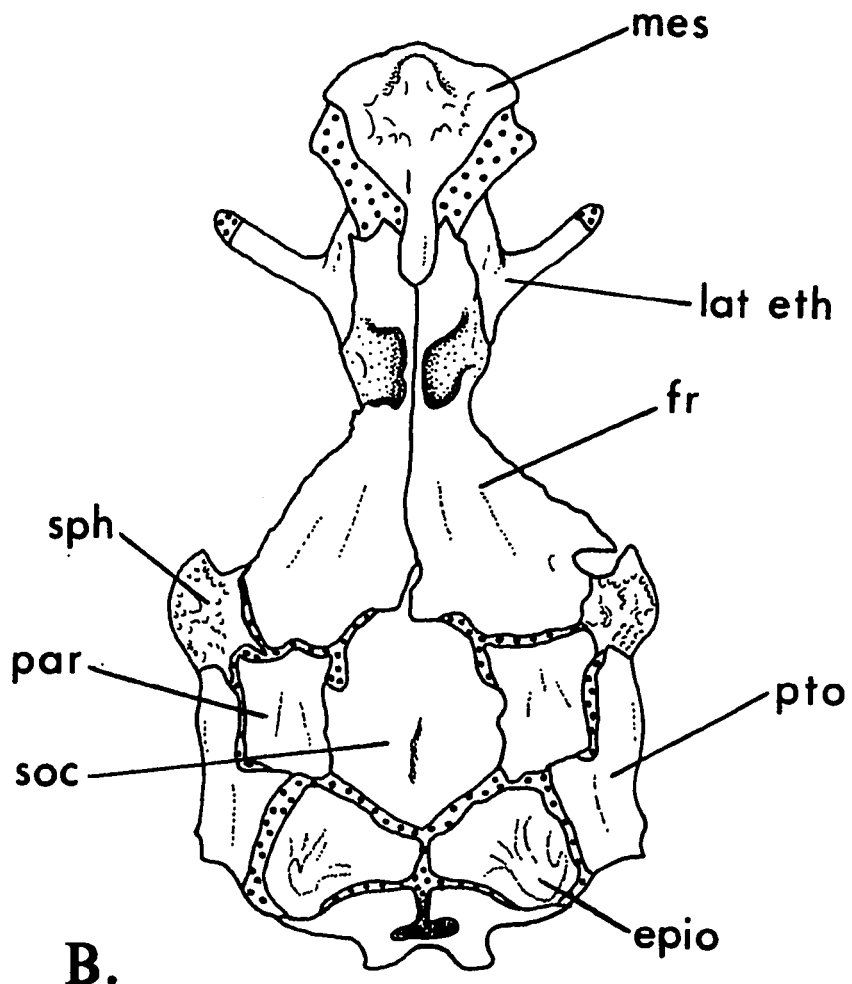
Cephalic lateralis pore system greatly reduced, pores small (Peden and Anderson, 1978, figs. 3, 7). Lateral extrascapulars absent. Suborbital pores absent, free lateralis organs under and behind eye, on cheeks and nape. Most suborbital bones lost, only lacrimal remains, very reduced. Only first postorbital pore present. Two nasal pores. Zero to two interorbital pores, usually only one. No occipital pores, no trace of bony supports across parietals. Preoperculomandibular system with first dentary foramen and first pore always absent; foramen and pore two absent in L. fierasfer and some L. dermatinus, L. australis and L. derjugini (fig. 36A). Preopercular canal passing through a shallow open trough in preopercle, or through four foramina, ventralmost always leading to a pore. Mandibular and preopercular branches separated by thick septum.

Teeth on jaws of adult males caniniform; teeth more numerous and smaller in females than males except in L. parviceps (Peden and Anderson, 1978, figs. 8-10). Vomerine and palatine teeth most often present, except most specimens of L. leptus lack palatine teeth (Peden and Anderson, 1981, tab. 2). Palatal arch reduced; endopterygoid weakly articulating with quadrate, not overlapping its dorsal surface; metapterygoid small. Hyomandibula posterior ramus normal. Opercle and subopercle poorly ossified. Symplectic strongly fused with quadrate (fig. 36B). Ceratohyal-epihyal juncture smooth. Fourth branchiostegal ray shifted

Figure 35. Lycodapus mandibularis, 126 mm SL. A) Left lateral, 3/4 view of neurocranium. B) Dorsal view of neurocranium of same specimen in A.

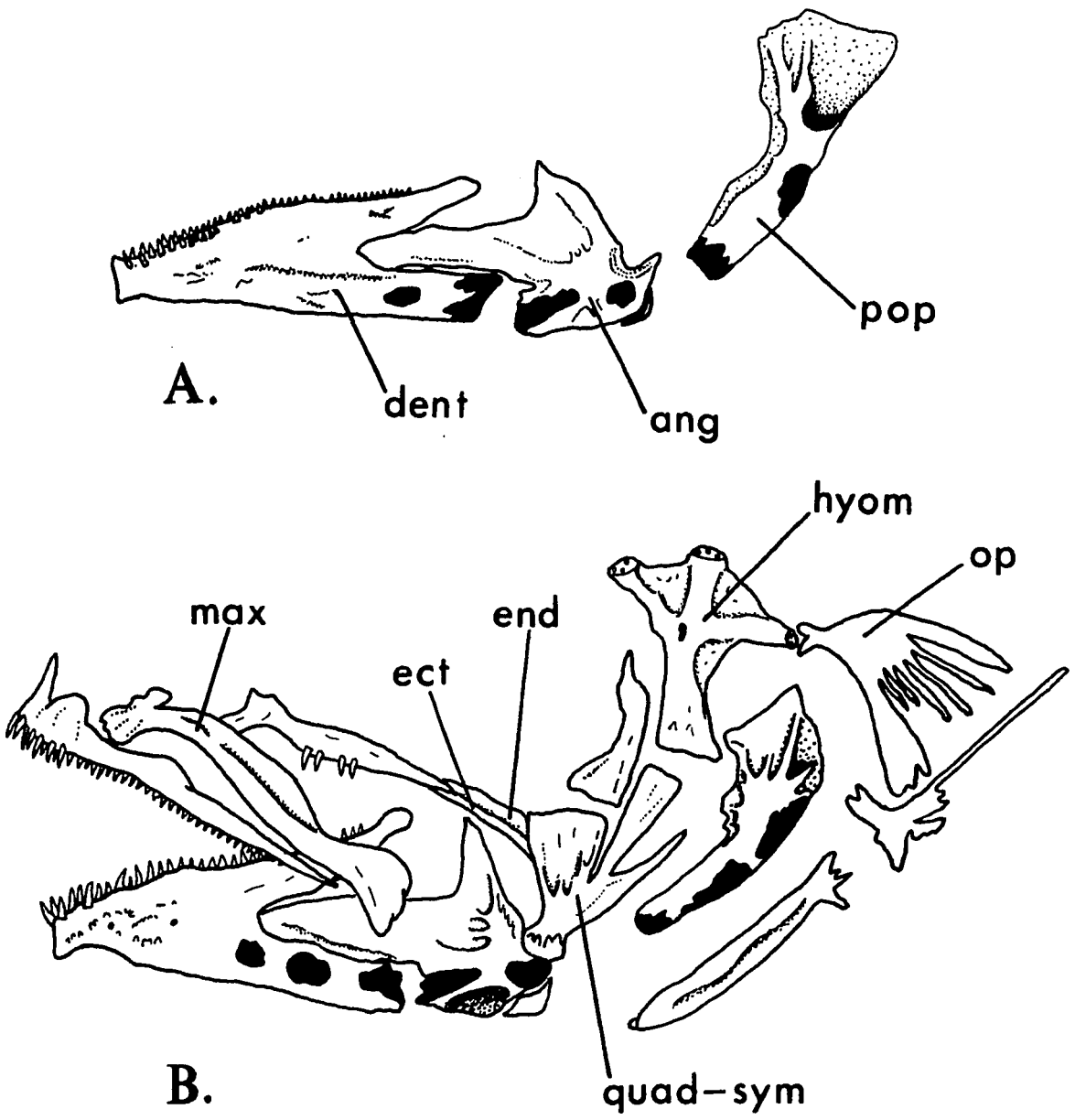


A.



B.

Figure 36. Some osteological features of Lycodapus. A) Left lateral view of bones passing preoperculomandibular canal of L. fierasfer, 99 mm SL. B) Left lateral view of suspensorium, jaws and opercular bones of L. mandibularis, 126 mm SL.



posteriorly onto epihyal (fig. 37A). Ceratobranchial 5 with single row of small teeth; three pairs infrapharyngobranchials and tooth plates (fig. 37B). Gill rakers short or long, three length patterns discernible (Peden and Anderson, 1978, figs. 5, 6). Gill rakers 0-2 + 9-13 = 9-14.

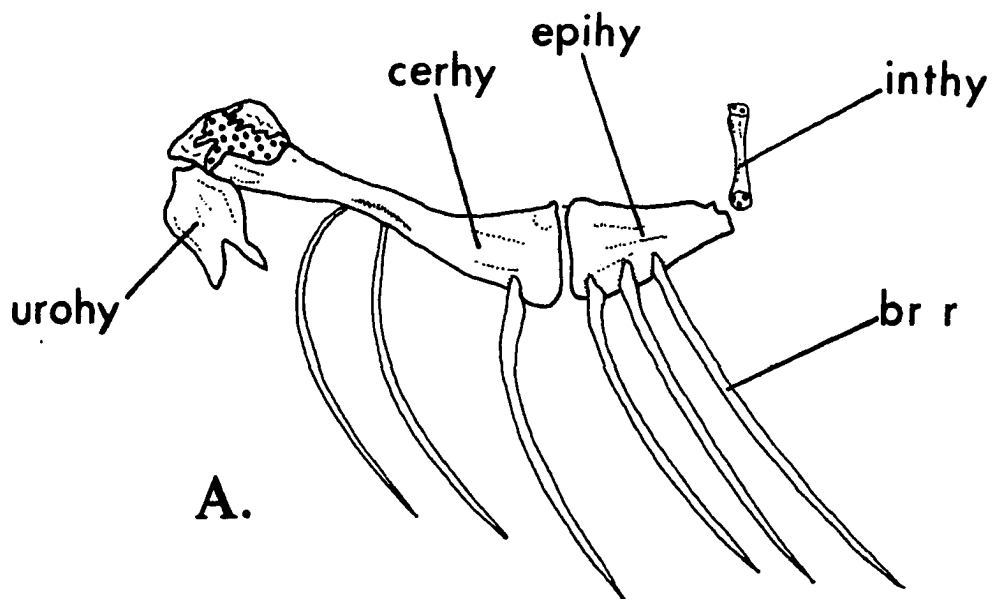
Posttemporal ventral strut weak. Scapular foramen enclosed; scapular posterior ramus absent. Two or three actinosts bearing 5-9 pectoral fin rays (fig. 10C). Pelvic fins absent, pelvic bone a small splint, or absent.

Epipleural ribs beginning on first or third vertebra, extending to sixth to ninth vertebra. Pleural ribs beginning on third or fourth vertebra, extending to seventh or eighth vertebra. Dorsal fin origin associated with vertebrae 4-5, with no free pterygiophores. All dorsal fin elements soft rays. One or two anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one or two fin rays, hypurals with 6-10 rays, total caudal rays 8-12 (Peden and Anderson, 1978, fig. 2). Parhypural partially separated from hypurals in some specimens. Last dorsal fin ray associated with fourth preural vertebra; last anal ray associated with second preural vertebra.

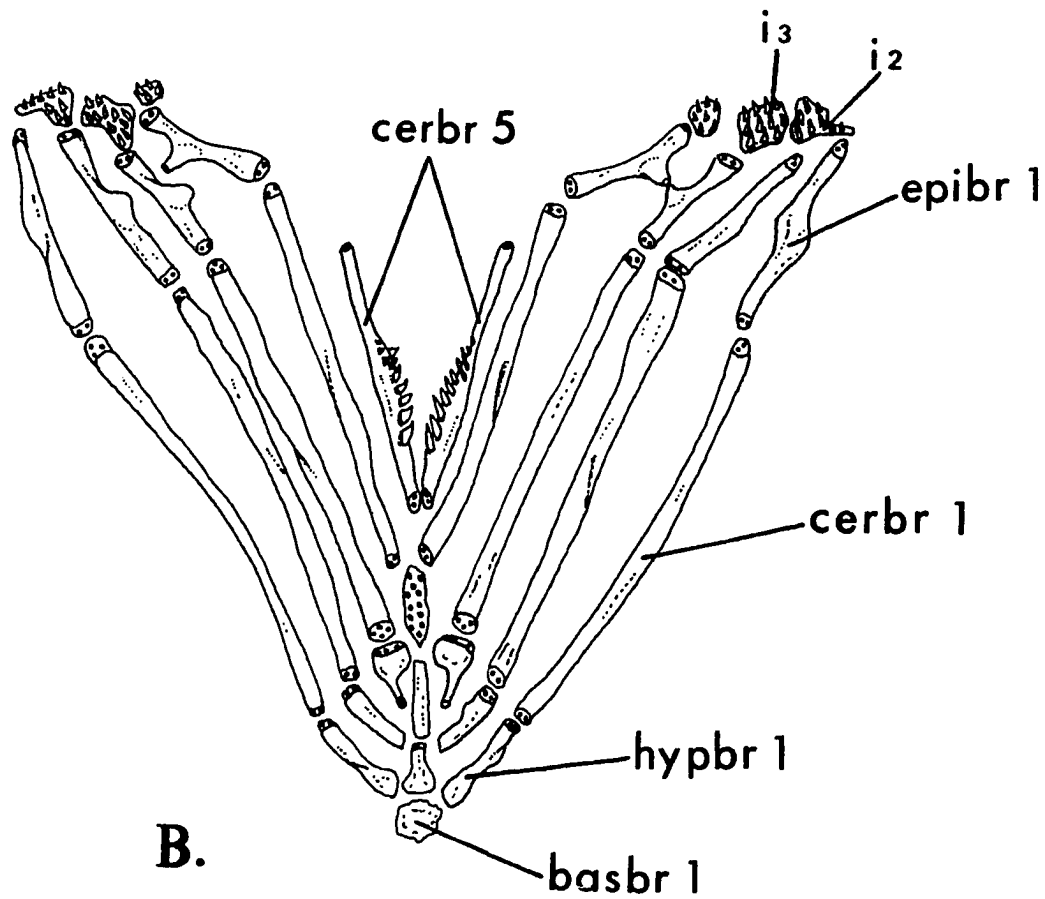
Palatine membrane absent, no vestiges remain. Pseudobranchial filaments 0-3, very short when present. Two nub-like pyloric caeca. Peritoneum black. All species oviparous, spawning in midwater (Anderson, 1981). Vertebrae symmetrical.

Distribution and species. All the species of Lycodapus are probably deep-pelagic, although only L. mandibularis, L. australis and L. dermatinus have been taken in midwater nets. Because the species are coastal

Figure 37. Lycodapus mandibularis, 126 mm SL. A) Left lateral view of hyoid bar. B) Bones of the branchial basket, gill rakers not shown.



A.



B.

or thalassobathyal, most may periodically associate near the bottom where their prey (mostly pelagic crustaceans) concentrate (Markle and Wenner, 1979; Anderson, 1981). Lycodapus australis Norman, 1937: Straits of Magellan and adjacent regions. Lycodapus derjugini Andriashev, 1937: coast of Kamchatka and Okhotsk Sea. Lycodapus dermatinus Gilbert, 1895: Welker Seamount (55°08'N, 140°20'W) to Gulf of California. Lycodapus endemoscotus Peden and Anderson, 1978: central British Columbia to Gulf of California. Lycodapus fierasfer Gilbert, 1891: Bering Sea to Gulf of Panama. Lycodapus leptus Peden and Anderson, 1981, L. poecilus Peden and Anderson, 1981 and L. psarostomatus Peden and Anderson, 1981 are so far known only from the eastern Bering Sea. Lycodapus mandibularis Gilbert, 1915: central Alaska to southern California. Lycodapus microchir Schmidt, 1950: Okhotsk Sea and east coast of Kamchatka. Lycodapus pachysoma Peden and Anderson, 1978: central British Columbia to Oregon (probably widely distributed in temperate eastern North Pacific in very deep water) and a separate population in the Scotia Sea. Lycodapus parviceps Gilbert, 1915: central Bering Sea to British Columbia. There is still one undescribed species known from the Scotia Sea and Kerguelen Plateau (S. Johnson, A. Andriashev, pers. comm.).

Comments. Peden and Anderson (1978, 1981) revised Lycodapus on the basis of most of the world's material. These papers provide complete synonymies, illustrations and distributions of all 13 species. Much new material taken by vessels of the Soviet Union in the Bering Sea is expected to extend the ranges of many species when data is available.

Additional references. Jordan and Evermann (1898: 2492, fig. 870); Bayliff (1959: 79, 80); Miller and Lea (1972: 78, 79, figs.); Hart (1973:

239-241, figs.); Fedorov (1973: 19, 24); McCosker and Anderson (1976: 214, 215).

Lycodes Reinhardt, 1831

(figs. 4D, 6A, 7A, 9B, 12A,B, 13C, 38; pl. VII)

Lycodes Reinhardt, 1831: 18 (type species: Lycodes vahlii, by monotypy); Reinhardt, 1837: 71; Lütken, 1880: 307-332; Collett, 1880: 77-116, pl. II, figs. 19-21, pl. III, pl. IV, fig. 28; Smitt, 1895: 607-609; Smitt, 1900: 56-58; Jensen, 1904: 1-49, 51-76, pls. I-X; Knipovich, 1906: 1-130, pls. I, II; Vladykov and Tremblay, 1936: 1-53, pls. I-VII; Schmidt, 1950: 84-105, pls. V-VIII, IX, fig. 2; Andriashev, 1954: 266-307, figs. 142-172.

Lycodalepis Bleeker, 1874: 369 (type species: Lycodes mucosus Richardson, 1855, by original designation).

Lycodopsis Collett, 1879: 382 (type species: Lycodes pacificus Collett, 1879, by original designation).

Leurynnis Lockington, 1880: 326-328 (type species: Leurynnis paucidens Lockington, 1880, by original designation).

Aprodon Gilbert, 1891: 106, 107 (type species: Aprodon corteziana Gilbert, 1891, by original designation).

Furcella Jordan and Evermann, 1896: 480 (type species: Lycodes diapterus Gilbert, 1891, by original designation; preoccupied by Furcella Lamark, 1801, in Mollusca).

Lycias Jordan and Evermann, 1898: 2461, 2463 (type species: Lycodes seminudus Reinhardt, 1837, original designation).

Furcimanus Jordan and Evermann, 1898: 2472 (type species: Lycodes diapterus Gilbert, 1891, by original designation; replacement name for Furcella Jordan and Evermann, 1896).

Bergeniana Popov, 1931a: 140 (subgenus; no type species).

Petroschmidtia Taranets and Andriashev, 1934: 506-512, figs. 1, 2 (type species: Petroschmidtia albonotata Taranets and Andriashev, 1934, by original designation). Katayama, 1941: 593; Matsubara and Iwai, 1951: 104-111.

Remarks. Lycodes contains a large number of species which exhibit a great deal of variation. Nine species have been divided previously into subspecies on the basis of characters now known to represent individual or populational variation. Some of the subspecies of L. palearis may,

in fact, be valid species. Previous extreme generic splitting in Lycodes has relied on very minor characters and is not recognized here, as all species possess one character that is unique among zoarcids, the development of mental crests, or cartilaginous ridges on the dentary.

Diagnosis. Body robust, tail relatively short; dentary with cartilaginous sheath enveloping and extending well under it, producing ridges running to chin tip (mental crests, character 30); parasphenoid wing well above mid-height of trigeminofacialis foramen; suborbital bones 7-11; palatine membrane weak or absent; palatal arch well developed; vertebrae 19-26 + 65-104 = 90-127; pseudobranchial filaments 6-9; pelvic fins present; scales, vomerine and palatine teeth present or absent; head usually acute anteriorly.

Description. Body robust, head usually pointed anteriorly, becoming rounded in older individuals of a few species. Scales usually present, complete; present and incomplete in L. seminudus; absent in L. mucosus (at least early stages), L. jugoricus, L. polaris and L. turneri. Lateral line present, quite variable in extent, as in Bothrocara (see Andriashev, 1954, fig. 142). Flesh firm, relatively thickened. Gill slit extending ventrally to pectoral base or almost to pelvic base.

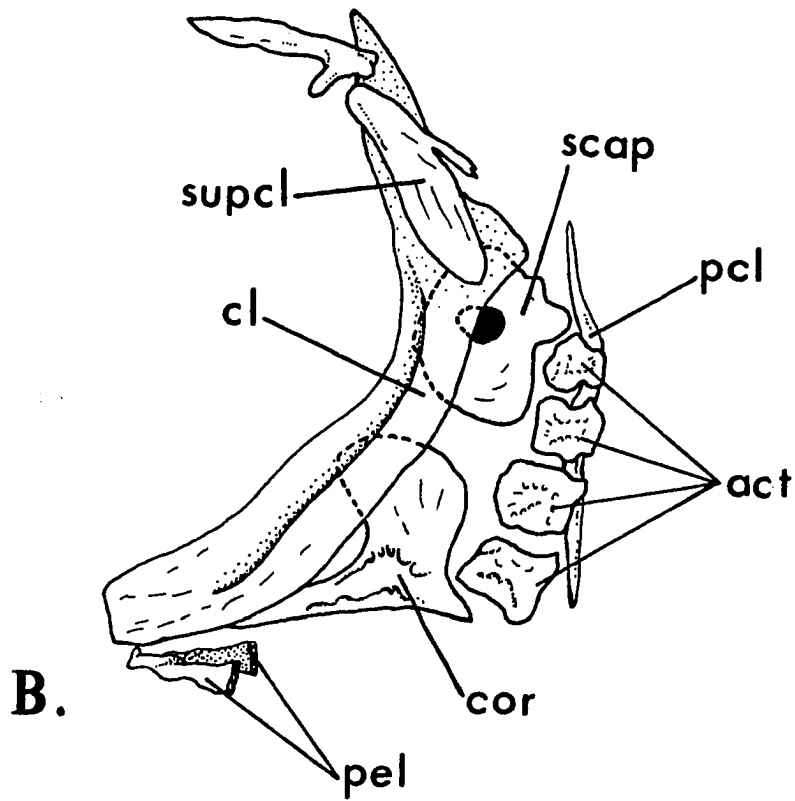
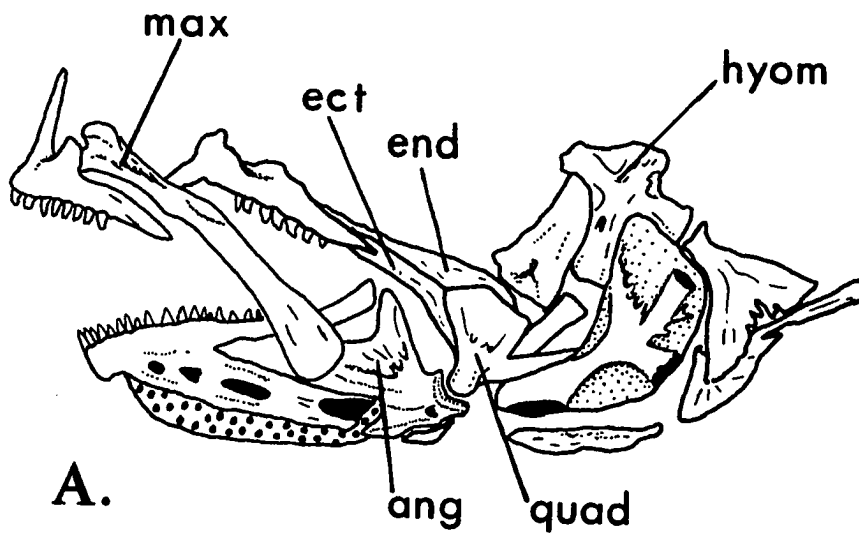
Parasphenoid wing well above mid-height of trigeminofacialis foramen, frontal descending wing reduced; frontal never separated from parasphenoid by pterosphenoid (fig. 6A). Sphenotic small, separated from parietal by frontal. Parietals separated from midline by supraoccipital. Supraoccipital extending well under frontal, with moderate mesial crest. Supraoccipital and exoccipital narrowly contacting posteriorly (fig. 7A).

Cephalic lateralis pores seem to completely close over in largest adults, or one or two pores of a given system remains open at random. Pores in adults extremely small. Pore systems of juveniles relatively complete in all species examined, pores rather large in very small juveniles. All four postorbital pores usually present in young. Two lateral extrascapulars. Two pair of nasal pores. One interorbital pore. Supratemporal commissure present in young of shallow dwelling species, closing over in adults; two or three occipital pores in this case. Suborbital pores 6-9 on lower branch, 0-3 on upper branch, total 6-12. Suborbital bones 7-11. Four dentary foramina for preoperculo-mandibular pores in all species examined, one in anguloarticular, three in preopercle (fig. 38 A). Mandibular and preopercular canals joined.

Jaw teeth moderate in adult males, more numerous than in females of most species; outer row enlarged. Teeth on vomer and palatines robust, sharp when present. Endopterygoid and ectopterygoid broadly articulating with quadrate. Metapterygoid large, thickened. Hyomandibula posterior ramus normal. Opercle and subopercle well ossified. Ceratohyal-epihyal juncture smooth; these bones thickened. Branchiostegal rays 4 + 2 (fig. 9B). Ceratobranchial 5 with large, numerous teeth. Three pairs of infrapharyngobranchials and tooth plates. Gill rakers 3-6 + 10-14 = 13-19.

Posttemporal ventral strut well developed in shallow-dwelling species (fig. 13C), more reduced in deeper living forms. Scapular foramen enclosed; scapula with well developed posterior strut (fig. 38 B). Four actinosts bearing 14-24 pectoral fin rays. Pectoral fin usually large. Pelvic fin rays 3, fin always present.

Figure 38. Some osteological features of Lycodes. A) Left lateral view of jaws, suspensorium and opercular bones of L. vahlii, 346 mm SL. B) Left lateral view of pectoral girdle of L. pallidus, 156 mm SL (pelvic rays not shown).



Epipleural ribs beginning on first or second vertebra, extending to vertebrae 12-18. Pleural ribs on third to ultimate precaudal vertebrae. Dorsal fin origin associated with vertebrae 3-8 or more posteriorly in L. uschakovi, with no free pterygiophores. All dorsal rays soft. Zero to four anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypural rays 8-10, thus total caudal rays 10-12. Last dorsal ray associated with fourth preural vertebra, last anal ray associated with second or third preural vertebra. Sometimes two anal rays attached to pterygiophore fused to haemal spine of second preural vertebra.

Palatine membrane weak or absent. Pseudobranchial filaments 6-9, rather large. Two nub-like pyloric caeca usually present, or pyloric caeca absent (L. esmarki, L. albonotatus, L. toyamensis). Peritoneum pale in shallow-dwelling species, black in slope dwelling forms. All well known species are oviparous. Vertebrae symmetrical or asymmetrical.

Distribution and species. The genus is widely distributed in boreal waters. Only one species, Lycodes agulhensis, is found in the southern hemisphere (Andriashev, 1959). The genus is in great need of revision, especially of North Pacific and western Arctic forms. In summary, in addition to L. agulhensis, I recognize 26-31 North Pacific endemic species (status of five names uncertain), two subarctic North Atlantic endemics, seven Arctic endemics and 10 species ranging from the high Arctic to the North Pacific or North Atlantic.

Additional references. Richardson (1855: 362, pl. XXVI); Gill (1862: 46); Günther (1862: 319-326); Jordan and Evermann (1898: 2460-2468,

figs. 853-856); Soldatov and Lindberg (1930: 492-497); Taranets (1937: 161-164); Okada and Matsubara (1938: 406); Leim and Scott (1966: 320-326); Andriashev (1973: 542-546); Hart (1973: 233, 234, 242-246); Lindberg and Krasnyukova (1975: 139-169, figs. 112-132); McAllister et al. (1981: 821-835, figs. 1-4).

Lycodichthys Pappenheim, 1911

(figs. 5B, 39; pl. VIII)

Lycodichthys Pappenheim, 1911: 382, 383 (type species: Lycodichthys antarcticus Pappenheim, 1911, by monotypy); Pappenheim, 1912: 180, pl. IX, fig. 6, pl. X, fig. 4.

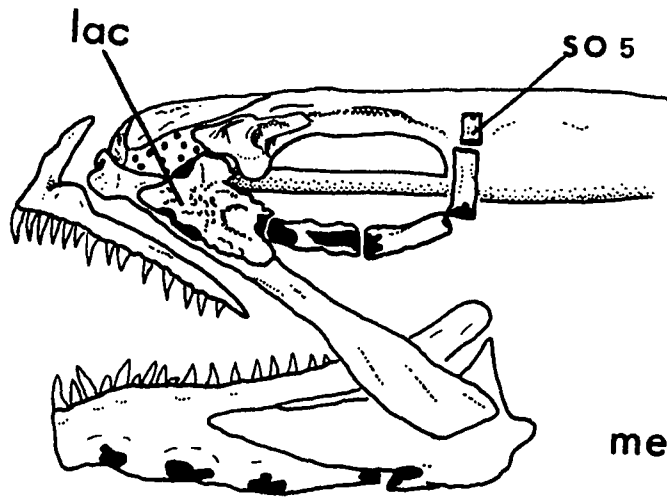
Rhigophila DeWitt, 1962: 819-826, figs. 1-4, tab. 1 (type species: Rhigophila dearborni, by original designation).

Remarks. This genus contains two species that are difficult to distinguish except that Lycodichthys antarcticus possesses pelvic fins and L. dearborni has lost them. As stated previously, this character is not used at the generic level here and the two species are placed in the same genus on the basis of their sharing a reduced number of suborbital bones in the tribe, similar dentition, vertebral counts, caudal skeleton, morphometry and even coloration.

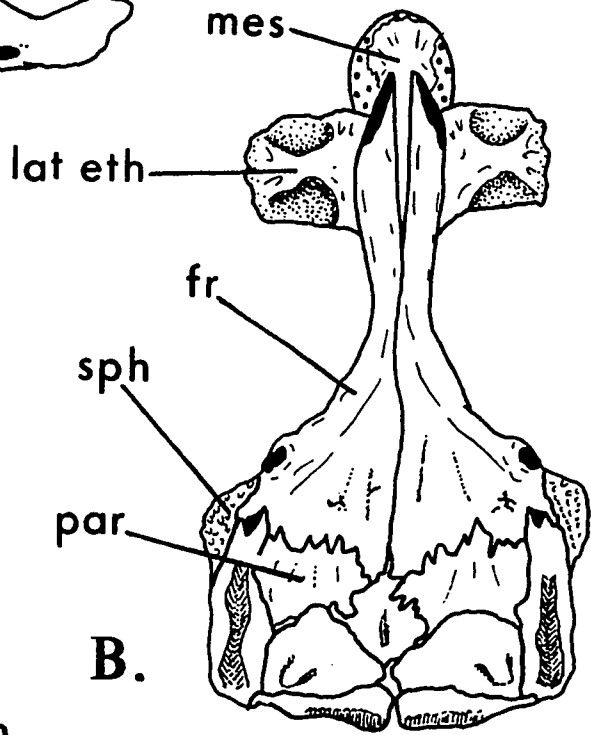
Diagnosis. Body robust, tail relatively short; suborbital bones and pores five, all pores on ventral ramus of canal (fig. 39A); gill slit not reaching ventral edge of pectoral base; vomerine and palatine teeth absent; parasphenoid wing below mid-height of trigeminofacialis foramen; palatal arch well developed; vertebrae 23-24 + 68-70 = 92-93; C 11; pyloric caeca and pseudobranch absent; supraoccipital separated from exoccipital by epioccipitals; pelvic fins present or absent.

Description. Head broad and ovoid, skull greatly depressed (fig. 39A).

