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THESIS – THÈSE

Title of Thesis – Titre de la thèse
The Systematic Position of Gasterosteiformes.

Degree for which thesis was presented
Grade pour lequel cette thèse fut présentée
Ph.D.

Year this degree conferred
Année d'obtention de ce grade
1985

University – Université
University of Alberta

Name of Supervisor – Nom du directeur de thèse
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The Systematic Position of Gasterosteiformes

by

P.S.Bowne

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Doctor of Philosophy

Zoology

EDMONTON, ALBERTA

Fall, 1985

THE UNIVERSITY OF ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The Systematic Position of Gasterosteiformes submitted by P.S.Bowne in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

J S Nelson

Supervisor

External Examiner

Date 1 October 1985

Abstract

The osteology of representatives of the taxa placed in Gasterosteiformes by Pietsch (1978), i.e. Nelson's (1976) Gasterosteiformes, Syngnathiformes, Indostomiformes, Hypoptychidae, Pegasiformes, and Dactylopteriformes, is examined in detail and compared with that of representatives of the major neoteleostean taxa. These taxa and the genera used as their representatives are: Stomiiformes, Diplophos; Aulopiformes, Saurida; Paracanthopterygii, Percopsis; Atherinomorpha, Fundulus, Allanetta, and Melanotaenia; Beryciformes, Holocentrus; Scorpaeniformes, Sebastes, Prionotus, Asterotheca, and Cottus; and Perciformes, Percalates, Plectroplites, Perca, and Ammodytes. Bones from all regions of the skeleton are examined and a total of 347 characters coded for analysis.

Analyses using the methods of phenetics, numerical phylogenetics, and evolutionary systematics indicate that Pegasiformes and Dactylopteriformes form a distinct lineage linked with the cottoid lineage of Scorpaeniformes. Gasterosteiformes also show affinities with Cottoidei. Phylogenetic and phenetic analyses support (Gasterosteiformes+Hypoptychidae) and (Indostomiformes+Pegasiformes+Dactylopteriformes) groups, but evolutionary systematics recognizes instead a (Gasterosteiformes+Syngnathiformes) grouping and removes Hypoptychidae and Indostomiformes to separate lineages. This difference in results is attributed to the more rigorous weighting used in the evolutionary analysis and the inclusion of apomorphic tendencies in this analysis.

The analyses based on apomorphy distribution are preferred to those based on overall similarity as more efficiently describing the distributions of both character states. Those based on rigorous weighting by comparison with outgroups are preferred as containing more accurate implied information about the absence in outgroups of those apomorphies used to define taxa. The use of apomorphic tendencies decreases the efficiency of diagnoses in the hierarchy unless they are viewed as statements about unexpressed genetic potential. Evolutionary systematic analyses and phylogenetic conventions for constructing an indented classification provide the most satisfactory classification, one most efficiently expressing information about character state distribution and hypothesized underlying genetic similarities.

Three new suborders of Scorpaeniformes are proposed: Gasterosteoidei, containing the present Gasterosteiformes and Syngnathiformes, Dactylopteroidei, containing Pegasus and Dactylopterus, and Indostomoidei, containing Indostomus. The interrelationships of these suborders are uncertain. Hypoptychus is removed from the grouping and made incertae sedis. It may be best placed with Atherinomorpha, but shows no strong affinities with any of the fishes examined.

Acknowledgements

The research for and writing of this thesis were made possible by many people, foremost are my committee members. Dr. J.S. Nelson, Dr. M.V.H. Wilson, and Dr. J.R. Nursall, who taught me what systematics was and provided, along with specific and general advice, unfailing examples of scholarship, courtesy, and enthusiasm. I wish to particularly thank Dr. Nelson for constant support and advice and the use of personal specimens, Dr. Wilson for advice and programs for numerical phylogenetics, and both for allowing me to run endless noisy programs on their computers.

Dr. Bruce Collette deserves my great thanks for allowing me to visit him at the Smithsonian, and to use his lab and specimens, and I wish to thank Sara Collette for her hospitality. Dr. V. Springer, Dr. David Stein, and Dr. S.H. W[illegible] allowed me to use their labs and specimens. These visits were uniformly delightful, and I am grateful for their kindness. Dr. K.E. Banister and Dr. T. Pietsch sent me badly needed specimens, as did Dr. R. Fritzsche, Mr. R. Carveth, Dr. Mary R. Dawson, Ms. S.L. Jewett, Dr. J.R. Paxton, Mr. J.A. Seigel, and Ms. Pearl M. Sonoda. Their help is greatly appreciated.

I benefitted greatly from many of the people and groups at the University of Alberta; in particular, from the advice of Terry Taerum and the MTS consulting room staff, from the exciting discussions of the Systematics Discussion Group and the Eco-lunch, and from many of the visitors invited for the Zoology Department Seminar Series and the Graduate Students' Visiting Professors Program, particularly Dr. E.O. Wiley and Dr. Dan Brooks. I wish to thank Dr. Brooks for allowing me to participate in his phylogenetics workshop and for his contagious enthusiasm.

Meghann Douglas, Kathy Smyth, Carol Derejko and the authors of the TEXTFORM program, University of Alberta, are responsible for any merit in the typing and formatting of this thesis. I wish to thank the faculty, staff and students of the Department of Zoology, who have made my stay at the University of Alberta both pleasant and edifying and whom I shall remember with affection.

I finally wish to thank my parents, whose love and support I have been able to rely upon in every endeavour.

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List of abbreviations used in figure labels

a - actinost(s)
accfo - accessory anterior foramen
amf - anteromedial pelvic flange
an - angular
app - anteromedial pelvic process
ar - articular
asp - pelvic ascending process
bbr - basibranchial
bh - basihyal
boc - basioccipital
brr - branchiostegal rays
bsp - basisphenoid
cb - canal bone
cbr - ceratobranchial
ch - ceratohyal
cl - cleithrum
cor - coracoid
dn - dentary
ebr - epibranchial
ect - ectocoracoid
eh - epihyal
eo - epiotic
eoc - exoccipital
ep - epural(s)
ept - ectopterygoid
fr - frontal
gh - glossohyal
hbr - hypobranchial
hhd - dorsal hypohyal
hhv - ventral hypohyal
hy - hyomandibula
hyp - hypural(s)
ih - interhyal
iop - interoperculum
lac - lachrymal
le - lateral ethmoid
me - median ethmoid
mpp - medial process of the pelvic
mpt - metapterygoid
mx - maxilla
na - nasal
npt - endopterygoid
op - operculum
pal - palatine
par - parietal
pb - prootic bridge
pbr - pharyngobranchial
pc - postcleithrum
pf - pelvic foramen(a)
phyp - parhypural
pm - premaxilla
pmp - posteromedial pelvic process
pop - preoperculum
pro - prootic
ps - pelvic spur
psp - parasphenoid
pt - pterotic

pts - pterosphenoid
ptt - posttemporal
PU1 - first preural centrum
PU2 - second preural centrum
q - quadrate
s - symplectic
sar - sesamoid articular
sb - scale bone
sc - scapula
scl - supracleithrum
scr - sclerotic bone(s)
se - supraethmoid
soc - supraoccipital
sop - suboperculum
sp - sphenotic
ss - suborbital stay
st - supratemporal
U1 - first ural centrum
U2 - second ural centrum
un - uroneural
v - vomer
vf - ventral foramen
vlp - pelvic ventrolateral projection

I. Introduction

> "The classification of the acanthopterygian fishes as it stands at present is an example of the ultimate futility of using assemblages of primitive characters to express relationship, with large, catch-all basal groups in effect defined arbitrarily by specializations that they do not have (Percoidei), leaving many derived and specialized groups of high rank and of uncertain relationships with one another and with the basal groups." Rosen and Patterson, 1969.

Whether one attributes it to the use of primitive characters or not, Rosen and Patterson's picture of acanthopterygian systematics is still accurate. Although schema of neoteleost relationships have been presented (Lauder and Liem, 1983; Nelson, 1984), many acanthopterygian taxa remain unattached, floating in controversy among their branches. The order Gasterosteiformes (sensu Nelson, 1976) [1] is one such taxon. This order contains five genera of sticklebacks, family Gasterosteidae (*Gasterosteus*, *Pungitius*, *Apeltes*, *Culaea*, and *Spinachia*) and two genera of tubesnouts, family Aulorhynchidae (*Aulichthys* and *Aulorhynchus*). All are restricted to the northern hemisphere, the sticklebacks occurring in both fresh and salt water and the tubesnouts confined to coastal Pacific waters. The order Gasterosteiformes is well-defined by both anatomical characteristics, notably the presence before the dorsal of a series of separated spines and the presence of lateral scutes instead of scales, and behavioral characteristics. It has been intensely studied by students of species- and subspecies-level evolutionary processes, but its affinities with other teleosts are not understood.

Banister (1967) presents a detailed review of the history of the classification of Gasterosteiformes. It has been traditionally placed with Syngnathiformes, the order containing the pipefishes, trumpetfishes, and snipefishes. Members of this widespread marine order are characterized by their elongate tubular snouts and rigid armored bodies. They have been linked with Gasterosteiformes on the basis of these characters and their reduced branchial skeletons. Several authors also include *Indostomus*, a similarly elongate and armored fish from Lake Indawgi, Upper Burma, in this grouping (Prashad and Mukerji, 1929; Bolin, 1936; Berg, 1940; Bertin and Arambourg, 1958). Pegasiformes (the sea-moths), a small order of demersal Indo-Pacific fishes with flattened armored bodies,

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[1] taxon names are usually according to Nelson, 1976; groupings of taxa are indicated by parentheses, e.g. (*Percopsis* + Acanthopterygii)

have been added to this assemblage by several authors (Gill, 1884; Smith-Woodward, 1901; Goodrich, 1909). There has been no consensus on the position of this composite group, which has usually been regarded as an independent lineage of fishes arising at either an advanced subacanthopterygian or a primitive acanthopterygian level. It has been placed with Atherinomorpha (Swinnerton, 1902; Branch, 1966), Scorpaeniformes (Artedi, 1738; Cuvier and Valenciennes, 1829), and as a primitive acanthopterygian group arising below Beryciformes (Jungersen, 1908; Regan, 1909; Jordan, 1923; Gosline, 1973; Lauder and Liem, 1983). Banister (1967), after a detailed examination of Gasterosteus aculeatus, Spinachia spinachia, Aulichthys japonicus, Indostomus paradoxus, and representative syngnathiforms, suggested that these fishes represented three different lineages. He included Gasterosteiformes (his Aulorhynchiformes) and Syngnathiformes (his Aulostomiformes) in Protacanthopterygii, suggesting that they arose from a "myctophoid" ancestor and that their acanthopterygian features were due to parallel evolution. Banister's only statement about the possible relationship of these orders was that they might have arisen from a common ancestor, since they shared modifications of the symplectic. Banister removed Indostomus to a separate order within Acanthopterygii, but in a later work (Banister, 1970) he revised this classification to place it within Paracanthopterygii, still in a separate order although he noted similarities which might link it with the batrachoid-gobiesocid lineage.

Since Banister's revision, fish systematics has undergone changes which make his conclusions difficult to interpret. The "Protacanthopterygii" within which he placed Gasterosteiformes and Syngnathiformes has been divided into four major taxa: Salmoniformes, Stomiiformes, Aulopiformes, and Myctophiformes (Lauder and Liem, 1983), and the "myctophoid" ancestor postulated might now belong in either of the last two orders. His placement of Indostomus within Paracanthopterygii has also been questioned by some ichthyologists (Pietsch, 1978; Nelson, 1984), as have the monophyly of Paracanthopterygii itself (Fraser, 1972) and the status of the specific lineage he related it to, the batrachoid-gobiesocid lineage (Gosline, 1970).

Ida (1976) united Gasterosteiformes and Syngnathiformes in one order, "Syngnathiformes", and removed the monotypic family Hypoptychidae from the ammodytid lineage within Perciformes to the gasterosteid lineage of this order. He suggested a relationship between Hypoptychus and Aulorhynchidae based on osteological and reproductive features, particularly the structures of the premaxillae, reduced numbers of branchiostegals, demarcation of the lower part of the coracoid into an "infraclavicle", hypural fusion, and hypothesized nest-building and egg-guarding behavior. He placed Hypoptychus in its own family within his suborder Gasterosteoidei.

Pietsch (1978) accepted Ida's classification, but renamed the taxon "Gasterosteiformes" and augmented it by the addition of Pegasiformes and their fossil relatives, the Rhamphosidae, which he placed in the syngnathid lineage. He also suggested replacing Indostomus in this group and adding Dactylopteriformes (his Cephalacanthidae; the flying gurnards) to it, but did not assign these fishes specific positions. He did not discuss the affinities of the group thus formed, except to note that Pegasidae are acanthopterygian fishes. Lauder and Liem (1983) accepted Pietsch's definition of "Gasterosteiformes" with the exception of the inclusion of Dactylopteriformes. They placed "Gasterosteiformes" and Dactylopteriformes in an unresolved trichotomy at the base of Percomorpha, between Lampridiformes and Beryciformes.

The groups Gasterosteiformes, Syngnathiformes, Indostomus, Hypoptychus, Pegasus, and Dactylopterus have been placed with almost every major group of Neoteleostei. To answer questions about their relationships with these groups and with one another, it is necessary to compare them with representatives of these groups, and for cladistic analysis it is also desireable to compare them to a more primitive outgroup. The representatives of these groups are referred to throughout the thesis as 'framework groups' or 'framework taxa'.

The outgroup chosen is Stomiiformes, which Lauder and Liem (1983) give as the primitive sister group of Aulopiformes and all higher Neoteleostei. The representative used is Diplophos, which is regarded as the most primitive stomiiform (Fink and Weitzman, 1982), and is therefore the best indicator of the probable characteristics of the common ancestor of Stomiiformes and their more advanced sister group.

The "myctophoid level" of Banister (1967) is represented by Saurida tumbil, a member of Aulopiformes. Paracanthopterygii are represented by Percopsis omiscomaycus, regarded as one of the most primitive members of that group (Rosen and Patterson, 1969).

Recent analysis of Atherinomorpha (Rosen and Parenti, 1981) suggests that Atheriniformes is its most primitive order. Two atherinoids (Allanetta harringtonensis and Melanotaenia nigrans) are examined in detail, as is one representative of the more advanced Cyprinodontoidei, Fundulus sp. Zehren (1979) suggests that Holocentrus arises at the base of Beryciformes, making it a reasonable representative of basal beryciform characteristics. I have examined Holocentrus laetoguttatus.

In the absence of an analysis of the relationships among scorpaeniforms, I have examined members of the scorpaenoid and cottoid lineages. Sebastes flavidus is chosen as a generalized scorpaenid and the triglids Prionotus carolinus and Peristedion truncatum are used because of superficial similarities with the study groups Pegasus and Dactylopterus and because of a suggested relationship between Triglidae and the latter (Starks, 1930; quoted in Gregory, 1933). The cottoids Cottus cognatus and Gilbertidia sigalutes and the agonid Asterotheca alascana are examined, the latter because relationships between Agonidae and Pegasiformes have been suggested (Günther, 1880; cited in Pietsch, 1978).

Relationships within Perciformes are also unresolved, but the family Percichthyidae is regarded as a primitive perciform group. Two species of Percichthyidae, Percalates novaemaculatus and Plectroplites ambiguus, are examined, as is the percid Perca flavescens. Since Hypoptychus has been placed within the perciform family Ammodytidae, a representative of this family (Ammodytes hexapterus) is also examined.

Representatives of all genera of Gasterosteiformes are examined, as are members of each family in Syngnathiformes: Aulostomidae (Aulostomus chinensis and A. maculatus), Fistuariidae (Fistularia tabacaria), Macrorhamphosidae (Macrorhamphosus gracilis, M. scolopax, and Notopogon lilliei), Centriscidae (Aeoliscus strigatus and Centriscus scutatus), Solenostomidae (Solenostomus paradoxus), and Syngnathidae (Syngnathus griseolineatus, Syngnathoides biaculeatus, Solegnathus spinosissimus, and Hippocampus hippocampus). Indostomiformes and Hypoptychidae are monotypic taxa. Pegasiformes is represented by Pegasus papilio and P. volitans, and Dactylopteriformes is represented by Dactylopterus volitans.

Although the osteology of many of the groups investigated has been studied, the published descriptions have concentrated on different characters. I have therefore presented descriptions of, and tables summarizing, the characters which are used in this study. These data appear in section III of the thesis, 'Comparative Skeletal Anatomy'. In Section IV, 'Systematic Analyses', I have investigated the relationships between study groups and framework groups and between study groups. The data are analysed separately by each of the three major schools of systematics: phenetic systematics, phylogenetic systematics (or cladistics), and evolutionary systematics (or synthetic systematics). Proponents of each of these schools have declared their merits, and their particular suitability for the investigation of higher taxa (e.g. Davies, 1983; Wiley, 1981; Mayr, 1969, respectively). My purpose in applying all three is not primarily to enter into the debate about their respective worths, but to gain whatever information about my study groups each can supply. Accordingly, each school and its methods will be briefly defined in its own section. A separate classification is constructed according to the methods of each school, and the three sets of results are compared in the final discussion and conclusions.

II. Methods and Materials

The specimens referred to are cleared and stained (for bone only), unless otherwise indicated. Measurements and counts were made according to Hubbs and Lagler's (1964) specifications with the following exceptions; the last two elements of the dorsal and anal fins were counted as two rays, regardless of whether they shared a common base, and the head lengths were measured from the anteriormost point of the snout to the posterior border of the occipital condyle. Osteological terminology follows Banister (1967) and Nelson (1971). Abbreviations used in the figures apear in the key on pages xxv-xxvi. Figures contain the lot number of the specimens illustrated when more than one lot of a species was examined. Data are presented both in descriptions, by anatomical region, and in tables. Mean values for meristic and morphometric data are presented, and missing data are indicated with 'X'. Much more variation exists within the groups represented than is listed in my data, which only refer to conditions within the specimens examined in detail. Variation as reflected in the literature is taken into account later in the thesis, in the sections on character weighting. The different systematic methods used are described in the 'Methods' sections of the separate chapters.

The specimens examined were from the following institutions: Australian Museum, Sydney (AMS), Humboldt State Universities Fishery Collection (HSU), California Academy of Sciences (CAS), Carnegie Museum of Natural History (CM), Harvard University Museum of Comparative Zoology (MCZ), Scripps Institution of Oceanography (SIO), United States National Museum, Smithsonian Institution (USNM), and the University of Alberta Museum of Zoology (UAMZ). Specimens from the laboratories of Dr. Bruce Collette, Dr. D. Stein, and Dr. S. Weitzman were also examined. Specimens examined in detail and used in the analyses are indicated with asterisks.