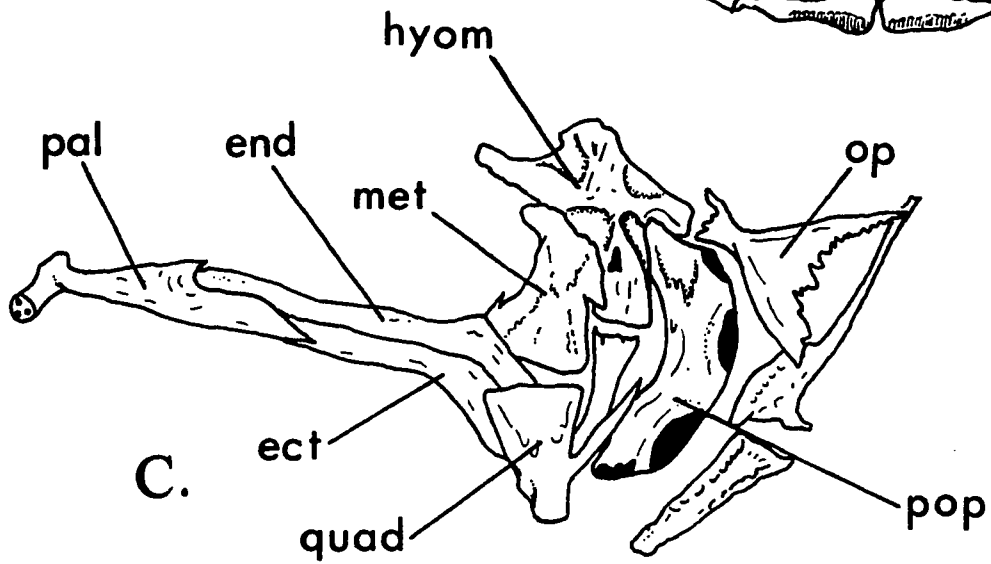
Figure 39. Lycodichthys dearborni, 206 mm SL. A) Left lateral view of head, jaws and suborbital bones. B) Dorsal view of neurocranium. C) Left lateral view of palatal arch, suspensorium and opercular bones.



A.



B.



C.

Body and tail moderately elongate, robust. Scales present, complete. Lateral line mediolateral, complete. Skin firm, moderately thickened. Gill slit extending ventrally to mid-pectoral fin base, or slightly beyond it.

Parasphenoid wing well below mid-height of trigeminofacialis foramen; frontal not separated from parasphenoid by pterosphenoid. Sphenotic small, separated from parietal by frontal and pterotic (fig. 39B). Parietals not meeting in midline. Supraoccipital relatively small, with small mesial crest, not contacting exoccipital posteriorly (fig. 39B).

Cephalic lateralis system reduced. Postorbital pores 1 and 4 present only. Two lateral extrascapulars. Two nasal pores. Interorbital and occipital pores absent. Three suborbital bones on lower branch, two on ascending branch, all five pores on lower branch (fig. 39A). Preoperculomandibular pores and bone foramina in primitive condition, with four dentary, one anguloarticular and three preopercular pores. Mandibular and preopercular branches joined.

Jaw teeth moderate, sexually dimorphic, males with larger and fewer teeth than females. Vomerine and palatine teeth always absent. Endopterygoid and ectopterygoid broadly articulating with quadrate (fig. 39C). Hyomandibula posterior ramus normal. Opercle and subopercle poorly ossified. Ceratohyal-epihyal juncture smooth. Branchiostegal rays 4 + 2; 3 + 2 rarely in L. dearborni (DeWitt, 1962). Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 1 + 8-10 = 9-11.

Posttemporal ventral ramus absent. Scapular foramen enclosed; scapula with well developed posterior strut. Four actinosts bearing

15-17 pectoral rays. Pelvic bone reduced, no pelvic rays in L. dearborni (DeWitt, 1962), but L. antarcticus with minute pelvic rays, each fin of three rays.

Epipleural ribs on vertebrae 1-11 or 12. Pleural ribs on third to ultimate precaudal or first caudal vertebra. Dorsal fin origin associated with third or fourth vertebra, with no free pterygiophores. First, or first and second, dorsal fin elements flexible spines. One to three anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural, with one fin ray, hypurals with 10 rays, thus total caudal rays 11. Last dorsal ray associated with third or fourth preural vertebra, last anal ray associated with second preural vertebra.

Palatine membrane weak. Pyloric caeca and pseudobranch always absent. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae symmetrical.

Distribution and species. Lycodichthys antarcticus Pappenheim, 1911: eastern Antarctica, from Enderby Land to Wilkes Land in about 300-600 m. Lycodichthys dearborni (DeWitt, 1962): Ross Sea, Antarctica in about 200-600 m. Both species are probably more widely distributed along Antarctic shores than present collections reflect, but both are probably restricted to the continent (Andriashev, 1965, 1977).

Additional references. Regan (1913: 244); Waite (1916: 14); Norman (1938: 82, fig. 53); Nybelin (1947: 54, 65); Andriashev (1959b: 7); Permitin (1969: 174); Wohlschlag (1963: 557-564, figs. 1-3); Lindberg (1974: 207, fig. 801).

Lycodonus Goode and Bean, 1883

(figs. 14, 40; pl. IX)

Lycodonus Goode and Bean, 1883: 208, 209 (type species: Lycodonus mirabilis Goode and Bean, 1883, by monotypy); Goode and Bean, 1896: 312, 313, pl. LXXX, fig. 280; Jensen, 1904: 83-86, 94-97, figs. 29-33; Barnard, 1927: 873, pl. XXXV, fig. 3; Andriashev, 1955a: 379-381; Gosztonyi, 1981: 151-159, figs. 1, 2, tab. 1.

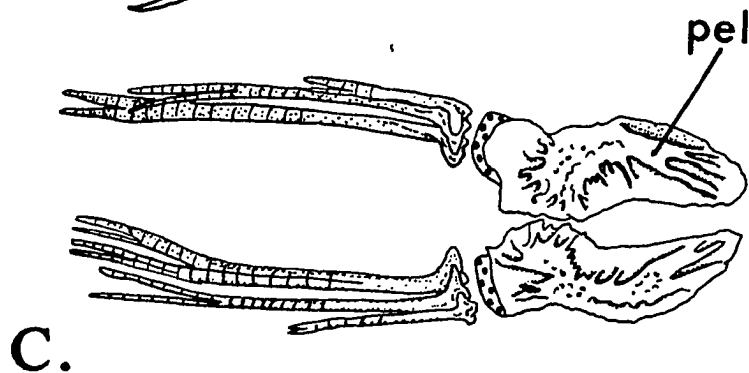
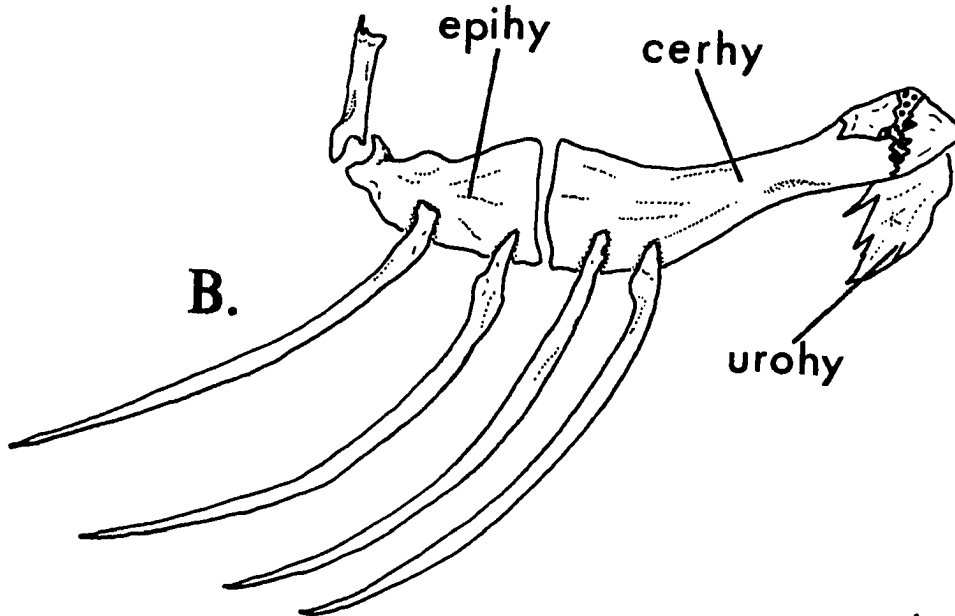
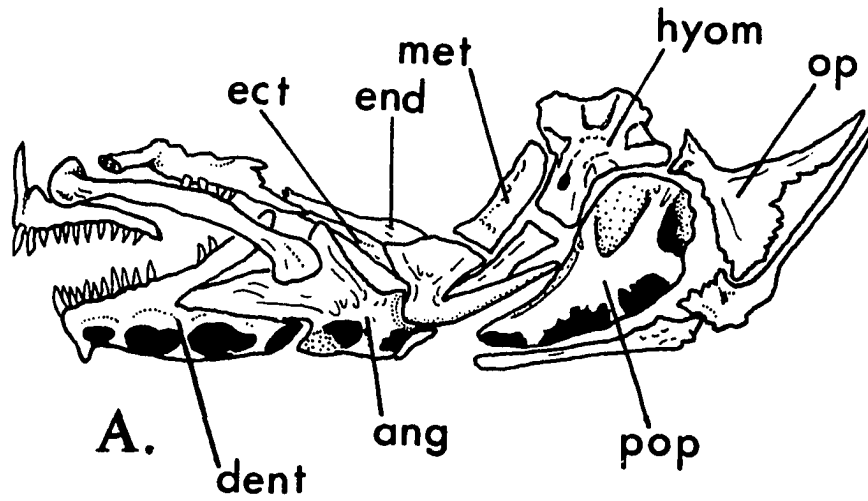
Diagnosis. Body low, tail elongate; dorsal and anal fin pterygiophores with broad, distal expansions, forming plates, or fin scutes, at fin bases (character 57); dorsal fin origin associated with vertebrae 11-15, with 8-11 free pterygiophores; vertebrae 21-25 + 85-105 = 110-128; branchiostegal rays 4-5; palatal arch weakly developed; suborbital bones 7-9.

Description. Scales present, complete, very small. Lateral line medio-lateral, complete. Flesh firm; on head, loose and thin. Gill slit extending ventrally to lower edge of pectoral base or just below it.

Parasphenoid wing well below mid-height of trigeminofacialis foramen; frontal and parasphenoid not excluded by pterosphenoid. Sphenotic and parietal excluded by frontal and pterotic. Parietals separated from midline. Supraoccipital moderate, mesial crest small; supraoccipital and exoccipital narrowly contacting posteriorly.

Cephalic lateralis pore system reduced, but anterior suborbital and preoperculomandibular pores enlarged. Postorbital pores 1, 3, 4 or 1 and 4 present. One lateral extrascapular. Two nasal pores. No interorbital or occipital or occipital pores, and supratemporal commissure absent. Suborbital bones 7-9, with 6-8 pores on ventral branch and no pores on ascending branch. Preoperculomandibular system in primitive condition, with four dentary, one anguloarticular and three preopercular pores and foramina; bone foramina very large (fig. 40A).

Figure 40. Some osteological features of Lycodonus. A) Left lateral view of jaws, suspensorium and opercular bones of L. mirabilis, 278 mm SL. B) Right lateral view of hyoid bar of L. vermiformis, 245 mm SL. C) Dorsal view of pelvic bones and fin rays of specimen in A.



Mandibular and preopercular branches joined.

Teeth in jaws small, not numerous, conical. Teeth present on vomer and palatine bones. Endopterygoid and ectopterygoid weakly articulating with quadrate. Hyomandibula posterior ramus normal. Opercle and subopercle moderately well ossified. Ceratohyal-epihyal juncture smooth (fig. 40B). Branchiostegal rays 3 + 2, except in L. vermiformis which has 2 + 2 (fig. 40 B). Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 1-2 + 8-11 = 9-13.

Posttemporal ventral strut moderately developed. Scapular foramen enclosed; scapular posterior strut moderately well developed. Four actinosts bearing 14-17 pectoral fin rays. Pelvic fins present, with three fin rays, proximalmost reduced (fig. 40C).

Epipleural ribs on vertebrae 1-14 or 15. Pleural ribs on third to ultimate precaudal vertebrae. Dorsal fin origin behind vertical through posterior margin of pectoral fin, associated with vertebrae 11-15, with 8-11 free pterygiophores. All dorsal elements soft rays. Four to six anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one or two fin rays, hypurals with 6-8 rays, thus total caudal rays 7-9. Last dorsal ray associated with third preural vertebra, last anal ray associated with second preural vertebra.

Palatine membrane weak. Pseudobranchial filaments 2-3, very short. Two nub-like pyloric caeca. Peritoneum black. This genus is oviparous. Vertebrae symmetrical.

Distribution and species. Lycodonus flagellicaudus (Jensen, 1902); Arctic portion of North Atlantic, from south of Spitsbergen to Faeroe

Channel and west to south of Iceland and southeastern Greenland, in 800-1992 m. Lycodonus ophidium (Jensen, 1902) is a junior synonym of L. flagellicaudus. Lycodonus malvinensis Gosztonyi, 1981; known from three specimens taken on the Falkland Plateau; probably widely distributed in temperate southwestern Atlantic at appropriate depths (1000-2000 m?). Lycodonus mirabilis Goode and Bean, 1883: western North Atlantic from Baffin Bay south to off Cape Hatteras, North Carolina. Lycodonus vermiformis Barnard, 1927: known only from off Cape Town, South Africa in 841-1152 m.

Comments. Oshima (1957) described Lycodonus dorsoscutatus from the Japan Sea. The description is so poor that it is difficult to tell what family this fish belongs to, but it is clearly not a zoarcid, as it is said to possess a supramaxilla, pelvic fins with one spine and five soft rays, two nostrils (pairs ?), a snout with "horny projections" (spines ?), vertical fins not continuous with the caudal, spines in the anal fin and a peculiar "bag-like" lower jaw.

Additional references. Collett (1878: 74); Collett (1880: 116 (partim), pls. 29, 31); Günther (1887: 79, pl. XII, fig. A); Lütken (1898: 20); Jensen (1902: 210-212); Smith (1965: 365); Andriashev (1973: 546, 547); Markle and Sedberry (1978: 23).

Lycogrammoides Soldatov and Lindberg, 1929

Lycogrammoides Soldatov and Lindberg, 1929: 39-42, fig. (type species: Lycogrammoides schmidti Soldatov and Lindberg, 1929, by original designation); Soldatov and Lindberg, 1930: 502-504; Shmidt, 1950: 117, 118.

Diagnosis. Body robust, tail relatively short; scales present, very extensive; branchiostegal membrane broad, attached to isthmus; six sub-

orbital bones and pores; branchiostegal rays 4 + 2; vertebrae 14 + 53 = 67 (in one); palatal arch weakly developed; palatine membrane and pelvic fins absent; adult males with caniniform dentition; mandibular and preopercular canals separated by septum.

Description. Squamation extensive, scales cover body, tail, bases of vertical fins, pectoral base, cheeks and nape anteriorly to nasal area. Lateral line complete, mediolateral; dorsal branch of few neuromasts running along base of dorsal fin. Flesh gelatinous, probably translucent in life. Branchiostegal membrane attached well anteriorly onto narrow isthmus. Upper lips coalesced with snout anteriorly.

Details of neurocranium not observed. Lycogrammoides schmidti exhibits many reductions in several characters. It probably has reduced the palatal arch, parasphenoid, supraoccipital, etc. Frontal width 19% its length.

Cephalic lateralis pores small, reduced in number. Postorbital pores 1 and 4 present, with probably two lateral extrascapulars. Two nasal pores. One interorbital pore. No occipital pores or supratemporal commissure. Six reduced suborbital bones, with five pores on ventral branch and one on ascending branch. Preoperculomandibular pores in primitive state, with four dentary, one anguloarticular and three preopercular pores. Mandibular and preopercular branches separated by septum.

Teeth on jaws, vomer and palatine bones. Anterior jaw teeth (outer row) of upper jaw caniniform, recurved in male examined. Vomerine teeth few, caniniform. Large caniniform tooth in outer row slightly away from symphysis in lower jaw, as in Lycodapus parviceps (Peden and Anderson, 1978, fig. 9). Hyomandibula posterior ramus normal. Ceratohyal-epihyal juncture smooth. Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed;

three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2 + 10 (in one).

Posttemporal ventral strut weak. Scapula not observed, foramen probably enclosed; posterior strut probably weak or absent. Four actinosts bearing 9 fin rays. Pelvic fins absent, pelvic bone a very small splint.

Epipleural ribs extend to about first half of precaudal vertebrae. Pleural ribs extend from third to ultimate precaudal vertebrae. Dorsal fin origin associated with third vertebra, with no free pterygiophores. All dorsal fin elements soft rays. No anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one fin ray, hypurals with seven rays, thus total caudal rays eight. Last dorsal fin ray associated with third preural vertebra; last anal ray associated with second preural vertebra.

Palatine membrane absent, no vestiges remain. Pseudobranchial filaments 10, rather long. Two well developed pyloric caeca. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae symmetrical.

Distribution and species. A single species in the genus, Lycogrammoides schmidti Soldatov and Lindberg, 1929, is known only from the five specimens reported by Shmidt (1950), one of which was donated to the Museum of Comparative Zoology, Harvard (MCZ 34050). Ranges throughout the Okhotsk Sea, from off the west coast of Kamchatka, Tauiskaya Bay and west of Iona Island in 68-200 m. Probably pelagic.

Lyconema Gilbert, 1895

(figs. 3D, 4I; pl. VII)

Lyconema Gilbert, 1895: 471, pl. 35 (type species: Lyconema barbatum Gilbert, 1895, by original designation); Gotshall, 1971: 295-297, fig. 1, tab. 1.

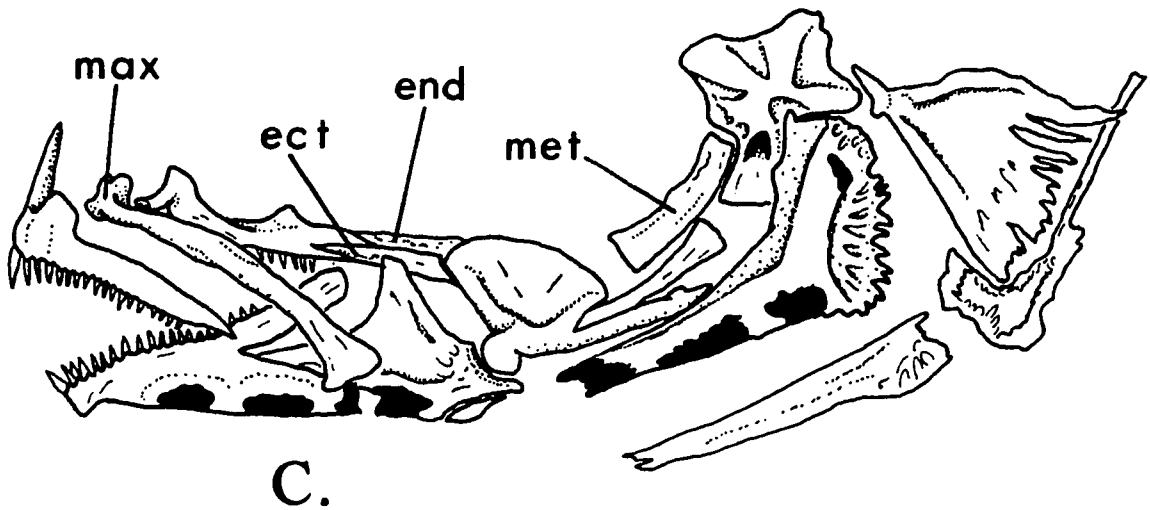
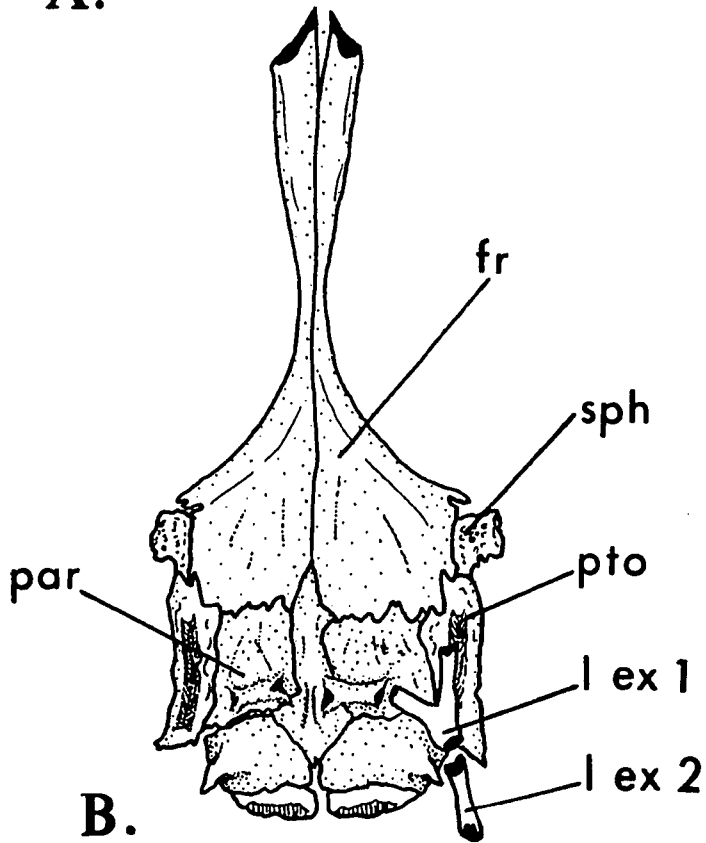
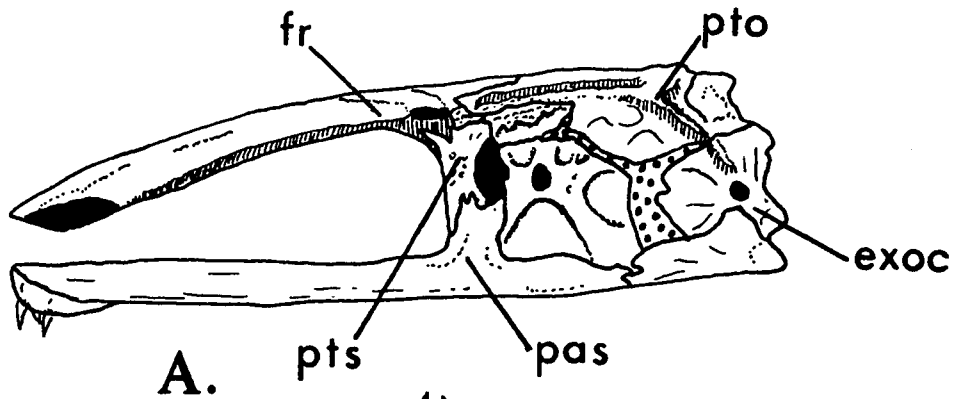
Diagnosis. Body low, tail elongate; two parallel rows of filamentous cirri on lower jaw, cirri often present on throat and branchiostegal membranes in large adults; frontal separated from parasphenoid by pterosphenoid; palatal arch weakly developed; suborbital bones and pores 9; vertebrae 20-21 + 86-93 = 106-114; scales, vomerine and palatine teeth present; pelvic fins each with two soft rays.

Description. Scales present, complete, very small. Lateral line medio-lateral, complete. Flesh firm. Gill slit extending ventrally to pelvic fin base or just above it (Fedorov, 1982: 17 stated the gill slit does not extend ventrally below pectoral fin base, repeating the error of Gilbert, 1895).

Parasphenoid wing very low, well below mid-height of trigemino-facialis foramen. Frontal descending wing small; frontal separated from parasphenoid wing by relatively large pterosphenoid (fig. 4IA). Sphenotic separated from parietal by frontal and pterotic. Parietals not meeting in midline, with well developed bony tubes posteriorly passing supratemporal commissure (fig. 4IB). Supraoccipital with well developed anterior ramus extending under frontals; mesial crest small; supraoccipital excluded from exoccipital by epioccipitals (fig. 4IB).

Cephalic lateralis pore system complete, pores moderate in size. Two lateral extrascapulars, first V-shaped (fig. 4IB). Postorbital pores 1-4 present. Two nasal pores. One interorbital pore. Three

Figure 41. Lyconema barbatum, 160 mm SL. A) Left lateral view of neurocranium, ethmoid region not shown. B) Dorsal view of neurocranium, left lateral extrascapulars and ethmoid region not shown. C) Left lateral view of jaws, suspensorium and opercular bones.



occipital pores. Suborbital bones usually 9; fragmentation of some produces up to 12 ossifications (fig. 3D). Suborbital pores seven on ventral branch, two on ascending branch. Preoperculomandibular system in primitive state, with four dentary, one anguloarticular and three preopercular pores and bone foramina (fig. 41C). Mandibular and preopercular branches joined.

Teeth on jaws small, conical, sharp. Teeth present on vomer and palatines. Dentition seems to be sexually dimorphic, but this requires further statistical testing; dimorphism does not appear to be related to tooth size, but to tooth numbers. Endopterygoid and ectopterygoid weakly articulating with quadrate (fig. 41C). Hyomandibula posterior ramus normal. Metapterygoid reduced. Opercle and subopercle not well ossified, with cartilaginous posterior borders. Ceratohyal-epihyal juncture smooth. Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2 + 8-9 = 10-11.

Posttemporal ventral strut well developed. Scapular foramen enclosed; scapular posterior strut well developed. Four actinosts, with 15-17 pectoral fin rays. Pelvic fins present, each with two soft rays.

Epipleural ribs on vertebrae 2-10 or 11. Pleural ribs on fourth to ultimate precaudal vertebra. Dorsal fin origin associated with vertebrae 4-6, with no free pterygiophores. Dorsal fin elements all soft rays. Three or four anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with 10 rays, thus total caudal rays 12. Last dorsal ray associated with fourth preural vertebra, last anal ray associated with second preural vertebra.

Palatine membrane weak. Pseudobranchial filaments 5-6, relatively long. Two nub-like pyloric caeca. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae symmetrical.

Distribution and species. A single species in the genus, Lyconema barbatum Gilbert, 1895, is found in the eastern North Pacific, from Bahia San Quintin, Baja California, to southern Oregon in 82-373 m.

Additional references. Gilbert (1915: 362); Barnhart (1936: 90, 181, fig. 273); Miller and Lea (1972: 78, fig.); Mearns and Allen (1973: 4); Eschmeyer and Herald (1983: 106, pl. 11).

Maynea Cunningham, 1871
(figs. 8D, 42-44; pl. XV)

Maynea Cunningham, 1871: 471, 472 (type species: Maynea patagonica Cunningham, 1871 (= Conger punctus Jenyns, 1842), by monotypy); Jordan and Davis, 1891: 663; McAllister and Rees, 1964: 105-107 (partim); Gosztonyi, 1977: 220-223.

Remarks. This monotypic genus has had a very confused history, having many unrelated species placed within it (i.e., species of Austrolycichthys, Bothrocara, Gymnelopsis and Redirolycus). Maynea is here restricted to the South American M. puncta (Jenyns), known in most of the literature as M. patagonica Cunningham. I have re-examined the type of Jenyns' (1842) Conger punctus (collected by Darwin in the Falkland Islands) and concur that Jordan and Davis' (1891) overlooked nomenclature for the species is correct.

Diagnosis. Body robust, tail moderately long; frontal bones squared-off (character 13); hyomandibula posterior ramus elongate (character 14); ceratohyal-epihyal juncture interdigitating (character 15); scales,

vomerine and palatine teeth present; pelvic fins absent; eight suborbital bones with 5-6 moderate pores; palatal arch well developed; parietals meeting in midline; supraoccipital separated from exoccipital; branchiostegal rays 5; vertebrae 29-30 + 89-98 = 119-128; C 7.

Description. Scales present, moderate, absent on nape. Lateral line mediolateral, complete. Flesh firm, barred or monotone. Gill slit extending ventrally to mid-pectoral fin base or just slightly below that.

Parasphenoid wing moderate, anterior ramus not extending to mid-height of trigeminofacialis foramen (fig. 42A); frontal and parasphenoid not separated by pterosphenoid, which is rather small. Sphenotic moderate, separated from parietal by frontal and pterotic. Parietals large, meeting in midline (fig. 42B). Supraoccipital large, widely separated from exoccipital by epioccipitals (fig. 42B).

Cephalic lateralis pore system reduced in number, pores small and rounded. One small lateral extrascapular. Postorbital pores 1 and 4 present. Two nasal pores. No interorbital or occipital pores. No supratemporal commissure or bony supports across parietals. Eight relatively small suborbital bones, with five or six pores on ventral branch and no pores on ascending branch (fig. 42C). Preoperculomandibular system in primitive state, with four dentary, one anguloarticular and three preopercular pores and bone foramina (fig. 43A). Preopercular and mandibular branches joined.

Teeth small, conical, no dimorphism in dentition. Teeth present on vomer and palatine bones. Endopterygoid and ectopterygoid broadly articulating with quadrate. Hyomandibula posterior ramus elongate (fig. 43A). Opercle, subopercle and metapterygoid large and well ossified. Ceratohyal-epihyal juncture with bone interdigitating dorsally (fig. 43B).

Figure 42. Maynea puncta, 149 mm SL. A) Left lateral view of neurocranium. B) Dorsal view of neurocranium. C) Left lateral view of head, upper jaw bones and suborbitals.

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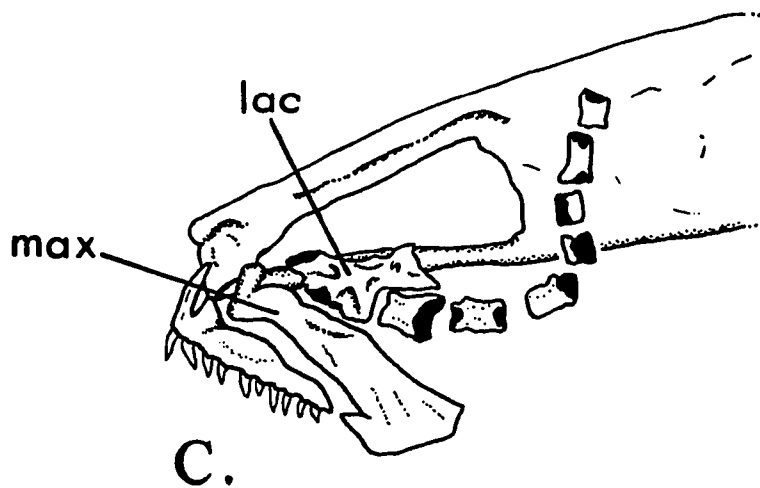
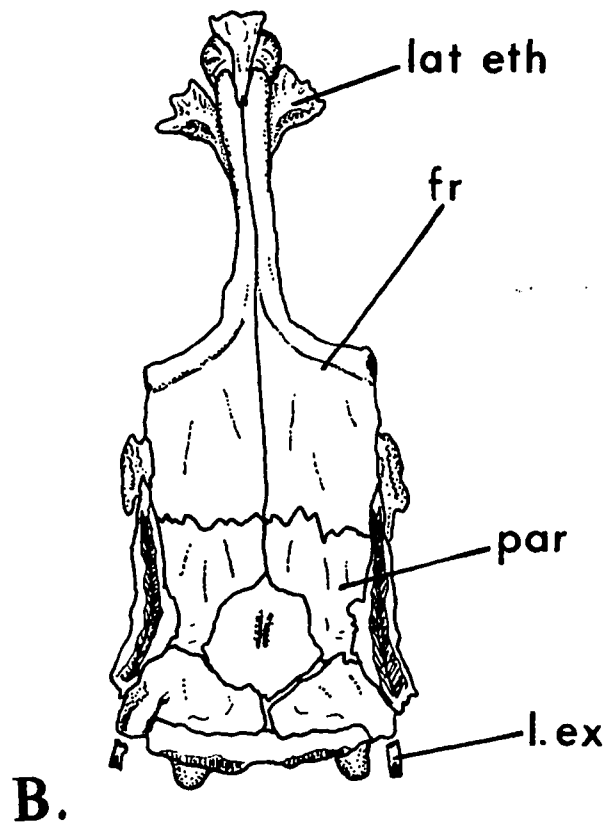
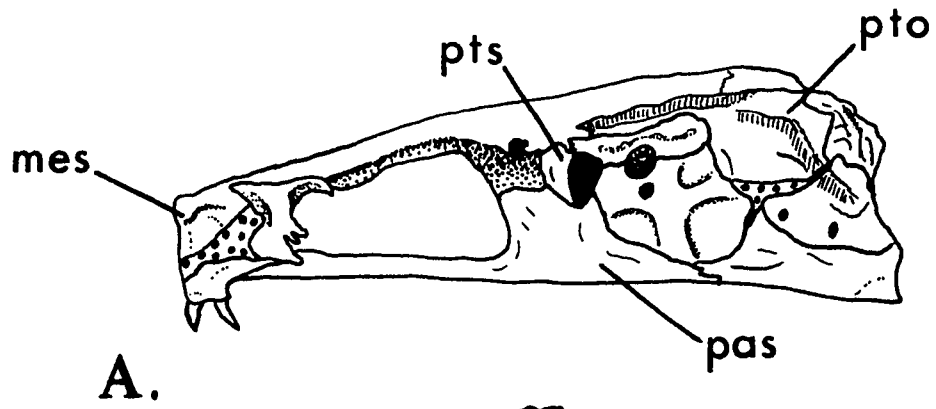
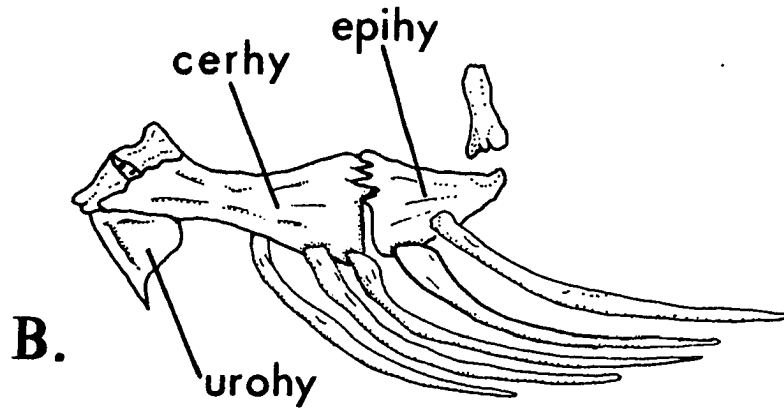
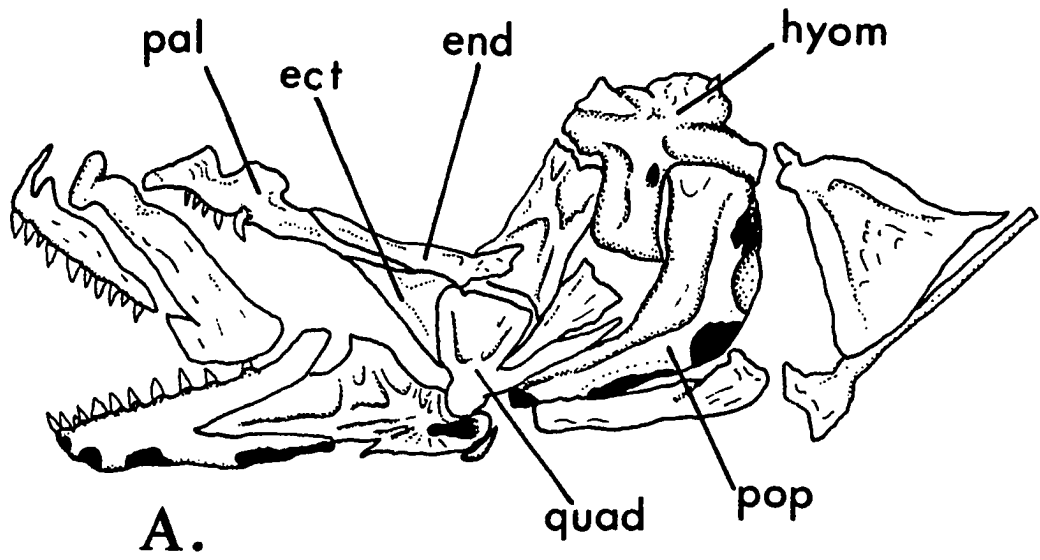


Figure 43. Maynea puncta, 149 mm SL. A) Left lateral view of jaws, suspensorium and opercular bones. B) Left lateral view of hyoid bar.



Branchiostegal rays 3 + 2. Ceratobranchial 5 toothed, three pairs of infrapharyngobranchials and tooth plates. Gill rakers 3 + 10-11.

Posttemporal ventral strut well developed (fig. 44A). Scapular foramen enclosed; scapular posterior ramus moderately well developed. Four actinosts bearing 14-16 pectoral fin rays. Pelvic fins absent, pelvic bones normal size.

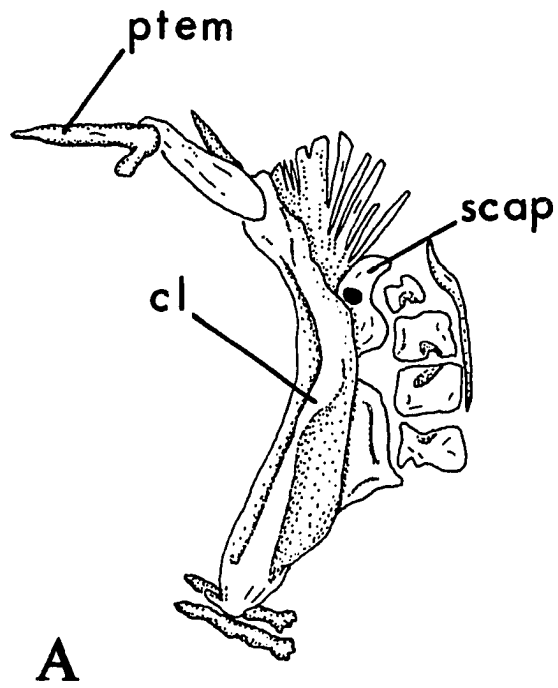
Epipleural ribs on vertebrae 1-18 or to 21. Pleural ribs on third through ultimate or penultimate precaudal vertebra. Dorsal fin origin associated with first vertebra, with no free pterygiophores. All dorsal fin elements soft rays. Three anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one fin ray, hypurals with six rays, thus total caudal rays seven in all four specimens known (fig. 44B). Last dorsal ray associated with third or fourth preural vertebra; last anal ray associated with second preural vertebra.

Palatine membrane weak. Five rather long pseudobranchial filaments. Two nub-like pyloric caeca. Peritoneum light. Maynea is oviparous, spawning and guarding egg masses in the intertidal zone. Vertebrae symmetrical.

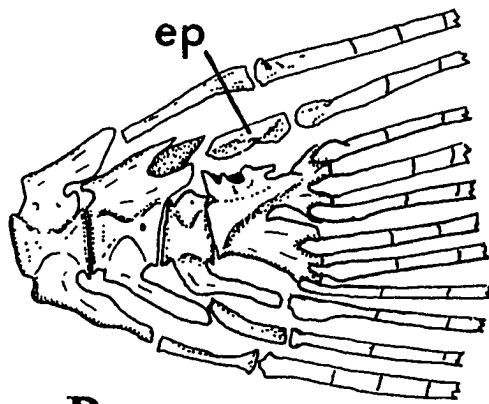
Distribution and species. A single species in the genus, Maynea puncta (Jenyns, 1842) is found in intertidal and shallow subtidal regions of southern Chile, Tierra del Fuego and the Falkland Islands. Also found on the outer shelf (probably when not spawning) to a depth of 101 m, possibly to 300 m.

Additional references. Günther (1870: 41, 42); Günther (1881: 20, pl. II, figs. C, D); Steindachner (1898: 318); Lonnberg (1905: 20); Lahille (1908: 438, 439, fig. 8); Regan (1913: 248); Hussakof (1914): 92;

Figure 44. Maynea puncta, 149 mm SL. A) Left lateral view of pectoral girdle. B) Left lateral view of caudal skeleton.



A



B

Norman (1937a: 108); Norman (1966: 477, 482); Nybelin (1969: 120); Lindberg (1974: 207, fig. 804).

Notolycodes Gosztonyi, 1977

(pl. VIII)

Notolycodes Gosztonyi, 1977: 224-227, figs. 13-15 (type species: Notolycodes schmidti Gosztonyi, 1977, by original designation).

Diagnosis. Body robust, tail relatively short; frontal bones squared-off (character 13); hyomandibula posterior ramus normal (character 14); ceratohyal-epihyal juncture interdigitating (character 15); chin pad present (character 29); squamation extensive, scales covering body, tail, fins, nape and cheek; gill slit extending ventrally to pelvic base; pelvic fins very long, one eye diameter in length or longer; eight sub-orbital bones, with seven small pores; branchiostegal rays 3 + 2; vomerine and palatine teeth absent; no occipital pores; P 18-21; vertebrae 23-26 + 66-69 = 89-94.

Description. Squamation very extensive for an eelpout, scales cover entire body, abdomen, tail, nape, cheeks and vertical fins to more than half their height. Lateral line mediolateral, complete. Flesh firm, thickened. Gill slit long, extending ventrally to pelvic fin insertion (Gosztonyi, 1977, fig. 13).

Details of neurocranium and suspensorium not seen. Bones appear well ossified and not reduced.

Cephalic lateralis pore system reduced in number, pores small and rounded. Postorbital pore 1 and 4 present. Probably only one lateral extrascapular. Two nasal pores. No interorbital or occipital pores. Eight suborbital bones with seven pores on ventral branch and none on

ascending branch. Preoperculomandibular system in primitive state, with four dentary, one anguloarticular and three preopercular pores; not all pores are open in large adults, as in Lycodes. Mandibular and preopercular branches joined.

Teeth small, conical, not dimorphic. No vomerine or palatine teeth. Endopterygoid and ectopterygoid probably broadly articulating with quadrate. Hyomandibular posterior ramus normal. Ceratohyal-epihyal juncture interdigitating dorsally, closely joined ventrally. Branchiostegal rays 3 + 2, thickened. Ceratobranchial 5 toothed, rather heavily; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 1-2 + 8-9 = 10-11.

Posttemporal ventral strut very weak. Scapula not seen. Four actinosts bearing 18-21 rather long, thick pectoral fin rays. Pelvic fins very long for an eelpout, of three rays each, equal to or longer than one eye diameter.

Epipleural ribs on vertebrae 1-2, extending to vertebrae 12-13. Pleural ribs on vertebrae 3-4, extending to ultimate precaudal vertebra. Dorsal fin origin associated with vertebrae 3-5, with no free pterygiophores. All dorsal fin elements soft rays. Three anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with nine rays, thus total caudal rays 11. Last dorsal fin ray associated with fourth preural vertebra; last anal ray associated with second preural vertebra.

Palatine membrane well developed, proximally bearing low sensory papillae. Seven pseudobranchial filaments, rather thick and long. Two nub-like pyloric caeca. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae symmetrical.

Distribution and species. A single species in the genus, Notolycodes schmidti Gosztonyi, 1977, is known from six specimens taken between Cabo Frio, Brazil, to off Rio de la Plata, Argentina, in 400-800 meters.

Oidiphorus McAllister and Rees, 1964
(figs. 45-47; pl. XV)

Oidiphorus McAllister and Rees, 1964: 104-105, fig. 1 (type species: Maynea brevis Norman, 1937a, by original designation; Gosztonyi, 1977: 228-229, fig. 17.

Remarks. Torno et al. (1977) described a new zoarcid from the South Sandwich Islands (Scotia Sea) as Oidiphorus laevifasciatus. The very short description is poor, but a photograph and some passages permit the conclusion that this species cannot be placed in Oidiphorus McAllister and Rees. The head of laevifasciatus is narrow, there are none of the uniquely placed dermal papillae and a body lateral line is present (although they report this to be composed of pores, this must be incorrect). In fact, this species appears to represent an undescribed genus allied to, and more primitive than, Melanostigma. The long gill slit, extending to the ventral edge of the pectoral base, presence of body lateral line and presence of two preopercular pores support this conclusion. Re-examination of the only known specimen of laevifasciatus is critically needed before further considerations are warranted.

Diagnosis. Body robust, tail very short; dermal papillae present on jaws, cheeks, nape and above eyes; flesh gelatinous; scales absent; vertebrae 15-17 + 43-50 = 58-64; gill slit extending ventrally to mid-pectoral base; frontal bones extremely wide, their width 82-84% of length at widest point; no teeth on ceratobranchial 5; two pairs of infrapharyngobranchials; palatal arch weak; C 7-9; suborbital bones and

pores six; pelvic fins absent.

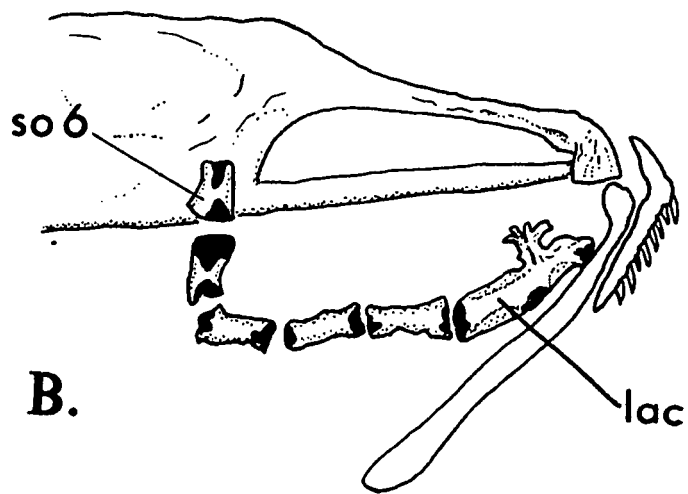
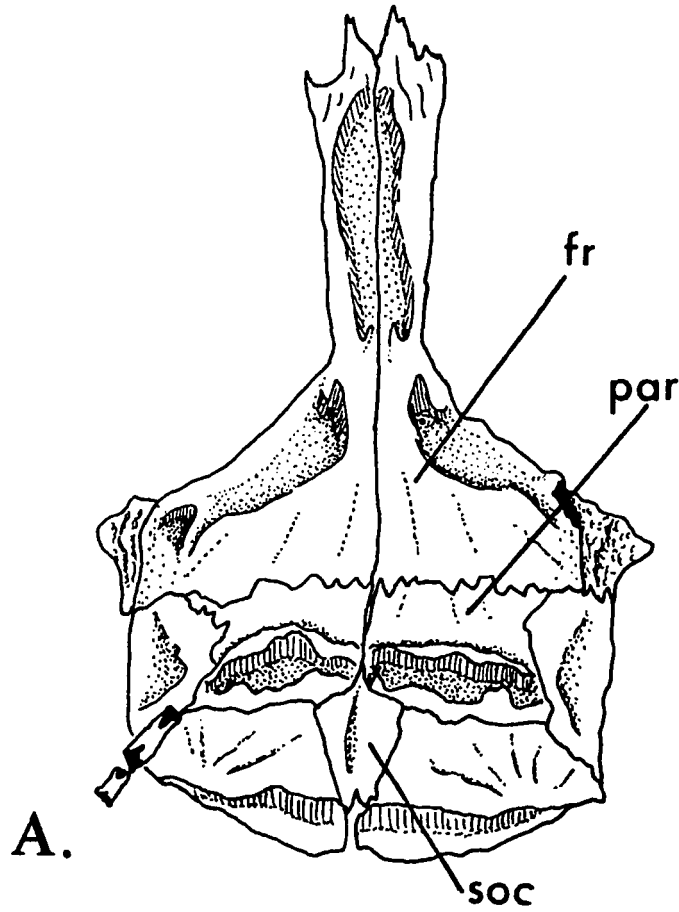
Description. Body and tail relatively short. Head very broad and rounded. Skin thin and delicate, with thick gelatinous layer. Low, triangular papillae on jaws and suborbital region in single row; on cheeks, nape and directly above eye. Papillae often poorly developed above eye and nape in large adults and subject to shrinkage in preservative. Lateral line mediolateral, complete. Gill slit extending ventrally to mid-pectoral base or slightly above or below it, never to pectoral base.

Parasphenoid wing greatly reduced, single ramus present, extending well below mid-height of trigeminofacialis foramen. Frontal and parasphenoid not separated by pterosphenoid, which is large and ovoid. Neurocranium greatly truncated, frontals extremely wide in relation to length (fig. 45A). Sphenotic and parietal separated by frontal and pterotic. Parietals large, meeting in midline. Supraoccipital relatively small, but with moderate mesial crest, narrowly contacting exoccipital behind.

Cephalic lateralis system reduced in number. Postorbital pores 1 and 4 present only. Two lateral extrascapulars. Two nasal pores. No occipital or interorbital pores. Supratemporal commissure present, wide trough through parietals for it (fig. 45A). Six suborbital bones with six pores in ventral branch, no pores in ascending branch. (fig. 45B). Preoperculomandibular pores and bone foramina in primitive condition, with four dentary, one anguloarticular and three preopercular pores. Mandibular and preopercular branches joined.

Teeth of adult males fang-like, but not greatly produced, less numerous than females. Vomerine teeth present; palatine teeth absent.

Figure 45. Oidiphorus brevis, 115 mm SL. A) Dorsal view of neurocranium, right lateral extrascapulars and ethmoid region not shown. B) Right lateral view of head, upper jaw and suborbital bones.



Endopterygoid and ectopterygoid weak; narrowly articulating with quadrate. Hyomandibula posterior ramus normal. Opercle with high dorsal ramus; subopercle dorsal ramus high, both producing high, broad opercular flap (fig. 46A; Norman, 1937a, fig. 57). Ceratohyal-epihyal juncture smooth. Branchiostegal rays 4 + 2, vert long (fig. 46B). Ceratobranchial 5 without teeth; two pairs of infrapharyngobranchials and tooth plates, corresponding to gill arches two and three (fig. 47A). Gill rakers 1-2 + 6-8 = 8-10.

Posttemporal ventral ramus weak. Postcleithrum reduced to small splint. Scapular foramen enclosed; scapular posterior ramus not well developed. Four actinosts bearing 16-19 pectoral fin rays. Pelvic fins absent, pelvic bone relatively large (fig. 47B).

Epipleural ribs beginning on second or third vertebra, extending to ultimate precaudal vertebra. Pleural ribs beginning on third or fourth vertebra, extending to ultimate precaudal vertebra. Dorsal fin origin associated with vertebrae 1-3, with no free pterygiophores. D 56-61, of all soft rays. Zero to two anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one fin ray, hypurals with 6-8 rays, thus total caudal rays 7-9. Last dorsal and last anal ray associated with third preural vertebra in all known specimens.

Palatine membrane weak. Pyloric caeca and psuedobranch absent in all specimens. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae symmetrical.

Distribution and species. A single species in the genus, Oidiphorus brevis (Norman, 1937) is known from about 30 specimens taken in the temperate southwestern Atlantic from off southern Brazil south to

Figure 46. Oidiphorus brevis, 115 mm SL. A) Right lateral view of jaws, suspensorium and opercular bones. B) Right lateral view of hyoid bar.

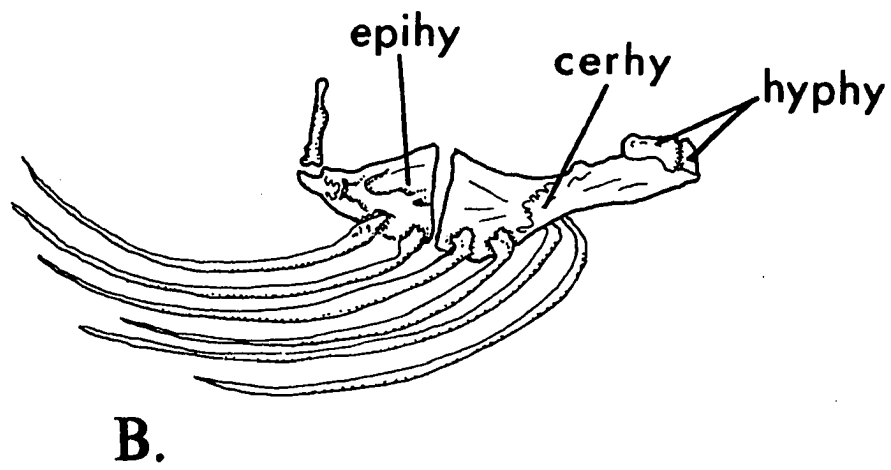
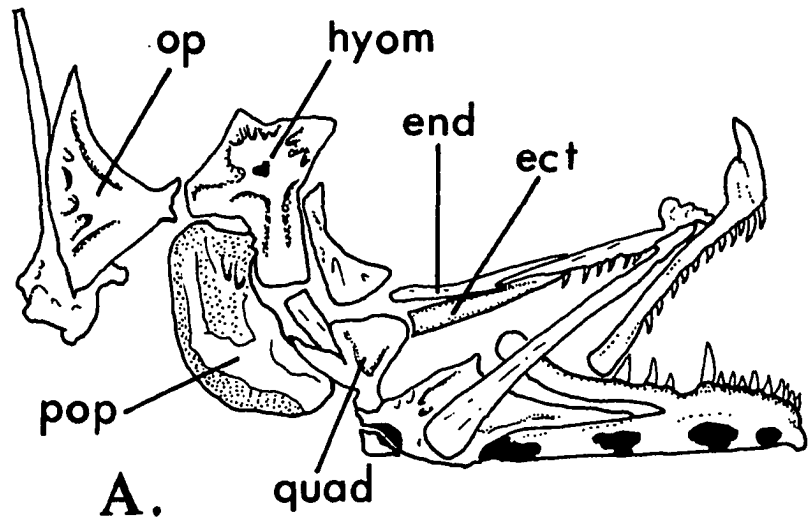
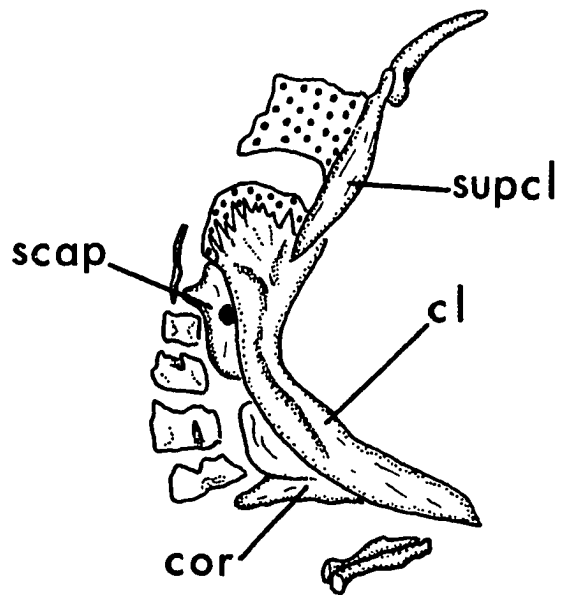
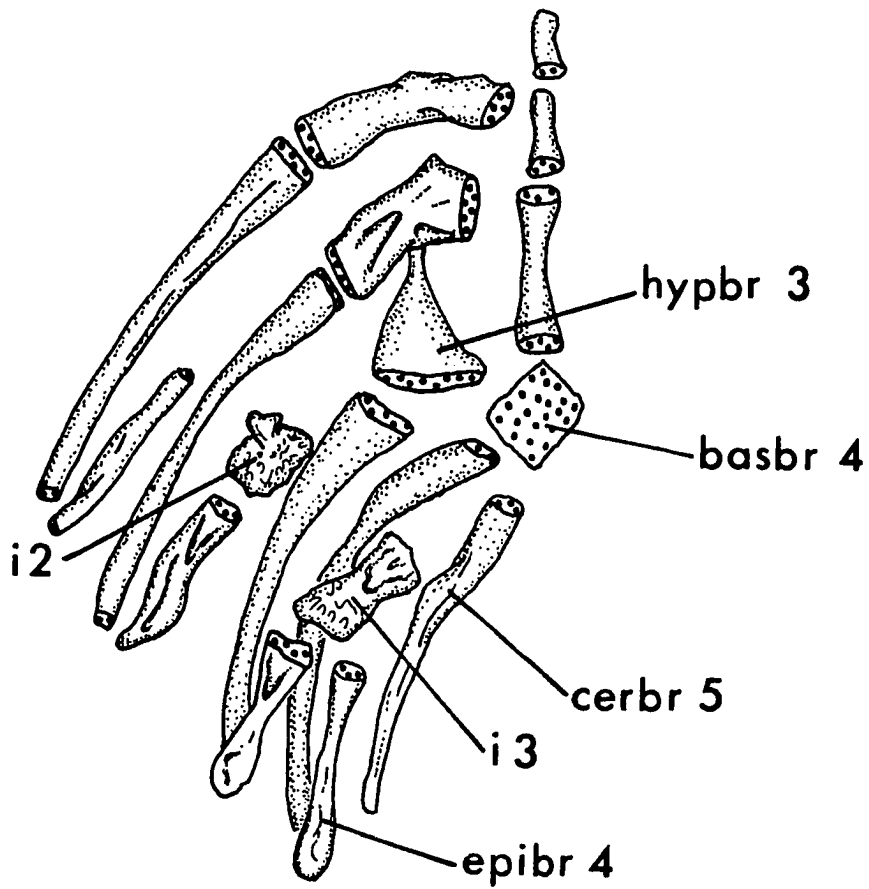


Figure 47. Oldiphorus brevis, 115 mm SL. A) Dorsal view of the bones of the left gill arches. B) Right lateral view of pectoral girdle.



Burdwood Bank in 133-1000 meters.

Ophthalmolycus Regan, 1913

(figs. 12D, 48, 49; pl. XI)

Ophthalmolycus Regan, 1913: 243 (type species: Lycodes macrops Günther, 1880, by original designation); Norman, 1937a: 98, 99, fig. 49; Gosztonyi, 1977: 229, 230, fig. 17.

Remarks. This genus contains three species, two of which have been regarded as belonging in Austrolycichthys Regan. These are Roule and Despax's (1911) Lycodes concolor and Pappenheim's (1912) Lycodes bothriocephalus. These two species are very similar and inseparable from Ophthalmolycus macrops at the generic level. Even Regan (1913) suggested L. concolor may be referable to Ophthalmolycus. The confusion seems to stem from the fact that only one specimen of O. macrops is known in the literature. Gosztonyi's (1977) Ophthalmolycus stehmanni is very different from the three species recognized here and is placed in a new monotypic genus (see below).

Diagnosis. Body low, tail elongate; anterior portion of pterotic narrower or as wide as posterior portion; suborbital bones 7-8, with six pores; palatal arch well developed; cephalic lateralis pores enlarged; pelvic fins, scales, vomerine and palatine teeth present; vertebrae 22-23 + 72-88 = 94-110; tail tip not tapering sharply.

Description. Scales present, complete, moderate in size. Lateral line mediolateral, complete. Flesh firm. Gill slit extending ventrally to pectoral fin base, or, in O. bothriocephalus, to mid-pectoral base.

Parasphenoid wing extending to mid-height of trigeminofacialis foramen or just below it; frontal and parasphenoid narrowly contacting

anteriorly; pterosphenoid relatively large (fig. 48A). Sphenotic and parietal separated by frontal and pterotic. Pterotic normal, with anterior half narrower or as wide as posterior section (fig. 48B). Parietals not meeting in midline. Supraoccipital moderate, anterior ramus extending well under frontals; mesial crest small; supraoccipital and exoccipital narrowly contacting posteriorly.

Cephalic lateralis system reduced, but pores enlarged. One lateral extrascapular. Postorbital pores 1, 3, 4 or 1 and 4 present. Two nasal pores. Interorbital and occipital pores absent. Supratemporal commissure absent, no bony supports on parietal. Suborbital bones 7-8, with six pores on ventral branch and none on ascending branch. Preoperculo-mandibular system in primitive state, with four dentary, one anguloarticular and three preopercular pores and bone foramina (fig. 49A). Mandibular and preopercular branches joined.

Teeth on jaws small, conical. Teeth present on vomer and palatine bones. Endopterygoid and ectopterygoid broadly articulating with quadrate (fig. 49A), well ossified. Hyomandibula posterior ramus normal. Opercle and subopercle moderately well ossified. Ceratohyal-epihyal juncture smooth. Branchiostegal rays 4 + 2, except in O. macrops, which has 3 + 2. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 1-3 + 8-10 = 11-12.

Posttemporal ventral strut weak (fig. 49B). Scapular foramen enclosed; scapular posterior strut well developed. Four actinosts bearing 14-18 pectoral fin rays. Pelvic fins present, with two or three rays.

Epipleural ribs on first to eleventh through sixteenth vertebrae. Pleural ribs on third to ultimate or penultimate precaudal vertebra. Dorsal fin origin associated with vertebrae 3-8, with no free pterygio-

Figure 48. Ophthalmolycus macrops, 129 mm SL. A) Left lateral view of neurocranium, ethmoid region not shown. B) Dorsal view of neurocranium.

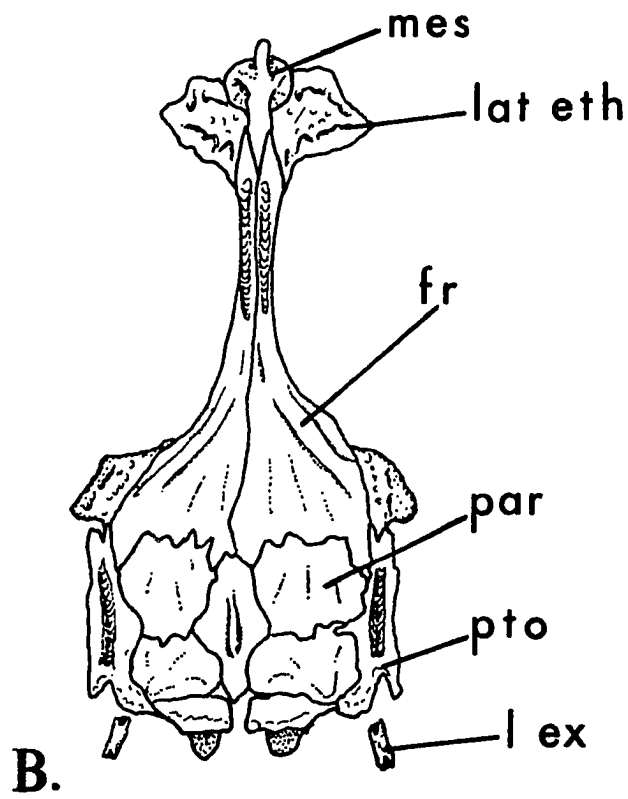
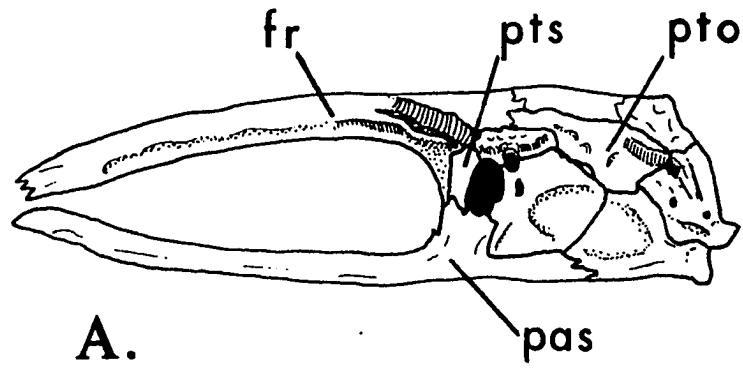
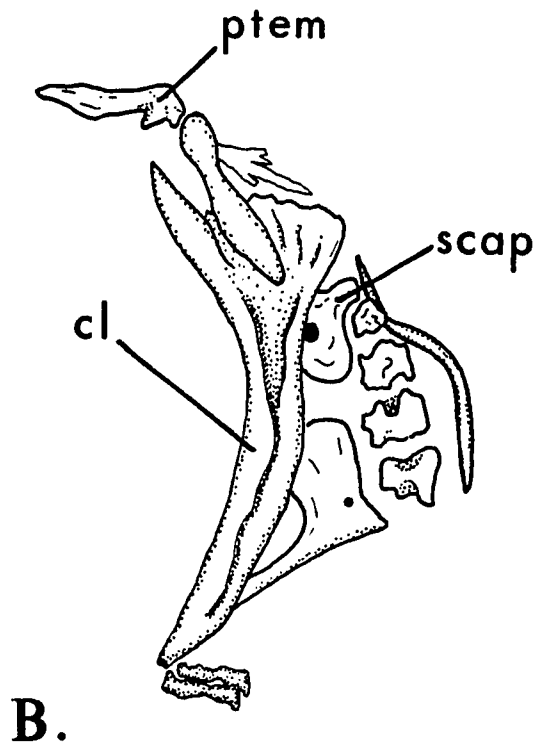
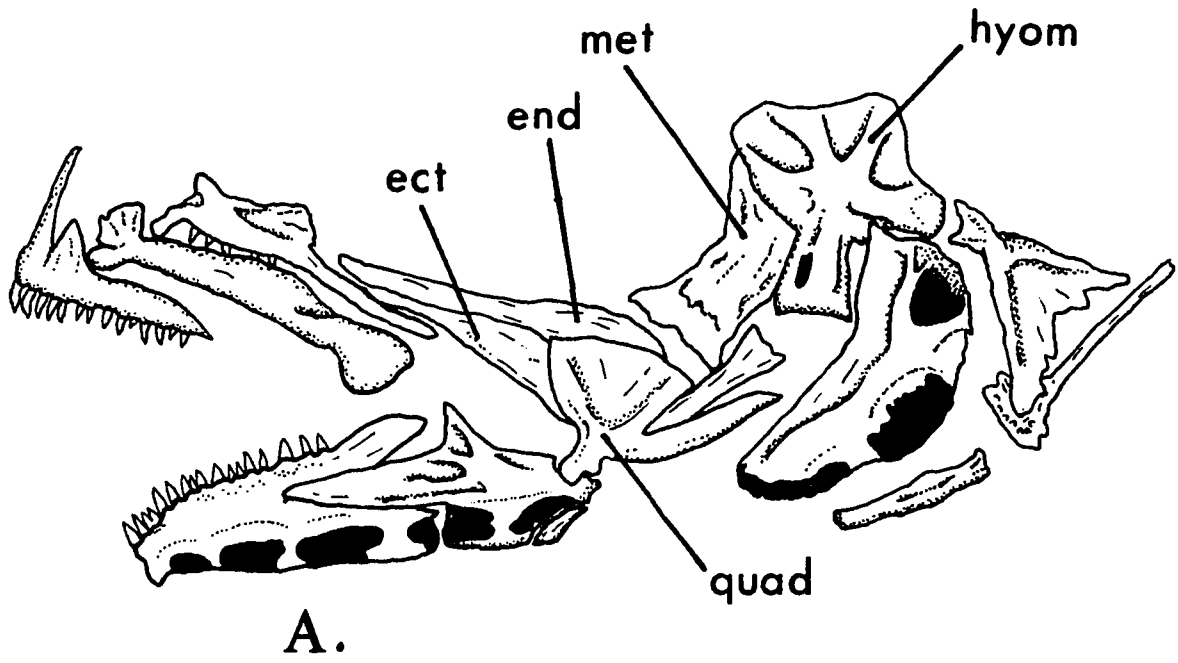


Figure 49. Ophthalmolycus concolor, 141 mm SL. A) Left lateral view of jaws, suspensorium and opercular bones. B) Left lateral view of pectoral girdle, pelvic fin rays not shown.



phores. Dorsal fin with anteriormost element a flexible spine, or of all soft rays. Two to five anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with eight rays, thus total caudal rays 10. Last dorsal ray associated with fourth preural vertebra, last anal ray associated with second preural vertebra.