List of specimens examined

Stomiiformes

Diplophos _greyae_ USNM 135691, 1 specimen

*_Diplophos_ _maderensis_ USNM 186364 1 specimen, 11.6 cm. standard length (SL)

*_Diplophos_ _taenia_ USNM 206614, 1 specimen, 17.1 cm. SL

collection of Dr. S. Weitzman, IIOE Station 294 A, 1 specimen, 12.19 cm. SL

Gonostoma _elongatum_, collection of Dr. S. Weitzman, Oregon Station 3219, 1 specimen

Polymetme corythaeola, USNM 158797, 1 specimen

Thorophos eryops, USNM 3736, 1 specimen

Aulopiformes

*Saurida tumbil, UAMZ 4046, 2 specimens, 13.6 and 15.5 cm. SL; 1 specimen not cleared and stained, 18.3 cm. SL

Percopsiformes

*Percopsis omiscomaycus, UAMZ 1577, 3 specimens; 6.64, 6.5, and 7.19 cm. SL

Atherinomorpha

Atherinoidei

*Allanetta harringtonensis, UAMZ 2673, 3 specimens, 5.92, 5.41, and 6.0 cm. SL

*Melanotaenia nigrans, USNM 173746, 2 specimens, 6.11 and 5.87 cm. SL

Exocoetoidei

Ablennes hians, collection of Dr. B. Collette, 1 specimen

Belone belone, USNM 198408, 1 specimen

Belonion apodion, USNM 199540 #44, 1 specimen and #26, 1 specimen

Cololabis saira, USNM 50744, 1 specimen

Danichthys rondeleti, collection of Dr. B. Collette, Delaware III:26-7:57, 1 specimen

Dermogenys viviparous, USNM 197727, 1 specimen

Euleptorhamphus velox, collection of Dr. B. Collette, 1 specimen

Fodiator acutus, collection of Dr. B. Collette, 1 specimen

Hemirhamphodon pogonognathus, USNM 94421, 1 specimen

Hemirhamphus bulao, collection of Dr. B. Collette, 1 specimen

Hyporhamphus acutus, USNM 115209, 1 specimen

Oxyporhamphus sp., USNM 158059, 1 specimen

Platybelone argala, collection of Dr. B. Collette, 1 specimen

Potamorrhaphus guianensis, USNM 179484, 1 specimen

Pseudotylosurus sp., USNM 167714, 1 specimen

Rhynchorhamphus mallabar, USNM 214937, 1 specimen

Tylosurus fodiator, USNM 82235, 1 specimen

Xenentodon sp., MCZ 8767, #7, 1 specimen

Zenarchopterus gilli, USNM 173765, 1 specimen

Cyprinodontoidei

*Fundulus sp., UAMZ 5565, 5 specimens, 3.11, 2.96, 3.09, 3.10, and 3.09 cm. SL

Xiphophorus maculatus, UAMZ uncatalogued, 1 adult, 15 embryos, counterstained for cartilage.

Beryciformes

*Holocentrus laetoguttatus, UAMZ 916, 1 specimen

*Holocentrus sp., UAMZ uncatalogued, 1 specimen, 7.86 cm. SL

Scorpaeniformes

*Asterotheca alascana, UAMZ 1985, 3 specimens; No.1 disarticulated, No.s 2 and 3 9.8 cm. and 10.0 cm. SL

*Cottus cognatus, UAMZ 2215, 6 specimens, 3.83, 4.42, 4.11, 3.88, 3.95, and 4.22 cm. SL

Gilbertidia sigalutes, UAMZ 1976, 2 specimens, 4.23 and 4.64 cm. SL

Liparis dannyi, CAS 14920, 1 specimen

Liparis florae, collection of D. Stein

Peristedion truncatum, USNM 199071, 3 specimens, 2 counterstained for cartilage, 11.54, 13.64, and 14.15 cm. SL

*Prionotus carolinus, UAMZ 1819, 1 specimen, 11.55 cm. SL; 1 specimen, not cleared and stained, 12.97 cm. SL

*Sebastes flavidus, UAMZ 3192, 3 specimens, 8.10, 8.22, and 7.5 cm. SL

*Sebastes ruberrimus, UAMZ 4817, prepared skeleton.

Perciformes

*Ammodytes hexapterus, UAMZ 1485, 2 specimens, 8.2 and 7.93 cm. SL

*Perca flavescens, UAMZ 1522, 3 specimens, 4.08, 5.56, and 5.53 cm. SL

*Percalates novaemaculatus AMSI 11607-002, 1 specimen, 5.13 cm. SL

*Plectroplites ambiguus, AMSI 18933-004, 1 specimen, 5.38 cm. SL

Gasterosteiformes

*Apeltes quadracus, UAMZ 5540, 8 specimens, 2.49, 2.63, 2.47, 2.32, 2.43, 2.37, 2.58, and 2.21 cm. SL

*Aulichthys japonicus, UAMZ 5543, 4 specimens, 9.34, 11.25, 11.88, and 9.61 cm. SL

*Aulorhynchus flavidus, UAMZ 5541, 3 specimens, 8.37, 7.9, and 5.85 cm. SL; UAMZ 1694, 4 specimens, 9.92, 10.56, 10.84, and 12.13 cm. SL

*Culaea inconstans, UAMZ 5023, 2 specimens, 5.38 and 6.09 cm. SL; UAMZ 5564, 3 specimens, 4.84, 4.29, and 4.12 cm. SL; UAMZ 559, 10 specimens, 1.77, 1.25, 1.75, 1.48, 1.88, 1.74, 1.90, 1.75, 2.55, and 2.13 cm. SL

*Gasterosteus aculeatus, UAMZ 5512, 3 specimens, 6.97, 4.37, and 2.8 cm. SL; UAMZ 4727, 2 specimens, 4.7 and 5.32 cm. SL

*Pungitius pungitius, UAMZ 4437, 2 specimens, 5.10 and 5.52 cm. SL; UAMZ 4754, 3 specimens, 3.05, 3.3, and 3.65 cm. SL

*Spinachia spinachia, UAMZ 5548, 6 specimens, 7.84, 5.47, 3.00, 6.14, 10.58, and 5.41 cm. SL

Syngnathiformes

*Aeoliscus strigatus, CAS 47118, 3 specimens, 10.12, 9.6, and 10.57 cm. SL; 2 specimens not cleared and stained, 10.51 and 10.92 cm. SL

Aulostomus chinensis, CAS 47120, 3 specimens, 15.87, 14.4, and 15.93 cm. SL; one specimen not cleared and stained, 16.23 cm. SL

*Aulostomus maculatus, SU 45551, 4 specimens, 12.78, 10.13, 9.28, and 8.99 cm. SL

Aulostomus sp., UAMZ uncatalogued, prepared skull

Centriscus scutatus, CAS 47121, 1 specimen, 9.39 cm. SL; one specimen not cleared and stained, 7.54 cm. SL; UAMZ 370, 2 specimens, 12.37 and 10.9 cm. SL

*Fistularia tabacaria, UAMZ 3781, 3 specimens, 26.6, 29.55, and 27.65 cm. SL

*Hippocampus hippocampus, SU 1536, 1 specimen, 10.54 cm. SL; 2 specimens not cleared and stained, 9.97 and 9.82 cm. SL

*Macrorhamphosus gracilis, CAS 47118, 4 specimens, 6.77 4.35, 5.97, and 7.12 cm. SL; 1 specimen not cleared and stained, 6.08 cm. SL

Macrorhamphosus scolopax, SU 68756, 3 specimens, 9.13, 9.01, and 9.03 cm. SL; one specimen not cleared and stained, 8.94 cm. SL

Notopogon lilliei, AMSI 10257, 1 specimen, 8.89 cm. SL; 1 specimen not cleared and stained, 12.17 cm. SL

Solegnathus spinosissimus, AMSI 10257, 1 specimen, 41.8 cm. SL

*Solenostomus paradoxus, Humboldt State Universities Fisheries Collection (AMSI-1) 18387-001, 1 specimen, 4.62 cm. SL; 2 specimens not cleared and stained, 6.49 and 6.05 cm. SL

*Syngnathoides biaculeatus, LACM 37398-16, 1 specimen, 20.39 cm. SL; SU 68757, 1 specimen, 16.15 cm. SL

*Syngnathus griseolineatus, UAMZ 3190, 5 specimens, 15.38, 13.27, 12.96, 15.58, and 13.51 cm. SL

Indostomiformes

*Indostomus paradoxus, USNM 203888, 1 specimen, 2.61 cm. SL ; UAMZ uncatalogued, from K. Banister, 1 specimen, 2.45 cm. SL; SIO 70-383, 1 specimen not cleared and stained, 2.54 cm. SL

Hypoptychidae

*Hypoptychus dybowskii, UAMZ 5550, 3 specimens, 8.09, 8.18, and 7.74 cm. SL

Pegasiformes

*Pegasus papilio, LACM 36886-1, 2 specimens, 5.54 and 5.45 cm. SL

*Pegasus volitans, LACM 36887-1, 36887-2, 2 specimens, 10.57 and 9.67 cm. SL

Rhamphosus aculeatus, CM 4213, 2 specimens; CM 5310, 2 specimens; CM 5312, 1 specimen; CM 5328, 1 specimen

C

Dactylopteriformes

*Dactylopterus volitans, USNM 261386, 3 specimens, 2 counterstained for cartilage, 5.16, 4.5, and 5.19 cm. SL

III. Comparative Skeletal Anatomy

The skeletons of the fishes examined are discussed in fourteen separate regions: the ethmoid region, orbital region, cranium roof, cranium floor, upper jaws and palatine-pterygoid arches, lower jaws and suspensoria, opercular series, hyoid arches, branchial basket, pectoral girdle, pelvic skeleton, dorsal and anal fins, axial skeleton, and caudal skeleton. Each anatomical section consists of brief descriptions of the bones of the framework fishes, detailed descriptions of the bones of the study groups, and summarizing tables containing the coded data used in the subsequent analyses.

A. The Ethmoid Region

The bones making up the ethmoid region are the median and lateral ethmoids, supraethmoid (in Syngnathiformes), rostrodermethmoid (in Diplophos), nasals, and vomer. The characters from the ethmoid region used in analyses are listed in Table A1. Coded data from framework groups are in Tables A2-3 and data from study groups are in Tables A4-5.

Framework

The ethmoid region in the stomiiform Diplophos is well described by Fink and Weitzman (1982) but homologies between the bones they describe and those in more advanced fishes are not all clear. The rostrodermethmoid, which forms the roof of the snout, does not appear to have a homologue in any of the other fishes I examined, nor does the 'anterior myodome bone'. The 'supraethmoid', which consists of a horizontal median plate with two laterally concave vertical flanges arising at its lateral edges, resembles and is probably homologous with the median ethmoid of higher fishes. The lateral ethmoids, nasals, and vomer appear to be homologous to the bones of the same names in the other fishes I examined. The nasals of Diplophos are small curved troughs open dorsally. The lateral ethmoids are vertical cylinders open medially, their lateral surfaces covered by antorbitals. The dorsal end of each lateral ethmoid (dorsomedial projection) touches the ventral surface of the frontal, and the ventral end (ventromedial projection) touches the parasphenoid. The head of the vomer is wide and bears a few large teeth on each edge; its shaft extends posteriorly to the middle of the orbit.

The lateral ethmoids and nasals of the aulopiform Saurida resemble those of Diplophos, but its median ethmoid consists of a flat dorsal plate with a mid-ventral flange running along it. The head of the vomer is toothed and firmly attached to the palatines; its shaft is short, not reaching the lateral ethmoids.

The lateral ethmoids of the paracanthopterygian Percopsis resemble those of Diplophos. Its median ethmoid consists of two vertical plates connected dorsally by a narrow horizontal plate which projects in a peak between the nasals. The nasals are wide and rectangular, bearing wide canals which are open dorsally. The vomer is toothless in Percopsis but toothed in Aphredoderus (Rosen & Patterson, 1969), and its shaft extends past the lateral ethmoids.

The nasals in Atherinomorpha, according to Rosen (1964), are usually flat and closely joined to the frontals. They are flat in the specimens I examined. In Fundulus and Melanotaenia the nasal lacks a sensory canal, but canals are present in Allanetta and Menidia. In Allanetta the canals are not closed dorsally. The vomer is toothed in Melanotaenia but is toothless in the others. The lateral ethmoids resemble those of Percopsis; in Allanetta their ventromedial projections bear anterior processes. The median ethmoid is a simple flat disc (Fig. A1). Rosen (1964) described it as double in most atherinomorphs, but it was single in the specimens I examined.

The nasals of Holocentrus are broad, curved laterally at their anterior ends, and do not meet in the midline. They bear broad indentations for the supraorbital canal and overlap the frontals without being strongly sutured to them. The head of the vomer is toothless and contacts the lateral ethmoids; its shaft extends past them into the orbit. The lateral ethmoids are similar to those of Saurida and Diplophos. The median ethmoid has wide vertical lateral plates and a narrow median plate. Its anterodorsal edge is deeply concave.

Nasals are present in most of the scorpaeniforms examined, and carry the supraorbital canals in complete bony tubes. In Asterotheca, Sebastes, Peristedion, and Prionotus they meet anteriorly, forming a firm symphysis in Asterotheca and Peristedion (Fig. A2). They are not firmly attached to the frontals. The vomers of Cottus, Sebastes, Asterotheca, and Prionotus are toothed, but those of Liparus are not. In Prionotus the head of the vomer bears lateral posterior extensions connecting the lateral ethmoids and posterodorsal extensions lying over the parasphenoid. In all, the shafts of the vomers extend to or past the posterior ends of the lateral ethmoids.

I did not examine enough specimens to determine the intrafamilial variability of the lateral ethmoids, but Quast (1965) considered them too variable for use in distinguishing scorpaeniform families. Their lateral faces are expanded into bony plates in Sebastes, Asterotheca (Fig. A3,A), and Prionotus, but are narrow edges in Cottus (Fig. A3,B). In Asterotheca and Sebastes the medial projections of each lateral ethmoid are fused into a single triangular cone opening medially and contacting the median ethmoid dorsally, the vomer anteriorly, and the parasphenoid ventrally; its posterior side is deeply concave. The median ethmoids of Cottus, Asterotheca, Prionotus, and Liparus have transverse ventral flanges.

The perciforms I examined have narrow tubular nasals separated posteriorly by the median ethmoids. The vomers are toothed in all except Ammodytes, and do not connect the lateral ethmoids or extend above the parasphenoids. The lateral ethmoids of perciforms are similar to those of Percopsis, lacking lateral faces or anterior and posterior projections. The median ethmoids have well-developed lateral faces, which meet anteriorly and posteriorly in Ammodytes.

Gasterosteiformes

Gasterosteiform nasals are relatively narrow and do not meet in the midline. In all except Gasterosteus a closed canal runs the full length of each nasal, which is loosely attached to the frontal; in Gasterosteus the canals are absent and the heavily ornamented nasals are sutured to the frontals. Gasterosteidae are distinguished by laminae which extend ventrally from the lateral edges of the nasals (Fig. A4), bending medially toward the vomers, often touching the lateral ethmoids in all genera except Spinachia.

The vomers are toothless, their heads not strongly attached to any of the surrounding bones. Their shafts extend past the posterior ends of the lateral ethmoids.

The lateral ethmoids in small Culaea are vertically placed cylinders between the frontals and the lachrymals. In larger specimens a lateral face covers each cylinder and its central portion is constricted, separating the dorsomedial and ventromedial projections. The former remains in contact with the frontal and the latter bends medially to lie with its open end parallel to the parasphenoid shaft. In Culaea it is augmented by a posterior process. In Spinachia the lateral face of the lateral ethmoid is expanded anteriorly and supported by an anterior lamina from the ventromedial projection. In Aulorhynchidae (Fig. A5) the anterior laminae extend further anteriorly than do the lateral faces of the bones.

There are no supraethmoids. The median ethmoids in Spinachia and Aulorhynchidae are flat, running most of the length of the snout. Their posterior portions bear ventral concavities whose lateral walls are expanded to contact the ventromedial projections of the lateral ethmoids. In Culaea and Apeltes the lateral walls are expanded both dorsally and ventrally and extend for most of the lengths of the median ethmoids. In Gasterosteus they are expanded, and the medial plate reduced, to the point where the bone appears a bilaminar vertical septum.

Syngnathiformes

Nasals are absent in Syngnathidae and Solenostomidae. In Aulostomus the nasal is a small tubular bone in the nasal cavity. The supraorbital sensory canal extends anteriorly from the nasal cavity in an unossified tube. In Fistularia no nasal appears in the nasal cavity but a series of tubular bones encloses the supraorbital canal. I view these as homologous to the nasals in Macrorhamphosus and Centriscidae (Fig. A6), in which the nasals consist of thin canals running from the frontals to the tip of the snout, augmented ventrally in Centriscidae by thin flanges which form part of the rostrum walls.

The vomer forms the dorsal surface of the tip of the rostrum in all Syngnathiformes, but is almost covered by the supraethmoid in Aulostomus and Fistularia. In other Syngnathiformes much of the shaft of the vomer is exposed dorsally. In all except Syngnathidae (Fig. A7) the head of the vomer is small, augmented laterally by the palatines, to which it is tightly sutured in Aulostomus and Fistularia. Only in Macrorhamphosus does the vomer shaft extend posteriorly past the lateral ethmoids.

The syngnathiform lateral ethmoids have strongly developed lateral faces, bearing long anterior projections in all except Syngnathidae. Jungersen (1910) identifies these as fused lachrymals; they are similar to the lachrymals of Centriscus, but cannot be separated from the lateral ethmoids in my specimens and, in all but Macrorhamphosus, are supported at least partially by anterior laminae from the ventromedial projections of the lateral ethmoids.

In Centriscidae and Syngnathidae the lateral faces of the lateral ethmoids are square and the dorsomedial and ventromedial projections of each are fused so that each bone resembles a cube with its medial side missing. A posterior process extends to the parasphenoid in most, and in Syngnathus and Syngnathoides an anterior process to the median ethmoid is also present.

The median ethmoid is covered by a sculptured supraethmoid. Its posterior portion forms a cone opening into the orbit, the anterior myodome. In Syngnathoides, Aulostomus, and Fistularia its ventrolateral edges are extended as bony ridges reaching the lateral surface of the snout. In Centriscidae each ridge is expanded dorsally and ventrally to form a lateral surface; in Macrorhamphosus two ridges, connected by struts, arise from each side. In both of these groups the ridges touch the nasals, which are thus firmly attached to the rostrum.

Indostomus

Indostomus (Fig. A8) has no separate nasals. Instead, the entire dorsal surface of the snout is covered by a sculptured median bone which Banister (1970) calls the supraethmoid. This bone both lies over and anterior to the vomer head and bears the anterior extensions of the supraorbital canals, leading me to believe that it is at least partly homologous to the nasals. The median ethmoid proper was unossified in my specimens, as in Banister's.