Palatine membrane weak. Pseudobranchial filaments 1-4, relatively short. Two pyloric caeca; nub-like in O. macrops, rather long in both O. concolor and O. bothriocephalus. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae asymmetrical anteriorly, either symmetrical or asymmetrical posteriorly.

Distribution and species. Ophthalmolycus bothriocephalus (Pappenheim, 1912): eastern Antarctica, from Enderby Land to Wilhelm Land in 300-380 meters. Ophthalmolycus concolor (Roule and Despax, 1911): eastern Antarctica to South Shetland Islands in 140-453 meters. Ophthalmolycus macrops (Günther, 1880): Straits of Magellan, Chile, in 73-552 meters.

Additional references. Lahille (1908: 412); Roule et al. (1913: 19, pl. II, fig. 3, pl. III, fig. 6); Norman (1937b: 80, fig. 10); Norman (1938: 83-85 (partim), fig. 54); Nybelin (1947: 55, 65, 66); Andriashev (1965: 513); Permitin (1977: 714); Daniels and Lipps (1982: 3, 4).

Pachycara Zugmayer, 1911

(figs. 12C, 13F, 50, 51; pls. IV, V, VI)

Pachycara Zugmayer, 1911a: 12; Zugmayer, 1911b: 134-136, pl. VI, fig. 6 (type species: Pachycara obesa Zugmayer, 1911, by monotypy); Markle and Sedberry, 1978: 22-25, fig. 1.

Remarks. This genus is very poorly known and there are more undescribed

species than described. Markle and Sedberry (1978) mistakenly reported their specimen of P. obesum to possess seven preoperculo-mandibular pores (it has eight). This, plus misinterpretation of allometry and individual variation in vertebral number prompted Andriashev (1979) to refer this specimen to Lycenchelys, an irregular reference for that author, who erected a genus for a species of Lycenchelys without pelvic fins (Apodolycus; P. obesum lacks pelvics too).

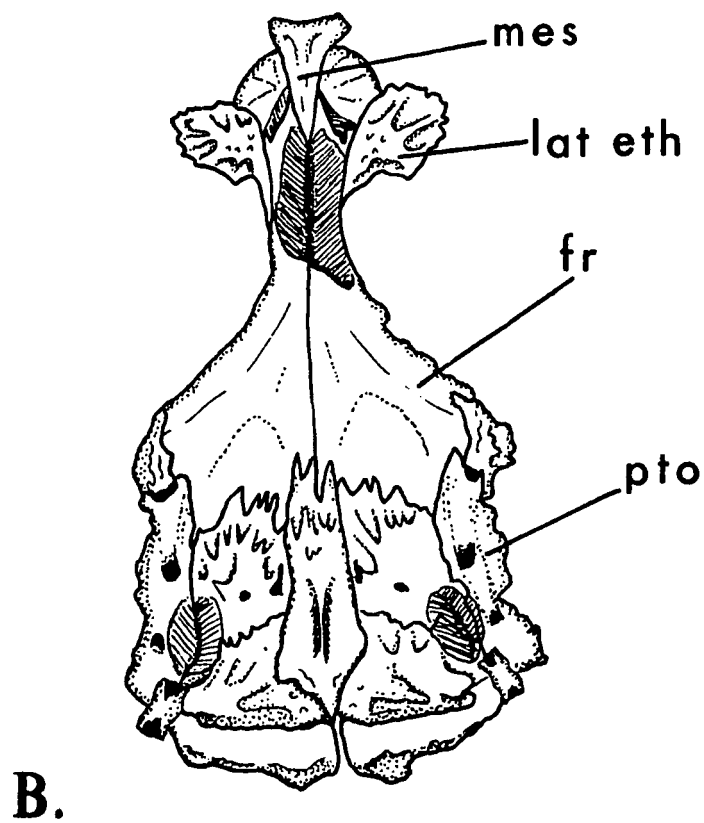
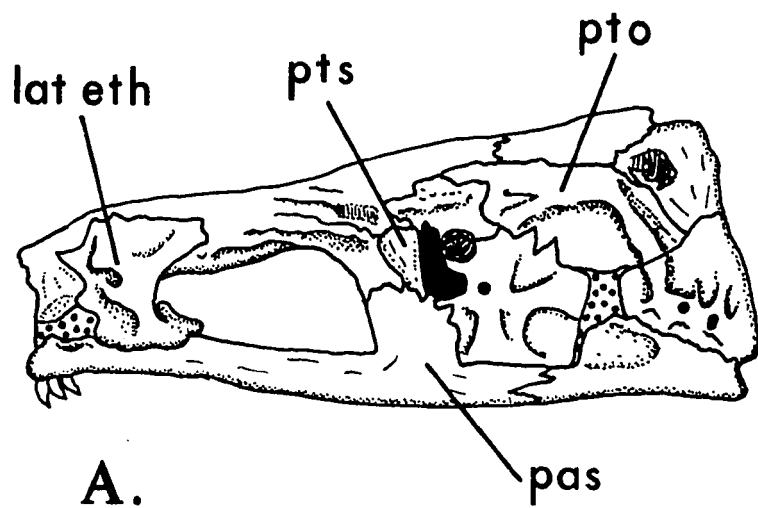
Diagnosis. Body robust, tail short; mental crests absent; parasphenoid wing below mid-height of trigeminofacialis foramen; precaudal vertebrae (25) 26-32 (total vertebrae 103-122); suborbital bones 6-8; pseudobranchial filaments 0-6; palatal arch well developed; pelvic fins present or absent; head blunt, rounded.

Description. Body moderately elongate, very robust; tail relatively long and high. Scales present, complete, on nape in one species. Lateral line mediolateral or mediolateral and ventrolateral. Flesh firm, thickened. Gill slit extending ventrally to pectoral base or below.

Osteological observations based on cleared and stained material of four species. Parasphenoid wing below mid-height of trigeminofacialis foramen, posterior ramus of wing poorly expressed or absent (fig. 50A). Frontal and parasphenoid not separated by pterosphenoid. Sphenotic and parietal separated by frontal and pterotic (fig. 50B). Parietals separated from midline with no channel through posterior margin bracing supratemporal commissure. Supraoccipital relatively large, anterior ramus extending well under frontals, mesial crest well developed; supraoccipital narrowly contacting exoccipital posteriorly.

Cephalic lateralis pore system reduced in number and size. Post-

Figure 50. Pachycara sp. A, 281 mm SL. A) Left lateral view of neurocranium. B) Dorsal view of neurocranium.



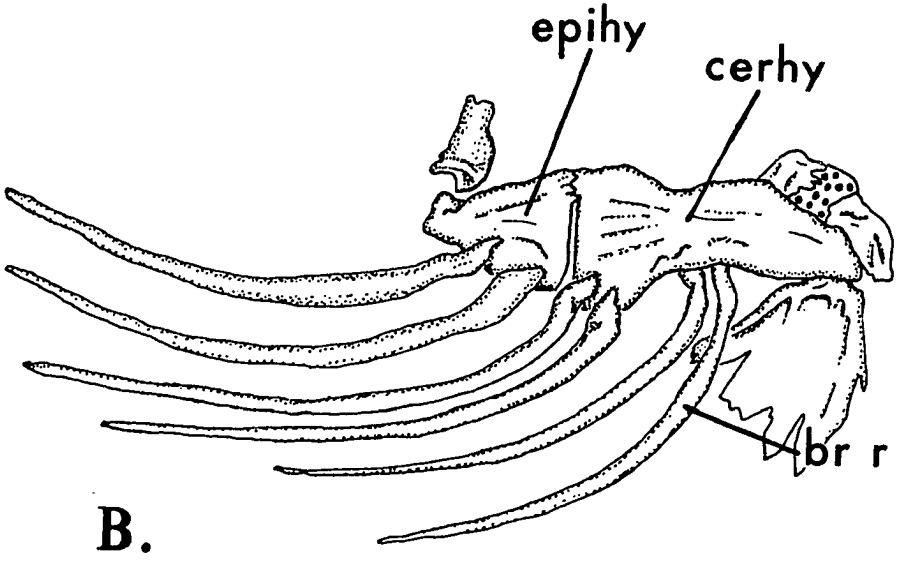
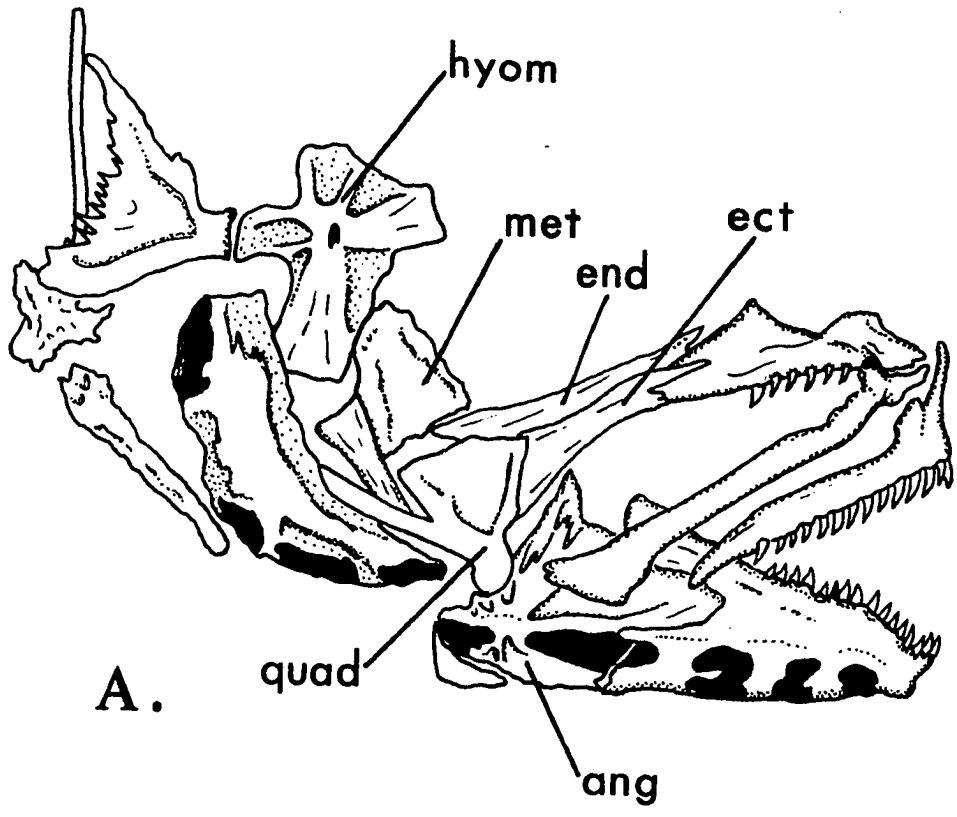
orbital pores present are 1, 3, 4; 1 and 4, or 1 only. One lateral extrascapular. Two nasal pores. No interorbital or occipital pores. Six suborbital bones, except in P. crassiceps, which has eight. Six suborbital pores, all on ventral branch, except P. crassiceps, which has six on ventral and one on ascending branch. Preoperculo-mandibular pore and bone foramina system in primitive state, with four dentary, one anguloarticular and three preopercular pores (fig. 51A). Mandibular and preopercular branches joined.

Teeth on jaws small but stout. Teeth present on vomer and palatines, also quite stout. Endopterygoid and ectopterygoid broadly articulating with quadrate (fig. 51A). Hyomandibula posterior ramus normal. Opercle and subopercle moderately well ossified. Ceratohyal-epihyal juncture smooth, except small, dorsal area in Pachycara sp. A (fig. 51B). Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed; teeth numerous, stout. Three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2-5 + 9-15 = 11-19, with one or two on hypobranchials.

Posttemporal ventral strut weak or absent (fig. 13F). Scapular foramen enclosed; scapula with well developed posterior strut. Four actinosts bearing 14-19 pectoral fin rays. Pelvic fins absent or present with three short rays.

Epipleural ribs on vertebrae 1 to 21 or 22. Pleural ribs on third to ultimate precaudal vertebra. Dorsal fin origin associated with vertebrae 3-8, with no free pterygiophores. D I, 95-113; first always a flexible spine. Three to six anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypural rays 8-10, thus total caudal rays 10-12. Last dorsal ray associated with third or fourth preural vertebra, last anal ray associated with

Figure 51. Some osteological features of Pachycara. A) Right lateral view of jaws, suspensorium and opercular bones of P. obesum, 332 mm SL. B) Right lateral view of hyoid bar of Pachycara sp. A.



second preural vertebra.

Palatine membrane weak. Pseudobranchial filaments 0-6, usually four or less. Two nub-like pyloric caeca. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae symmetrical.

Distribution and species. Pachycara bulbiceps (Garman, 1899): Queen Charlotte Islands, British Columbia, south to Gulf of Panama in 2601-3229 meters. Pachycara crassiceps (Roule, 1916): southwest of Ireland to off Namibia (A. Andriashev, pers, comm.) in 900-2191 meters. Pachycara obesum Zugmayer, 1911: east of the Azores, off Cap Blanc, Mauritania and Middle Atlantic Bight of the U.S. in 2400-4780 meters. Pachycara sp. A: Queen Charlotte Islands, British Columbia, to off Oregon in 2743-2889 meters. Pachycara sp. B: Queen Charlotte Islands to off Oregon in 1500-2889 meters. Pachycara sp. C: Bay of Bengal, Indian Ocean, in 2600 meters. Pachycara sp. D: Venezuela Basin, Caribbean Sea, in 3469-3510 meters. Pachycara sp. E: Galapagos Rift Zone in about 2500 meters (Cohen and Haedrich, 1983).

Additional references. Garman (1899: 140, 141, pl. E, fig. 1); Roule (1916: 23); Roule (1919: 64, pl. V); Fowler (1936: 1056, 1057, fig. 437); Golovan' (1978: 226 (ref. to Lycodes atlanticus)); Merrett and Marshall (1981: 240); Percy et al. (1982: 387, 399, 400).

Phucocoetes Jenyns, 1842

(figs. 52, 53; pl. XV)

Phucocoetes Jenyns, 1842: 168, 169, pl. 29, fig. 3 (type species: Phucocoetes latitans Jenyns, 1842, by monotypy); Norman, 1937a: 104, 105, fig. 54; Gosztonyi, 1977: 233-235, figs. 17, 18).

Diagnosis. Body robust, tail relatively short; frontal bones squared-off;

(character 13); hyomandibula posterior ramus elongate (character 14); ceratohyal-epihyal juncture interdigitating (character 15); scales, vomerine and palatine teeth present; pelvic fins present, with three rays each; ventral edge of gill slit above mid-pectoral base; palatal arch well developed; suborbital bones 7, with 5-6 small pores; supraoccipital separated from exoccipital; branchiostegal rays 4 + 2; C 10; vertebrae 24-27 + 75-82 = 102-108.

Description. Scales present, small, absent on nape and vertical fins. Lateral line mediolateral, complete. Flesh firm. Gill slit very reduced, extending ventrally to slightly above pectoral base or to opposite sixth pectoral fin ray (about mid-pectoral base).

Parasphenoid wing moderately well developed, but not reaching above mid-height of trigeminofacialis foramen (fig. 52A). Pterosphenoid small, not separating frontal from parasphenoid. Sphenotic small, separated from parietal by pterotic and frontal. Parietals moderate, not meeting in midline (fig. 52B). Supraoccipital anterior ramus long, extending well under frontals. Supraoccipital separated from exoccipital by very large epioccipitals (fig. 52B).

Cephalic lateralis pore system reduced in number, pores moderate in size. One lateral extrascapular. Postorbital pores 1 and 4 present. Two nasal pores. Interorbital and occipital pores absent. No supratemporal commissure and no bony supports across parietals. Seven suborbital bones with 5-6 pores on ventral branch and none on ascending branch (fig. 52C). Preoperculomandibular system in primitive state, with four dentary, one anguloarticular and three preopercular pores and bone foramina (fig. 53A). Mandibular and preopercular branches joined.

Teeth on jaws small, conical, males with lateral canines anteriorly

Figure 52. Phucocoetes latitans, 109 mm SL. A) Left lateral view of neurocranium, ethmoid region not shown. B) Dorsal view of neurocranium, left lateral extrascapular and ethmoid region not shown. C) Left lateral view of head, upper jaw and suborbital bones.

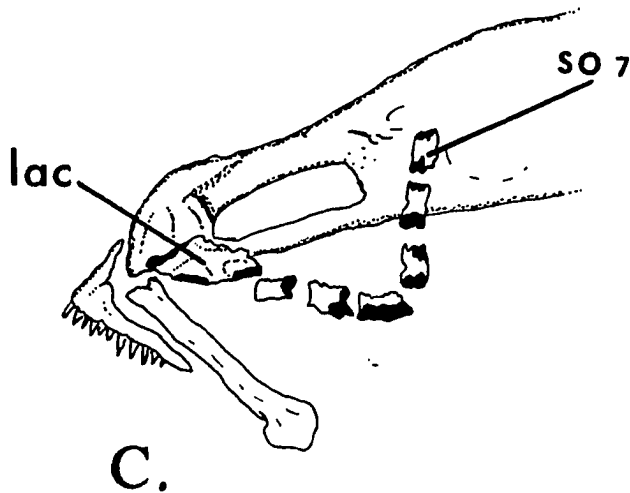
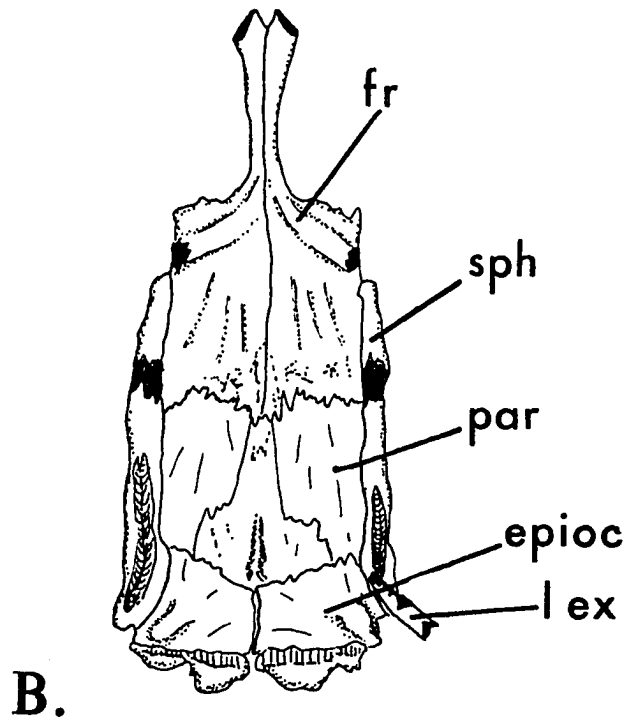
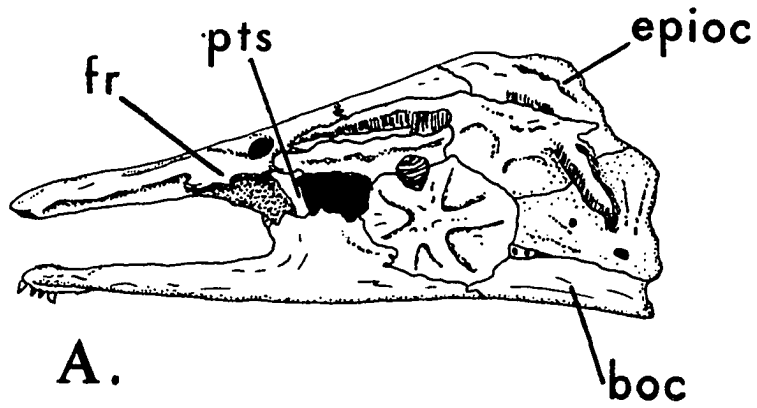
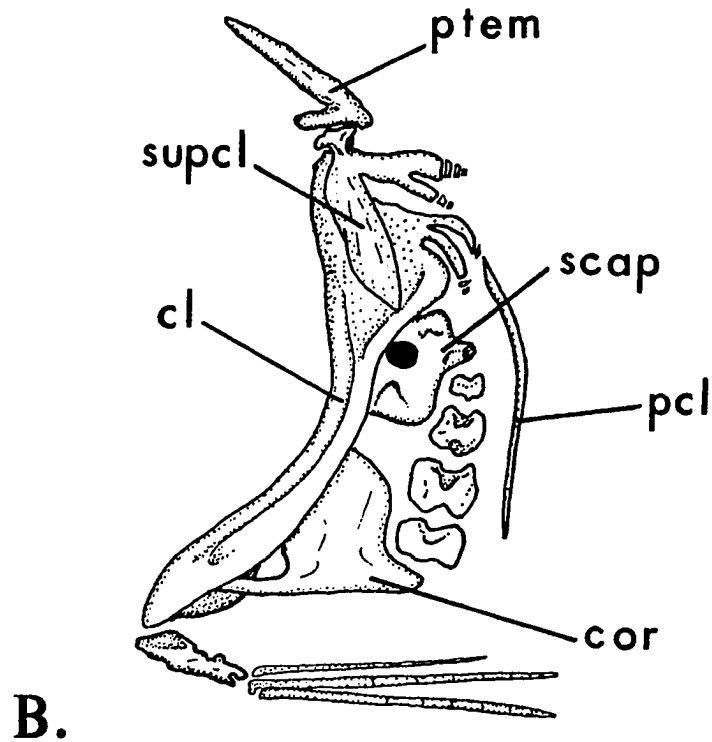
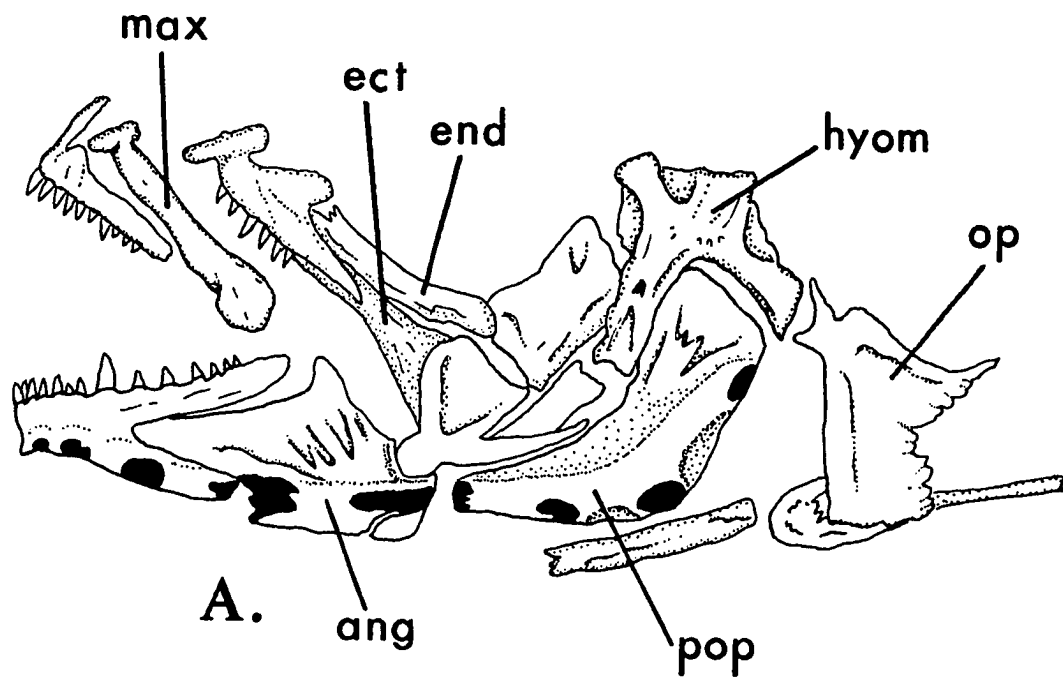


Figure 53. Phucocoetes latitans, 109 mm SL. A) Left lateral view of suspensorium, jaws and opercular bones. B) Left lateral view of pectoral girdle.



(Gosztonyi, 1977, fig. 18). Teeth present on vomer and palatine bones. Endopterygoid and ectopterygoid broadly articulating with quadrate (fig. 53A). Hyomandibula posterior ramus elongate (fig. 53A). Ceratohyal-epihyal juncture strongly interdigitating. Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2 + 9 (in three fish).

Posttemporal ventral strut well developed (fig. 53B). Scapular foramen enclosed; scapular posterior strut well developed. Four actinosts bearing 14-16 pectoral fin rays. Pelvic fins present, with three small rays each (fig. 53B).

Epipleural ribs on vertebrae 1 through 22 or 25. Pleural ribs on third to ultimate precaudal vertebra. Dorsal fin origin associated with second vertebra, with no free pterygiophores. All dorsal fin elements soft rays. One or two anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with two fin rays, hypurals with eight rays, thus total caudal rays 10. Last dorsal ray associated with fourth preural vertebra; last anal ray associated with second preural vertebra.

Palatine membrane weak. Five rather long pseudobranchial filaments. Two nub-like pyloric caeca. Peritoneum light. This genus is oviparous. Vertebrae asymmetrical.

Distribution and species. A single species in the genus, Phucocoetes latitans Jenyns, 1842, spawns in the intertidal zone of Patagonia, the Falkland Islands and Tierra del Fuego. Non-spawning adults have been found as deep as 85 meters on the Patagonian shelf. The species associates with seaweed and kelp holdfasts.

Additional references. Regan (1913: 246, 247); Norman (1966: 476, 482);
Cunningham (1871: 471); Boulenger (1900: 53).

Piedrabuenia Gosztonyi, 1977

(figs. 54, 55; pl. X)

Piedrabuenia Gosztonyi, 1977: 235-238, figs. 19, 20, 22 (type species:
Piedrabuenia ringueleti Gosztonyi, 1977, by original designation).

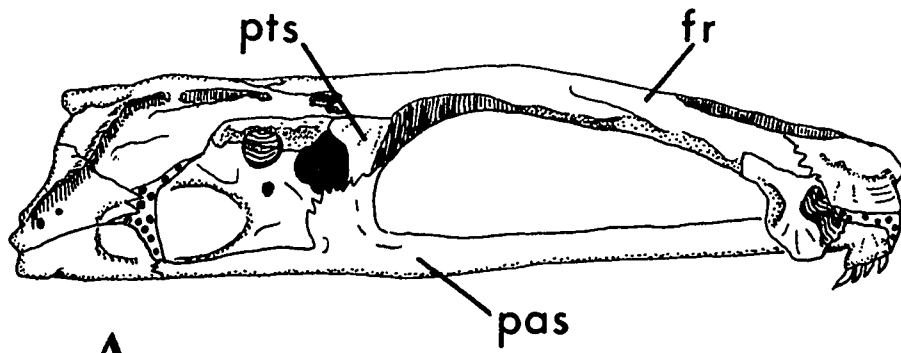
Diagnosis. Body low, tail elongate; double row of short, triangular papillae on lower jaw, single row set between anterior suborbital pores; suborbital bones usually eight, with nine pores; palatal arch weakly developed; vertebrae 24-25 + 95-101 = 120-126; branchiostegal rays 3 + 2; C 8; scales, vomerine and palatine teeth present; pelvic fin rays 2.

Description. Scales present, small, absent on head and vertical fins. Lateral line with mediolateral and ventrolateral branches. Flesh firm, with characteristic light banding on body and tail (pl. X). Gill slit extending ventrally to, or almost to, lower edge of pectoral base.

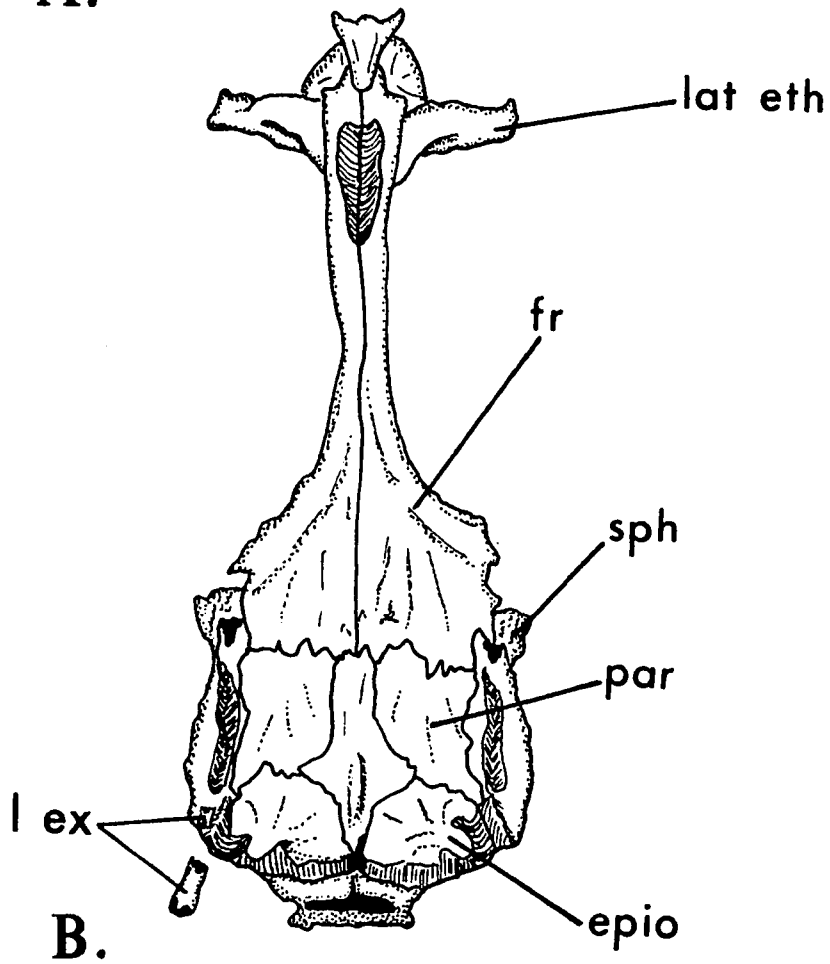
Parasphenoid wing below mid-height of trigeminofacialis foramen, no posterior ramus of wing (fig. 54A); frontal and parasphenoid narrowly contacting anteriorly, pterosphenoid relatively large. Sphenotic and parietal separated by pterotic and frontal (fig. 54B). Parietals not meeting in mid-line. Supraoccipital relatively large, with small mesial crest; supraoccipital and exoccipital narrowly contacting posteriorly.