The lateral ethmoids are situated dorsally, forming part of the orbit roofs. The medial projections of each lateral ethmoid are fused to form a single structure projecting directly inwards. The posterior faces of these structures form part of the anterior wall of the orbits. The ventral surfaces of the lateral ethmoids bear longitudinal flanges which touch the pterygoids; these flanges may be homologous to the palatines of the other fishes examined. The head of the vomer is toothless and indistinct, being completely fused to the ventral surface of the supraethmoid; its shaft extends posteriorly past the lateral ethmoids.

Hypoptychus

The nasals of Hypoptychus are wide (Fig. A9) and bear the supraorbital canal. The lateral ethmoids (Fig. A10) resemble those of the atherinoid Allanetta; their lateral surfaces are edges rather than plates and their ventromedial projections are expanded anteriorly and posteriorly to lie along the parasphenoid shaft. The median ethmoid has deep lateral plates. The vomer is toothless and extends posteriorly past the lateral ethmoids to mid-orbit. It is not expanded between the lateral ethmoids.

Pegasus

The rostrum in Pegasus is apparently formed from the nasals, since it shows a median line and the remnant of a canal on each side of its posterior end (Fig. A11). Its posteroventral portion is deeply excavated to form the cavity which receives the jaw bones. Posterolaterally, the rostrum touches the lateral ethmoids. These bones have expanded lateral faces (Fig. A12) and reach posterodorsally to form part of each orbit roof. Their ventromedial and dorsomedial projections are fused into triangular cones similar to those described in Asterotheca, and inclined posteriorly so that their posterior faces enter the orbit, forming the anterior portion of the interorbital septum.

The median ethmoid consists of a dorsal plate bearing an anteriorly concave transverse lamina which touc[illegible]he anterior sides of the lateral ethmoids. The toothless vomer occupies a posterior position, its head lying between the anterior corners of the lateral ethmoids and its shaft suturing to the parasphenoid between their posterior corners.

Dactylopterus

The ethmoid region in Dactylopterus is highly modified, the tip of the snout being formed dorsally by a single large bone (Fig. A13) which bends ventrally to form the anterior wall of a cavity which contains the upper jaw bones. This bone fills the position occupied by the nasals in Pegasus or Asterotheca, but it shows no evidence of being a paired structure. Its ventral surface bears lateral flanges resembling those of the median ethmoid in other fishes, so I believe this bone to be at least partially homologous to the median ethmoid. The highly sculptured component of this bone may be derived from either a supraethmoid or from fused nasals. The fact that it lies dorsal and anterior to the vomer head supports the latter view, the supraethmoids observed in Syngnathiformes being located far behind the vomer head.

The lateral ethmoids closely resemble those of Pegasus and Asterotheca in the fusion of their medial projections, but these do not extend posteriorly into the orbits. The broad sculptured dorsal surfaces of the lateral ethmoids form the anterior orbit roofs and curve forwards to form the anterior walls of the orbits and the snout. Their fused medial projections touch the wide vomer head. The wide toothless vomer head bears a ventral keel which terminates anteriorly in a transverse flange (Fig. A14).

Table A1 : Characters from the ethmoid region
(asterisks indicate those used in phenetic analyses)

*A1.nasals present (1)/ absent (0)

*A2.Lateral ethmoids with broad lateral faces/ with lateral edges

*A3.Lateral ethmoids extend posteriorly onto orbit roof/ confined to anterior orbit walls

*A4.Lateral ethmoids with/ without anterolateral extensions

A5.Median ethmoids with/ without ventral transverse flanges

*A6.Medial projections of each lateral ethmoid fused/ separate

*A7.Ventromedial projections with/ without anterior processes

*A8.Ventromedial projections with/without posterior processes

*A9.Ventromedial projections extend posteriorly into orbits/ lie anterior to orbits

*A10. Vomer with/ without dorsal projections over parasphenoid

A11. Median ethmoid with/ without vertical lateral plates

A12. Median ethmoid horizontal median plate reduced/ broad

A13. Median ethmoid with/ without ventral ossification

A14. Median ethmoid with/ without ventrolateral ridges

A15. Median ethmoid touches lateral ethmoids/ separate from lateral ethmoids

*A16. Vomer head toothed/ toothless

*A17. Vomer head tightly attached/ not tightly attached to palatines

*A18. Vomer head fused to median ethmoid/ separate from median ethmoid

*A19. Vomer head connects/ does not connect lateral ethmoids

*A20. Vomer shaft extends posteriorly past lateral ethmoids/ ends anterior to posterior tips of lateral ethmoids

*A21. Vomer shaft meets/ does not meet parasphenoid

*A22. Vomer shaft exposed dorsally/ covered dorsally

A23. Snout length/head length (%)

A24. Median ethmoid length/head length (%)

A25. Vomer length/head length (%)

Table A2 : Distributions of binary characters from the ethmoid region among framework taxa

Taxon	12345	67890	12345	67890	12
Diplophos	10100	00000	10000	10001	10
Saurida	10100	00000	00000	11000	10
Percopsis	10000	00000	11000	00001	10
Fundulus	10000	00000	00000	00001	10
Melanotaenia	10000	00000	0000X	10001	10
Allanetta	10000	01000	00001	00011	10
Holocentrus	10000	00000	11000	00011	10
Asterotheca	11101	11110	10001	10001	10
Cottus	10101	01000	11001	10001	10
Sebastes	11100	10001	00000	10000	10
Prionotus	11111	01101	00001	10011	10
Percalates	1000X	00000	10000	10001	10
Plectroplites	1000X	00000	10000	10001	10
Perca	10000	00000	11000	10001	10
Ammodytes	10100	00000	10000	00001	10

Table A3 : Distributions of numerical characters from the ethmoid region among framework taxa

Taxon	23	24	25
Diplophos	25.1	17.4	11.7
Saurida			
Percopsis	16.1	33.8	19.7
Fundulus	7.8	17.3	9.2
Melanotaenia	X	23.5	X
Allanetta	11.2	29.7	25.5
Holocentrus	X	X	X
Asterotheca	16.2	24.6	20.2
Cottus	15.5	21.3	10.7
Sebastes	18.0	27.0	15.4
Prionotus			
Percalates	12.5	28.6	15.5
Plectroplites	14.9	36.7	14.4
Perca	10.2	27	14.4
Ammodytes	23.5	38.3	22.5

Table A4 : Distributions of binary characters from the ethmoid region among study groups

Taxon	12345	67890	12345	67890	12
Gasterosteus	11000	00000	11000	00001	10
Pungitius	11000	00000	10000	00001	10
Culaea	11000	00100	10000	00001	10
Apeltes	11000	00000	10000	00001	10
Spinachia	11110	01000	10000	00001	10
Aulichthys	11110	00100	10000	00001	10
Aulorhynchus	11110	00100	10000	00001	10
Syngnathus	01000	11100	1010X	00000	01
Syngnathoides	01000	11100	1010X	00000	01
Hippocampus	01000	10100	1010X	00000	01
Solenostomus	01010	01000	10110	00000	11
Aulostomus	11010	01000	10110	01000	11
Fistularia	11010	01000	10110	11000	11
Macrorhamphosus	11010	11100	10110	00001	11
Aeoliscus	11010	11100	10110	00000	11
Indostomus	11100	10000	XXXXX	00101	10
Hypoptychus	10000	01100	11000	00001	10
Pegasus	11101	10010	00001	00010	10
Dactylopterus	11100	10000	10000	00011	10

Table A5 : Distributions of numerical characters from the ethmoid region among study groups

Taxon	23	24	25
Gasterosteus	31.4	8.3	31.9
Pungitius	26.4	8.2	20.2
Culaea	28.1	5.2	18.4
Apeltes	25.1	9.6	5.2
Spinachia	47.4	16.6	37.1
Aulichthys	55.8	27.6	38.7
Aulorhynchus	56.8	25.6	56.1
Syngnathus	55.2	31.0	45.2
Syngnathoides	60.6	47.0	32.5
Hippocampus	44.1	23.0	33.0
Solenostomus	77.7	46.3	26.2
Aulostomus	70.8	61.8	48.5
Fistularia	82.2	23.6	34.1
Macrorhamphos	62.4	41.5	68.9
Aeoliscus	76.3	31.1	40.2
Indostomus	38.1	X	X
Hypoptychus	36.9	15.6	37.2
Pegasus	49-61	8.7	9.9
Dactylopterus	22.8	16.8	23.5

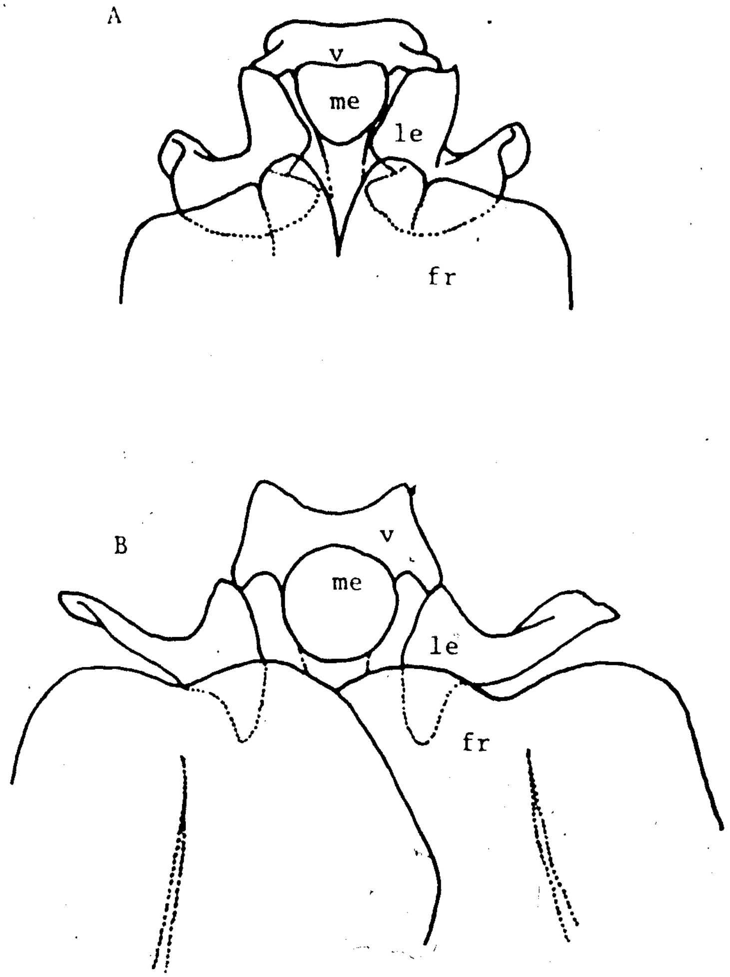


Figure A1 : Ethmoid regions of Atherinomorpha, dorsal view

A - <u>Allanetta</u> <u>harringtonensis</u> X23.5

B - <u>Fundulus</u> sp., X23.5

(abbreviations are listed on pages xxv-xxvi)

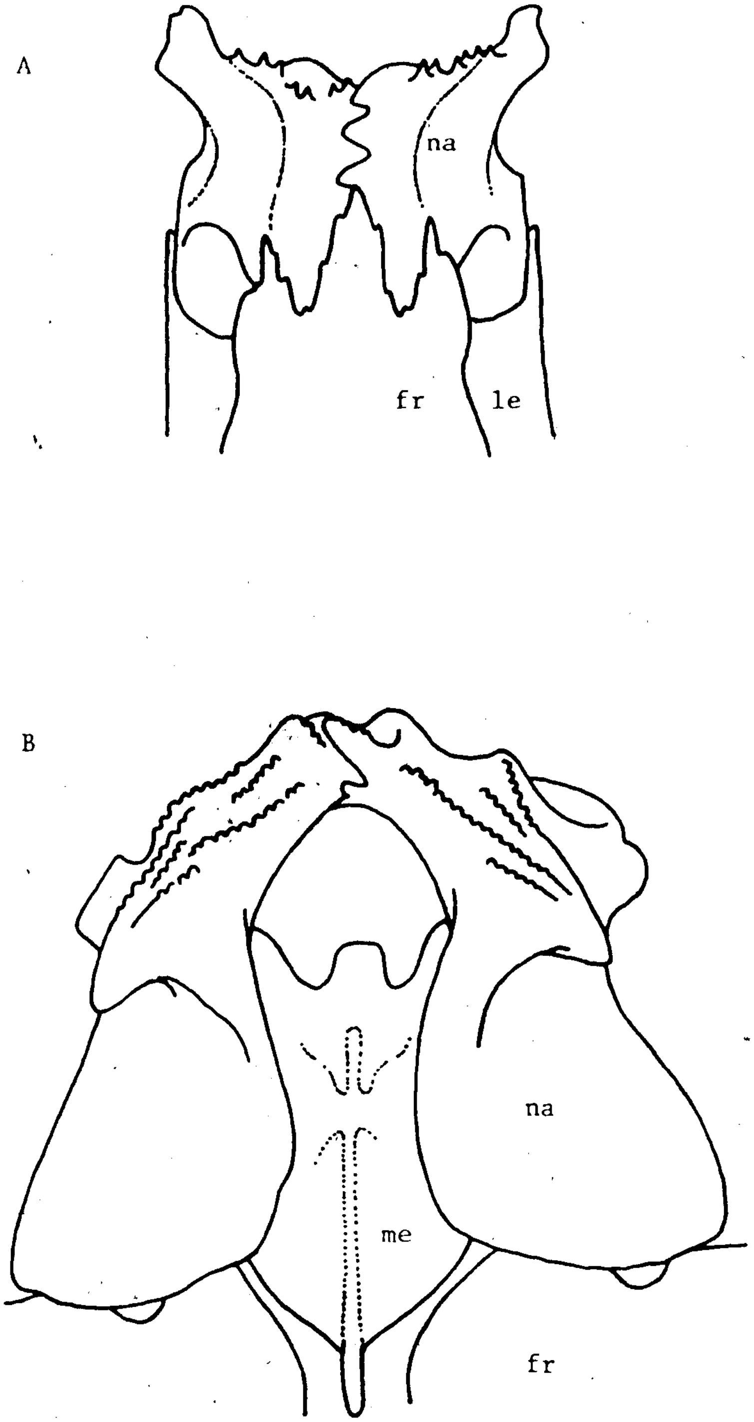


Figure A2 : Nasal regions of Scorpaeniformes, dorsal view

A. Peristedion truncatum, X5.6

B. Asterotheca alascana, X23.5

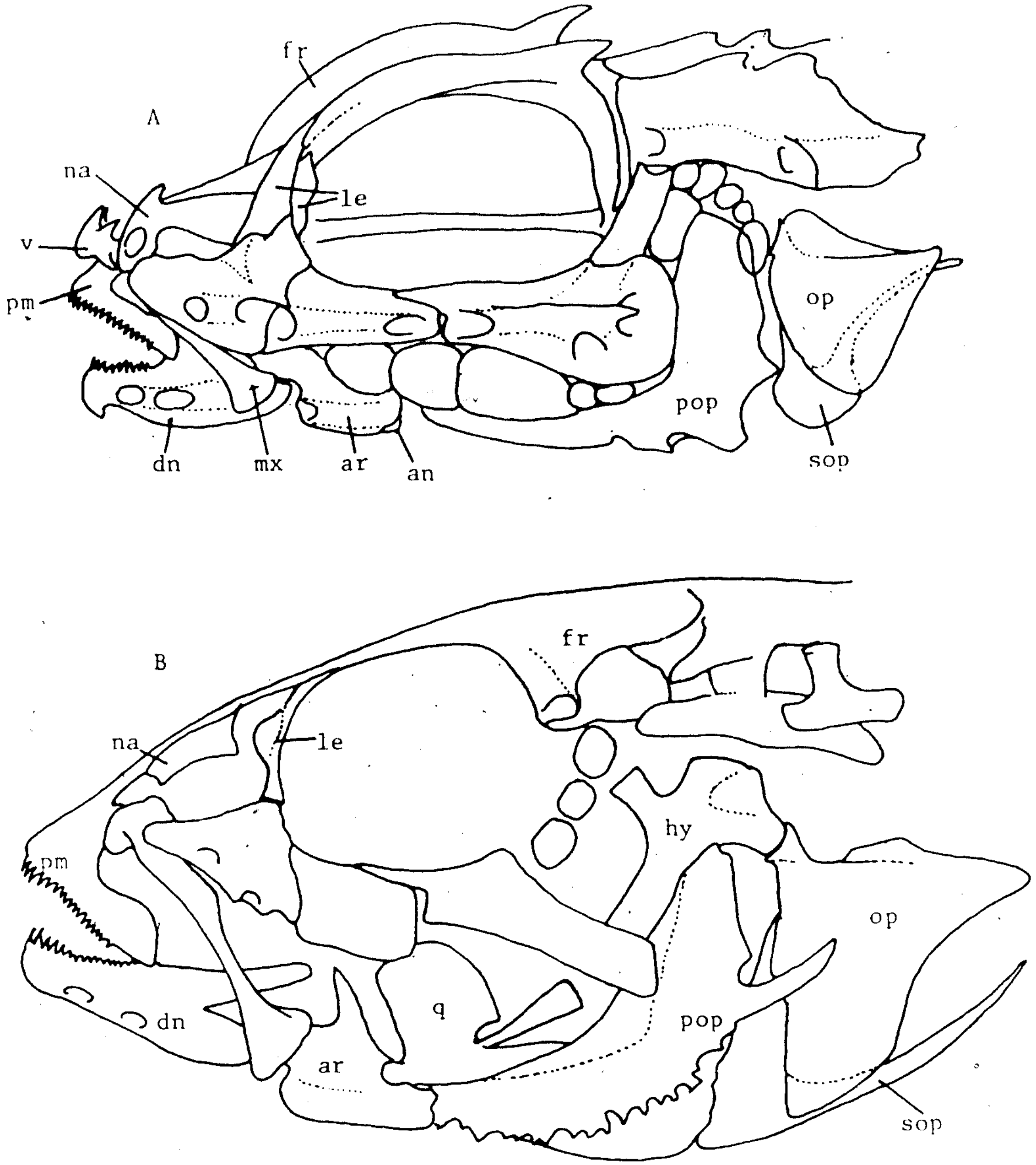


Figure A3 : Whole heads of Cottoidei, left lateral views

A. Asterotheca [illegible]ascana, X5.6

B. Cottus cognatus, X11.5

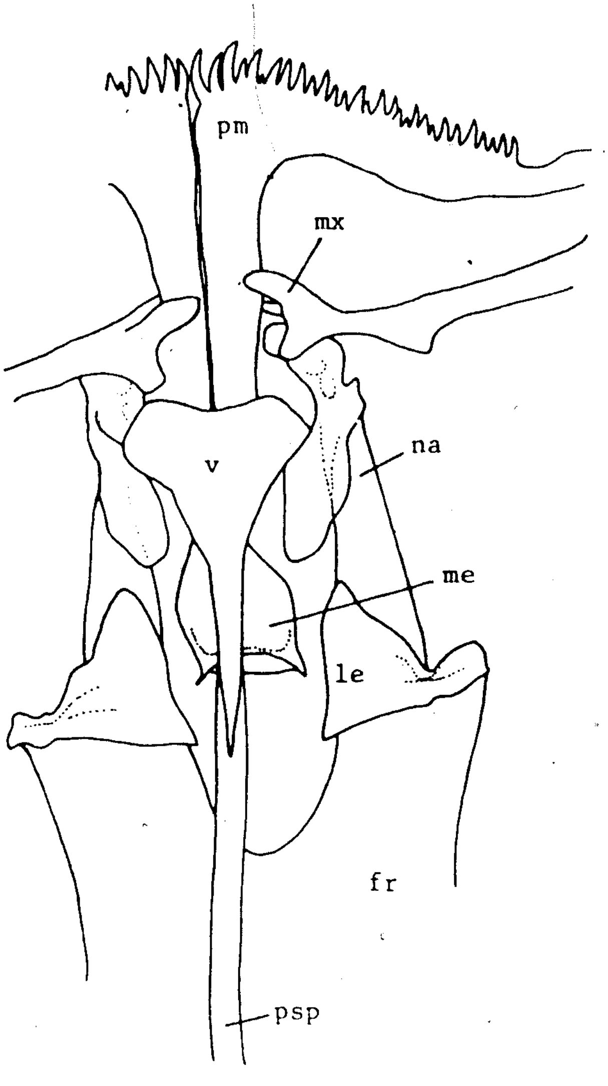


Figure A 4: Pungitius pungitius, ethmoid region, ventral view. X 23.5 (UAMZ 4754)

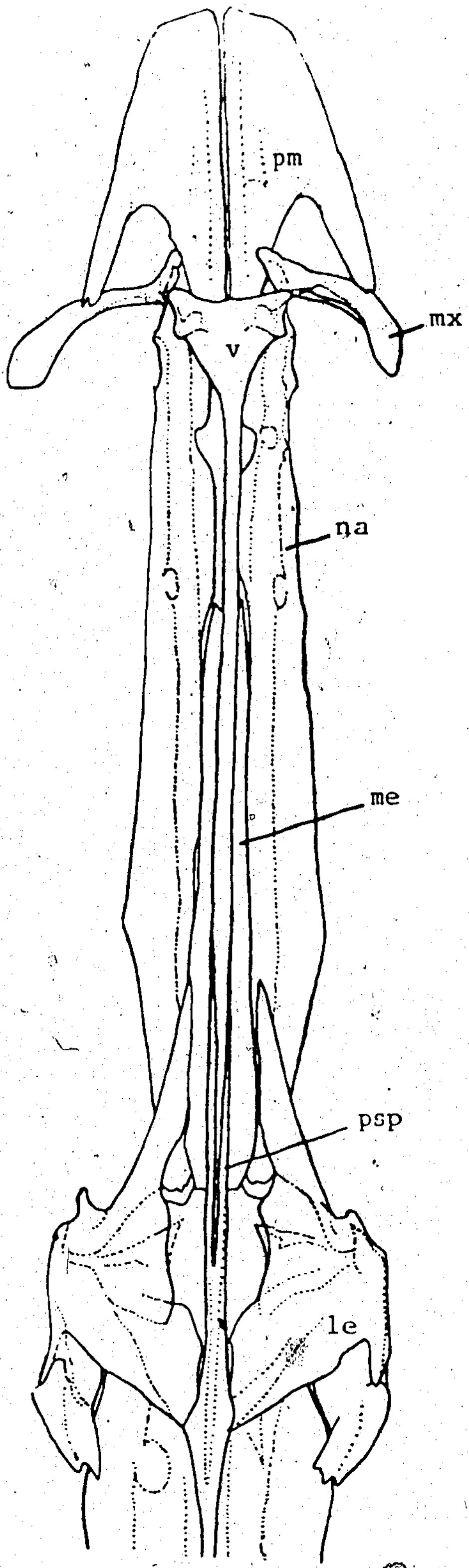


Figure A5: <u>Aulorhynchus flavidus</u>, ethmoid region, ventral view, X 11.5 (UAMZ 1694)

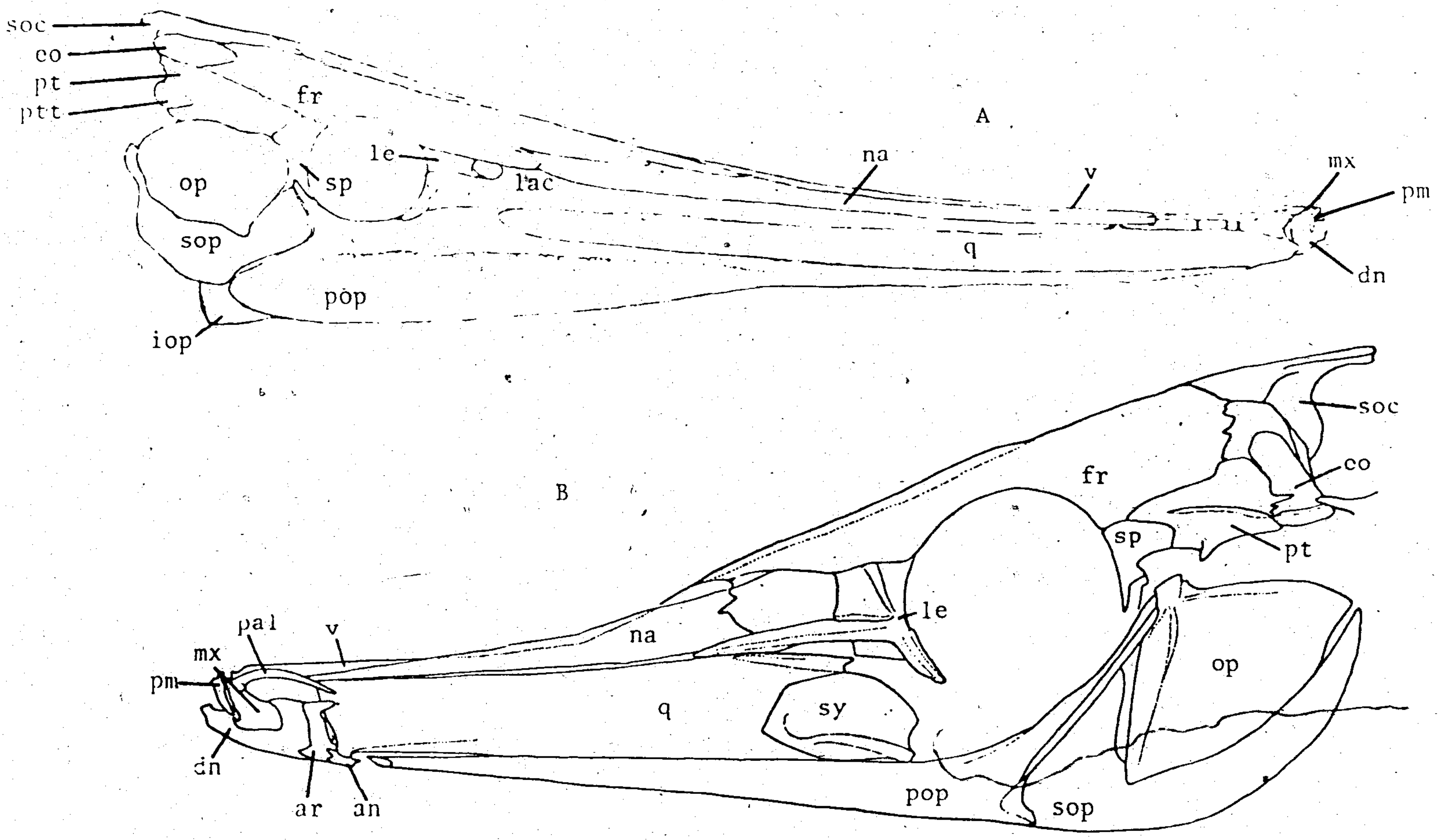


Figure A6 : Whole heads of Syngnathiformes

A. Centriscus scutatus, right lateral view, X 3.5 (UAMZ 370)

B. Macrorhamphosus gracilis, left lateral view, X 8.6

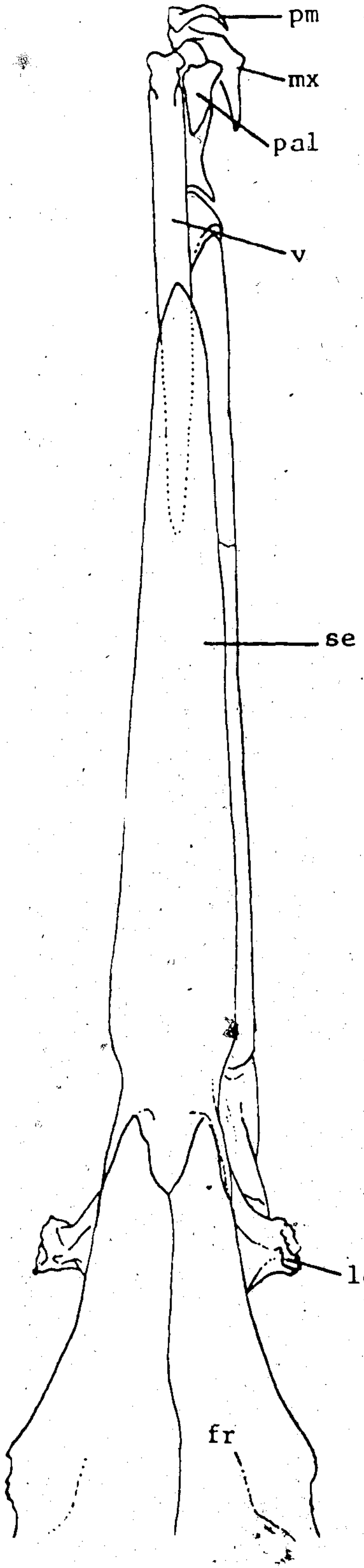


Figure A7: Syngnathoides biaculeatus, snout with left jaws and suborbitals removed, dorsal view. X 11.5 (LACM 37398-16)

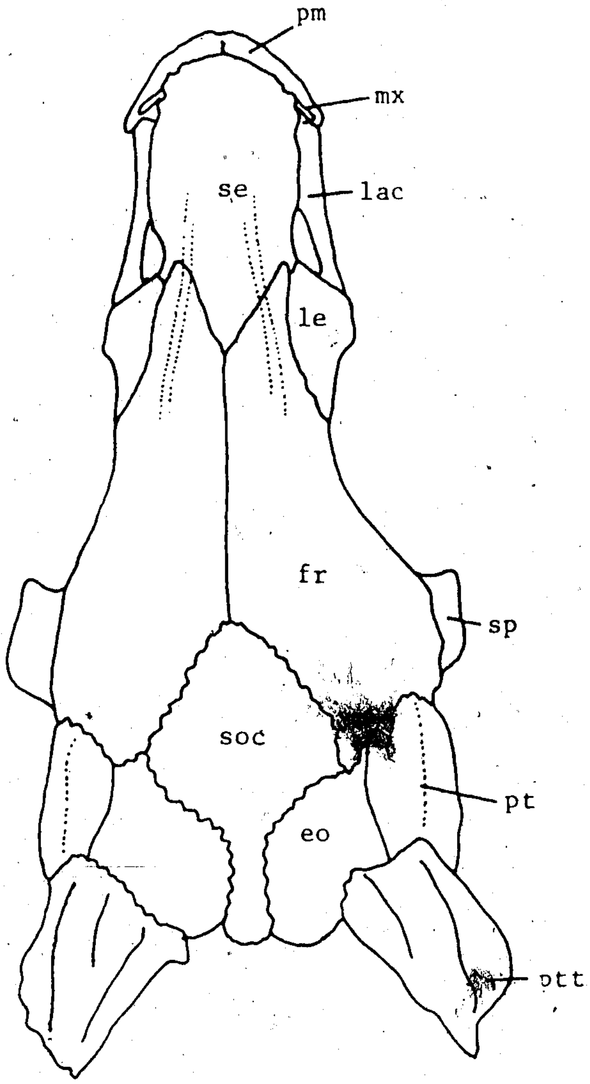
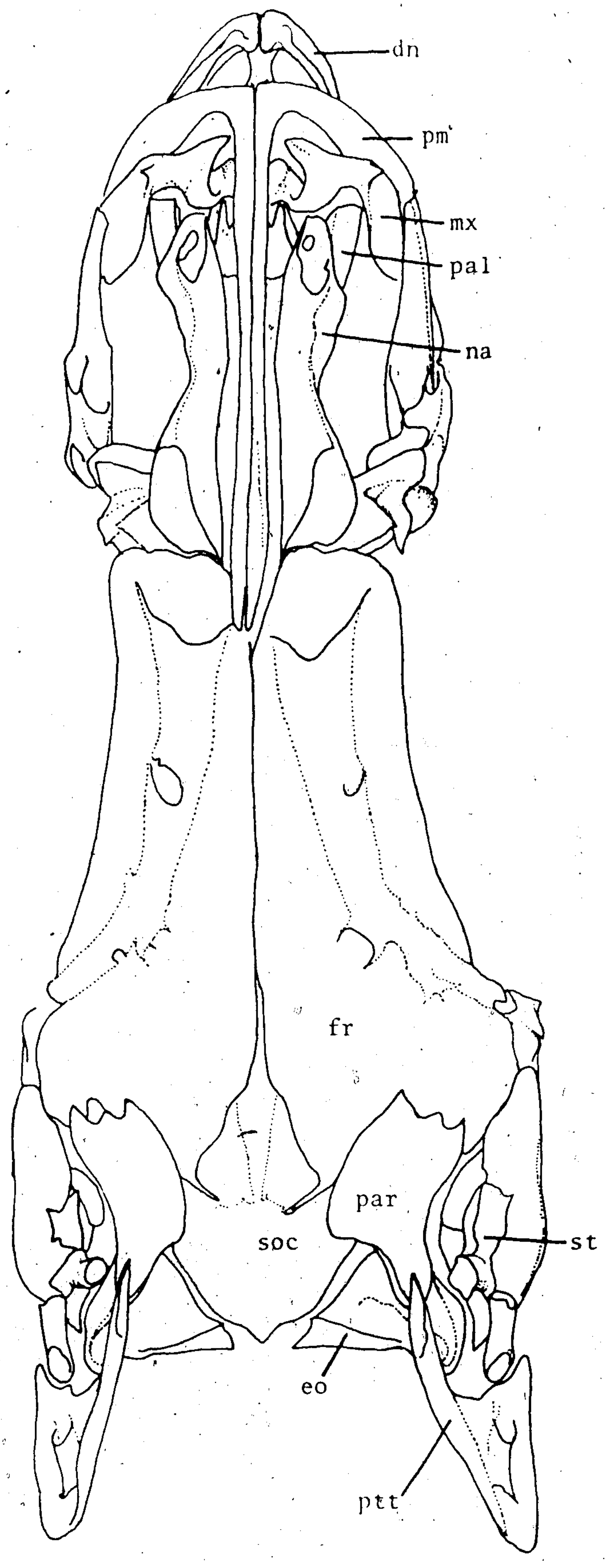


Figure A8 : Indostomus paradoxus, neurocranium, dorsal view, X 23.5 (UAMZ uncatalogued)