Cephalic lateralis pores reduced in number, but anterior suborbital and preoperculo-mandibular pores enlarged. One or two lateral extrascapulars (proximalmost a small splint or absent). Postorbital pores 1-4, or 1, 3 and 4 present. Two nasal pores. No interorbital or occipital pores. Supratemporal commissure absent and no bony supports on parietal

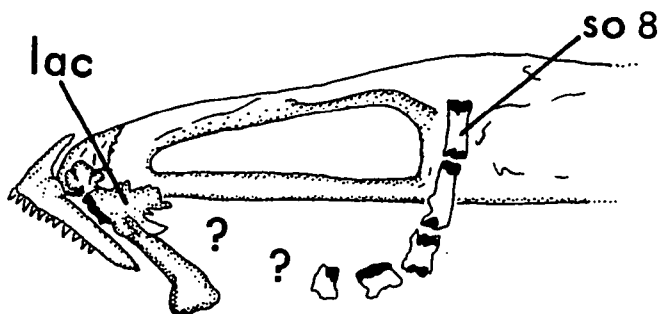
Figure 54. Piedrabuenia ringueleti, 209 mm SL. A) Right lateral view of neurocranium. B) Dorsal view of neurocranium, right lateral extrascapulars not shown. C) Left lateral view of head, upper jaw and suborbital bones (bones 2 and 3 absent in this specimen).



A.



B.



C.

remain. Suborbital bones normally eight (?), bones two and three absent in the one cleared and stained specimen (fig. 54C). Suborbital pores seven on ventral branch, two on ascending branch. Four preoperculo-mandibular pores exiting from dentary, one from anguloarticular and three from preopercle; posteriormost four exiting from relatively large bone foramina, dentary with shallow trough (fig. 55A).

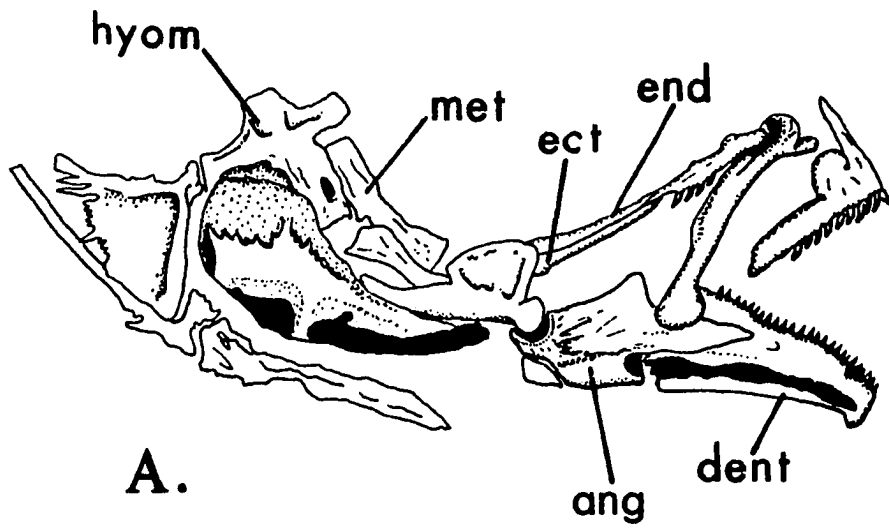
Teeth on jaws small, conical. Teeth present on vomer and palatine bones. Endopterygoid and ectopterygoid weakly articulating with quadrate. Hyomandibula posterior ramus normal, but just slightly produced (fig. 55A). Ceratohyal-epihyal juncture smooth. Branchiostegal rays 3 + 2 in all specimens (fig. 55B). Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 2-3 + 8-11 = 10-14.

Posttemporal ventral strut weak. Scapular foramen enclosed; scapula with well developed posterior strut. Four actinosts bearing 17-18 pectoral fin rays. Pelvic fin rays two in all specimens.

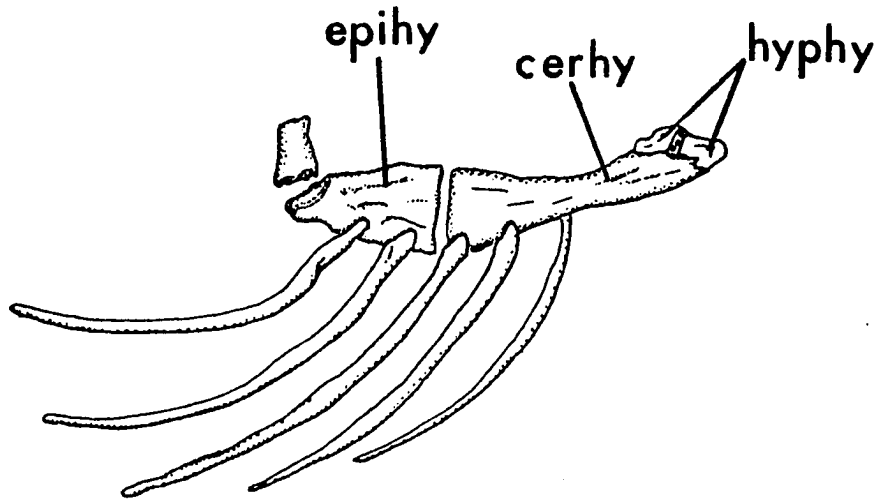
Epipleural ribs on vertebrae 1 through 12 or 13. Pleural ribs on third to ultimate or penultimate precaudal vertebra. Dorsal fin associated with vertebrae 8-11, with no free pterygiophores. Dorsal fin elements all soft rays. Four or five anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one fin ray, hypurals with seven rays, thus total caudal rays 8. Last dorsal fin ray associated with fourth preural vertebra, last anal fin ray associated with second preural vertebra.

Palatine membrane weak. Pseudobranchial filaments 4-5. Two nub-like pyloric caeca. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae symmetrical.

Figure 55. Piedrabuenia ringueleti, 209 mm SL. A) Right lateral view of jaws, suspensorium and opercular bones. B) Right lateral view of hyoid bar.



A.



B.

Distribution and species. A monotypic genus, Piedrabuenia ringueleti Gosztonyi, 1977, was described on the basis of two specimens taken on the Patagonian slope in 1971. Since then I have obtained five more from the same locality. Depths of capture: 480-500 meters. Probably widely distributed along the slopes of temperate South America at appropriate depths.

Plesienchelys gen. nov.

(figs. 56-58; pl. XIII)

Ophthalmolycus (non Regan, 1913). Gosztonyi, 1977: 230-233, figs. 16, 17 (partim).

Type species. Ophthalmolycus stehmanni Gosztonyi, 1977; herein designated.

Remarks. This genus is erected for Gosztonyi's (1977) single species. It differs from Ophthalmolycus mainly on the basis of its longer, thinner tail with fewer vertebrae, minute lateralis pores, structure of the bony passages of the preoperculomandibular canal and structure of the pterotic bones.

Etymology. From the Greek πλειώ, "majority," used as "primitive" in zoology, and ερχελης, "eel," referring to this species many plesiomorphous characters compared to its near relatives.

Diagnosis. Body low, tail elongate; anterior portion of pterotic bones wider than posterior portion; preoperculomandibular canal passing through trough in preopercle and dentary; cephalic lateralis pores minute; palatal arch well developed; suborbital bones seven, with six pores; vertebrae 19-21 + 66-73 = 86-93; lateral line with incomplete mediolateral and complete ventrolateral branches; scales, pelvic fins, vomerine and

palatine teeth present; tail sharply tapering posteriorly; no pyloric caeca.

Description. Scales present, very small, absent on head and vertical fins. Lateral line with mediolateral branch running to middle of tail and ventrolateral branch running to tip of tail. Flesh moderately firm, thin, without gelatinous layer. Gill slit extending ventrally to below lower edge of pectoral base.

Parasphenoid wing low, with short posterior ramus, not reaching mid-height of trigeminofacialis foramen; frontal and parasphenoid not separated by pterosphenoid (fig. 56A). Ethmoid cartilage extensive, protruding well into orbit. Sphenotic and parietal separated by pterotic and frontal. Anterior portion of pterotic very wide, overlapping parietal in part, wider anteriorly than posteriorly (fig. 56B). Supraoccipital moderate, narrowly contacting exoccipital posteriorly, with low mesial crest.

Cephalic lateralis pore system reduced in number, pores very small and rounded. One very small (distalmost) lateral extrascapular. Postorbital pores 1, 3 and 4 present. One or two nasal pores, when one, only anteriormost present. Interorbital and occipital pores absent. No supratemporal commissure, but low bony shelves remain on parietals (fig. 56B). Seven suborbital bones, with six pores on ventral branch and none on ascending branch. Preoperculo-mandibular system with four dentary, one anguloarticular and three preopercular pores. Only first preoperculo-mandibular pore exiting from a foramen in bone (dentary), remaining pores from open, shallow troughs in preopercle and dentary (fig. 57A). Mandibular and preopercular branches joined.

Teeth on jaws very small, conical. Teeth present on vomer and

Figure 56. Plesienchelys stehmanni, 192 mm SL. A) Left lateral view of neurocranium. B) Dorsal view of neurocranium.

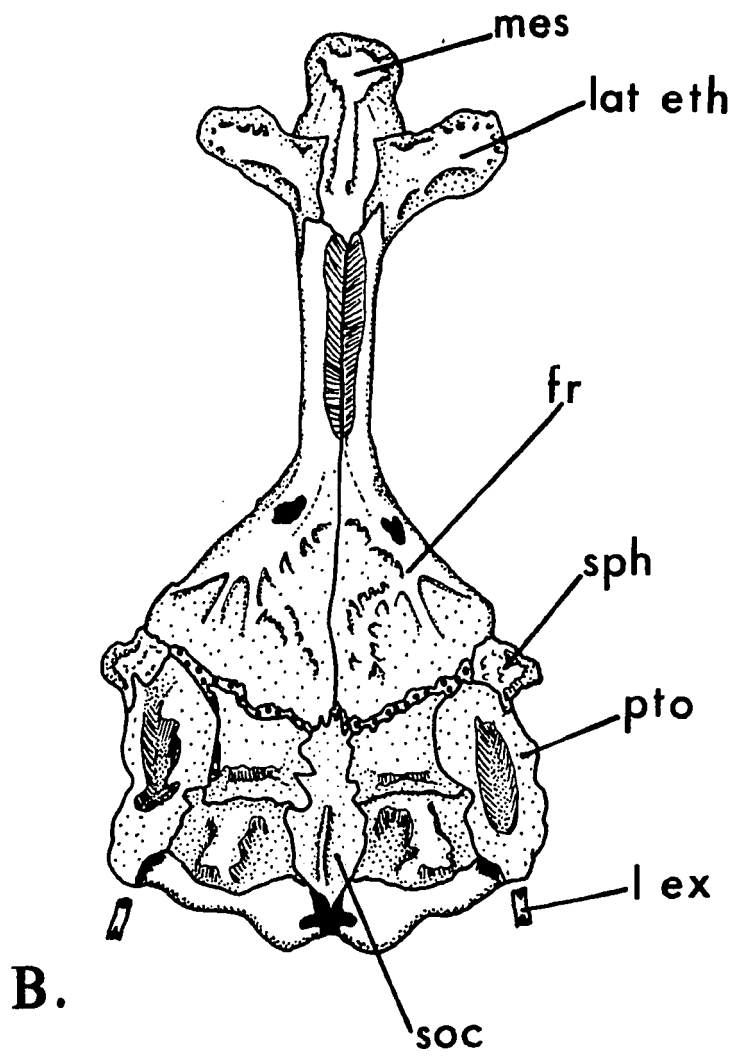
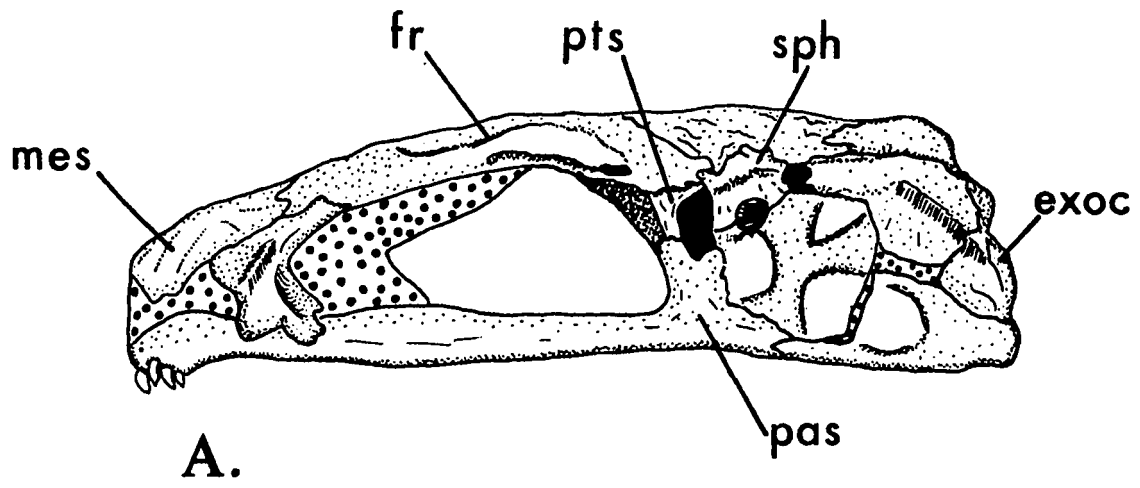
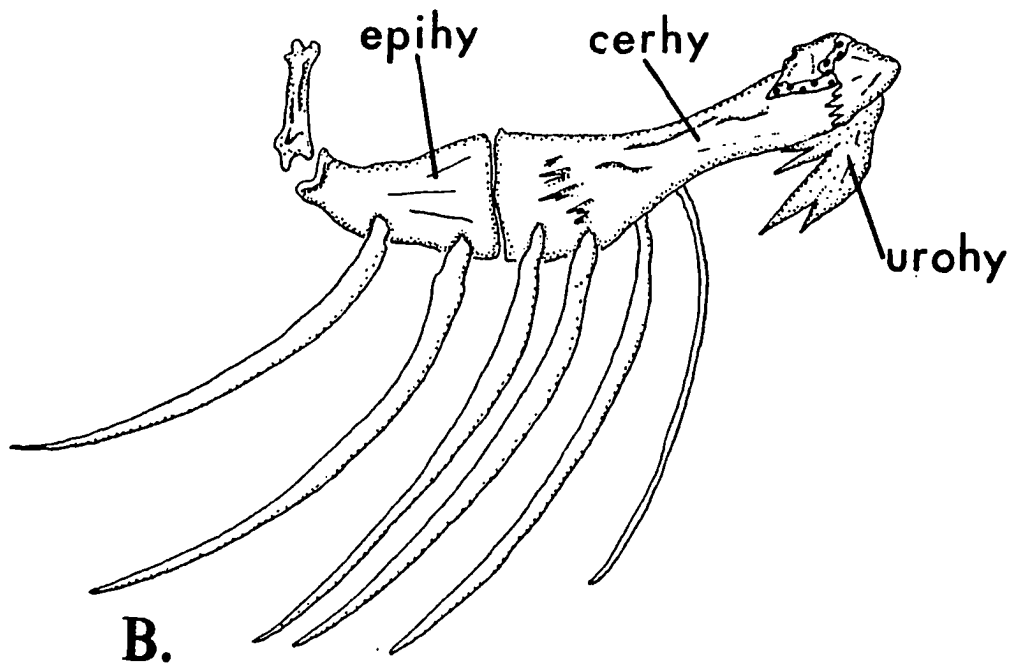
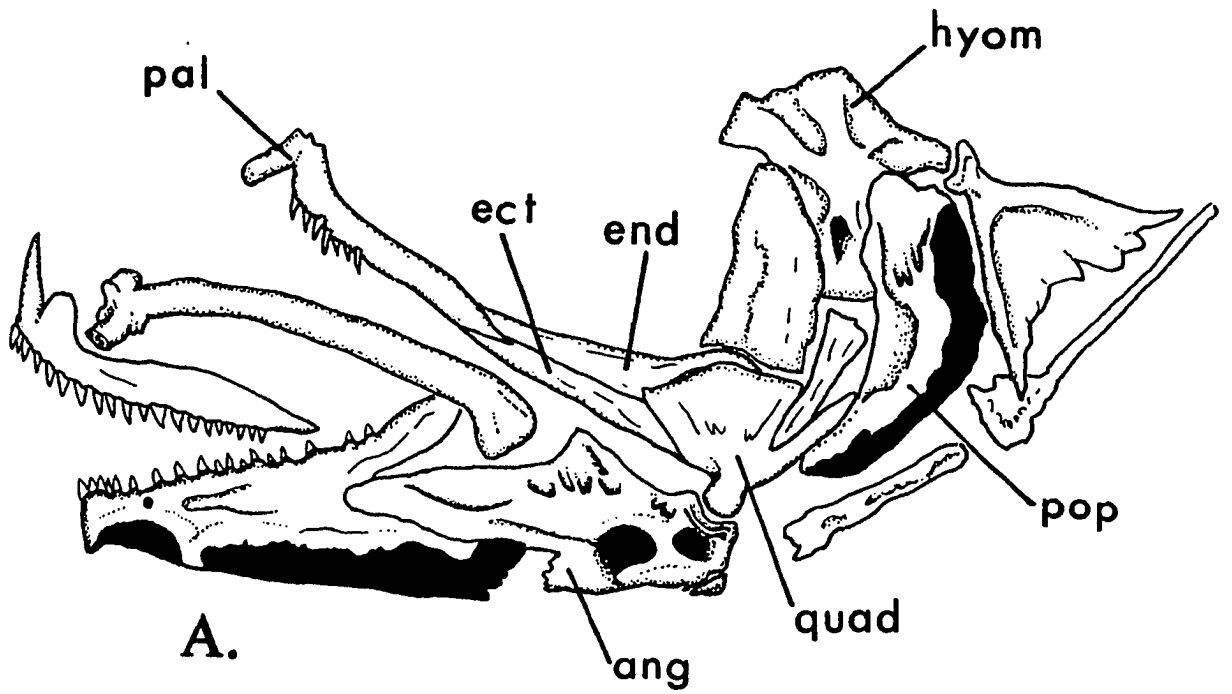


Figure 57. Plesienchelys stehmanni, 192 mm SL. A) Left lateral view of suspensorium, jaws and opercular bones. B) Right lateral view of hyoid bar.



palatine bones, relatively strong on vomer. Endopterygoid and ectopterygoid broadly articulating with quadrate (fig. 57A). Hyomandibula posterior ramus normal. Ceratohyal-epihyal juncture smooth (fig. 57B). Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed; only a single row of small teeth remain (fig. 58A). Three pairs of infrapharyngobranchials and tooth plates. Gill rakers 1-3 + 7-9 = 8-11.

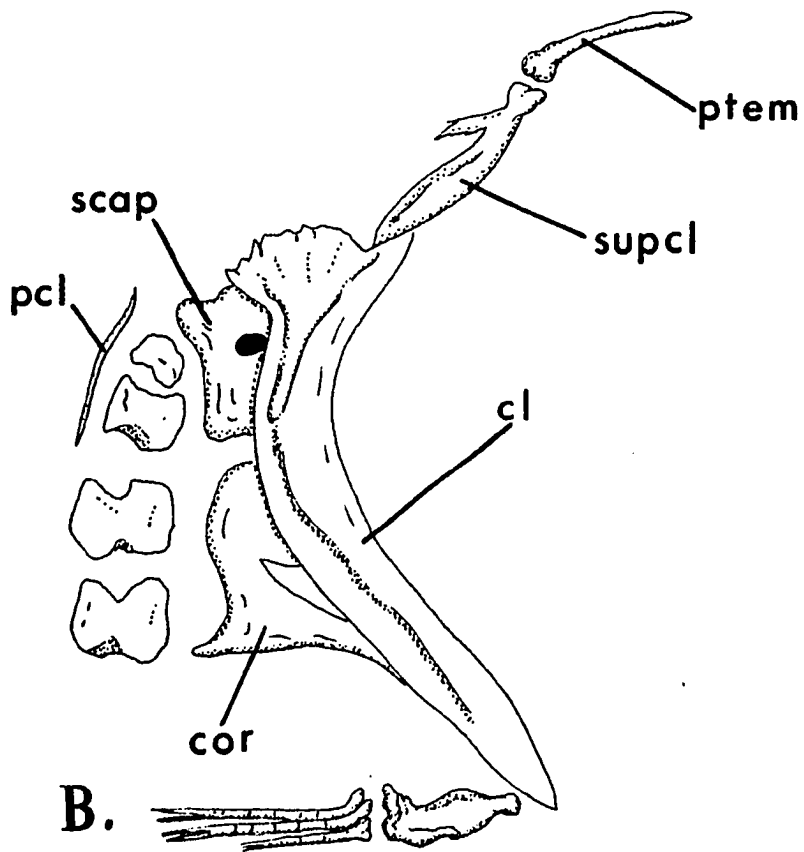
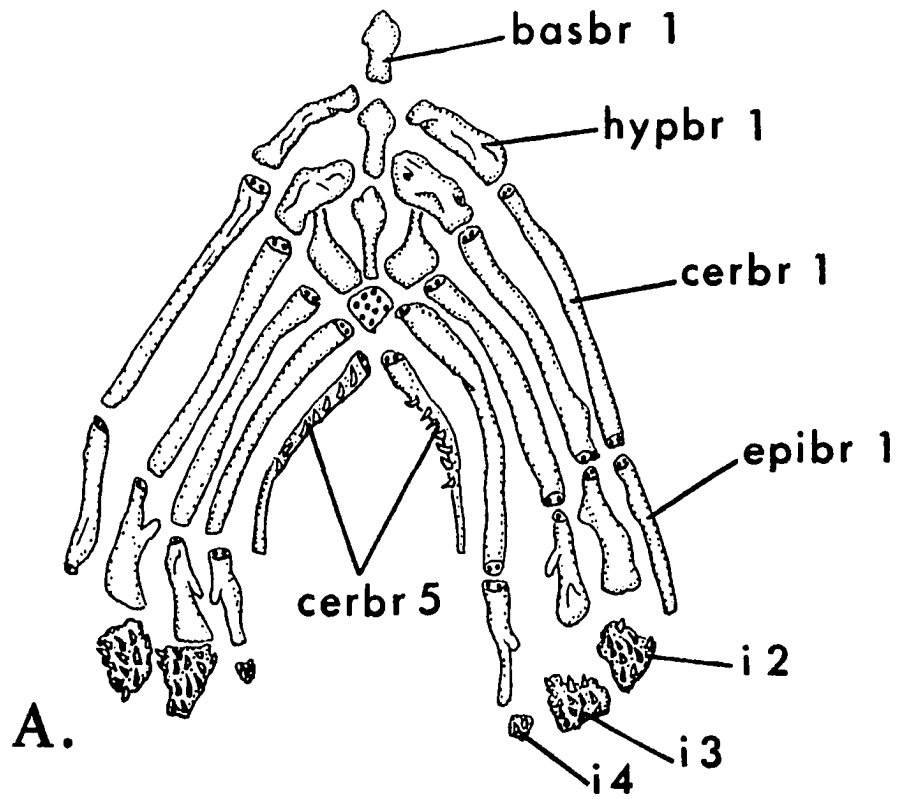
Posttemporal ventral strut weak or absent (fig. 58B). Scapular foramen enclosed; scapular posterior strut well developed. Four actinosts bearing 17-19 pectoral fin rays. Pelvic fin rays three, distalmost reduced (fig. 58B).

Epipleural ribs on vertebrae 1-17. Pleural ribs on fourth to ultimate precaudal vertebra. Dorsal fin origin associated with vertebrae 6-8, with no free pterygiophores. All dorsal fin elements soft rays. Four to five anal pterygiophores anterior to first caudal vertebra. One epural with two fin rays, hypurals with 7-8 rays, thus total caudal rays 9-10. Last dorsal fin ray associated with fourth preural vertebra; last anal associated with second preural vertebra.

Palatine membrane weak. Pseudobranchial filaments 3-4, relatively short. Pyloric caeca absent. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae symmetrical.

Distribution and species. Plesienchelys stehmanni (Gosztonyi, 1977) was originally described on the basis of a single specimen. I have located eight more, all taken on the Argentine slope. At present, the species known range is off Rio de la Plata south to Burdwood Bank in 340-975 m.

Figure 58. Plesienchelys stehmanni, 192 mm SL. A) Dorsal view of branchial basket. Epihyals and upper pharyngeal bones pulled backward 180° from in situ position. B) Right lateral view of pectoral girdle.



Pogonolycus Norman, 1937

(pl. XV)

Pogonolycus Norman, 1937a: 106, 107, fig. 55 (type species: Pogonolycus elegans Norman, by original designation); Gosztanyi, 1977: 238-240, figs. 21, 22.

Diagnosis. Body robust, tail relatively short; frontal bones squared-off (character 13); hyomandibula posterior ramus elongate (character 14); ceratohyal-epihyal juncture interdigitating (character 15); fringed cirri present on lower jaw, chin, rictus of mouth and between anterior suborbital pores; branchiostegal rays 3 + 2; suborbital bones 6-7, with six pores; pelvic fins present, with two rays each; C 9; scales, vomerine and palatine teeth present; vertebrae 20 + 71-73 = 91-93; pseudo-branchial filaments 2-3.

Description. Scales present, small, absent on nape and pectoral fin base; present on basal portion of vertical fins. Lateral line mediolateral, complete. Flesh firm. Gill slit extending ventrally to mid-pectoral base. Facial cirri mostly fringed, especially in larger fish; cirri located on lower lip, jaw, chin, mouth rictus and between anteriormost suborbital pores (see Gosztanyi, 1977, fig. 21).

Details of neurocranium not observed due to scarcity of specimens, except through radiographs. Skull appears similar to Phucocoetes and Maynea in every respect.

Cephalic lateralis pore system reduced in number; pores moderate in size, rounded. Probably only one lateral extrascapular present. Postorbital pores 1 and 4 present. Two nasal pores. Interorbital and occipital pores absent, no supratemporal commissure. Suborbital bones seven, with six pores on ventral branch and none on ascending branch.

Preoperculo-mandibular system in primitive state, with four dentary, one angulo-articular and three preopercular pores. Mandibular and preopercular branches joined.

Teeth small, conical, sexual dimorphism not noticed. Vomerine and palatine teeth present, small. Palatal arch appears to be strong. Hyomandibula posterior ramus elongate. Ceratohyal-epihyal juncture interdigitating dorsally. Branchiostegal rays 3 + 2. Ceratobranchial 5 toothed; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 1 + 9 (in one fish).

Posttemporal ventral strut weak. Scapula not seen, probably normal. Four actinosts bearing 17 pectoral fin rays. Pelvic fins present, with two rays each. Epipleural ribs on vertebrae 1-17. Pleural ribs on third through penultimate vertebra. Dorsal fin origin associated with third vertebra, with no free pterygiophores. Dorsal fin elements all soft rays. Two pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one fin ray, hypurals with eight rays, thus total caudal rays 9. Last dorsal fin ray associated with fourth preural vertebra; last anal ray associated with second preural vertebra.

Palatine membrane weak. Pseudobranchial filaments 2-3, small. Two nub-like pyloric caeca. Peritoneum dusky. Pogonolycus is probably oviparous. Vertebrae asymmetrical.

Distribution and species. A single species in the genus, Pogonolycus elegans Norman, 1937 is known from only six specimens taken on the outer continental shelf of southern Chile and the Patagonian-Fuegian-Falklands region in 100-480 meters.

Additional references. Norman (1966: 476, 482); Lindberg (1974, fig. 802).

Redirolycus gen. nov.
(figs. 59, 60; pl. XI)

Melanostigma (non Günther, 1881). Norman, 1937a: 110, fig. 58.

Maynea (non Cunningham, 1871). McAllister and Rees, 1964: 106, 107, appendix; Gosztonyi, 1977: 223, 224, fig. 12.

Type species. Melanostigma microphthalmus Norman, 1937; herein designated.

Remarks. This genus is erected for Norman's (1937a) Melanostigma microphthalmus and one undescribed species, both from the Patagonian-Falkland slope. They are separated from Maynea, placed there by McAllister and Rees (1964), by their possession of only 4-5 suborbital bones, parietals not meeting in the midline, smooth ceratohyal-epihyal juncture, normal hyomandibula and six branchiostegal rays. The genus is known from only four specimens of R. microphthalmus, one of which was cleared and stained, and two of the undescribed species from the German WALTHER HERWIG collections.

Etymology. From the Latin rēdirē, to be reduced, and the Greek λυχῶδης, wolfish, after Lycodes, commonly used as a suffix for southern hemisphere zoarcids (Pogonolycus, Ophthalmolycus, Austrolycus, etc.).

Diagnosis. Body low, tail elongate; suborbital bones 4-5; gill slit above pectoral fin base, or extending ventrally to mid-pectoral base; palatal arch reduced; C 7-8; P 9-14; scales, vomerine and palatine teeth present; pelvic fins absent; vertebrae 24-27 + 67-75 = 93-101.

Description. Scales present, small, absent on head. Lateral line mediolateral, complete. Flesh firm, but thin. Gill slit entirely above pectoral base in R. microphthalmus, extending ventrally to mid-pectoral base in Redirolycus sp. A.

Parasphenoid wing below mid-height of trigeminofacialis foramen; frontal and parasphenoid not separated by pterosphenoid; frontal descending wing small (fig. 59A). Sphenotic and parietal separated by pterotic and frontal. Parietals not meeting in midline, relatively small (fig. 59B). Supraoccipital moderate, with small mesial crest; supraoccipital and exoccipital separated by relatively large epioccipitals (fig. 59B).

Cephalic lateralis pore system reduced in number, pores enlarged. One small lateral extrascapular (fig. 59B). Postorbital pores 1, 3, 4, or 1 and 4 only present. Two nasal pores. No interorbital pores. Occipital canal with one mesial pore in Redirolycus sp. A, or no occipital pores and no bony supports on parietal in R. microphthalmus. Suborbital bones 4-5, the fewest among the lycenchelyines (fig. 59C). The unusual length of the fourth suborbital bone suggests it may represent fusion between two elements in R. microphthalmus. Suborbital pores 4-5 on ventral branch only, except one specimen of Redirolycus sp. A, which has one pore on ascending branch.

Preoperculomandibular pore system with four dentary, one anguloarticular and three preopercular pores and bone foramina in Redirolycus sp. A; R. microphthalmus with four dentary foramina, with first not leading to a pore in these specimens, one anguloarticular and two preopercular pores and bone foramina (uppermost lost; fig. 59C). Mandibular and preopercular branches joined.