Figure A9 : *Hypoptychus dybowski*

whole head, dorsal view, X11.6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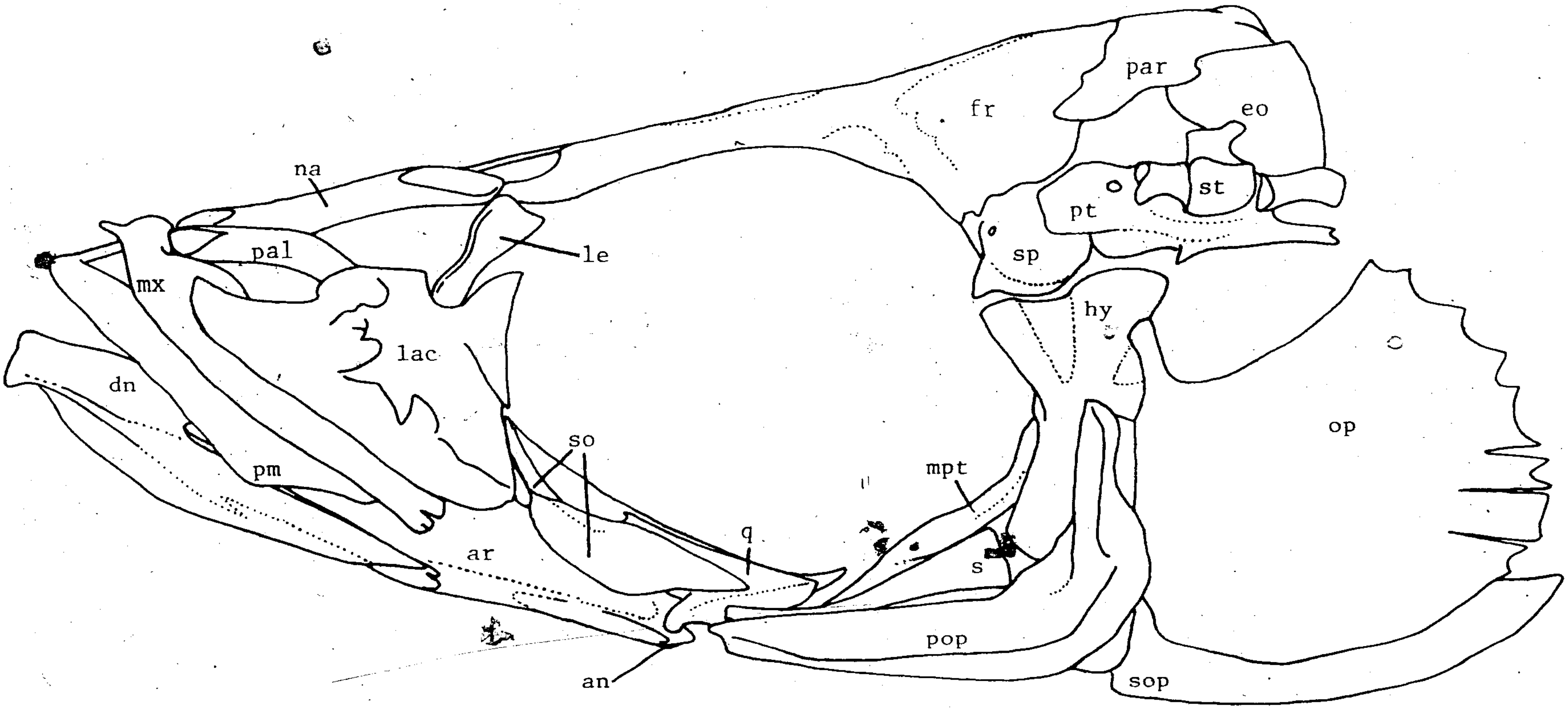
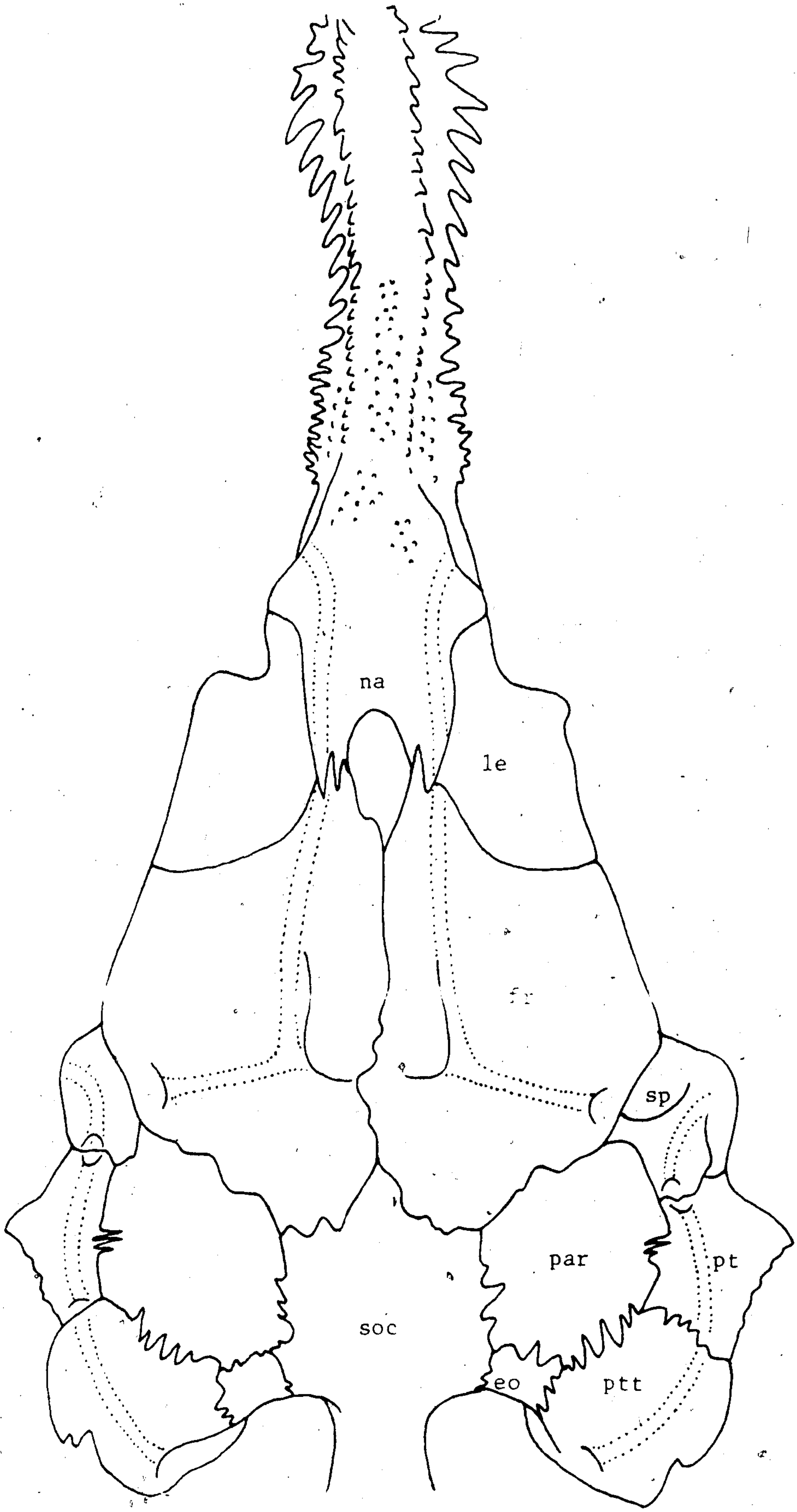


Figure A10 : Hypoptychus dybowski, whole head, left lateral view, X 11.5

Figure A11 : Pegasus papilio, whole head, dorsal view, X11.5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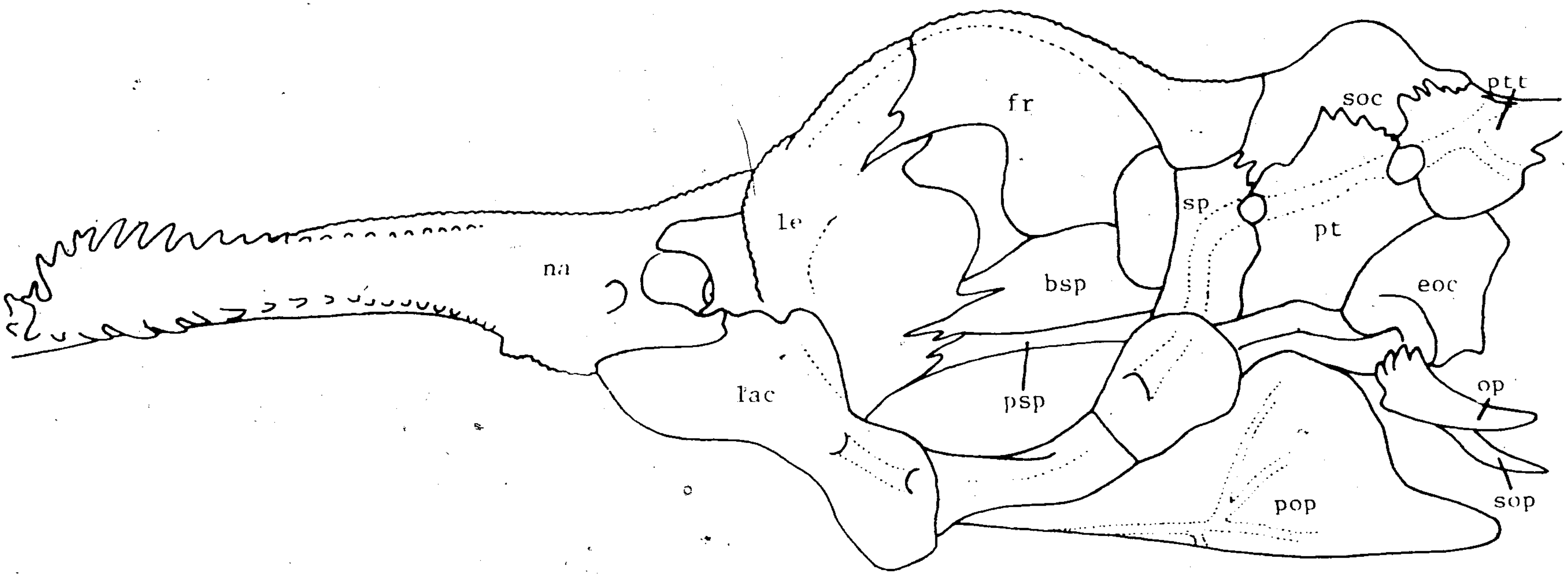

Figure A12 : Pegasus papilio, whole head, left lateral view,   X11.5

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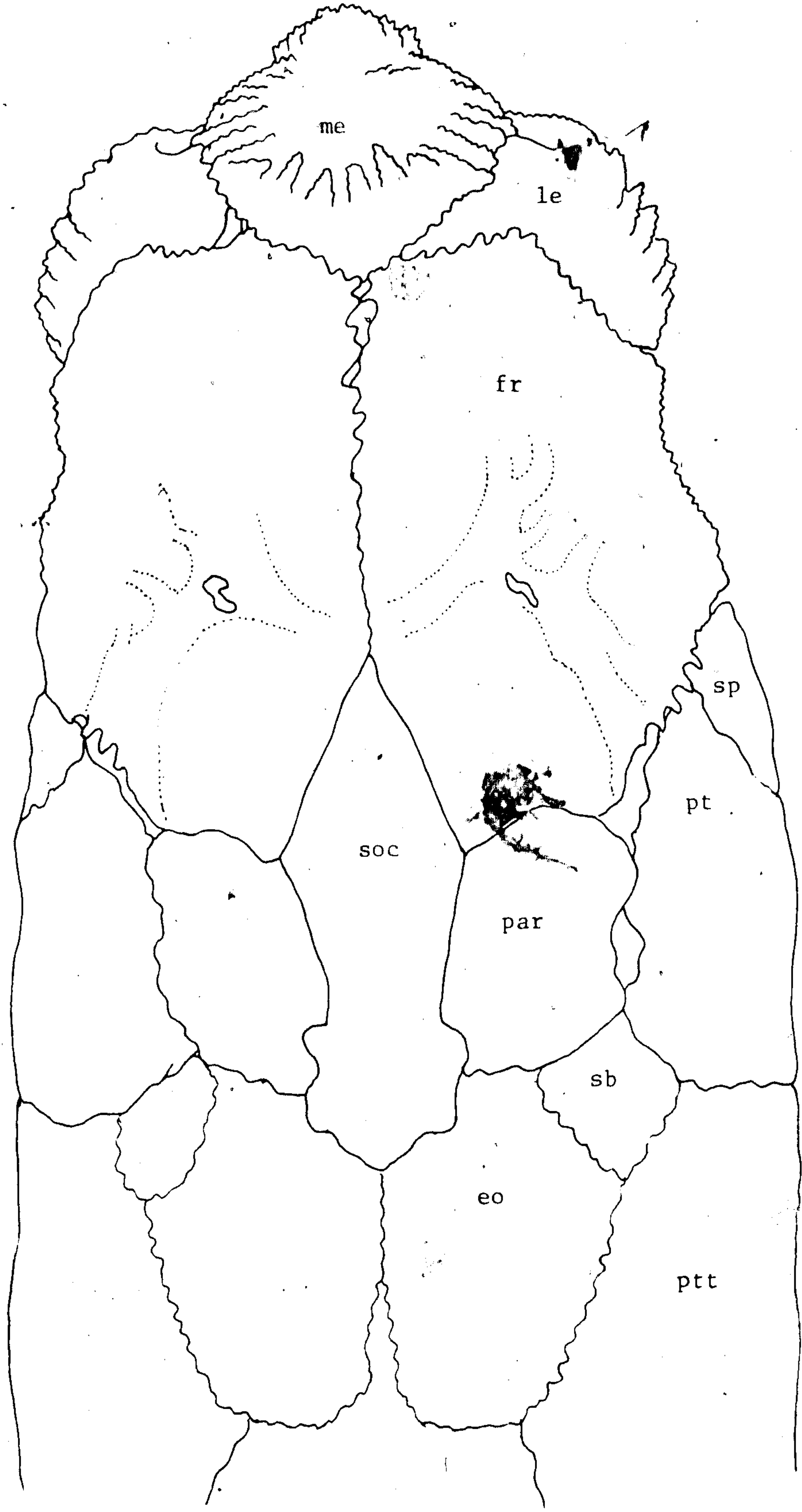
Figure A 13 : *Dactylopterus volitans*, whole head, dorsal view,

X 11.6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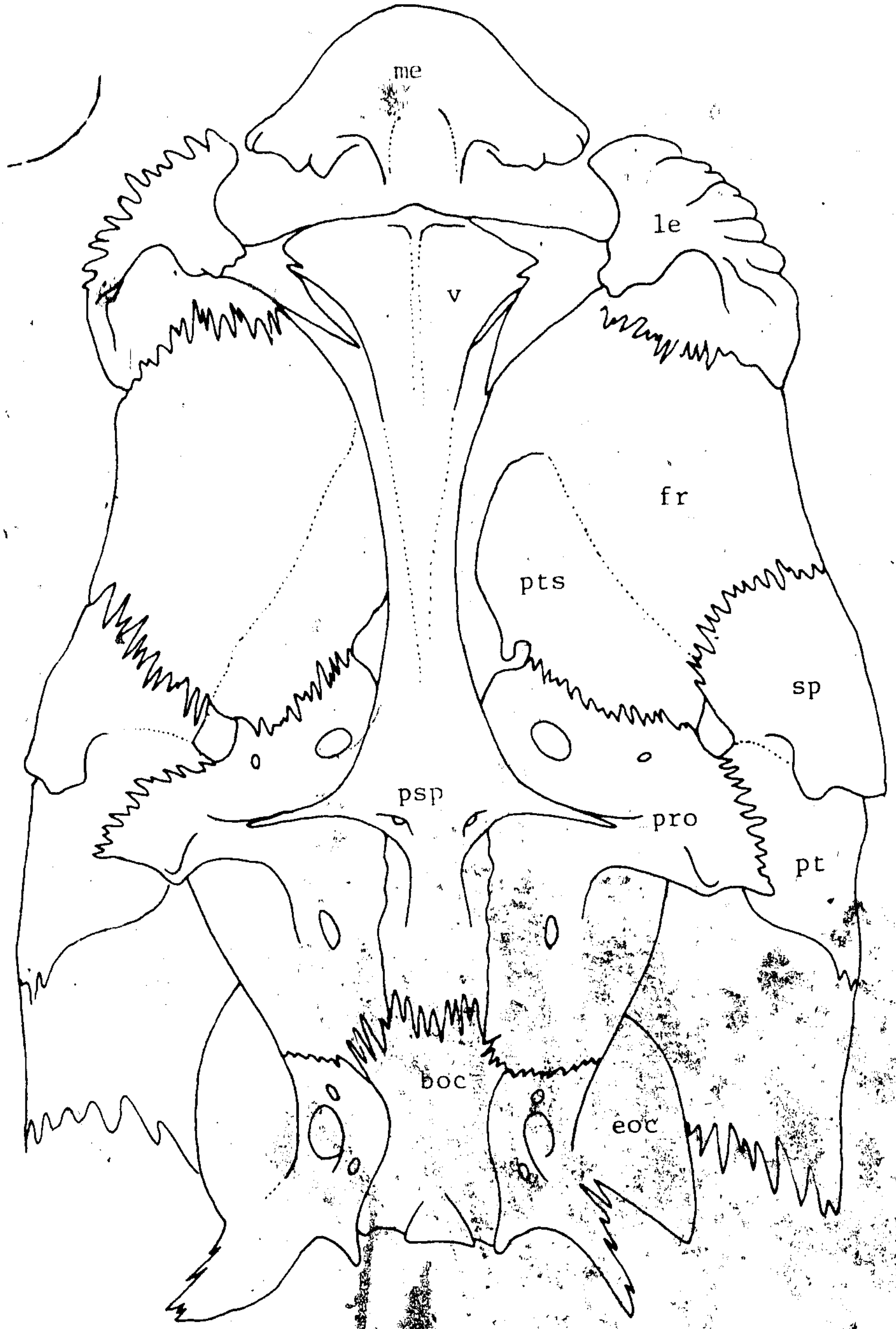

Figure A14: Dactylopterus volitans, neurocranium, ventral view, X11.6

B. The Orbital Region

The orbital region is composed of the frontals, circumorbitals, sphenotics and dermosphenotics, orbitosphenoids, pterosphenoids, basisphenoid, and sclerotic bones (when present). The characters from this region are listed in Table B1; coded data for framework groups appear in Table B2, data for study groups in Table B3.

Framework

The frontals in Diplophos are plain flat bones carrying the supraorbital canals and the lateral ends of the mental cross-canal. They lack both lateral and medial postorbital processes. Each circumorbital series consists of an antorbital, a supraorbital, five delicate suborbitals, and the dermosphenotic. The supraorbital covers the lateral ethmoid; the antorbital lies before the eye in the position occupied by the anterior portion of the first suborbital (or lachrymal) in most other fishes. The remaining six circumorbital bones and the dermosphenotics bear the infraorbital canal in open troughs along their orbital edges.

The posterior walls of the orbits are almost horizontal and are composed of the large flat pterosphenoids, which meet in the midline, and the single basisphenoid lying posterior to and between the pterosphenoids and extending to the parasphenoid shaft via a ventral process. A large posterior myodome is present.

The frontals in Saurida have slight lateral postorbital processes and bear the supraoccipital canals but no mental cross-canal. They bear small medial postorbital processes which contact the pterosphenoids. A basisphenoid is present but the posterior myodome is not visible. The lachrymals extend anteriorly to the tips of the nasals; there are four additional suborbitals and a dermosphenotic in each suborbital series, all bearing the infraorbital canal. Each eye is stiffened by an ossified sclerotic ring formed of anterior and posterior bones.

Each of the frontals in Percopsis bears a single short canal on its posterior half; these canals extend obliquely forward, like supraorbitals, but instead of curving to follow the orbit margins they open medially. Rosen and Patterson (1969) give as a characteristic of Percopsiformes the continuation of each supraorbital canal in a broad trough on the frontal, but I did not observe this. They also note that the posterior canal is absent in Aphredoderus. There are no lateral postorbital processes, but a medial postorbital process extends from each frontal to touch the pterosphenoid. There is no basisphenoid, but a myodome is present. Each suborbital series consists of the lachrymal, four suborbitals, and the dermosphenotic. The lachrymals are large and extend to the tips of the nasals, their dorsal margins folded laterally to form open troughs for the infraorbital canals. The dorsal margin of each lachrymal also bears a posteriorly concave preorbital process and an anterodorsal process which Rosen and Patterson (1969) identify as an antorbital. The remaining suborbitals and the dermosphenotic bear the infraorbital canal in wide troughs. There is no sclerotic ring.

The frontals in Melanotaenia and Allanetta bear a supraorbital canal but no vestige of the interorbital commisures. Lateral postorbital processes are short or absent and medial postorbital processes are short and touch the pterosphenoids (Fig. B1). The basisphenoid and posterior myodome are present.

Rosen (1964) describes Atherinomorpha as distinguished by an incomplete suborbital series consisting only of the lachrymal and dermosphenotic, except in melanotaeniids, which have a second suborbital. My observations agree with his. The lachrymals, and the second suborbitals in Melanotaenia, bear the infraorbital canals in troughs. The dermosphenotics consist of vertical troughs or of flanges along the posterior rims of the orbits; in Fundulus both the flanges and troughs are present, the troughs lying free along the orbital sides of the flanges. The sclerotic rings are present and well-developed as in Saurida.

The frontals in Holocentrus bear the supraorbital canals but no mental cross canals. Their postorbital processes are large, almost excluding the dermosphenotics from the orbit rims; the ventromedial processes are very short and contact the pterosphenoids. Orbitosphenoids and a basisphenoid are also present, as is the posterior myodome. Each suborbital series consists of an antorbital, the lachrymal, four suborbitals, and the dermosphenotic. All except the antorbital bear the infraorbital canal in bony troughs. A suborbital shelf extends inward from the median face of each suborbital. The dermosphenotics are separated from the sphenotics and developed into tubular bones along the posterior margins of the orbits. Each sclerotic ring is reduced to two small bones, one on the anterior side of the eye and one on the posterior side.

The frontals of *Sebastes*, *Asterotheca*, and *Prionotus* bear both supraorbital and mental cross canals. Medial postorbital processes extend to the pterosphenoids in all. The basisphenoid is present in *Sebastes* but not in *Asterotheca*, *Cottus* (Fig. B2), or *Prionotus*; the posterior my[illegible]s present in *Sebastes* and *Prionotus*. Quast (1965) states that the presence of th[illegible]henoid distinguishes Scorpaenidae and Hexagrammidae from the cottid and agonid lines.

The suborbital rings are incomplete in *Sebastes alutus* and the posterior three suborbitals in *Cottus* are small and separated from one another. Quast (1965) notes that the third and fourth suborbitals are often absent in Scorpaenidae. In all, the lachrymals contact the lateral ethmoids and the tips of the nasals and the suborbitals bear the infraorbital canals. Subocular shelves are present in all but *Cottus* and *Prionotus*. The third suborbitals meet the preopercula to form suborbital stays (Fig. A3).

The dermosphenotics in *Prionotus* and *Sebastes* form the posterior edges of the orbits ; those of *Asterotheca* are reduced to small bones at the tips of the frontal postorbital processes. The dermosphenotics in *Cottus* are of normal size but do not participate in the orbit margins. Sensory canals are born by the dermosphenotics in *Sebastes*. Sclerotic bones similar to those of *Holocentrus* are present in *Prionotus*.

The frontals in all perciforms examined bear both supraorbital canals and, in all except *Ammodytes* and *Perca*, interorbital commisures. Their lateral and medial postorbital processes are small. Pterosphenoids, basisphenoids, and myodomes are present. The suborbital rings of *Percalates*, *Plectroplites*, and *Perca* are complete, without suborbital shelves or stays. In *Ammodytes* the suborbital rings are open ventrally; each consists of an anterior lachrymal, a small splint-like second suborbital, and two small, tubular posterior bones. These may be dermosphenotics, but if so they are further separated from the sphenotics than are the dermosphenotics of any other fishes examined. The dermosphenotics in *Percalates* and *Plectroplites* bear the junctions of the lateral and infraorbital canals; those of *Perca* bear no canals.

Gasterosteiformes

Gasterosteiform frontals bear the supraorbital canals and, in all except *Gasterosteus*, the interorbital commisures. Lateral postorbital processes are present, as are large medial postorbital processes which contact the lateral processes of the parasphenoid; there are no separate pterosphenoids (Fig. B3). Banister (1967) found separate pterosphenoids in *Aulichthys* and *Aulostomus*, suggesting that there may be variability in these species with respect to this character. The suborbital series of Gasterosteidae are incomplete posteriorly (Figs. B4-5). Each consists of a lachrymal, a small second suborbital, and a large third suborbital which extends to touch the preoperculum. In *Spinachia* the third suborbital is extended posteriorly toward the angle of the preoperculum; in other Gasterosteidae it extends ventrally to touch the anterior limb of the preoperculum. In Aulorhynchidae the suborbital series each consist of the lachrymal and five narrow tubular suborbitals (Fig. B6). All bear the infraorbital canal. The sphenotics are covered posteriorly by the dermopterotics, and their anterior borders are almost completely excluded from the orbits by the lateral postorbital processes of the frontals. The dermosphenotics and dermopterotics in Aulorhynchidae (Fig. B7) are fused into one long tubular bone. Sclerotic bones are present in *Aulichthys* (Fig. B6).

Syngnathiformes

In *Aulostomus* and *Fistularia* the frontals bear the supraorbital canals and remnants of the interorbital commisures. The interorbital commisures are reduced in *Macrorhamphosus* and Centriscidae; Syngnathidae and *Solenostomus* have no canals on the frontals. The frontals lack postorbital processes and only in *Aulostomus* and Syngnathidae are medial postorbital processes present. In *Syngnathoides*, *Syngnathus*, and *Solenostomus* the frontals meet the parasphenoid lateral processes (Fig. B8), but in *Hippocampus*, Centriscoidei (Fig. B9,A), and Aulostomoidei (Fig. B9,B) the frontals and parasphenoids are separated by very narrow gaps which are bridged by the pterosphenoids. Pterosphenoids are present in all Syngnathiformes, and *Fistularia tabacaria* has a process on the dorsal side of the parasphenoid shaft, at the posterior end of the orbit, which may be homologous to a basisphenoid. Myodomes are present in all the syngnathiforms examined except *Syngnathus* and *Syngnathoides*.

Two families of Syngnathiformes have conspicuous suborbital bones. Centriscidae have a single bone extending the full length of each side of the snout (Fig. A6,A). Jungersen (1908) calls these bones the antorbitals, but Banister (1967) calls them infraorbitals and suggests that they may be homologous with the lachrymals. I agree with Banister, since these bones occupy the positions usually filled by the lachrymals, between the anterior margins of the orbits and the tip of the snout. In Centriscidae, however, the "lachrymals" also occupy the positions filled by the anterior and ventral parts of the lateral ethmoids in Macrorhamphosus, Aulostomus, Fistularia, and Solenostomus, which suggests that they are compound bones formed by the fusion of the lachrymals and lateral ethmoids. There are no canals along these "lachrymals"; their anterior ends are often subdivided into small bony plates. There are no posterior infraorbitals.

Syngnathidae have a different suborbital series, again confined to the anterior margins of the orbits and the sides of the snout. A series of three flat bones fills the space between the tip of the snout and the orbit (Fig. B10). I believe these also to be homologous to the lachrymals, resulting from a subdivision similar to that at the anterior tips of the "lachrymals" in Centriscidae.

The dermosphenotics are wide and flat in all Syngnathiformes, extending ventrally to form the posterodorsal orbit margins. In Centriscidae they bear the infraorbital canals, but no traces of the interorbital commisures. Sclerotic bones are present only in Aulostomus.

Indostomus

In Indostomus the frontals bear the supraorbital canals, but no traces of the interorbital commisures were observed. Their lateral postorbital processes are large and their medial postorbital processes small, touching the pterosphenoids (Fig. B11). The basiocciptal and myodome are absent. The lachrymals are the only suborbitals present. The posterior edge of each is expanded medially into a narrow plate forming the anterior wall of the orbit and an anterior vestige of the suborbital shelf. There are no canals on the lachrymals. The dermosphenotics are reduced to tiny plates on the posteroventral corners of the lateral postorbital processes of the frontals. They also bear no canals. There are no sclerotic bones.

Hypoptychus

The frontals in Hypoptychus bear supraorbital and interorbital commisures (Fig. A9) but lack marked lateral and medial postorbital processes. The posterior myodome is present, as are the pterosphenoids (Fig. B12), and the basisphenoid is absent. The circumorbital rings are incomplete, each consisting only of the lachrymal and two suborbitals. The lachrymals extend anteriorly to the tips of the nasals; each bears the infraorbital canal in a wide trough formed by its laterally folded dorsal edge. The posterior margin of each is expanded into a wide posteriorly concave flange forming the anterior orbit wall (Fig. A10). The remaining two suborbitals are flat and delicate, without canals. There are no suborbital shelves or stays. The sphenotics bear no canals. Sclerotic bones are absent.

Pegasus

The frontals of Pegasus papilio and P. volitans bear complete supraorbital canals and rudimentary interorbital commisures (Fig. A11). Large medial postorbital processes extend from them to the basisphenoid, which forms part of the interorbital septum (Fig. B13). Posterior to these processes the frontals meet the pterosphenoids, which curve backwards to suture to the sphenotics. The suborbital rings are complete, each consisting of a lachrymal and two suborbitals. All three bones in each series bear the infraorbital canal (Fig. A12). The lachrymals form the anterior halves of the ventral margins of the orbits and each has a thin anterior process lying along the side of the rostral cavity. Suborbitals 2 and 3 lie in an almost horizontal plane below the eyes, both strongly attached to the preoperculum. As well as forming a horizontal platform under the eye, they and the lachrymals bear internal flanges forming subocular shelves.

The sphenotics bear the posterior portions of the infraorbital canals and the anterior portions of the lateral canals. They form the posterior margins of the orbits, the frontals lacking lateral postorbital processes. Sclerotic bones are absent.

Dactylopterus

The frontals in Dactylopterus bear supraorbital and mental cross-canals (Fig. A13), but lack lateral and medial postorbital proceses. Large pterosphenoids extend ventrally from the frontals to form the interorbital septum (Fig. B14,A) along with a large basisphenoid which extends dorsally from the parasphenoid. There is no posterior myodome. The sphenotics are small and confined to the posterior corners of the orbits. Each bears the lateral canal.

Each orbital ring is complete, formed of a lachrymal and three other suborbitals (Fig. B14,B). Both the second and third suborbitals touch the lachrymal, the second being excluded from the orbit margin. It forms a long spined strut which extends posteriorly to touch the ascending limb of the preoperculum. Gregory (1933) identified the terminal part of this strut as a separate suborbital, but I was unable to separate it from the strut. These struts are very similar in shape and position to the suborbital stays of Scorpaeniformes (Fig. A3), differing mainly in their origin from the second rather than the third suborbital. The fourth suborbital is a slender tubular bone. All the bones in each orbital ring bear the infraorbital canal.

Table B1 : Characters from the orbital region

(asterisks indicate characters used in phenetic analyses)

*B1. Frontals bear(1)/ do not bear(0) supraorbital canals

*B2. Frontals bear / do not bear interorbital commisures

*B3. Frontals with/ without lateral postorbital processes

*B4. Frontals reach/ do not reach near posterior end of skull

*B5. Frontals touch/ do not touch parasphenoid lateral processes

*B6. Lachrymals bear/ do not bear infraorbital canals

*B7. Antorbitals present/ absent

B8. Lachrymals subdivided anteriorly/ not subdivided

B9. Suborbital rings complete/ incomplete

*B10. Suborbitals extend to touch preopercula/ do not touch preopercula

*B11. Pterosphenoids present/ absent

*B12. Basisphenoid present/ absent

*B13. Posterior myodome present/ absent

*B14. Dermosphenotics bear/ do not bear lateral canals

*B15. Dermosphenotics attached to sphenotics/ separate from sphenotics

*B16. Frontals with/ without distinct medial postorbital processes

*B17. Dermosphenotics bear/ do not bear infraorbital canals

*B18. Sclerotic rings present/ absent

B19. Orbit length/head length (%)

B20. Frontal length/head length (%)

Table B2 : Distributions of characters from the orbital region among framework taxa

Taxon	12345	67890	12345	678	9	0
Diplophos	11000	11010	11101	011	21.4	36.8
Saurida	10100	10010	11001	101	27.7	X
Percopsis	11000	11010	10101	111	31.8	55.0
Fundulus	10110	10000	11100	111	30.6	41.2
Melanotaenia	10100	10000	11101	111	36.3	43.3
Allanetta	10010	10000	11101	101	47.2	56.1
Holocentrus	10110	11010	11100	111	45.8	X
Asterotheca	11100	10011	10001	100	37.5	56.3
Cottus	10100	10001	10001	100	26.6	44.4
Sebastes	11000	10XX1	11101	100	23.4	38.7
Prionotus	11000	10011	11101	101	X	X
Percalates	11110	10010	11111	111	35.6	60.9
Plectroplites	11110	10010	11111	111	34.0	53.1
Perca	10110	10010	11101	100	32.2	50
Ammodytes	10110	10000	11100	101	32.5	44.6

Table B3 : Distributions of characters from the orbital region among study groups

Taxon	12345	67890	12345	678	9	0
Gasterosteus	10101	10001	00101	100	29.2	51.6
Pungitius	11101	10001	00101	100	31.2	46.7
Culaea	11101	10001	00101	100	29.9	48.6
Apeltes	11101	10001	00101	100	35.4	53.2
Spinachia	11101	10001	00101	100	23.3	50.9
Aulichthys	11101	10010	00101	101	21.8	37.2
Aulorhynchus	11101	10010	00101	101	18.1	44.0
Syngnathus	00001	00100	10001	100	14.9	34.2
Syngnathoides	00001	00100	10001	100	14.5	31.6
Hippocampus	00000	00100	10101	100	17.0	44.8
Solenostomus	00010	00000	10101	000	13.6	25.5
Aulostomus	11010	00000	10101	100	11.1	45.4
Fistularia	11010	00000	11101	000	9.5	10.1
Macrorhamphosus	10010	00000	10101	000	18.3	55.1
Aeoliscus	10010	00100	10101	011	X	47.9
Indostomus	10100	00000	10001	010	23.9	52.8
Hypoptychus	11000	10000	10101	000	35.1	42.2
Pegasus	11000	10011	11011	110	18-27	10.9
Dactylopterus	11000	10011	11001	011	34.8	46.3

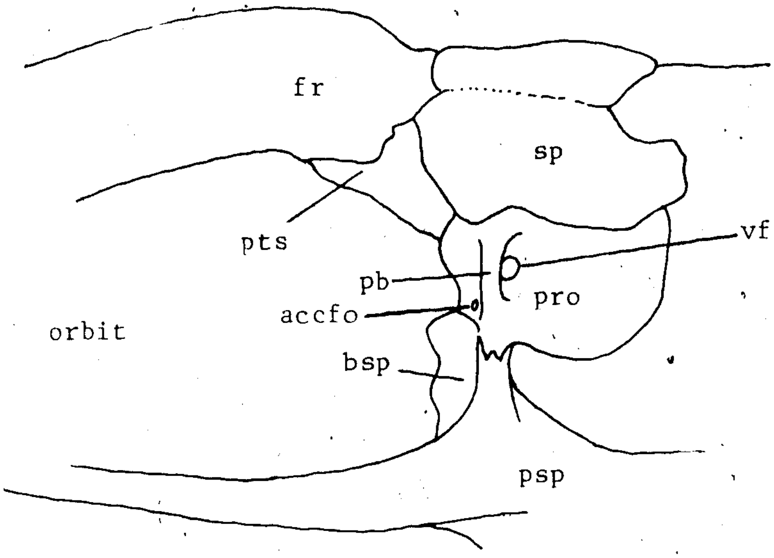

Figure B 1 : <u>Allanetta</u> <u>harringtonensis</u> posterior orbit wall, X 11.5

left ventrolateral view

(abbreviations are listed on pages xxv-xxvi)