Teeth on jaws small, few. Teeth present on vomer and palatine bones, also small. Endopterygoid and ectopterygoid weakly articulating with quadrate (fig. 59C). Hyomandibula posterior ramus normal. Ceratohyal-epihyal juncture smooth (fig. 60A). Branchiostegal rays 4 + 2, except one specimen with 4 + 2 on one side, 5 + 2 on the other. Ceratobranchial

Figure 59. Redirolycus microphthalmus, 90 mm SL. A) Right lateral view of neurocranium, ethmoid region not shown. B) Dorsal view of neurocranium, ethmoid region not shown. C) Right lateral view of jaws, suspensorium, opercular and suborbital bones.

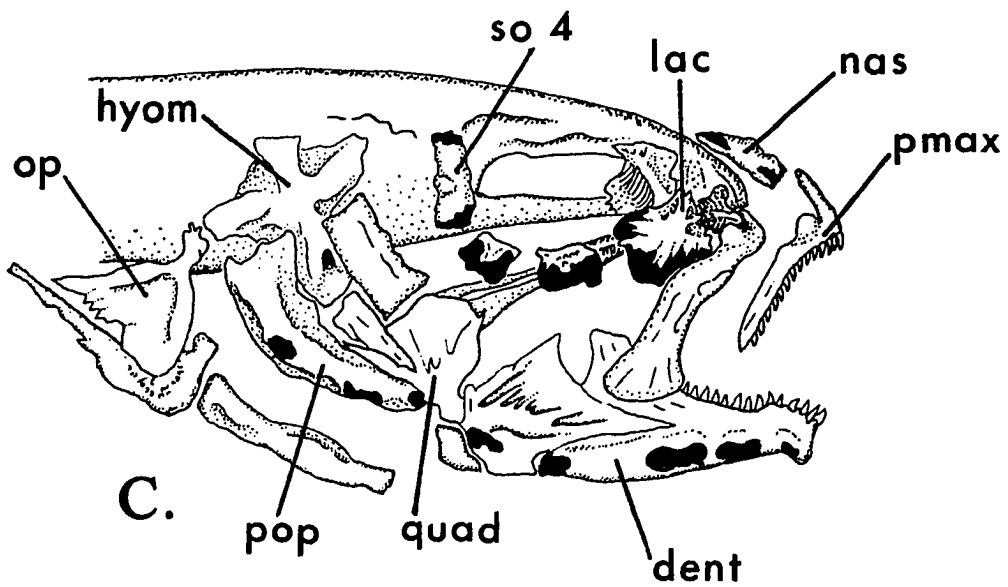
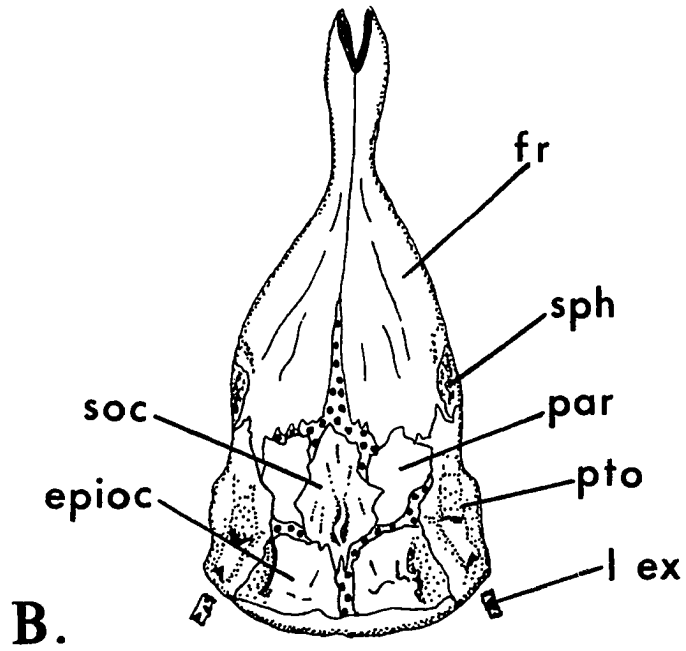
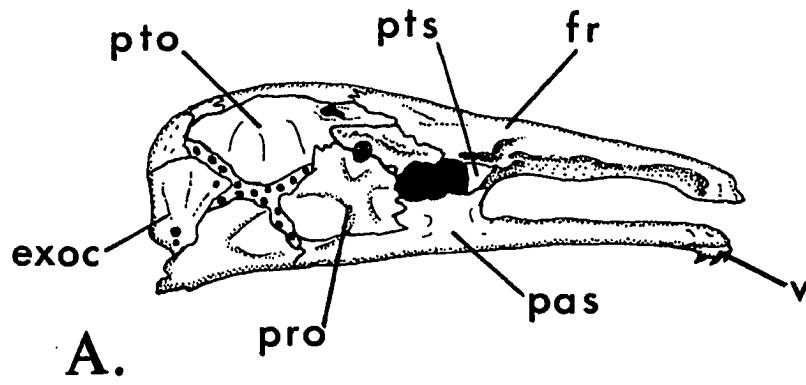
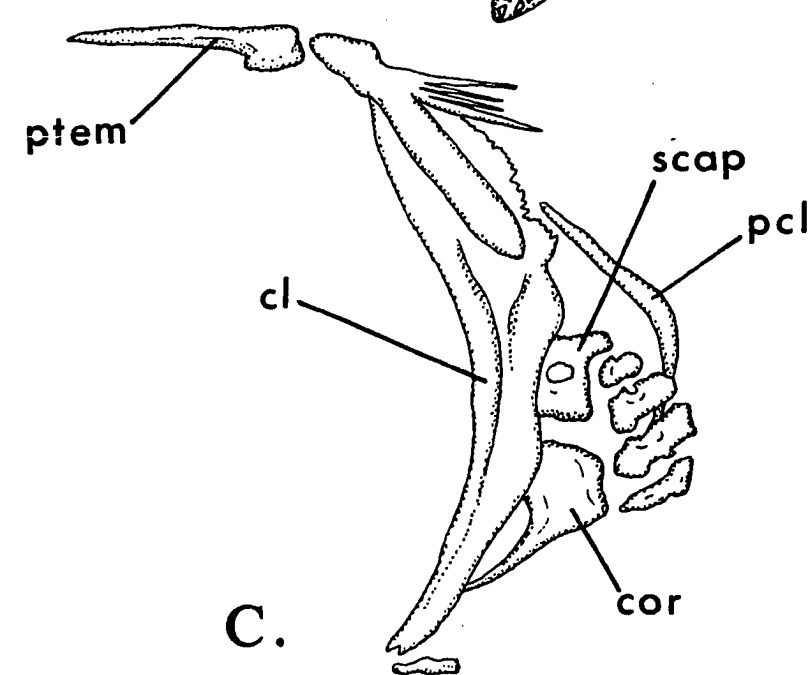
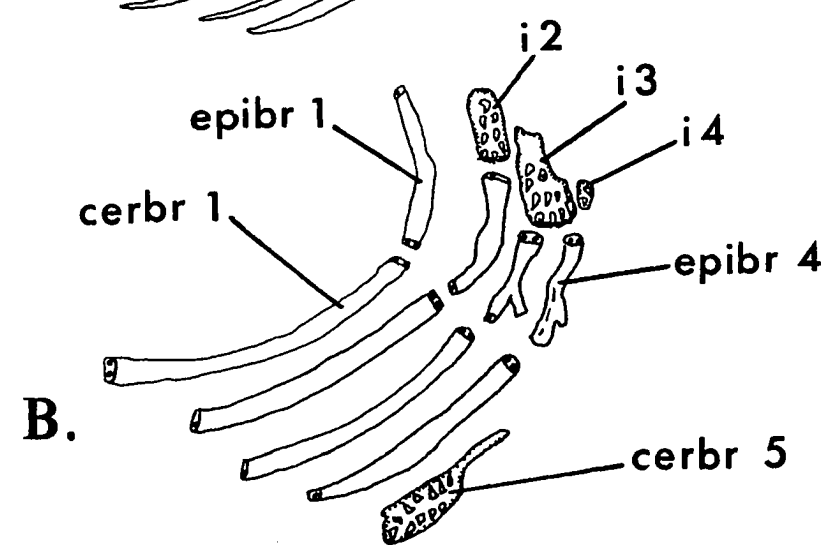
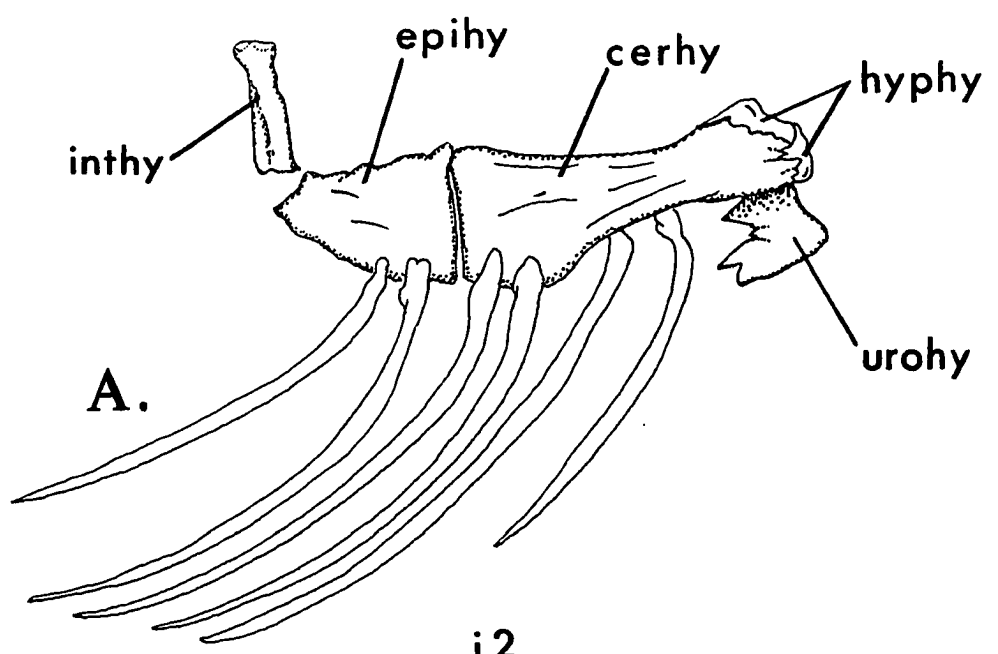


Figure 60. Redirolycus microphthalmus, 90 mm SL. A) Right lateral view of hyoid bar. B) Dorsal view of bones of left gill arches, basibranchials not shown. C) Left lateral view of pectoral girdle; pelvic fin rays absent in this species.



five toothed; three pairs of infrapharyngobranchials and tooth plates; infrapharyngobranchial of fourth gill arch reduced, with only two small teeth (fig. 60B). Gill rakers 1-2 + 7-8 = 8-10.

Posttemporal ventral strut very weak (fig. 60C). Scapular foramen enclosed; scapula with well developed posterior strut. Four actinosts bearing 9-14 short pectoral fin rays. One specimen, a 45 mm SL juvenile, has only four pectoral rays on each side, apparently adult complement not yet formed. Pelvic fins absent; pelvic bone reduced (fig. 60C).

Epipleural ribs extending from vertebrae 1 through 16 or to 22 (in Redirolycus sp. A). Pleural ribs on vertebrae 3-4 to ultimate or penultimate vertebra. Dorsal fin origin associated with vertebrae 3-4, with no free pterygiophores. All dorsal fin elements soft rays. Two to four anal pterygiophores anterior to haemal spine of first caudal vertebra. One epural with one ray, hypurals with six rays, thus total caudal rays seven in all known specimens. Last dorsal ray associated with third or fourth preural vertebra; last anal ray associated with second preural vertebra in all specimens.

Palatine membrane weak. Pseudobranchial filaments 2-4, very small. Two nub-like pyloric caeca. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae slightly asymmetrical, constriction not shifted anteriorly as strongly as in most species with asymmetrical vertebrae.

Distribution and species. Redirolycus microphthalmus (Norman, 1937): four specimens known from the Argentine slope between 46° S and 56° S in 115-580 m. Redirolycus sp. A: two specimens known from approximately 46° S, 60° W in 580-900 m.

Taranetzella Andriashev, 1952

(pl. IX)

Taranetzella Andriashev, 1952: 415-417, fig. (type species: Taranetzella lyoderma Andriashev, by original designation); Andriashev, 1955a: 381-382, fig. 22; Percy et al., 1982: 387.

Diagnosis. Body low, slender, tail elongate; flesh gelatinous; lateral line absent; palatal arch weakly developed; suborbital bones eight, with seven pores; vertebrae 20 + 69-74 = 89-94; scales, pelvic fins, vomerine and palatine teeth present.

Description. Scales present only on tail in two juveniles seen by me; adults may have more extensive squamation. No trace of lateral line neuromasts. Flesh gelatinous, especially on head and body; fleshy lobes present between suborbital pores, but not produced as papillae. Gill slit extending ventrally to pectoral base.

Osteology of neurocranium limited to observations from radiographs only. General features of palatal arch reduced, endopterygoid and ectopterygoid probably weakly articulating with quadrate. Parasphenoid wing probably not high. Sphenotic and parietal probably separated if this species is like all other lycenchelyines. Parietals probably do not meet in midline.

Cephalic lateralis pore system reduced in number, pores enlarged anteriorly. Probably only one lateral extrascapular. Postorbital pores 1 and 4 present. Two nasal pores. No interorbital or occipital pores, no supratemporal commissure. Apparently eight suborbital bones; suborbital pores seven on ventral branch, none on ascending branch. Preoperculo-mandibular system with four dentary, one anguloarticular and three preopercular pores. Mandibular and preopercular branches joined.

Teeth moderate, conical, recurved inwardly. Two strong canines at

symphysis of premaxilla. Teeth present on vomer and palatine bones. Hyomandibula posterior ramus normal. Ceratohyal-epihyal juncture smooth. Branchiostegal rays 4 + 2. Ceratobranchial 5 toothed, single row present; three pairs of infrapharyngobranchials and tooth plates. Gill rakers 3 + 13 in one specimen.

Posttemporal ventral strut weak. Scapular foramen not observed, probably enclosed and with posterior strut. Four actinosts bearing 15 pectoral fin rays. Pelvic fin rays three.

Epipleural ribs appear to extend to about middle of precaudal vertebrae. Pleural ribs from second to ultimate precaudal vertebra. Dorsal fin origin associated with third vertebra, with no free pterygiophores. All dorsal fin elements soft rays. Three anal pterygiophores anterior to haemal spine of first caudal vertebra.

One epural with one fin ray, hypurals with seven rays, thus total caudal rays eight (in one specimen). Last dorsal ray associated with third preural vertebra; last anal ray associated with second preural vertebra.

Palatine membrane weak. Pseudobranchial filaments 2-3, very short. Two nub-like pyloric caeca. Peritoneum black. Reproductive mode unknown, probably oviparous. Vertebrae symmetrical.

Distribution and species. A single species in the genus, Taranetzella lyoderma Andriashev, 1952, is known from Olyutorskiy Bay, Kamchatka, in 986 m (holotype) and off Oregon in 2225-3000 m (Pearcy et al., 1982).

ZOOGEOGRAPHY

Distributional patterns of the shelf-dwelling zoarcids generally support zoogeographic areas proposed by Briggs (1974). Many coastal zoarcid genera are confined within one of Briggs' Regions, or Provinces within a Region. Few slope-dwelling genera, however, are so confined within Briggs' shelf regions, as these are defined by physical parameters and endemic groups that generally do not occur on continental slopes. Although he did not elaborate, Briggs postulated recognition of a large number of deep-slope provinces based on differing patterns of endemism (Briggs, 1974: 377). As Vinogradova (1979) observed with macrobenthic invertebrates, eurybathic-slope and abyssal zoarcids at present appear to be widely distributed, but most species are known from few specimens. Indeed, 45% of the zoarcid genera recognized here are based on 15 or fewer specimens each.

A few general distributional patterns of the zoarcids emerged on analysis of marine zoogeographic regions, while considering genera and areas of endemism. No attempt is made here to analyze the ancestral zoarcid biota through track analysis, due to imprecise knowledge about the geographic ranges of most genera. Instead, I have subdivided the northern and southern hemispheres into 12 faunal areas based on Briggs (1974), but emended as necessary to accurately reflect zoarcid distributions (table 2). Those patterns at variance with Briggs' scheme are seen to be caused by wide-ranging, deep-sea genera.

Table 2. Geographical distribution of zoarcid genera, after Briggs (1974). Numbers refer to areas listed below. See text.

1. Arctic Region.
2. Western Pacific Boreal Region.
3. Eastern Pacific Boreal plus California Regions.
4. Eastern Tropical Pacific plus Western South America Regions.
5. Indo-West Pacific Region.
6. Eastern Atlantic and Mediterranean Region.
7. Western Atlantic Boreal Region.
8. Tropical-Subtropical Western Atlantic Regions.
9. Magellan Province plus Eastern South America Region.
10. South Africa Region.
11. Subantarctic Region.
12. Antarctic Region.

Genus	Zoogeographic Area											
	1	2	3	4	5	6	7	8	9	10	11	12
Lycozoarces		X										
Macrozoarces							X					
Zoarces		X				X						
Bilabria		X										
Davidijordania		X										
Hadropareia		X										
Krusensterniella		X										
Gymnelopsis		X										
Gymnelus	X	X	X				X					
Melanostigma		X	X	X	X	X	X		X	X	X	
Puzanovia		X	X									
Nalbantichthys			X									
Andriashevia		X										
gen. nov.			X									
Lycodes	X	X	X			X	X	X		X		
Pachycara			X	X	X	X	X	X		X		
Austrolycichthys				X				X			X	
Exechodontes								X				
Lycodichthys												X
Oidiphorus									X			
Plesienchelys									X			
Ophthalmolycus									X		?	X

Genus	Zoogeographic Area											
	1	2	3	4	5	6	7	8	9	10	11	12
Redirolycus									X			
Taranetzella		X	X									
Lycinema			X									
Eucryphycus			X									
Lycenchelys	X	X	X	X		X	X	X	X		X	X
Lycodonus	X					X	X		X	X		
Hadropogonichthys		X										
Piedrabuenia									X			
Derepodichthys			X									
Bothrocarara		X	X	X								
Bothrocarina		X										
Lycogrammoides		X										
Lycodapus		X	X	X					X		X	X
Notolycodes									X			
Aiakas									X			
Iluocoetes									X			
Austrolycus									X			
Dadyanos									X			
Crossostomus									X			
Phucocoetes									X			
Pogonolycus									X			
Maynea									X			

Northern Hemisphere

Arctic Region.

This area includes the Arctic Ocean, northern Bering Sea and a portion of the western North Atlantic south to the Straits of Belle Isle, Labrador (Briggs, 1974, fig. 9-10). The northeastern Atlantic is not included because there is a northward extension of the temperate fauna into Arctic areas (Briggs, 1974: 259).

Four genera occur in the Arctic: Gymnelus, Lycenchelys, Lycodes and Lycodonus, and none are endemic. However, Gymnelus, Lycenchelys and Lycodes have species that are endemic to the Arctic.

North Pacific Ocean.

Western Pacific Boreal Region.

This area of high endemism extends from Cape Olyutorskiy, Kamchatka, south to the Yellow Sea. It includes the Oriental, Okhotsk and Kurile Provinces of Briggs (1974: fig. 9-5).

Nineteen zoarcid genera occur in the Region, ten of which (53%) are endemic (endemism 23% of total): Andriashevia, Bilabria, Bothrocarina, Davidijordania, Gymnelopsis, Hadropareia, Hadropogonichthys, Krusensterniella, Lycogrammoides, and Lycozoarces. The non-endemic genera in this Region are: Bothrocara, Gymnelus, Lycenchelys, Lycodapus, Lycodes, Melanostigma, Puzanovia, Taranetzella and Zoarces. All the non-endemic genera have endemic species in the Region except Gymnelus, Puzanovia and Taranetzella.

Eastern Pacific Boreal Region plus California Region.

This area extends from the eastern Bering Sea south to Magdalena Bay, Baja California, and includes the northern Gulf of California. The two Regions of Briggs (1974: figs. 8-2, 9-8) are combined, as there are no endemic zoarcids in the California Region, and all species found in that Region are deep-sea.

Fourteen genera occur in this northeastern Pacific area, five of which (36%) are endemic (endemism 11% of total): Derepodichthys, Eucryphycus, Lyconema, Nalbantichthys and Bond and Stein's new genus. The non-endemic genera are: Bothrocarra, Gymnelus, Lycenchelys, Lycodapus, Lycodes, Melanostigma, Pachycara, Puzanovia and Taranetzella. The non-endemic genera have endemic species in the area except Gymnelus, Puzanovia and Taranetzella, as in the northwestern Pacific (above).

Eastern Tropical Pacific Region plus Western South America Region.

This area extends from central Mexico south to southern Chile, and includes the Galapagos Islands (Briggs, 1974: figs. 2-2, 6-2). The two adjacent Regions are combined, as there are no endemic genera in either, and all species are deep-sea. All zoarcids inhabiting the eastern tropical Pacific are rare in collections, but the best known are widely distributed throughout both Regions.

The six zoarcid genera in the eastern tropical Pacific are: Austrolycichthys, Bothrocarra, Lycenchelys, Lycodapus, Melanostigma and Pachycara. All have endemic species in the area except Lycodapus, which is represented by a single specimen (Garman, 1899; Peden and Anderson, 1978).

Indo-West Pacific Region

Zoarcids in this broad tropical area are known only from the Indo-

Polynesian Province (Briggs, 1974: fig. 1-2). There is no generic endemism in the Indo-West Pacific. Recognition of this geographic area for Zoarcidae is based on three collections of the only specimens known of Melanostigma inexpectatum (off New Guinea), M. vitiazi (Banda Sea) and Pachycara sp. C (Bay of Bengal).

North Atlantic Ocean.

Eastern Atlantic Boreal Region plus Mediterranean-Atlantic Region.

These two Regions include the entire northeastern Atlantic, extending from the Kola Peininsula, USSR, south to Senegal, including Iceland, and the Baltic and Mediterranean seas. The two adjacent Regions are combined, as there are no endemic genera in either and all species are deep-sea, except Zoarces viviparus.

The six genera in the northeastern Atlantic are: Lycenchelys, Lycodes, Lycodonus, Melanostigma, Pachycara and Zoarces. Only Lycodes and Melanostigma do not have endemic species occurring in this area. Lycodonus and Lycenchelys are the only genera found in one of the Regions (the Eastern Atlantic Boreal).

Western Atlantic Regions.

There are two components of zoarcid distribution in the northwestern Atlantic; one boreal, consisting of genera also occurring in the northeastern Atlantic and Arctic, the other tropical-subtropical, consisting of only a few species of restricted distribution.

The Western Atlantic Boreal Region extends from the Straits of Belle Isle south to Cape Hatteras, North Carolina (Briggs, 1974: fig. 9-1). Seven zoarcid genera occur here: Gymnelus, Lycenchelys, Lycodes, Lycodonus, Macrozoarces, Melanostigma and Pachycara. Macrozoarces is the only endemic

genus (generic endemism 14%, or 2% of total). There are no endemic species of the other genera in this Region.

A tropical-subtropical component of zoarcid distribution in the northwestern Atlantic includes the Carolina Region, extending from Cape Hatteras south to Tampico, Mexico, and the Caribbean and West Indian Provinces of the Tropical Western Atlantic Region (Briggs, 1974: figs. 3-2, 8-2). The geographic ranges of the zoarcids occurring in this area are imprecisely known; all species are known from fewer than 15 specimens each (two are known from one each). Six species, representing six genera, are found here: Austrolycichthys sp. A, Exechodontes daidaleus, Lycenchelys bullisi, L. verrillii, Lycodes atlanticus and Pachycara sp. D. All species in this area are deep-sea and most, if not all, will probably be found to overlap Briggs' shelf Regions eventually. Exechodontes is the only endemic genus (generic endemism 17%, or 2% of the total). Lycenchelys verrillii and Lycodes atlanticus are the only non-endemic species in the tropical-subtropical northwestern Atlantic.

Southern Hemisphere

Zoarcids occurring in the Western South America Region were treated above under the section on the eastern tropical Pacific. This is because the southern hemisphere Region is an extension of the northern, and all species are deep-sea. The deep waters of the Western South America Region are, however, still very poorly known, and less than 20 zoarcid specimens are known to me.

South America Regions.

South of Chiloe Island, Chile, around Tierra del Fuego and north to

southern Brazil is the area of highest zoarcid generic endemism. The area includes the Magellan Province of the Southern South America Region and the southern part of the warm temperate Eastern South America Region (Briggs, 1974: figs. 6-2, 7-1).

Eighteen genera are found in this area, 13 of which (72%) are endemic (endemism 30% of total): Aiakas, Austrolycus, Crossostomus, Dadyanos, Iluocoetes, Maynea, Notolycodes, Oidiphorus, Piedrabuenia, Plesienchelys, Phucoetes, Pogonolycus and Rediolycus. The non-endemic genera are: Lycodapus, Lycodonus, Melanostigma and Ophthalmolycus, all of which have endemic species in the area except Melanostigma. The high endemism in this area is primarily due to the mayneines, that monophyletic group of nine genera (fig. 15).

Southern Africa Region.

All four zoarcids off southern Africa are found in deep water off the coastal Southwest Africa and Agulhas Provinces (Briggs, 1974: fig. 6-3). Three are lower slope-dwelling species: Lycodes agulhensis, Lycodonus vermiformis and Pachycara crassiceps. Melanostigma gelatinosum is deep-pelagic and circum-subantarctic. All the genera occurring here are found along several of Briggs' Regions, but Lycodes agulhensis and Lycodonus vermiformis are endemic species.

Subantarctic Region.

This area includes the island Provinces of Briggs (1974: fig. 7-4) in the Antarctic Convergence, the center of which lies at about 55° S. Each island group is considered a Province by Briggs, but the biota of most of these areas is poorly known. Thus, their relationship to the

Antarctic coastal fauna is tenuous. The Provinces include the Kerguelen, Macquarie, South Georgia, Bouvet and Prince Edward-Crozet islands.

There are no endemic zoarcid genera in this Region. In fact, only Lycenchelys, with two species (both endemic), Lycodapus, with two species (one endemic) and Melanostigma gelatinosum are so far recorded from the Subantarctic Region.

Antarctic Region.

This area includes coastal and slope waters of Antarctica and the Scotia Sea island arc (Briggs, 1974: 179). The coastal fishes of South Georgia Island were considered by Briggs to be part of this Region. As there are no coastal zoarcids recorded from South Georgia, and only the wide-ranging, deep-sea genera Lycenchelys, Lycodapus and Melanostigma are known from near the island, I include it in the subantarctic area (above).

Six genera occur in this Region, two of which (33%) are endemic (endemism 4.5% of total): Lycodichthys and one unnamed, based on "Oidiphorus" laevifasciatus (see p. 155). The non-endemic genera are: Austrolycichthys, Lycenchelys, Lycodapus and Ophthalmolycus. Of the non-endemic genera, only Lycodapus does not have endemic species in Antarctica.

In summary, the greatest radiation of zoarcid genera has occurred in temperate seas (table 2). The Western and Eastern Pacific Boreal Regions have 53% (23% of total) and 36% (11% of total) zoarcid generic endemism, respectively, and there is 72% (30% of total) endemism in the Magellan Province of temperate South America (extended northward to southern Brazil by slope-dwelling forms). On the basis of zoarcid

distributions, Briggs' (1974: 377) postulation of differing (broader) continental slope Regions and Provinces from those of adjacent shelves seems warranted, especially with regard to the eastern tropical Pacific and both sides of the Atlantic. Of all the shallow, shelf-dwelling zoarcid genera, only one genus (2% of total), Gymnelus, is found in three or more of Briggs' Regions, while 20% of the deep-sea (slope and abyss) genera are found in three or more Regions. Dispersion of deep-sea zoarcids is probably aided by the short, demersal larval period of these fishes (Anderson, In Press).

APPENDIX I

Specimens studied in detail are listed below. Radiographs and preserved material of many common zoarcids not listed were used to aid the work. Given are museum number, followed by number of specimens and size in mm standard length (in parentheses), and general capture locality. Asterisced specimens were cleared and stained for osteological observations. Non-asterisced specimens were superficially dissected when permissible, radiographed and are currently stored in alcohol. Museum abbreviations are as follows:

BCPM: British Columbia Provincial Museum, Victoria.

BMNH: British Museum (Natural History), London.

CAS: California Academy of Sciences, San Francisco.

HSU: Humboldt State University, Arcata.

HUMZ: Museum of Zoology, Hokkaido University, Hakodate.

ISH: Institut fur Seefischerei, Hamburg.

LACM: Natural History Museum of Los Angeles County, Los Angeles.

MACN: Museo Nacional de Ciencias Naturales, Buenos Aires.

MCZ: Museum of Comparative Zoology, Cambridge.

MNHN: Museum National d'Histoire Natural, Paris.

NMC: National Museum of Natural Sciences, Ottawa.

SAM: South African Museum, Cape Town.

SAMA: South Australian Museum, Adelaide.

SIO: Scripps Institution of Oceanography, La Jolla.

- SU: Museum of Zoology, Stanford University; now housed at CAS.
- UA: University of Alaska Marine Collections, Fairbanks.
- UMML: Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami.
- USNM: National Museum of Natural History, Washington, D.C.
- UWZ: Museum of Zoology, University of Wisconsin, Madison.
- VIMS: Virginia Institute of Marine Science, Gloucester Point.
- ZIL: Zoological Institute, Academy of Sciences, Leningrad.
- ZMUC: Zoologiske Museum, University of Copenhagen.
- ZMUO: Zoologiske Museum, University of Oslo.

Family Zoarcidae

Aiakas kreffti Gosztonyi, 1977. ISH 385/71 (holotype, 247 mm), slope off Patagonia; ISH 274/78 (1, 301 mm), Patagonian slope.

Andriashevia aptera Fedorov and Neyelov, 1978. ZIL 43449 (holotype, 173 mm), Pacific coast of Japan.

Austrolycichthys brachycephalus (Pappenheim, 1912). CAS uncat. (1, 263 mm)*, Antarctic Peninsula. BMNH 1913.4.15: 58-59 (2 syntypes, 148, 152 mm), Antarctica: Wilhelm Land. BMNH 1937.7.12: 793 (1, 278 mm), Antarctica: Ross Sea. CAS uncat. (1, 205 mm), Antarctic Peninsula.

Austrolycichthys conorhynchus (Garman, 1899). UMML 22862 (1, 211 mm), Gulf of Panama. MCZ 28690 (3 syntypes, 182-230 + mm), Gulf of Panama.

Austrolycichthys suspectus (Garman, 1899). ZMUC P761085 (1, 280 mm)*, Gulf of Panama. SIO 68-106 (1, 216 mm), Gulf of California. MCZ 28683 (holotype, 230 mm), Gulf of Panama.

Austrolycichthys sp. A. USNM 233626 (1, 170 mm), USA: Straits of Florida, 867 m.

Austrolycus depressiceps Regan, 1913. VIMS 05942 (1, 209 mm)*; and LACM 11153-1 (3, 104-268 mm)*, all Chile: Tierra del Fuego. VIMS 05401 (2, 138, 155 mm), Argentina: Tierra del Fuego. USNM 88806 (1, 445 + mm), Falkland Islands.

Austrolycus laticinctus Regan, 1913. VIMS 05400 (1, 194 mm)*, Argentina: Puerto Deseado. ISH 1422/66 (1, 109 mm), Argentina: Tierra del Fuego.

Bilabria ornata (Soldatov, 1922). Four specimens, 166-219 mm. See Anderson (1982b).

Bothrocara alalongum (Garman, 1899). MCZ 28694 (2 syntypes, 235 + and 432 mm), Gulf of California. SU 5256 (1, 323 mm), Gulf of California.

Bothrocara brunneum (Bean, 1890). CAS 34355 (, 338 mm)*, California: Monterey Bay. USNM uncat. (3, 165-368 mm)*, Bering Sea. USNM uncat. (6, 278-360 mm), Bering Sea. VIMS 07112 (1, 455 mm), California: Monterey Bay.

Bothrocara elongatum (Garman, 1899). MCZ 28691 (holotype, 515 mm), Gulf of Panama. MCZ 28692 (1, 310 mm +), Gulf of Panama.