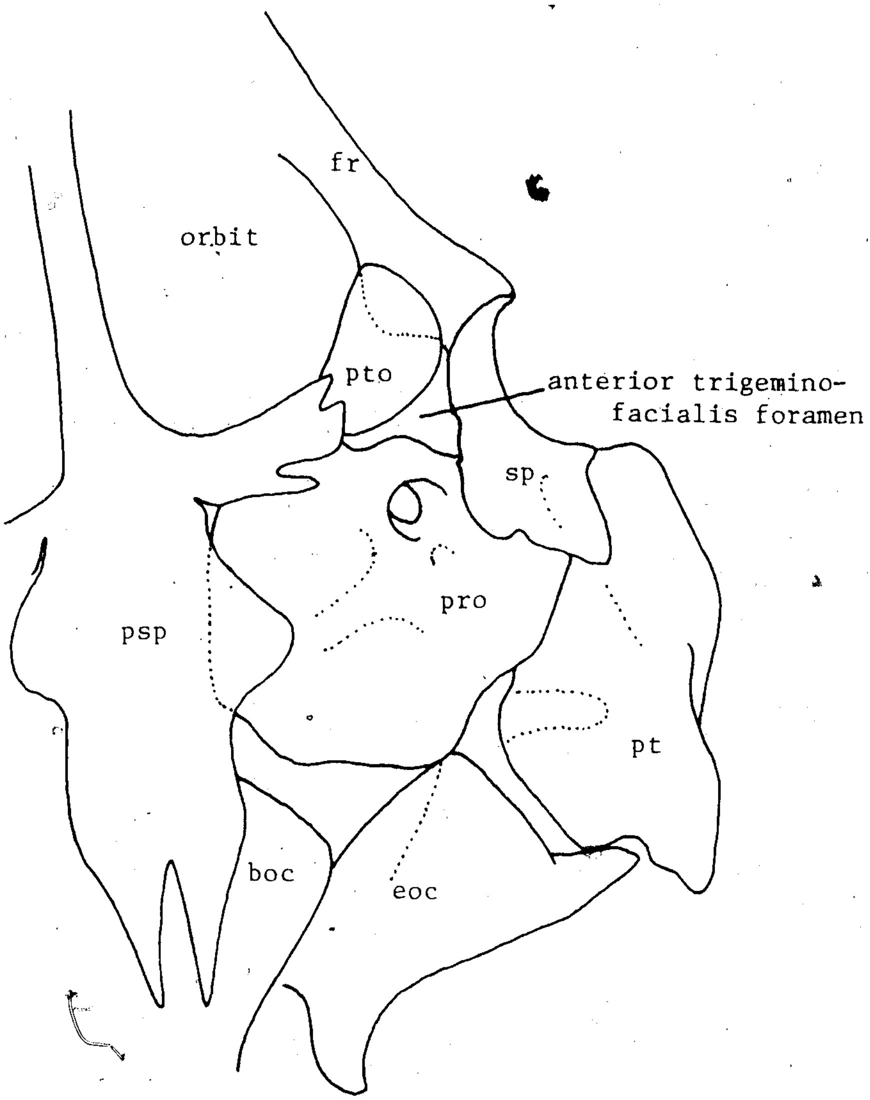

Figure B 2 : Cottus cognatus postorbital region, ventral view.
X 23.5

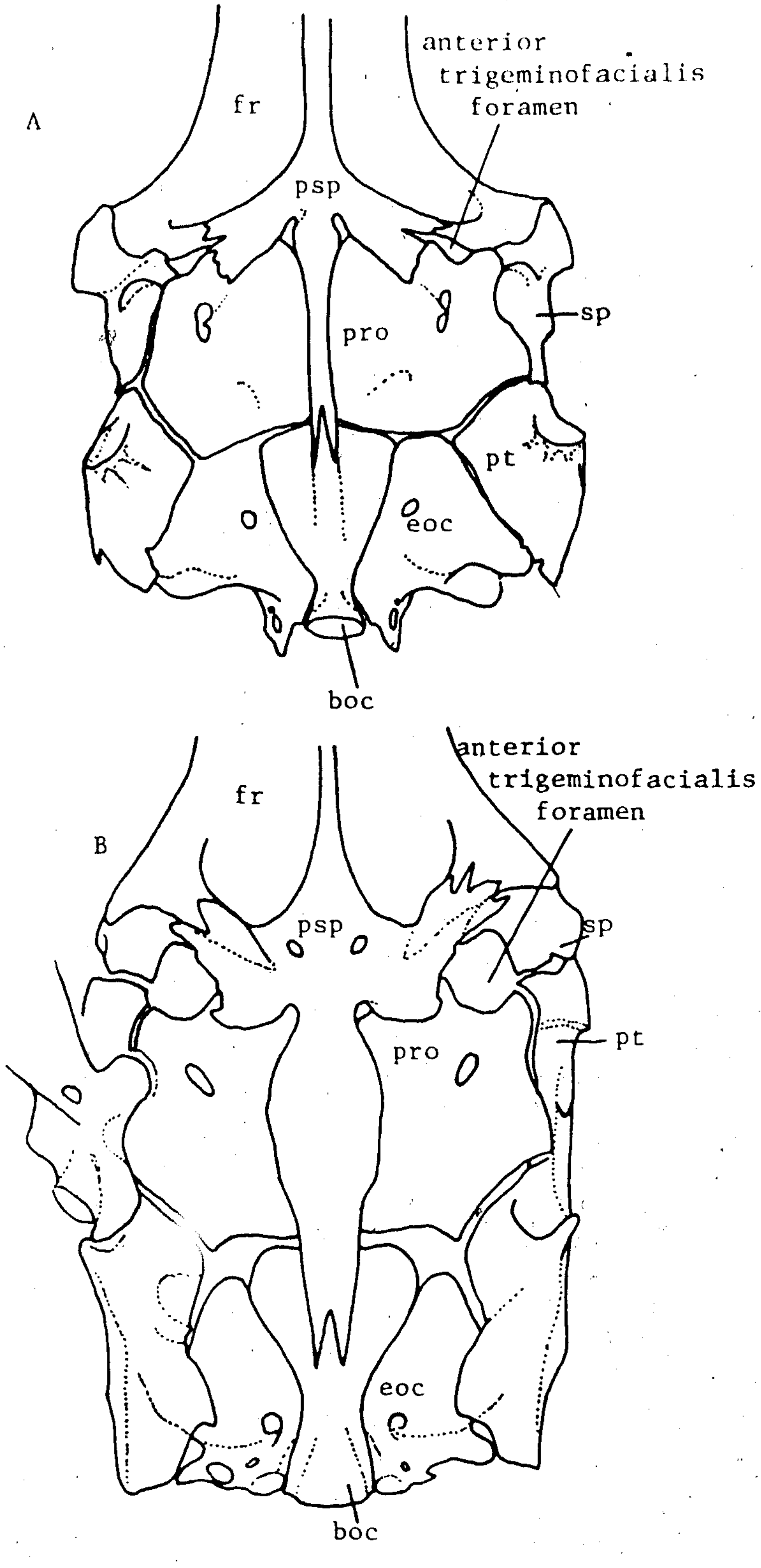

Figure B 3 : Postorbital regions of Gasterosteiformes, ventral views

A. Culaea inconstans, X 11.5 (UAMZ 5023)

B. Aulorhynchus flavidus, X 11.6 (UAMZ 1694)

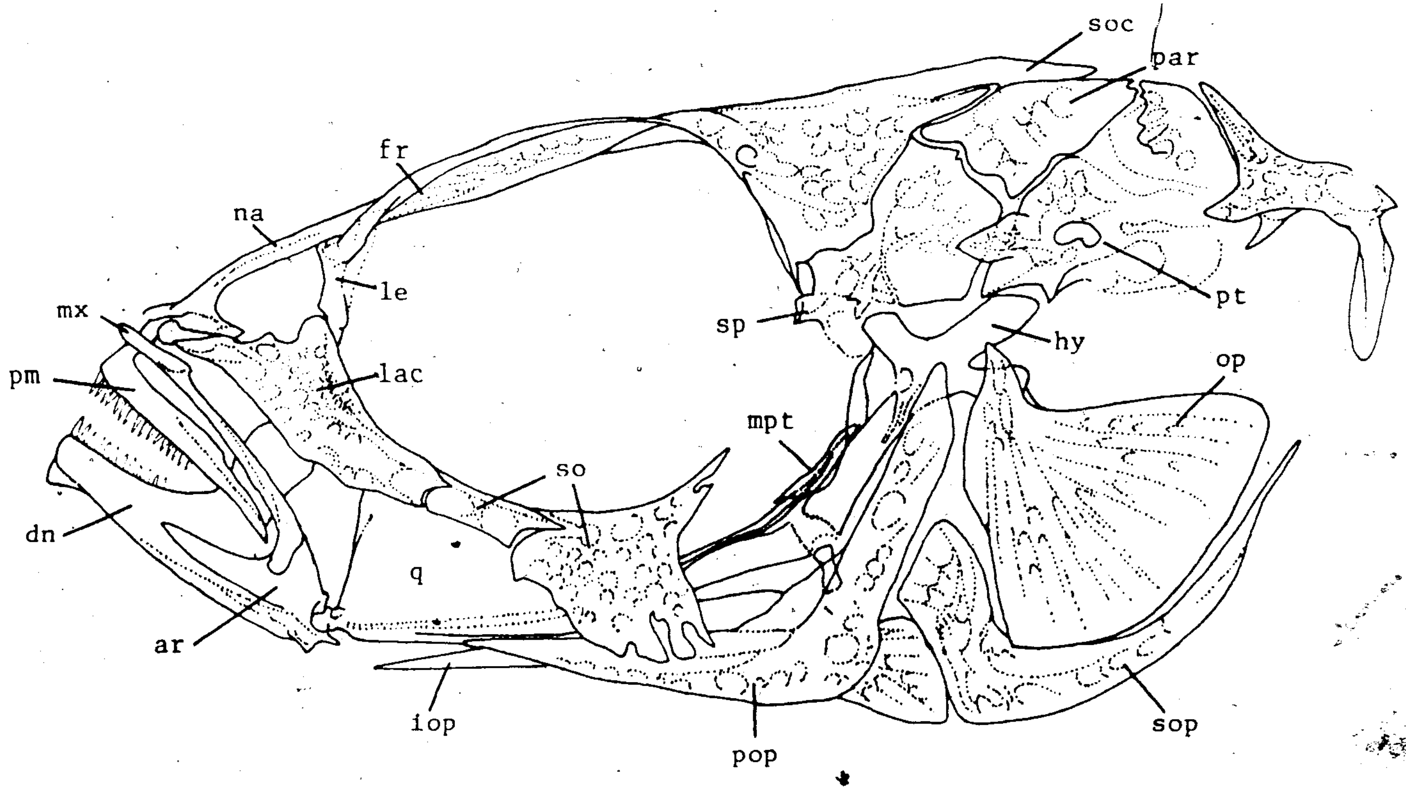

Figure B 4 : *Pungitius pungitius*, whole head, left lateral view, × 18 (UAMZ 4754)

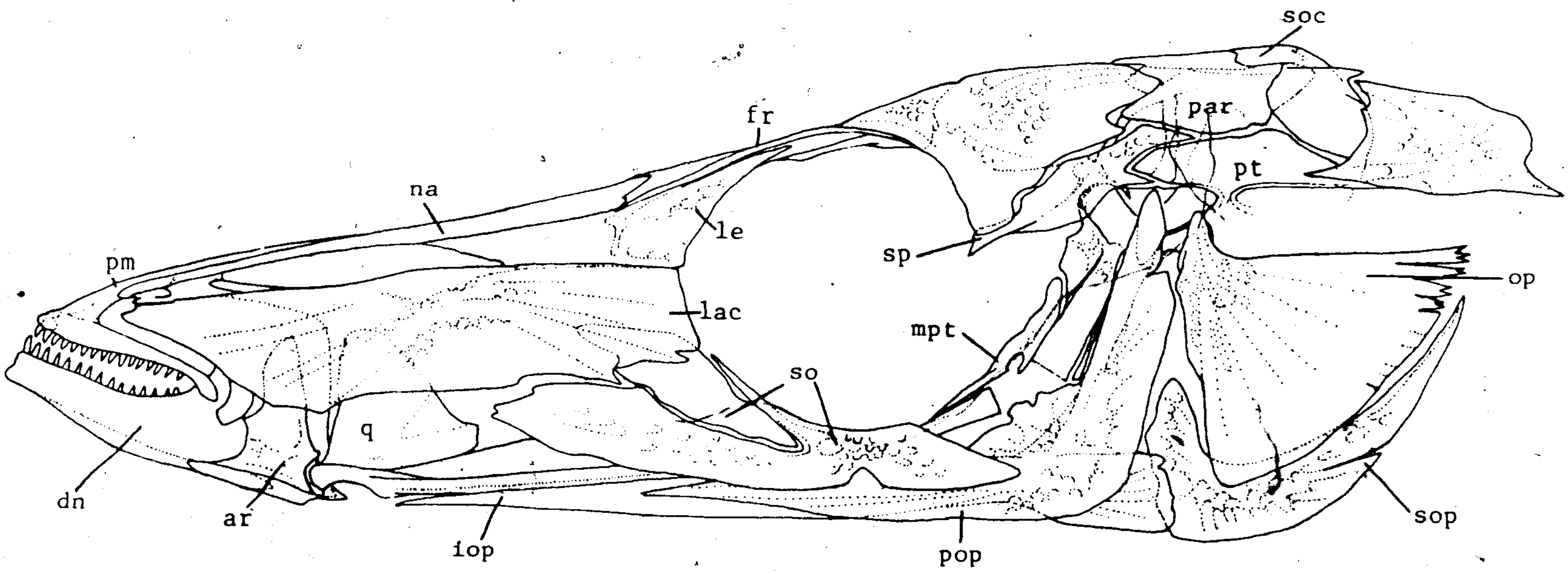

Figure B 5 : Spinachia spinachia, whole head, left lateral view, X 15

Figure B6 : Whole heads of Aulorhynchidae, left lateral views

A. *Aulorhynchus flavidus*, X 7.15 (UAMZ 5541)

B. *Aulichthys japonicus*, X 7.15


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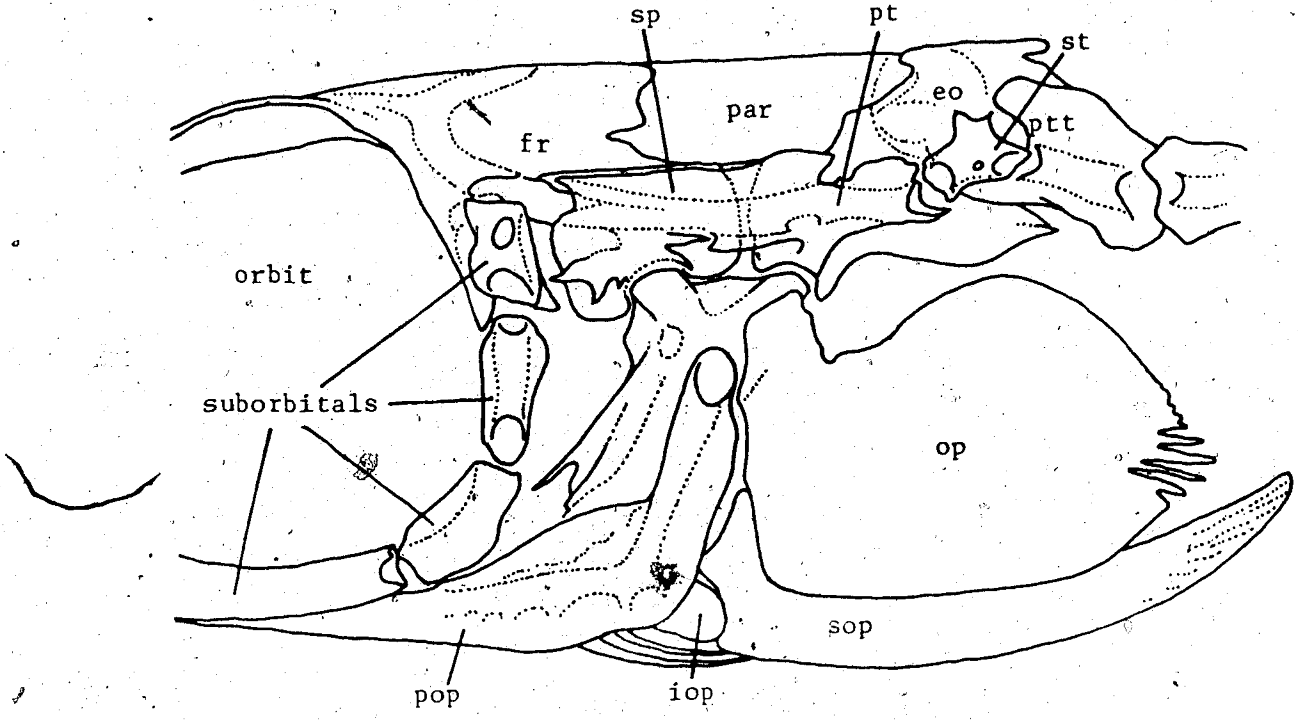


Figure B 7: *Aulorhynchus flavidus*, postorbital region, left lateral view, X 11.5 (UAMZ 5541)

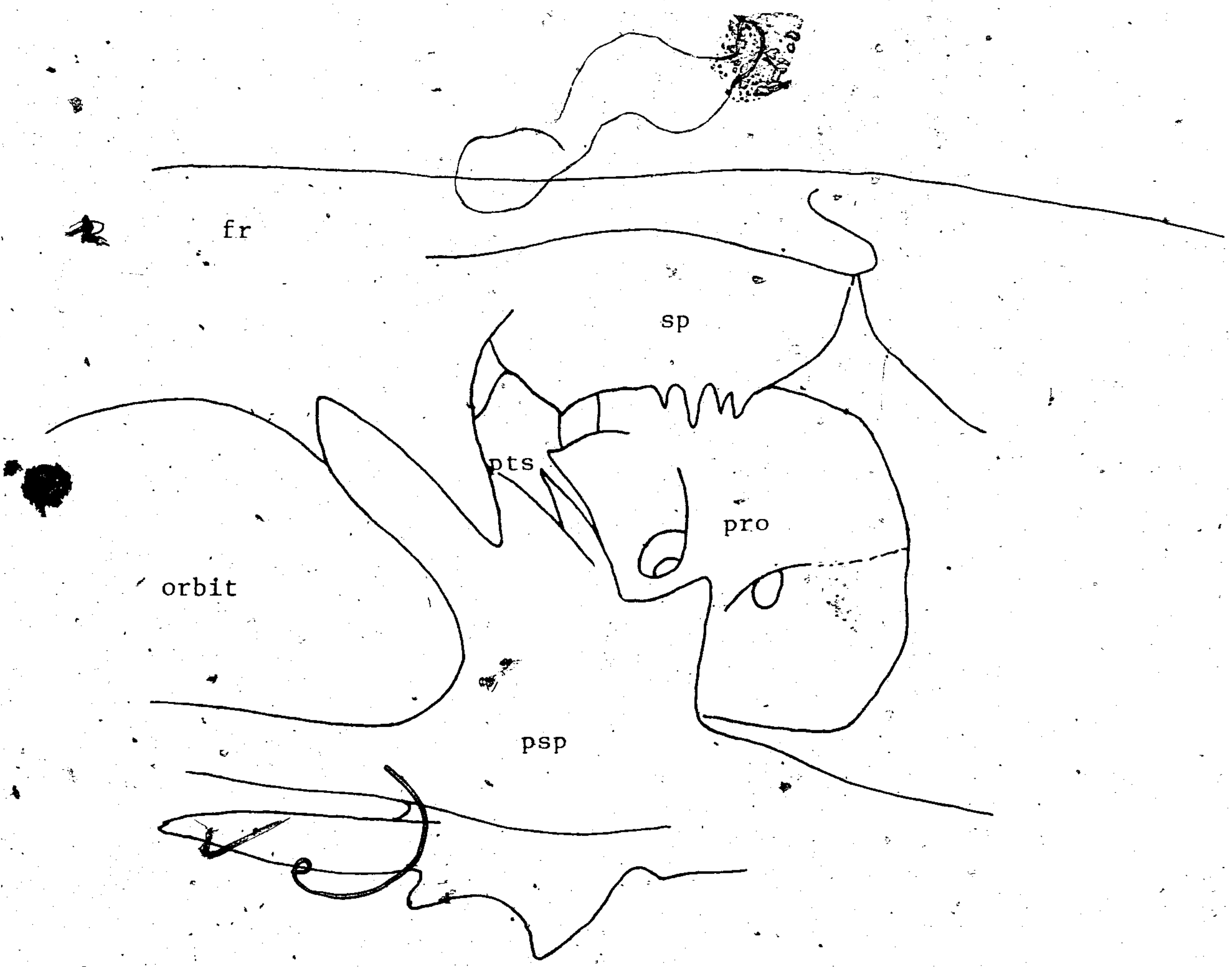


Figure B 8 : Syngnathus griseolineatus posterior orbit wall, left oblique view, X 48.5