Bothrocara hollandi (Jordan and Hubbs, 1925). SU 3535 (cotype, 248 mm), off Japan. USNM 117950 (1, 252 mm); USNM 117966 (11, 189-253 mm); USNM 117934 (1, 202 mm); USNM 149617 (2, 241-246 mm); USNM 150295 (1, 233 mm); USNM 150296 (1, 318 mm), all Japan Sea.

Bothrocara molle Bean, 1890. USNM 75820 (holotype of B. remigerum,

281 mm), California: Monterey Bay. SIO 71-190 (1, 480 mm), California. SU 22987 (paratype of B. remigerum, 250 mm), California: Monterey Bay. SU 21349 (1, 72 mm), Mexico: Coronado Isl. SU 475 (1, 181 mm), California. BCPM 982-93 (1, 145 mm), off Oregon.

Bothrocara pusillum (Bean, 1890). LACM 1199 (6, 133-145 mm)*, and (6, 126-149 mm), Alaska: off Petersburg.

Bothrocara rictolatum (Garman, 1899). MCZ 28693 (holotype, 427 mm), Gulf of Panama. Probable synonym of B. alalongum.

Bothrocara tanakai (Jordan and Hubbs, 1925). USNM 150363 (1, 323 mm)*, (1, 409 mm), Japan: off Hokkaido. USNM 161445 (1, 305 mm); USNM 161495 (1, 645 mm); USNM 160718 (1, 319 mm); SU 32252 (1, 266 mm); all Japan.

Bothrocara zestum Jordan and Fowler, 1902. USNM 50576 (holotype, 475 mm), Japan: Sagami Bay. SU 7122 (paratypes, 464-499 mm), Sagami Bay.

Bothrocarina microcephala (Shmidt, 1938). HUMZ 55484 (1, 338 mm)*; HUMZ 34001 (1, 430 mm), both Okhotsk Sea.

Crossostomus chilensis (Regan, 1913). SIO 74-110 (1, 55 mm), Argentina: Staten Island. MACN 4403 (1, 165 mm), Argentina: Tierra del Fuego.

Crossostomus fasciatus (Lonnberg, 1905). VIMS 05402 (1, 118 mm)*, Argentina: Puerto Deseado. ISH 328/71 (1, 335 mm), Patagonian shelf.

Dadyanos insignis (Steindachner, 1898). VIMS 05403 (1, 198 mm)*, Argentina: Puerto Deseado. ISH 6/75 (2, 168, 209 mm), same collection.

Davidijordania jordaniana Popov, 1936. USNM 92585 (1, 118 mm), Okhotsk Sea.

Davidijordania poecilimon (Jordan and Fowler, 1902). Two specimens, 106, 135 mm; see Anderson (1982b).

Derepodichthys alepidotus Gilbert, 1895. See Anderson and Hubbs (1981).

Eucryphycus californicus (Starks and Mann, 1911). VIMS 05806 (16, 48-173 mm)*; CAS 38667 (4, 123-196 mm); VIMS 05394 (1, 118 mm), all California: Monterey Bay.

Exechodontes daidaleus DeWitt, 1977. USNM 211797 (holotype, 96 mm), Gulf of Mexico. USNM 233628 (1, 65 mm)*, Straits of Florida. VIMS 05406 (1, 92 mm)*, (1, 97 mm), Florida: off Daytona Beach. UMML 3818 (2, 93, 98 mm), off Daytona Beach. UMML 5362 (1, 113 mm), Florida: off Dry Tortugas. UMML 15913 (2, 73-87 mm), Straits of Florida. UMML 16074 (1, 103 mm), Straits of Florida. UMML 18365 (2, 91, 100 mm), Straits of Florida. UMML 32308 (1, 95 mm), off Miami Beach.

Gymnelopsis brashnikovi Soldatov, 1922. ZIL 13029 (1, 97 mm), Okhotsk Sea; see Anderson (1982b).

Gymnelopsis brevifenestrata Anderson, 1982. Thirteen specimens, 74-120 mm, Okhotsk Sea; see Anderson (1982b).

Gymnelopsis ocellata Soldatov, 1922. Six specimens, 82-140 mm, Okhotsk Sea; see Anderson (1982b).

Gymnelopsis ochotensis (Popov, 1931). UMMZ 202550 (1, 252 mm)*, USNM 117956 (1, 222 mm)*, both Japan Sea; eight specimens 108-243 mm, Okhotsk and Japan seas; see Anderson (1982b).

Gymnelus hemifasciatus Andriashev, 1937. NMC 75-165 (1, 105 mm)*, Arctic Canada; 112 specimens, 28-140 mm; see Anderson (1982b).

Gymnelus retrodorsalis Le Danois, 1913. ZMUC 208 (1, 107 mm)*, Greenland; 107 specimens, 38-135 mm; see Anderson (1982b).

Gymnelus pauciporus Anderson, 1982. Five specimens. 106-136 mm, Okhotsk and Bering seas; see Anderson (1982b).

Gymnelus popovi (Taranets and Andriashev, 1935). UWZ 3558 (3, 55-100 mm)‡ Aleutian Islands; 96 specimens 24-163 mm; see Anderson (1982b).

Gymnelus viridis (Fabricius, 1780). Thirteen cleared and stained, 60-215 mm, and 274 alcohol specimens; see Anderson (1982b).

Hadropareia middendorffi Schmidt, 1904. ZIL 20147 (3, 219-238 mm), Okhotsk Sea: Shantar Islands.

Iluocoetes effusus (Smitt, 1898). VIMS 05398 (2, 131, 147 mm)*, (2, 109, 110 mm), Argentina: Puerto Deseado. ISH 25/70 (5, 131-161 mm), same collection.

Iluocoetes fimbriatus Jenyns, 1842. ISH 1401/66 (1, 302 mm)*, South Atlantic: Burdwood Bank. BMNH 1917.7.14: 69 (holotype, 140 mm), Chile: Chiloe Isl. (coll.: Charles Darwin, 1833). ISH 1219/66 (3, 334-365 mm); ISH 1359/66 (3, 305-344 mm); ISH 386/78 (1, 127 mm); ISH 397/78 (1, 177 mm); ISH 388/78 (1, 125 mm), all off Argentina and Falkland Isl.

Krusensterniella maculata Andriashev, 1938. ZIL 29989 (2, 121, 140 mm), Okhotsk Sea: Tatar Strait. ZIL 40166 (1, 97 mm), Japan Sea.

Krusensterniella multispinosa Soldatov, 1922. USNM 92592 (1, 125 mm).

Krusensterniella notabilis Schmidt, 1904. USNM 92591 (syntype, 109 mm), Okhotsk Sea.

Lycenchelys alba (Vaillant, 1888). MNHN 86-590 (syntypes, 190-195 + mm), off the Azores Isl. MNHN 1970-31 (holotype of Lycenchelys labradorensis Geistdorfer et al., 1970, 213 mm), North Atlantic: Davis Strait. VIMS 05388 (1, 267 mm), off Virginia.

Lycenchelys antarcticus Regan, 1913. LACM 11043-5 (1, 242 mm)*, Scotia Sea: off South Orkney Isl.

Lycenchelys bachmanni Gosztonyi, 1977. ISH 306/71 (holotype, 315 mm), Argentine slope.

Lycenchelys bellingshauseni Andriashev and Permitin, 1968. ISH 402/76 (1, 266 mm)*, Scotia Sea. ISH 351/76 (1, 234 mm), Scotia Sea.

Lycenchelys bullisi Cohen, 1964. USNM 188232 (holotype, 176 mm), UMML 5363 (paratype, 170 mm) and UMML 28665 (1, 170 mm), all Gulf of Mexico.

Lycenchelys camchatica (Gilbert and Burke, 1912). SIO 74-166 (9, 121-145 mm)*; many alcohol specimens, see Anderson et al. (1979).

Lycenchelys cicatrifer (Garman, 1899). MCZ 28684 (holotype, 230 mm), Gulf of Panama.

Lycenchelys crotalina (Gilbert, 1891). VIMS 07198 (2, 212-342 mm)*, (2, 220-309 mm), California: off Cape Mendocino. USNM 44279 (holotype of Lycodopsis crotalinus, 318 mm), California: off Santa Barbara Isl. USNM 44280 (holotype of Lycodopsis crassilabris, 295 mm), off southern California. USNM 75818 (holotype of Embryx parallelus, 388 mm), Calif-

ornia: Monterey Bay. HSU 29000-10 (18, 137-422 mm), California: off Cape Mendocino. SIO 74-166 (3, 333-414 mm), off southern California.

Lycenchelys hippopotamus Schmidt, 1950. ZIL 32958 (2, 170, 200 mm); ZIL 32959 (1, 205 mm), all Okhotsk Sea.

Lycenchelys hureaui (Andriashev, 1979). ZIL 44333 (holotype of Apodolycus hureaui Andriashev, 260 mm), Kerguelen Plateau. MNHN uncat. (10, 245-271 mm), Kerguelen Plateau.

Lycenchelys incisa (Garman, 1899). MCZ 28685 (syntypes, 195 + 240 mm), Gulf of Panama.

Lycenchelys ingolfiana Jensen, 1902. ZMUC 20 (holotype, 278 mm), North Atlantic: Davis Strait.

Lycenchelys jordani (Evermann and Goldsborough, 1907). USNM 57828 (holotype of Lycodes jordani Ev., Golds., 330 + mm). SU 20014 (paratype, 208 mm), both off southeastern Alaska. BCPM 71-242 (2, 255-296 mm), off Oregon.

Lycenchelys kolthoffi Jensen, 1904. ZMUC P76335-76343 (9, 151-232 mm), northwestern Greenland.

Lycenchelys microcephala Jensen, 1902. ZMUC 78 (holotype, 79 mm), North Atlantic: Reykjanes Ridge.

Lycenchelys monstrosa Anderson, 1982. Twelve specimens, 164-276 mm; see Anderson (1982a).

Lycenchelys muraena (Collett, 1879). ZMUO 4538 (1, 123 mm), coast of

Norway. ZMUO 4539 (1), Faeroe Ridge. ISH AD 262/64 (2, 191, 226 mm),
North Atlantic: Denmark Strait.

Lycenchelys nigripalata DeWitt and Hureau, 1979. MNHN 1974-86 (holotype,
280 mm), Antarctic Peninsula.

Lycenchelys paxilla (Goode and Bean, 1879). VIMS 03802 (3, 121-173 mm)*,
VIMS 06543 (13, 109-175 mm), all off Virginia.

Lycenchelys platyrhina (Jensen, 1902). ZMUC 119 (holotype, 146 mm),
North Atlantic: off Jan Mayen Isl.

Lycenchelys porifer (Gilbert, 1891). USNM 44384 (holotype of Lycodes
porifer Gilbert, 299 mm), Gulf of California. SIO 70-248-61 (3, 220-
255 mm), SIO 70-247-61 (1, 257 mm), all Gulf of California. MCZ 28687,
28688 (4, 165-225 + mm; syntypes of Lycodes anguis Garman, 1899), Gulf
of California. MCZ 28686 (1, 255 mm; syntype of Lycodes serpens Garman),
Gulf of California.

Lycenchelys rassi Andriashev, 1955. ZIL 32962 (holotype, 192 mm),
Okhotsk Sea. MCZ 34074 (1, 145 mm), Okhotsk Sea.

Lycenchelys ratmanovi Andriashev, 1955. USNM 221249 (1, 136 mm), USNM
221250 (1, 132 mm), both Bering Sea.

Lycenchelys sarsi (Collett, 1871). ZMUC P761014-761017 (4, 147-165 mm),
North Atlantic: Rockall Bank. ISH 13/74 (2, 115-169 mm), southwest of
Faeroe Islands. ZMUO 4555 (1, 96 mm), Norway: Hardangerfjord. ZMUO
sta. 133/71 (10, 96-145 mm), Norway: Glomfjord.

Lycenchelys scaura (Garman, 1899). MCZ 28689 (holotype, 175 mm), Gulf

of Panama. LACM 11577-2 (1, 192 mm)*, Chile: off Valpariso.

Lycenchelys tristichodon DeWitt and Hureau, 1979. MNHN 1974-87 (holotype, 304 mm), Antarctic Peninsula.

Lycenchelys verrillii (Goode and Bean, 1877). VIMS 06169 (4, 116-160 mm)*, off Atlantis Canyon, USA. VIMS 06509 (16, 79-162 mm), off Norfolk Canyon, USA.

Lycenchelys sp. A. ISH 381/78 (1, 234 mm), South Atlantic: Burdwood Bank. ISH 382/78 (1, 176 mm), off Falkland Islands.

Lycenchelys sp. B. USNM 218475 (1, 259 mm), USSR: Kuril Islands.

Lycodapus australis Norman, 1937. Fifty-seven specimens, 39-95 mm; see Peden and Anderson (1978).

Lycodapus derjugini Andriashev, 1935. Five specimens, 52-125 mm; see Peden and Anderson (1978).

Lycodapus dermatinus Gilbert, 1895. VIMS 07117 (1, 89 mm)*, California: Monterey Bay. Thirty six specimens in alcohol, 44-122 mm; see Peden and Anderson (1978).

Lycodapus endemoscotus Peden and Anderson, 1978. Thirty-four specimens, 63-127 mm; see Peden and Anderson (1978).

Lycodapus fierasfer Gilbert, 1891. VIMS 07116 (1, 99 mm)*, off Oregon. Forty-six specimens in alcohol, 35-140 mm; see Peden and Anderson (1978).

Lycodapus leptus Peden and Anderson, 1981. Fifteen of 41 specimens, 80-99 mm; see Peden and Anderson (1981).

Lycodapus mandibularis Gilbert, 1915. VIMS 07114 (5, 85-126 mm)*, CAS 36726 (4, 48-130 mm)*, all California: Monterey Bay. Three hundred forty-three specimens in alcohol, 18-164 mm; see Peden and Anderson (1978); Anderson (1981).

Lycodapus microchir Schmidt, 1950. ZIL 24848 (holotype, 77 mm), Okhotsk Sea. ZIL uncat. (13, 56-98 mm), Bering Sea; see Peden and Anderson (1981).

Lycodapus pachysoma Peden and Anderson, 1978. Nine specimens, 87-161 mm; see Peden and Anderson (1978). ISH 403/76 (2, 143, 184 mm), off South Georgia Island.

Lycodapus parviceps Gilbert, 1915. VIMS 07118 (1, 98 mm)*, British Columbia: Vancouver Island. Twenty-seven specimens 54-116 mm; see Peden and Anderson (1978).

Lycodapus poecilus Peden and Anderson (1981). Fifteen of 43 specimens, 69-109 mm; see Peden and Anderson (1981).

Lycodapus psarostomatus Peden and Anderson, 1981. Five specimens, 74-155 mm; see Peden and Anderson (1981).

Lycodapus sp. A. BCPM 975-221 (2, 145, 162 mm), off South Georgia Isl.

Lycodes albolineatus Andriashev, 1955. ZIL 34581 (holotype, 596 mm), Kamchatka coast.

Lycodes agulhensis Andriashev, 1959. BMNH 1927,12.6: 69 (2, 223, 235 + mm), off Cape Town, South Africa.

Lycodes atlanticus Jensen, 1902. VIMS 05407 (4, 288-319 mm)*; VIMS 06471 (4, 269-334 mm); VIMS 03864 (1, 86 mm); VIMS 03795 (1, 116 mm), all off Norfolk Canyon, USA.

Lycodes brevicaudus Taranets and Andriashev, 1935. BMNH 1970.2.12: 1 (1, 163 mm), Okhotsk Sea.

Lycodes brevipes Bean, 1890. LACM 33295-1 (3, 121-188 mm), Gulf of Alaska.

Lycodes brunneofasciatus Suvorov, 1935. BMNH 1970.2.12: 2 (1, 240 mm), Okhotsk Sea. USNM 233629 (3, 345-365 mm), Alaska: Aleutian Islands.

Lycodes caudimaculatus Matsubara, 1936. BMNH 1938.6.23: 26 (1, 222 mm), Japan Sea. CAS 39576 (1, 191 mm), Japan: Suruga Bay.

Lycodes cortezianus (Gilbert, 1891). VIMS 07109 (3, 52-292 mm)*, VIMS 07110 (1, 196 mm)*, both California: off San Miguel Isl. VIMS 06477 (5, 235-270 mm), California: Monterey Bay.

Lycodes concolor Gill and Townsend, 1897. USNM 48764 (holotype, 545 mm), Bering Sea. LACM 35768-2 (1, 179 mm); LACM 35752-4 (1, 281 mm), both Gulf of Alaska. LACM 34164-1 (1, 325 mm), Bering Sea.

Lycodes diapterus Gilbert, 1892. VIMS 07095 (5, 167-234 mm)*, (15, 190-249 mm), all California: Monterey Bay.

Lycodes esmarki Collett, 1875. VIMS 05758 (1, 129 mm); VIMS 03247 (1, 145 mm), both off Norfolk Canyon, USA. ZMUC uncat. (10, 343-441 mm), Greenland.

Lycodes eudipleurostictus Jensen, 1902. VIMS 05756 (1, 257 mm)*, off Iceland. NMC 74-275 (2, 309-340 mm), Alaska: Beaufort Sea. NMC 80-415 (1, 291 mm), Greenland. ZMUC 138 (syntype, 255 mm), north of Faeroe Islands.

Lycodes frigidus Collett, 1879. ZMUC P76830-76832 (3, 142-198 mm), north of Iceland. ZMUC 40-43 (4, 133-157 mm), north of Iceland. MCZ 40707 (1, 140 mm), Chukchi Sea. ZMUO 4517-4520 (4 syntypes, 270-375 mm), Arctic Atlantic.

Lycodes japonicus Matsubara and Iwai, 1952. USNM 150066 (3, 120-124 mm)*; (12, 100-129 mm), Japan Sea.

Lycodes jugoricus Knipovich, 1906. NMC 75-1924 (1, 159 mm), NMC 64-358 (1, 211 mm), both Arctic Canada.

Lycodes lavalaei Vladykov and Tremblay, 1936. VIMS 02215 (2, 444, 480 mm), off Nova Scotia. NMC 70-296 (2, 232, 345), coast of Labrador.

Lycodes luetkeni Collett, 1880. ZMUO 4536 (holotype, 355 mm), west of Spitsbergen.

Lycodes mucosus Richardson, 1855. BMNH 1855.9.19: 760 (holotype, 171 mm), Arctic Canada. NMC 77-1541 (1, 204 mm), Arctic Canada. NMC 75-1946 (1, 116 mm), Arctic Canada. UA 1151 (6, 98-161 mm), Chukchi Sea.

Lycodes pacificus Collett, 1879. CAS uncat. (3, 70-160 mm)*, California: off San Luis Obispo Bay. VIMS 05392 (1, 180 mm); VIMS 05393 (1, 222 mm), both California: Monterey Bay.

Lycodes palearis Gilbert, 1895. VIMS 07074 (1, 240 mm)*, (8, 288-390 mm), all Bering Sea.

Lycodes pallidus Collett, 1879. NMC 70-29 (3, 128-156 mm)*, (4, 136-147 mm), Canada: Saguenay Fjord, Quebec. VIMS 01221 (1, 105 mm), off Nova Scotia. USNM uncat. (1, 217 mm), Barents Sea.

Lycodes polaris (Sabine, 1824. MCZ 27570 (1, 167 mm), Kara Sea. NMC 69-115 (1, 225 mm); NMC 67-301 (1, 162 mm), both Arctic Canada. UA 1225 (5, 91-173 mm), Alaska: Beaufort Sea.

Lycodes raridens Taranets and Andriashev, 1937. UA 1918 (1, 221 mm), Bering Sea. UA 1476 (1, 179 mm), Beaufort Sea. UA 1161 (1, 252 mm), Beaufort Sea.

Lycodes reticulatus Reinhardt, 1835. ZMUC 21 (syntype, 335 mm), Greenland. VIMS 03594 (1, 280 mm)*, Gulf of St. Lawrence. VIMS 03596 (2, 372-397 mm), Gulf of St. Lawrence.

Lycodes rossi Malmgren, 1864. Twenty specimens, 51-223 mm, Arctic Canada; see McAllister et al. (1981).

Lycodes sagittarius McAllister, 1976. Ten specimens, 98-180 mm, Arctic Alaska and Canada; see McAllister et al. (1981).

Lycodes seminudus Reinhardt, 1837. Six specimens, 101-193 mm, Arctic Canada; see McAllister et al. (1981).

Lycodes soldatovi Taranets and Andriashev, 1935. ZIL 37978 (1, 380 mm), Bering Sea.

Lycodes squamiventer (Jensen, 1904). ISH 807/64 (12, 70-220 mm), North Atlantic: Denmark Strait. ISH 146/59 (13, 157-228 mm), North Atlantic: Faeroe Channel. ZMUC 235 (holotype, 245 mm), Norwegian Sea.

Lycodes tanakai (Jordan and Thompson, 1914). USNM uncat. (4, 323-602 mm), Japan Sea.

Lycodes toyamensis (Katayama, 1941). HUMZ 42728 (1, 317 mm)*; HUMZ 53067 (1, 324 mm); HUMZ 42717 (1, 325 mm), all Japan Sea.

Lycodes turneri Bean, 1878. VIMS 05389 (1, 141 mm), Beaufort Sea. UA 1161 (1, 209 mm); UA 1209 (2, 116-173 mm), both Chukchi Sea. UA 230 (1, 191 mm), Bering Sea.

Lycodes vahlii Reinhardt, 1831. VIMS 05815 (1, 346 mm)*, (1, 246 mm); VIMS 05818 (2, 185, 292 mm), all Greenland.

Lycodichthys antarcticus Pappenheim, 1911. BMNH 1913.4.15: 60-61 (2 syntypes, 174, 199 mm): VIMS 05777 (1, 179 mm)*; SAMA F353 (1, 181 mm), all Antarctica: Wilkes Land.

Lycodichthys dearborni (DeWitt, 1962). VIMS 05404 (1, 206 mm)*, and (5, 142-198 mm), Antarctica: McMurdo Sound.

Lycodonus flagellicaudus (Jensen, 1902). ISH 9/74 (3, 108-115 mm)*, North Atlantic: Wyville-Thompson Ridge. ZMUC 21-29 and 31 (10 syntypes, 105-199 mm), Spitsbergen to Faeroe Islands.

Lycodonus mirabilis Goode and Bean, 1883. VIMS 03086 (1, 125 mm)*; VIMS 06499 (1, 278 mm)*, VIMS uncat. (10, 115-282 mm)*; VIMS 05385 (1, 281 mm); VIMS 05459 (1, 302 mm), all off Norfolk Canyon, USA.

Lycodonus vermiformis Barnard, 1927. BMNH 1927.12.6: 71 (syntype, 245 mm); SAM 12906 (1, 268 + mm), both off Cape Town, South Africa.

Lycogrammoides schmidti Soldatov and Lindberg, 1929. MCZ 34050 (1, 205 mm), Okhotsk Sea: off Iona Island.

Lycinema barbatum Gilbert, 1895. LACM 34151-2 (2, 155, 160 mm)*, California: off Trinidad Head. VIMS 05391 (4, 124-155 mm)*, (3, 135-164 mm), California: off San Miguel Island.

Lycozoarces regani Popov, 1931. USNM 105219 (1, 152 mm)*, 4 alcohol specimens, 106-178 mm; see Anderson (1982b).

Macrozoarces americanus (Schneider, 1801). VIMS uncat. (11, 34-268 mm)*, (17, 189-1180 mm), all USA: off Nantucket Shoals.

Maynea puncta (Jenyns, 1842). VIMS 05783 (1, 149 mm)*, Argentina: Ushuaia. LACM 10722-1 (1, 250 mm); LACM 10724-1 (1, 77 mm), both Chile: Straits of Magellan. SIO 74-109-61 (1, 76 mm), Argentina: Staten Isl.

Melanostigma atlanticum Koefoed, 1952. VIMS 05646 (6, 69-115 mm)*, (41, 53-113 mm), USA: off Cape Cod, Massachusetts.

Melanostigma bathium Bussing, 1965. MCZ 54038 (1, 87 mm)*, MCZ 54040 (1, 77 mm), both Chile: off Valpariso. SIO 72-31 (3, 69-76 mm), off Galapagos Islands.

Melanostigma gelatinosum Günther, 1881. MCZ 54035 (1, 62 mm)*, MCZ 54034 (1, 46 mm), both Chile: off Valpariso. BMNH 1937.7.12: 795 (holotype, 200 mm); BMNH 1939.6.20: 36 (1, 225 mm), both off South Georgia Is.

Melanostigma inexpectatum Parin, 1978. ZIL 42640 (holotype, 101 mm), off New Guinea.

Melanostigma orientale Tominaga, 1971. NMC 71-208 (paratype, 45 mm), Japan: Suruga Bay.

Melanostigma pammelae Gilbert, 1895: VIMS 05408 (8, 69-99 mm)*; VIMS 07156 (10, 58-95 mm); VIMS 07155 (10, 41-80 mm), all California: Monterey Bay.

Nalbantichthys elongatus Schultz, 1967. USNM 200671 (holotype, 135 mm), Bering Sea.

Notolycodes schmidti Gosztonyi, 1977. ISH 1134/66 (holotype, 319 mm), Argentina: off Rio de la Plata. ISH 1977/66 (paratype, 175 mm), Brazil: off Cabo de São Tomé. ISH 391/78 (1, 386 mm), off Rio de la Plata.

Oidiphorus brevis (Norman, 1937). ISH 175/78 (1, 115 mm)*; BMNH 1936.8.36: 1042-1045 (4 syntypes, 37-84 mm); ISH 379/78 (5, 71-110 mm); ISH 1146/66 (1, 125 mm); ISH 1444/66 (1, 70 mm), all Argentine slope.

Ophthalmolycus bothriocephalus (Pappenheim, 1912). BMNH 1937.7.12: 159 (1, 112 mm), Antarctica: Enderby Land.

Ophthalmolycus concolor (Roule and Despax, 1911). CAS uncat. (1, 141 mm)*, Antarctic Peninsula. LACM 11357-2 (1, 215 mm)*, Antarctica: Ross Sea. MNHN 244.2.1.1 (holotype, 167 + mm), Antarctica: Ross Sea. BMNH 1937.7.12: 794 (1, 120 mm), Antarctica: South Shetland Islands. CAS uncat. (2, 109, 142 mm), Antarctic Peninsula.

Ophthalmolycus macrops (Gunther, 1880). LACM 11759-4 (1, 129 mm)*;

BMNH 1879.5.14: 48 (holotype, 127 mm), both Chile: Straits of Magellan.

Pachycara bulbiceps (Garman, 1899). UMML 33485 (1, 313 mm)*, (1, 255 mm)

and UMML 33484 (1, 380 mm), both Gulf of Panama. SIO 73-286 (2, 425, 455 mm), off Costa Rica, eastern Pacific.

Pachycara crassiceps (Roule, 1916). BMNH 1981.6.23: 3 (1, head only,

445 mm)* (1, 449 mm), southwest of Ireland. BMNH 1981.6.23: 1-2 (2, 432-512 mm), off Cap Blanc, Mauritania.

Pachycara obesum Zugmayer, 1911. BMNH 1981.6.16: 15 (1, head only,

332 mm)*, off Cap Blanc, Mauritania. USNM 215611 (1, 82 mm); MCZ 57612 (1, 498 mm), both USA: Middle Atlantic Bight.

Pachycara sp. A. BCPM 980-100 (1, 281 mm)*; BCPM 980-121 (2, 185, 421

mm); BCPM 979-11365 (1, 221 mm); BCPM 979-11368 (1, 247 mm); BCPM 979-11369 (6, 247-391 mm), all British Columbia: off Queen Charlotte Isl.

Pachycara sp. B. BCPM 980-98 (1, 507 mm); BCPM 980-99 (1, 261 mm);

BCPM 979-11365 (2, 300, 593 mm); BCPM 980-121 (2, 463, 552 mm), all British Columbia: off Queen Charlotte Islands.

Pachycara sp. C. ZMUC P761147 (1, 236 mm), Indian Ocean: Bay of Bengal.

Pachycara sp. D. USNM 233627 (1, 161 mm), Caribbean Sea: Venezuela Basin.

Pachycara sp. E. LACM 43531-1 (1, 403 mm), Galapagos Rift Zone.

Phucocoetes latitans Jenyns, 1842. BMNH 1917.7.14: 67 (lectotype, 115

mm), Falkland Isl. VIMS 05399 (1, 109 mm)*, (1, 87 mm), Argentina:

Puerto Deseado. SIO 74-109 (1, 72 mm), Argentina: Staten Isl.

Piedrabuenia ringueleti Gosztonyi, 1977. ISH 279/71 (holotype, 227 mm), Patagonian slope. ISH 378/78 (1, 209 mm)*, (3, 141-219 mm), Patagonian slope. ISH 389/78 (1, 233 mm), north Argentine slope.

Plesienchelys stehmanni (Gosztonyi, 1977). ISH 249/78 (1, 192 mm)*; ISH 377/78 (1, 200 mm); ISH 383/78 (1, 245 mm); ISH 392/78 (1, 214 mm); ISH 393/78 (1, 205 mm); ISH 317/71 (holotype, 165 mm), all slope off Argentina and Falkland Islands.

Pogonolycus elegans Norman, 1937. BMNH 1936.8.26: 1031 (holotype, 152 mm), off Falkland Islands. ISH 1445/66 (1, 65 mm), Patagonian shelf.

Puzanovia rubra Fedorov, 1975. ZIL 39213 (holotype, 227 mm), Bering Sea.

Redirolycus microphthalmus (Norman, 1937). ISH 376/78 (1, head only, 90 mm)*, Patagonian shelf. BMNH 1936.8.26: 1046 (paratype, 68 mm), off Falkland Islands. LACM 10062-1 (1, 45 mm), Argentina: Tierra del Fuego.

Redirolycus sp. A. ISH 164/78 (1, 150 mm), ISH 173/78 (1, 152 mm), both Patagonian slope.

Taranetzella lyoderma Andriashev, 1952. ZIL 32813 (holotype, 100 mm), Bering Sea. CAS 38921 (1, 142 mm), off Oregon.

Zoarces elongatus Kner, 1868. MCZ 32492 (1, 242 mm)*; USNM 105154 (1, 203 mm)*, both Okhotsk Sea.

Zoarces gillii Jordan and Starks, 1905. CAS 17746 (4, 178-229 mm)*, (11, 182-263 mm), East China Sea.

Zoarces viviparus (Linnaeus, 1758). ISH 9/59 (1, 193 mm)*, Netherlands.

Family Zaproridae

Zaprora silenus Jordan, 1896. UMMZ 179527 (1, 80 mm)*, southeast Alaska: Chatham Strait.

Family Anarhichantidae

Anarhichas lupus Linnaeus, 1758. VIMS 02346 (1, 147 mm), off Nova Scotia.

Anarhichas minor Olafsen, 1772. VIMS 01225 (1, 332 mm), Gulf of St. Lawrence.

Anarrhichthys ocellatus Ayers, 1855. LACM 36177-1 (1, 428 mm)*, California: Monterey Bay.

Family Stichaeidae

Acantholumpenus mackayi (Gilbert, 1893). LACM 33864-4 (2, 205-211 mm)*, Bering Sea.

Anoplarchus purpureus Gill, 1861. VIMS 07495 (11, 41-136 mm)*, California, Monterey Bay.

Azygopterus corallinus Andriashev and Makushok, 1955. ZIL 33444 (holotype, 94 mm), USSR: Kuril Islands.

Chirolophis nugator (Jordan and Williams, 1895). LACM 31977-8 (4, 35-105 mm)*, California: Mendocino Co.

Cryptacanthodes maculatus Storer, 1839. VIMS 03388 (1, 226 mm)*, Virginia: off Norfolk Canyon. VIMS 07427 (1, 401 mm), off Cape Cod.

Eulophias tanneri Smith, 1902. USNM 49798 (holotype, 41 mm), Japan.

Eumesogrammus praecius (Krøyer, 1837). VIMS 02264 (1, 156 mm), Gulf of St. Lawrence.

Neozoarces steindachneri Jordan and Snyder, 1903. SU 4025 (3, paratypes, 53-62 mm), Japan: Hakodate.

Xiphister atropurpureus (Kittlitz, 1858). VIMS 07494 (9, 48-165 mm)*, California: Monterey Bay.

Zoarchias glaber Tanaka, 1908. UMMZ 207710 (3, 89-1-9 mm), Japan.

Zoarchias veneficus Jordan and Snyder, 1903. SU 7104 (6 paratypes, 38-55 mm)*, Japan, Hakodate. UMMZ 202575 (11, 54-76 mm)*, (40, 51-70 mm), Japan, near Nagasaki.

Family Pholididae

Ulvicola sanctaerosae Gilbert and Starks, 1896. VIMS 07496 (1, 153 mm)*, California: Carmel Bay.

Xererpes fucorum (Jordan and Gilbert, 1880). VIMS 07497 (13, 71-131 mm)*, California: Monterey Bay.

Family Scytalinidae

Scytalina cerdale Jordan and Gilbert, 1880. CAS 30960 (2, 50-79 mm)*, California: Mendocino County shore.

Family Bathymasteridae

Bathymaster signatus Cope, 1873. NMC 61-53 (3, 189-252 mm)*, southeastern Alaska.

APPENDIX II

Osteological abbreviations used in the text figures are listed below.

ACT-actinosts	HYPHY V-ventral hypohyal
ANG-anguloarticular	I 2-4-infrapharyngobranchials
BASBR-basibranchials	INTHY-interhyal
BOC-basioccipital	L EX-lateral extrascapulars
BR R-branchiostegal rays	LAC-lacrima
CERBR-ceratobranchial	LAT ETH-lateral ethmoid
CL-cleithrum	MAX-maxilla
COR-coracoid	MES-mesethmoid
DENT-dentary	MET-metapterygoid
D 1-first dorsal ray	NAS-nasal bone
ECT-ectopterygoid	OP-opercle
END-endopterygoid	PAL-palatine
EP epural	PAR-parietal
EPIBR-epibranchials	PAS-parasphenoid
EPIHY-epihyals	PCL-postcleithrum
EPIOC-epioccipital	PEL-pelvic bone
EXOC-exoccipital	PH-parhypural
FR-frontal	PMAX-premaxilla
H-hypurals	POP-preopercle
HYOM-hyomandibula	PTEM-posttemporal
HYPBR-hypobranchials	PTO-pterotic
HYPHY D- dorsal hypohyal	PTS-pterosphenoid

PU-preural vertebrae

QUAD-quadrate

SCAP-scapula

SO-suborbital bones

SOC-supraoccipital

SPH-sphenotic

SUPCL-supracleithrum

SYM-symplectic

TAR-terminal anal ray

TDR-terminal dorsal ray

U 1-first ural vertebra

UROHY-urohyal

V-vomer

APPENDIX III

Zoarcid character matrix. Matrix numbers refer to states, pp. 23-42.

Genus	Character												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Lycozoarces</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Macrozoarces</i>	0	0	0	1	0	0	0	1	0	0	0	0	0
<i>Zoarces</i>	0	0	0	1	0	0	0	1	0	0	0	0	0
<i>Bilabria</i>	0	0	0	2	0	0	0	0	0	0	-	-	0
<i>Davidijordania</i>	0	0	0	2	0	0	0	0	0	0	0	0	0
<i>Hadropareia</i>	0	0	0	2	0	0	0	0	0	0	-	-	0
<i>Krusensterniella</i>	0	0	0	2	0	0	0	0	0	0	-	-	0
<i>Gymnelopsis</i>	0	0	0	2	0	0	0	0	0	0	0	0	0
<i>Gymnelus</i>	0	0	0	2	0	0	0	0	0	0	0	0	0
<i>Melanostigma</i>	0	0	0	2	0	1	0	0	0	1	1	0	0
<i>Puzanovia</i>	1	1	0	2	0	0	0	0	0	0	1	-	0
<i>Nalbantichthys</i>	1	1	0	2	0	0	0	0	0	0	1	-	0
<i>Andriashevia</i>	1	1	0	2	0	0	0	0	0	0	-	-	0
gen. nov.	1	1	0	2	0	0	0	-	-	-	-	-	-
<i>Lycodes</i>	0	0	0	1	0	1	1	0	0	0	0	0	0
<i>Pachycara</i>	0	0	0	1	0	1	1	0	0	0	0	1	0
<i>Austrolycichthys</i>	0	0	0	1	0	1	1	0	0	0	0	1	0
<i>Exechodontes</i>	0	0	-1	1	0	1	1	0	0	0	0	1	0
<i>Lycodichthys</i>	0	0	0	1	0	1	1	0	0	0	0	1	0
<i>Oidiphorus</i>	0	0	0	1	0	1	1	0	0	1	1	1	0
<i>Plesienchelys</i>	1	1	0	1	0	1	1	0	0	0	0	1	0
<i>Ophthalmolycus</i>	1	1	1	1	0	1	1	0	0	0	0	1	0

APPENDIX III

Zoarcid character matrix. Matrix numbers refer to states, pp. 23-42.

Genus	Character												
	14	15	16	17	18	19	20	21	22	23	24	25	26
Lycosoarces	0	0	0	0	0	0	0	0	1	1	0	0	0
Macrozoarces	0	0	0	0	2	1	1	0	1	1	0	0	0
Zoarces	0	0	0	0	2	1	1	0	1	1	0	0	0
Bilabria	0	-	-	0	2	0	1	0	1	1	0	0	0
Davidijordania	0	0	0	0	2	0	1	0	1	1	0	0	0
Hadropareia	0	-	-	0	2	0	1	0	1	1	1	0	0
Krusensterniella	0	1	-	1	2	1	1	0	1	1	0	0	0
Gymnelopsis	0	1	0	1	2	0	1	0	1	1	0	0	0
Gymnelus	0	0	0	1	1	0	1	0	1	1	1	0	0
Melanostigma	0	0	0	2	1	0	1	0	1	1	1	1	1
Puzanovia	0	-	0	2	3	0	1	0	1	1	0	0	0
Nalbantichthys	0	-	0	2	3	0	1	0	1	1	1	1	0
Andriashevia	0	-	0	2	3	0	1	0	1	1	1	0	0
gen. nov.	-	-	0	2	3	0	1	0	1	1	1	0	0
Lycodes	0	0	0	0	1	0	1	0	1	1	0	0	0
Pachycara	0	0	0	0	2	0	1	0	1	1	0	0	0
Austrolycichthys	0	0	0	0	1	0	1	0	1	1	0	0	0
Exechodontes	0	0	0	0	1	0	1	0	1	1	1	1	1
Lycodichthys	0	0	0	0	1	0	1	0	1	1	0	0	0
Oidiphorus	0	0	0	0	0	0	1	0	1	1	1	0	1
Plesienchelys	0	0	0	0	1	0	1	0	1	1	0	0	0
Ophthalmolycus	0	0	0	0	1	0	1	0	1	1	0	0	0

APPENDIX III

Zoarcid character matrix. Matrix numbers refer to states, pp. 23-42.

Genus	Character												
	27	28	29	30	31	32	33	34	35	36	37	38	39
Lycozoarces	0	0	0	0	0	0	0	0	0	1	0	0	0
Macrozoarces	1	0	0	0	0	0	0	0	0	1	0	1	1
Zoarces	0	0	0	0	0	0	0	0	0	1	0	1	1
Bilabria	1	0	0	0	0	0	0	0	0	1	0	1	0
Davidijordania	0	0	0	0	0	0	0	0	0	1	0	0	0
Hadropareia	0	0	0	0	0	0	0	0	0	1	0	1	0
Krusensterniella	0	0	0	0	0	0	0	0	1	1	0	0	0
Gymnelopsis	0	0	0	0	0	0	0	0	1	1	0	0	0
Gymnelus	0	0	0	0	0	0	0	0	0	1	0	0	0
Melanostigma	0	0	0	0	0	1	1	-1	0	1	0	0	0
Puzanovia	0	0	0	0	-	0	0	0	0	1	0	0	1
Nalbantichthys	0	0	0	0	-	0	0	1	0	1	0	1	1
Andriashevia	1	0	0	0	-	0	0	0	0	1	0	0	1
gen. nov.	0	0	0	0	-	-	-	0	0	1	0	-	-
Lycodes	0	0	0	1	0	1	1	0	0	1	0	0	0
Pachycara	0	0	0	0	1	1	1	0	0	1	0	0	0
Austrolycichthys	0	0	0	0	1	1	1	0	0	1	0	0	0
Exechodontes	0	0	0	0	1	1	1	0	1	1	0	1	0
Lycodichthys	0	0	0	0	0	1	1	0	0	1	0	1	1
Oidiphorus	0	1	0	0	0	1	1	0	0	1	0	0	0
Plesienchelys	0	0	0	0	1	1	1	0	1	1	0	0	0
Ophthalmolycus	0	0	0	0	1	1	1	0	0	1	0	0	0

APPENDIX III

Zoarcid character matrix. Matrix numbers refer to states, pp. 23-42.

Genus	Character												
	40	41	42	43	44	45	46	47	48	49	50	51	52
<i>Lycozoarces</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Macrozoarces</i>	0	0	0	0	1	0	0	0	1	1	0	0	0
<i>Zoarces</i>	0	0	0	0	1	0	0	0	1	1	0	0	0
<i>Bilabria</i>	-	-	-	0	-	0	0	0	0	-	0	0	0
<i>Davidjordania</i>	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Hadropareia</i>	-	-	-	0	-	0	0	0	0	-	0	0	0
<i>Krusensterniella</i>	-	-	-	0	-	1	0	0	0	-	0	0	0
<i>Gymnelopsis</i>	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Gymnelus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Melanostigma</i>	1	1	0	0	1	0	1	1	0	1	0	0	0
<i>Puzanovia</i>	-	-	-	0	-	0	0	0	1	-	0	0	0
<i>Nalbantichthys</i>	-	-	-	0	-	0	0	0	1	-	0	0	0
<i>Andriashevia</i>	-	-	-	0	-	0	0	0	1	-	0	0	1
gen. nov.	-	-	-	0	-	-	0	0	-	-	0	0	0
<i>Lycodes</i>	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Pachycara</i>	0	0	0	0	0	0	0	0	1	1	0	0	0
<i>Austrolycichthys</i>	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Exechodontes</i>	1	1	0	0	0	0	1	1	-1	1	0	0	0
<i>Lycodichthys</i>	0	0	0	0	0	0	0	0	-1	1	0	0	0
<i>Oidiphorus</i>	0	0	1	0	0	0	1	1	-1	1	0	0	0
<i>Plesienchelys</i>	0	0	0	0	0	0	0	0	-1	1	0	0	0
<i>Ophthalmolycus</i>	0	0	0	0	0	0	0	0	0	1	0	0	0

APPENDIX III

Zoarcid character matrix. Matrix numbers refer to states, pp. 23-42.

Genus	Character										
	53	54	55	56	57	58	59	60	61	62	63
<i>Lycozoarces</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Macrozoarces</i>	0	1	0	0	0	1	1	0	0	0	0
<i>Zoarces</i>	0	1	0	0	0	1	1	0	0	0	1
<i>Bilabria</i>	0	1	0	0	0	1	1	0	0	1	0
<i>Davidijordania</i>	0	1	1	0	0	1	1	0	0	1	0
<i>Hadropareia</i>	0	1	0	0	0	1	2	0	0	-	0
<i>Krusensterniella</i>	1	1	0	0	0	1	2	0	0	1	0
<i>Gymnelopsis</i>	1	1	1	1	0	1	2	0	0	0	0
<i>Gymnelus</i>	1	1	1	1	0	1	1	0	0	0	0
<i>Melanostigma</i>	1	1	1	0	0	0	2	0	1	1	0
<i>Puzanovia</i>	1	1	0	0	0	1	1	0	1	0	0
<i>Nalbantichthys</i>	1	1	0	0	0	1	1	-1	1	1	0
<i>Andriashevia</i>	1	1	0	0	0	1	-	-	1	-	0
gen. nov.	1	1	-	0	0	1	2	-	-	-	0
<i>Lycodes</i>	0	1	1	0	0	1	1	0	1	0	0
<i>Pachycara</i>	0	1	1	0	0	1	1	0	1	1	0
<i>Austrolycichthys</i>	0	1	1	0	0	1	1	0	1	1	0
<i>Exechodontes</i>	0	1	1	0	0	1	1	0	1	1	0
<i>Lycodichthys</i>	0	1	1	0	0	1	1	-1	1	1	0
<i>Oidiphorus</i>	1	0	0	0	0	1	2	-1	1	1	0
<i>Plesienchelys</i>	0	1	1	0	0	1	1	-1	1	1	0
<i>Ophthalmolycus</i>	0	1	1	0	0	1	1	1	1	1	0

APPENDIX III

Zoarcid character matrix. Matrix numbers refer to states, pp. 23-42.

Genus	Character												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Redirolycus	1	1	1	1	0	1	1	0	0	0	1	1	0
Taranetzella	1	1	1	1	0	1	1	0	0	0	-	1	-
Lyconema	1	1	1	1	0	1	1	0	0	0	1	1	0
Eucryphycus	1	1	1	1	0	1	1	0	0	0	1	1	0
Lycenchelys	1	1	1	1	0	1	1	0	0	0	1	1	0
Lycodonus	1	1	1	1	0	1	1	0	0	0	1	1	0
Hadropogonichthys	1	1	1	1	0	1	1	0	0	0	-	1	-
Piedrabuenia	1	1	1	1	0	1	1	0	0	0	1	1	0
Derepodichthys	1	1	1	1	0	1	1	0	0	1	1	1	0
Bothrocarara	0	0	0	1	0	1	1	0	0	0	1	1	0
Bothrocarina	0	0	0	1	0	1	1	0	0	0	1	1	1
Lycogrammoides	0	0	0	1	0	0	1	0	1	1	1	1	-
Lycodapus	0	0	0	0	0	0	1	0	1	1	1	1	1
Notolycodes	0	0	0	1	0	1	1	0	0	0	-	-	0
Aiakas	0	0	0	1	0	1	1	0	0	0	-	-	0
Iluocoetes	0	0	0	1	0	1	1	0	0	0	0	1	1
Austrolycus	0	0	0	2	0	1	1	0	0	0	0	1	1
Dadyanos	0	0	0	2	1	1	1	0	0	0	0	1	1
Crossostomus	0	0	0	2	1	1	1	0	0	0	0	1	1
Phucocoetes	0	0	0	2	0	1	1	0	0	0	0	1	0
Pogonolycus	0	0	0	2	0	1	1	0	0	0	-	-	0
Maynea	0	0	0	2	0	1	1	0	0	0	0	1	0

APPENDIX III

Zoarcid character matrix. Matrix numbers refer to states, pp. 23-42.

Genus	Character												
	14	15	16	17	18	19	20	21	22	23	24	25	26
Redirolycus	0	0	0	1	1	0	1	0	1	1	0	0	0
Taranetzella	0	0	-	0	1	0	1	0	1	1	0	1	1
Lycinema	0	0	0	0	2	0	1	0	1	1	0	0	0
Eucryphycus	0	0	0	0	2	0	1	0	1	1	0	0	0
Lycenchelys	0	0	0	0	2	0	1	0	1	1	0	0	0
Lycodonus	0	0	0	0	2	0	1	0	1	1	0	0	0
Hadropogonichthys	0	0	-	0	2	0	1	0	1	1	0	0	0
Piedrabuenia	0	0	0	0	2	0	1	0	1	1	0	0	0
Derepodichthys	0	0	0	1	2	0	1	0	1	1	1	1	1
Bothrocarara	0	0	0	0	2	0	1	1	1	1	0	0	0
Bothrocarina	0	0	1	1	2	0	1	1	1	1	0	0	0
Lycogrammoides	0	0	1	1	0	0	1	1	1	1	0	0	1
Lycodapus	0	0	1	1	0	0	1	1	1	1	1	1	1
Notolycodes	0	1	0	0	1	0	1	0	1	1	0	0	0
Aiakas	0	1	0	0	1	0	1	0	1	1	0	0	0
Iluocoetes	1	1	0	0	1	0	1	0	1	1	0	0	0
Austrolycus	1	1	0	0	2	0	1	0	1	1	0	0	0
Dadyanos	1	1	0	0	2	0	1	0	1	1	0	0	0
Crossostomus	1	1	0	0	1	0	1	0	1	1	0	0	0
Phucocoetes	1	1	0	0	1	0	1	0	1	1	0	0	0
Pogonolycus	1	1	0	0	1	0	1	0	1	1	0	1	0
Maynea	1	1	0	0	2	0	1	0	1	1	0	0	0

APPENDIX

Zoarcid character matrix. Matrix numbers refer to states, pp. 23-42.

Genus	Character												
	27	28	29	30	31	32	33	34	35	36	37	38	39
Redirolycus	0	0	0	0	1	1	1	0	0	1	0	0	0
Taranetzella	0	0	0	0	-	1	1	0	0	1	0	0	0
Lycinema	0	1	0	0	0	0	0	0	0	1	0	0	0
Eucryphycus	0	0	0	0	0	0	0	0	0	1	0	0	0
Lycenchelys	0	0	0	0	0	1	1	0	0	1	0	0	0
Lycodonus	0	0	0	0	1	1	1	0	0	1	0	0	0
Hadropogonichthys	0	1	0	0	-	0	1	0	0	1	0	0	0
Piedrabuenia	0	1	0	0	0	0	0	0	1	1	0	0	0
Derepodichthys	0	0	0	0	1	1	1	0	1	1	0	0	0
Bothrocarina	0	0	0	0	0	1	0	0	0	1	0	0	0
Bothrocarina	0	0	0	0	0	1	0	0	0	1	0	0	0
Lycogrammoides	0	0	0	0	-	1	0	0	0	0	0	0	0
Lycodapus	0	0	0	0	1	1	1	0	1	0	0	0	0
Notolycodes	0	0	1	0	1	1	1	0	0	0	0	1	1
Aiakas	1	0	0	0	-	0	1	0	0	0	0	1	1
Iluocoetes	0	0	0	0	1	1	1	0	0	0	0	0	0
Austrolycus	0	0	0	0	1	1	1	0	0	0	0	0	0
Dadyanos	0	0	0	0	1	1	1	0	0	0	1	1	1
Crossostomus	1	0	0	0	1	1	1	0	0	0	0	0	0
Phucocoetes	0	0	0	0	1	1	1	0	0	0	0	0	0
Pogonolycus	0	1	0	0	-	1	1	0	0	0	0	0	0
Maynea	0	0	0	0	1	1	1	0	0	0	0	0	0

APPENDIX III

Zoarcid character matrix. Matrix numbers refer to states, pp. 23-42.

Genus	Character												
	40	41	42	43	44	45	46	47	48	49	50	51	52
Redirolycus	0	0	0	0	0	0	0	0	-1	1	0	0	0
Taranetzella	-	-	0	0	0	0	0	0	0	1	0	0	0
Lycinema	1	0	0	0	0	0	0	0	-1	0	0	0	0
Eucryphycus	0	0	1	0	0	0	0	0	0	0	0	0	0
Lycenchelys	0	0	0	0	0	0	0	0	0	1	0	0	0
Lycodonus	0	0	0	0	0	1	0	0	0	1	0	0	0
Hadropogonichthys	-	-	0	0	0	0	0	0	0	-	0	0	0
Piedrabuenia	0	0	0	0	0	1	0	0	0	1	0	0	0
Derepodichthys	1	1	0	1	0	0	0	1	0	1	1	1	1
Bothrocarara	0	0	0	0	0	0	0	0	1	1	0	0	0
Bothrocarina	0	0	0	0	0	0	0	0	1	1	0	0	0
Lycogrammoides	-	0	0	0	0	0	0	0	0	1	0	0	0
Lycodapus	1	1	0	0	0	0	0	0	0	1	0	0	1
Notolycodes	-	-	0	0	0	1	0	0	-1	1	0	0	0
Aiakas	-	-	0	0	0	0	0	0	-1	-	0	0	0
Iluocoetes	0	0	1	0	0	0	0	0	1	1	0	0	0
Austrolycus	0	0	0	0	0	0	0	0	1	1	0	0	0
Dadyanos	0	0	1	1	0	0	0	0	0	1	0	0	0
Crossostomus	0	0	0	0	0	0	0	0	-1	1	0	0	0
Phucocoetes	0	0	0	0	0	0	0	0	-1	0	0	0	0
Pogonolycus	-	-	0	0	0	1	0	0	-1	1	0	0	0
Maynea	0	0	1	0	0	1	0	0	0	0	0	0	0

APPENDIX III

Zoarcid character matrix. Matrix numbers refer to states, pp. 23-42.

Genus	Character										
	53	54	55	56	57	58	59	60	61	62	63
Redirolycus	1	1	1	0	0	1	2	0	1	1	0
Taranetzella	0	1	1	0	0	1	2	0	1	1	0
Lycinema	0	1	1	0	0	1	1	0	1	0	0
Eucryphycus	1	1	1	0	0	1	1	0	1	1	0
Lycenchelys	0	1	1	1	0	1	1	0	1	1	0
Lycodonus	0	1	1	1	1	1	2	0	1	1	0
Hadropogonichthys	0	1	1	0	0	1	1	-1	1	-	0
Piedrabuenia	0	1	1	0	0	1	2	0	1	0	0
Derepodichthys	0	1	1	0	0	1	2	0	1	1	0
Bothrocara	1	1	0	0	0	1	1	0	1	0	0
Bothrocarina	1	1	1	0	0	1	1	1	1	0	0
Lycogrammoides	1	0	1	0	0	1	2	1	1	0	0
Lycodapus	1	0	1	0	0	1	1	0	1	1	0
Notolycodes	0	1	1	0	0	1	1	0	1	0	0
Aiakas	1	1	0	0	0	1	1	1	1	1	0
Iluocoetes	0	1	0	0	0	1	2	0	0	0	0
Austrolycus	0	1	0	0	0	1	1	-1	0	0	0
Dadyanos	0	1	0	0	0	1	1	0	0	0	0
Crossostomus	0	1	0	0	0	1	1	0	0	0	0
Phucocoetes	0	1	0	0	0	1	1	0	0	0	0
Pogonolycus	0	1	1	0	0	1	1	0	0	1	0
Maynea	1	1	0	0	0	1	2	0	0	0	0

Plate I.

- A) Zoarchias glaber Tanaka, 1908 (Stichaeidae); UMMZ 207710, 100 mm SL.
- B) Zoarces gillii Jordan and Starks, 1905; CAS 17746, 221 mm SL.
- C) Davidijordania poecilimon (Jordan and Fowler, 1902); UMMZ 202548,
123 mm SL.
- D) Krusensterniella multispinosa Soldatov, 1922; USNM 92592, 125 mm SL.

A



B



C



D



Plate II.

A) Melanostigma atlanticum Koefoed, 1952; VIMS 05646, 108 mm SL.

B) Nalbantichthys elongatus Schultz, 1967; USNM 200671, 135 mm SL.

A



B



Plate III.

- A) Austrolycichthys brachycephalus (Pappenheim, 1912); CAS uncat.,
205 mm SL.
- B) Austrolycichthys conorhynchus (Garman, 1899); UMML 22862, 211 mm SL.
- C) Austrolycichthys suspectus (Garman, 1899); SIO 68-106, 216 mm SL.

A



B



C



Plate IV.

A) Austrolycichthys sp. A; USNM 233626, 170 mm SL.

B) Head and body of A.

C) Pachycara sp. D; USNM 233627, 161 mm SL.

A



B



C



Plate V.

A) Pachycara obesum Zugmayer, 1911; MCZ 57612, 498 mm SL.

B) Pachycara bulbiceps (Garman, 1899); SIO 73-286, 455 mm SL.

C) Head and body of B.

A



B



C



Plate VI.

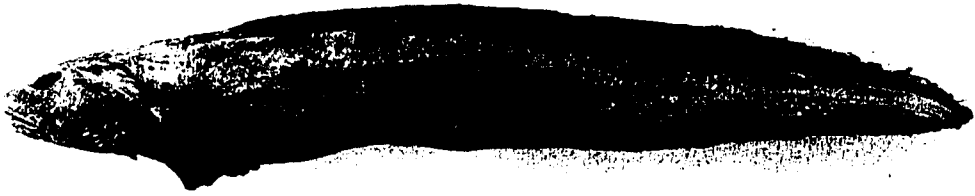
A) Pachycara crassiceps (Roule, 1916); BMNH 1981.6.23: 1-2, 512 mm SL.

B) Head and body of A.

C) Pachycara sp. C; ZMUC P761147, 236 mm SL.

D) Head and body of C.

A



B



C



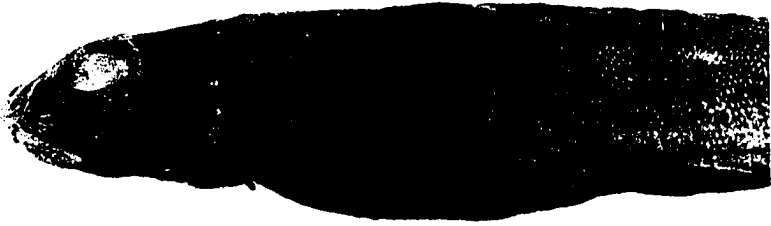
D



Plate VII.

- A) Lycodes concolor Gill and Townsend, 1897; LACM 34164-1, 325 mm SL.
- B) Lycodes squamiventer (Jensen, 1904); ISH 149/73, 217 mm SL.
- C) Lyconema barbatum Gilbert, 1895; VIMS 05391, 146 mm SL.
- D) Eucryphycus californicus (Starks and Mann, 1911); VIMS 05394, 118 mm.

A



B



C



D

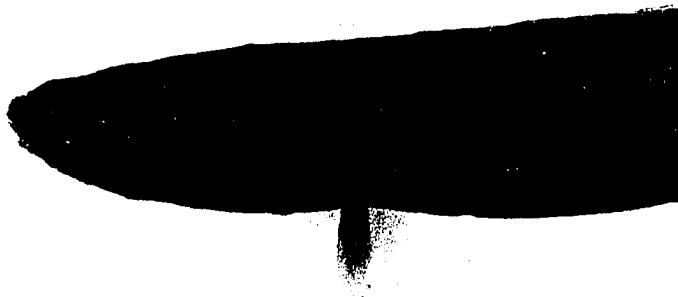


Plate VIII.

- A) Lycodichthys dearborni (DeWitt, 1962); VIMS 05404, 198 mm SL.
- B) Lycodichthys antarcticus Pappenheim, 1911; SAMA F353, 181 mm SL.
- C) Notolycodes schmidti Gosztanyi, 1977; ISH 391/78, 386 mm SL.

A



B



C

Plate IX.

- A) Taranetzella lyoderma Andriashev, 1952; CAS 38921, 142 mm SL.
- B) Lycodonus mirabilis Goode and Bean, 1883; VIMS 05459, 302 mm SL.
- C) Lycenchelys porifer (Gilbert, 1891); SIO 70-247-61, 257 mm SL.
- D) Lycenchelys paxilla (Goode and Bean, 1879); VIMS 06545, 248 mm SL.

A



B



C



D



Plate X.

- A) Lycenchelys sp. A; ISH 381/78, 234 mm SL.
- B) Piedrabuenia ringueleti Gosztonyi, 1977; ISH 389/78, 233 mm SL.
- C) Lycenchelys bellingshauseni Andriashev and Permitin, 1968; ISH 351/76, 234 mm SL.

A



B



C

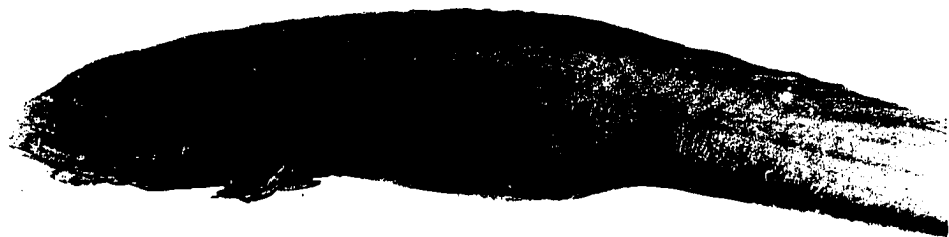


Plate XI.

- A) Ophthalmolycus bothriocephalus (Pappenheim, 1912); BMNH 1937.7.12: 159, 112 mm SL.
- B) Ophthalmolycus concolor (Roule and Despax, 1911); CAS uncat., 142 mm.
- C) Redirolycus microphthalmus (Norman, 1937); ISH 376/78, 90 mm SL.
- D) Redirolycus sp. A; ISH 164/78, 147 mm SL.

A



B



C



D

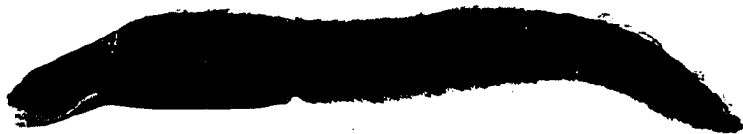


Plate XII.

- A) Bothrocarina microcephala (Shmidt, 1938); HUMZ 34001, 430 mm SL.
- B) Head and body of A.
- C) Bothrocara brunneum (Bean, 1890); VIMS 07686, 447 mm SL.
- D) Lycodapus pachysoma Peden and Anderson, 1978; ISH 403/76, 184 mm SL.

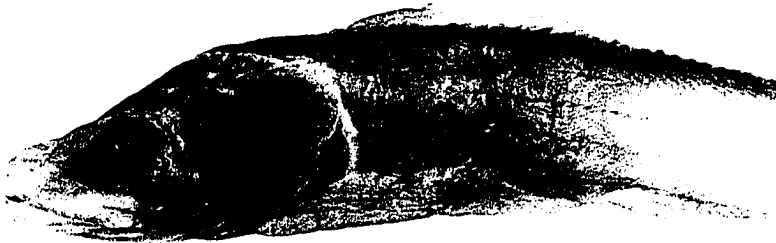
A



B



C



D



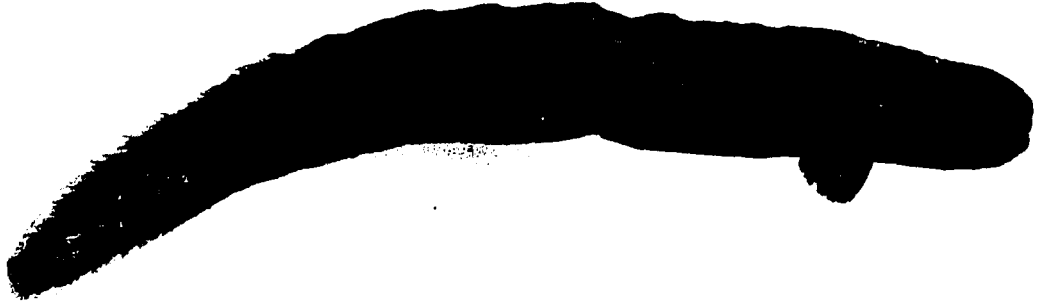
Plate XIII.

A) Aiakas krefftii Gosztonyi, 1977; ISH 274/78, 301 mm.

B) Head and body of A.

C) Plesienchelys stehmanni (Gosztonyi, 1977); ISH 377/78, 204 mm SL.

A



B



C



Plate XIV.

- A) Ilucoetes fimbriatus Jenyns, 1842; ISH 388/78, 125 mm SL.
- B) Austrolycus depressiceps Regan, 1913; VIMS 05401, 155 mm SL.
- C) Crossostomus chilensis (Regan, 1913); MACN 4403, 165 mm SL;
anomalously pigmented individual.

A



B



C



Plate XV.

- A) Maynea puncta (Jenyns, 1842); LACM 10722-1, 250 mm SL.
- B) Phucocoetes latitans Jenyns, 1842; VIMS 05399, 109 mm SL.
- C) Pogonolycus elegans Norman, 1937; ISH 1445/66, 65 mm SL.
- D) Oidiphorus brevis (Norman, 1937); ISH 380/78, 88 mm SL.

A



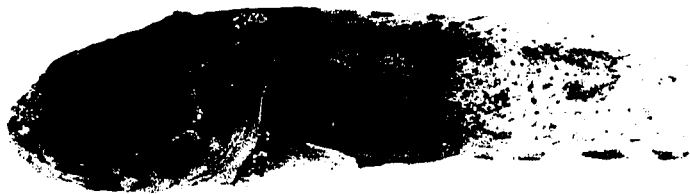
B



C



D



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