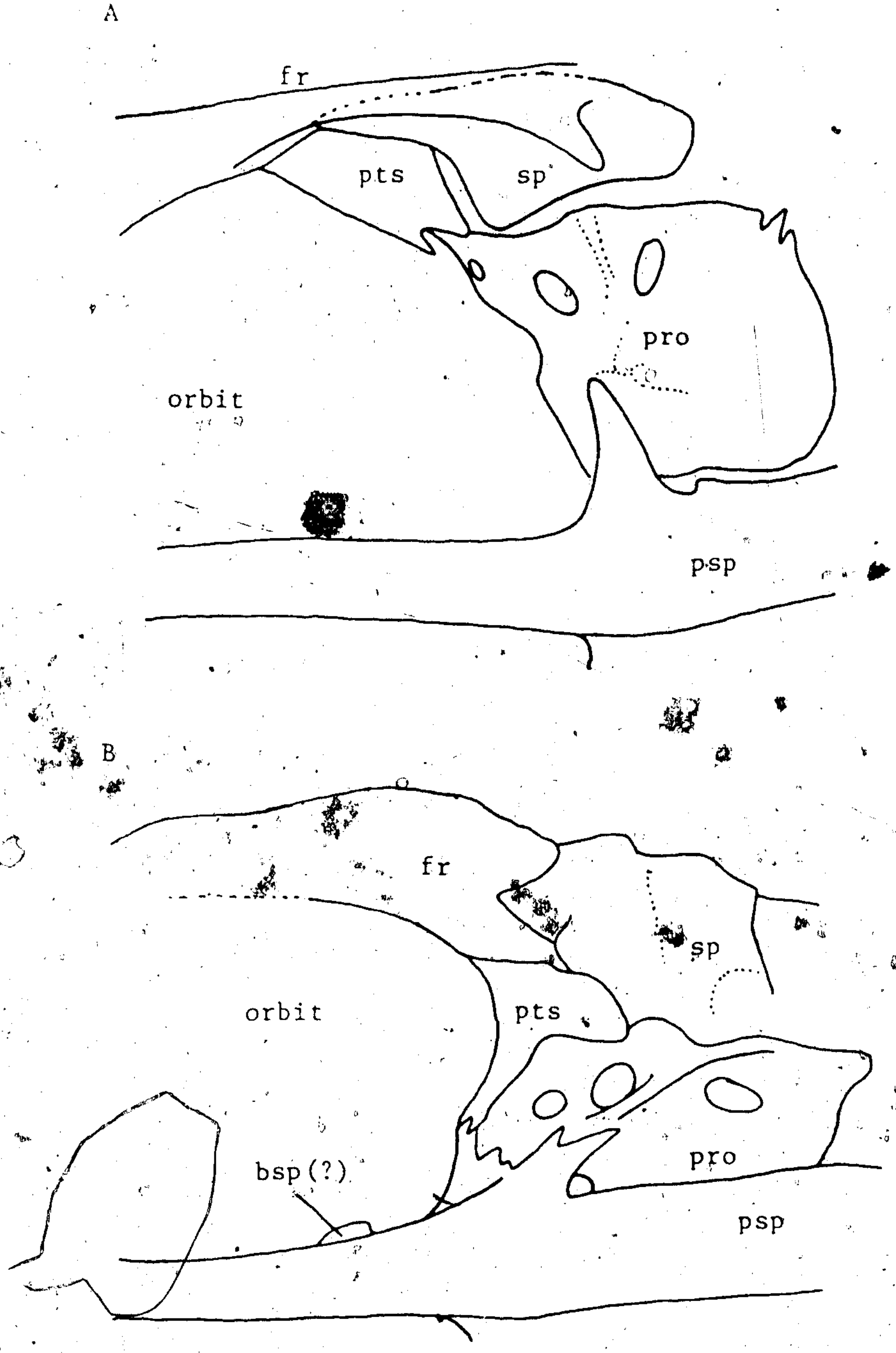


Figure B 9 : Postorbital regions of Syngnathiformes, left ventrolateral views

A. Macrorhamphosus gracilis, X 23.5

B. Fistularia tabacaria, X 11.5

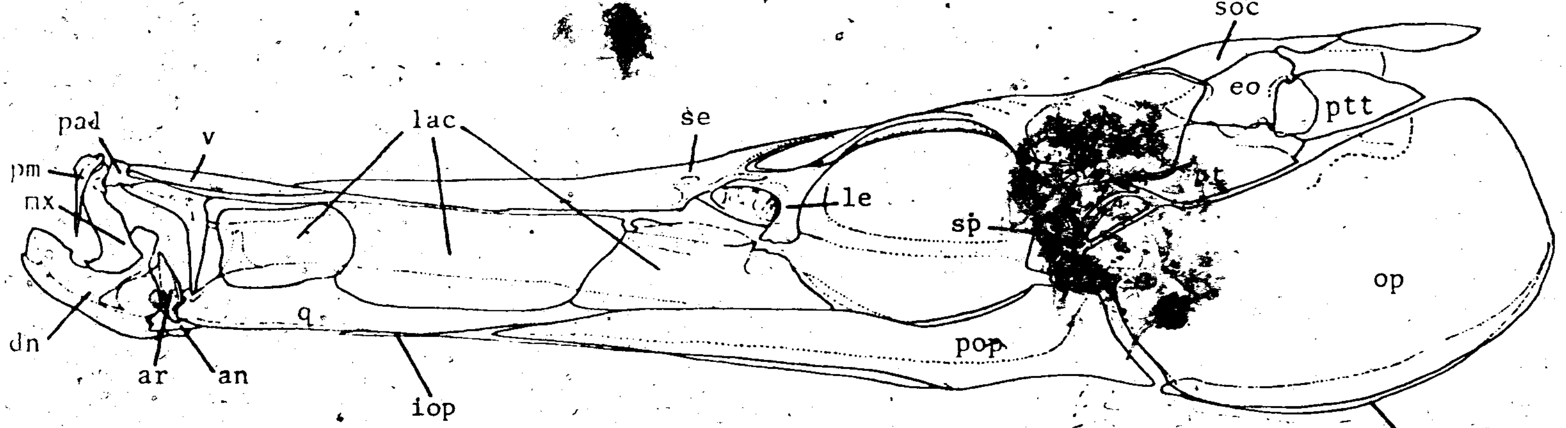


Figure B10: *Syngnathus griseolineatus*, whole head, left lateral view, X 8.6

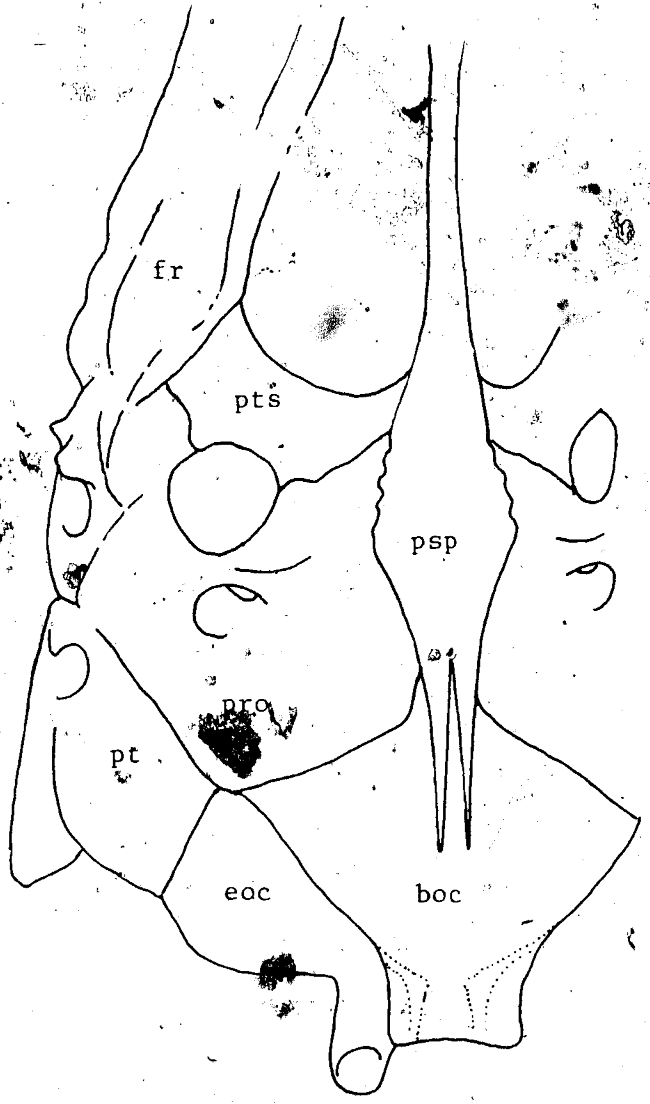
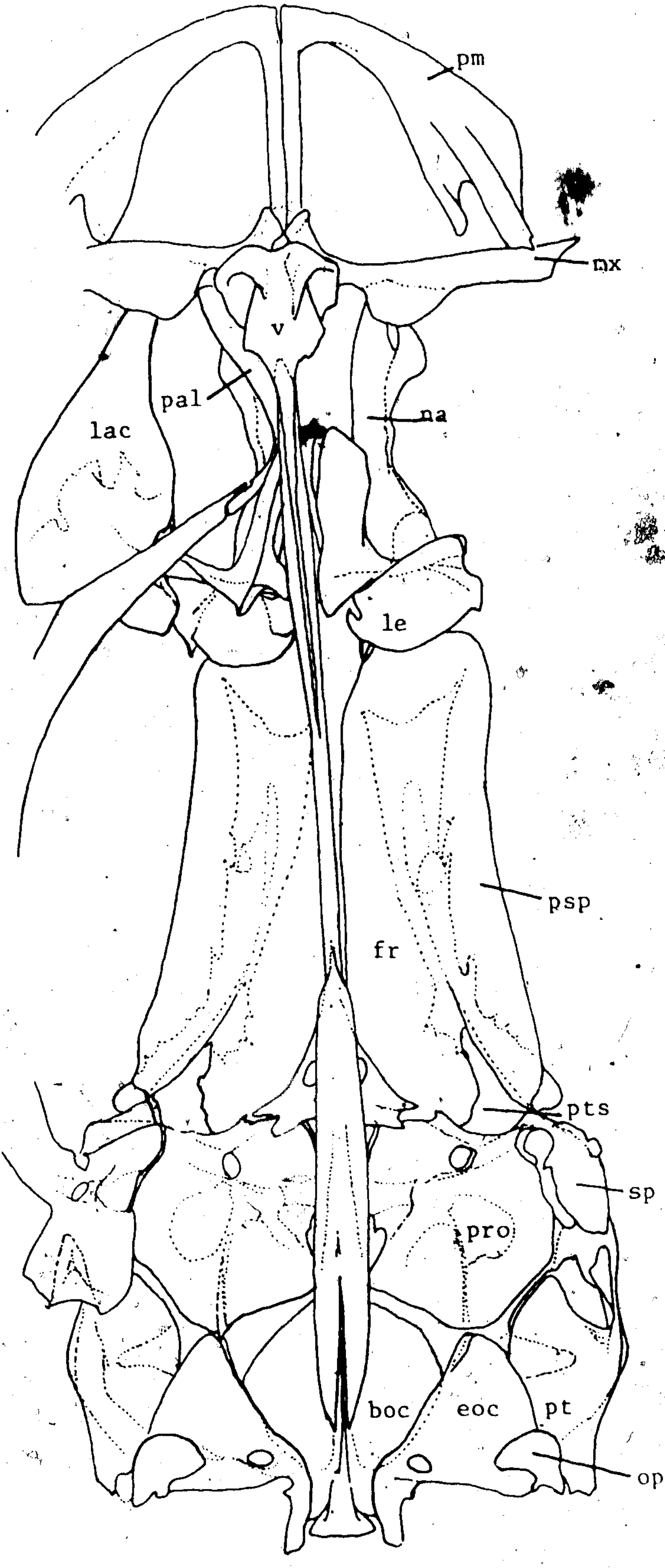


Figure B-11 : Indostomus paradoxus, postorbital region, ventral view,

X 48.5 (USNM 203888)

Figure B 12 : *Hypoptychus dybowski*, neurocranium, ventral view, X 11.5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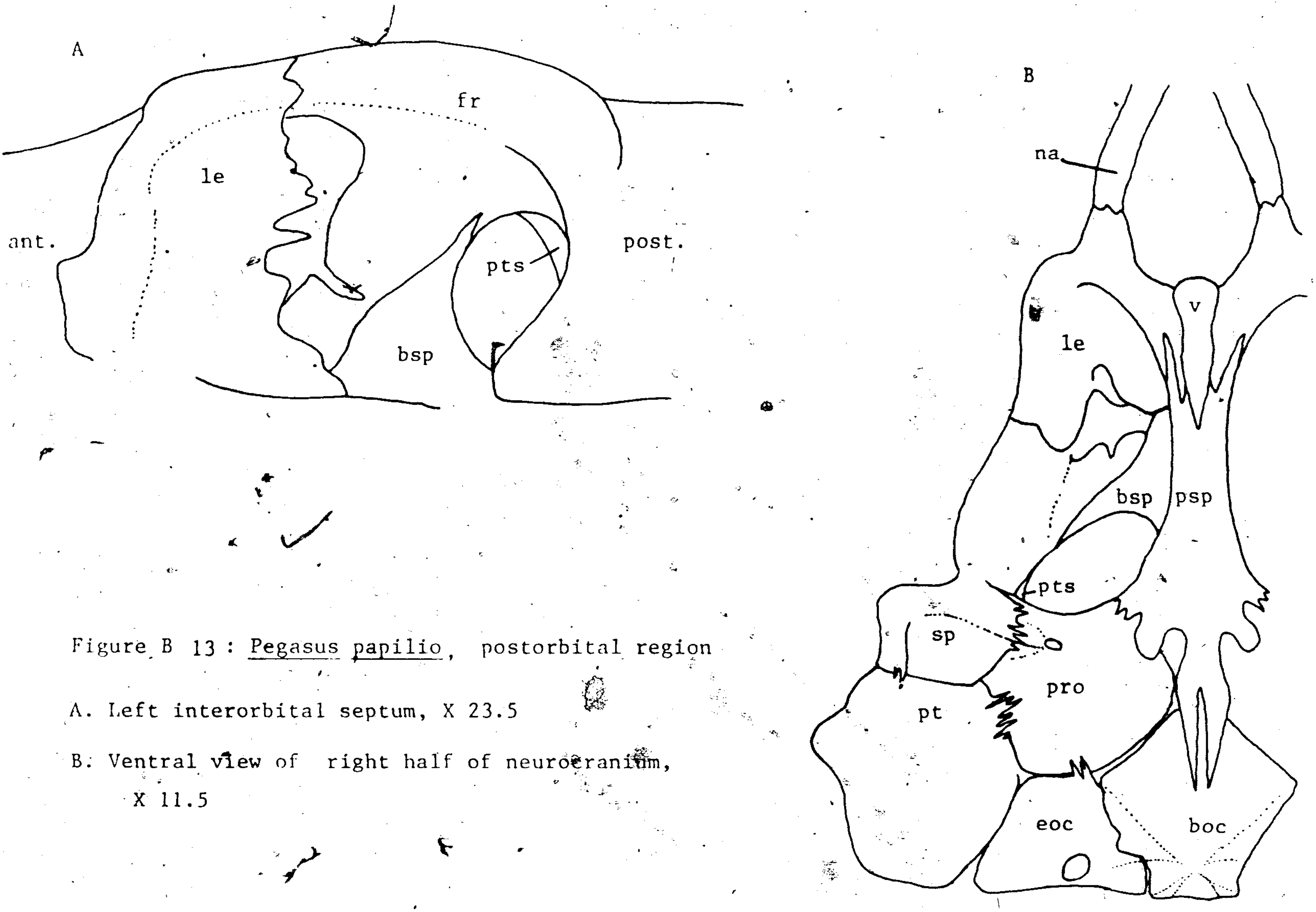


Figure B 13 : Pegasus papilio, postorbital region

A. Left interorbital septum, X 23.5

B. Ventral view of right half of neurocranium, X 11.5

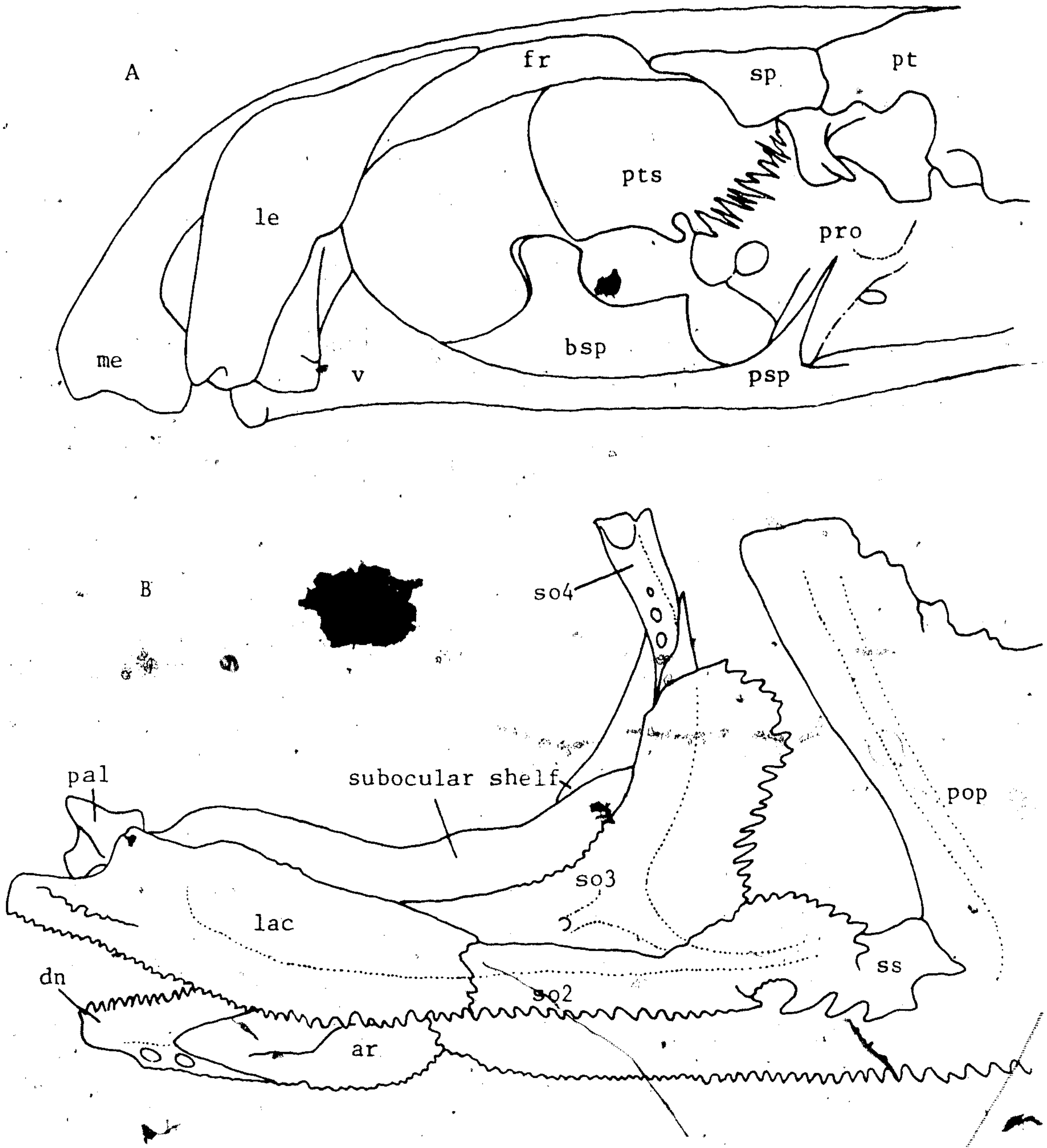


Figure B14 : Dactylopterus volitans

A. Left lateral view of neurocranium, X11.6

B. Lateral view of left suspensorium, X11.6

C. The Cranium Roof

The bones of the cranium roof are the supraoccipital, the parietals, the pterotics, and the epiotics. Extrascapulars are often present. Characters from the cranium roof are listed in Table C1, with coded data for framework and study groups in Tables C2 and C3, respectively.

Framework

In Diplophos the supraoccipital is small and is separated from the frontals by elongate parietals. The parietals meet in the dorsal midline and extend posteriorly along the anterolateral edges of the supraoccipital to meet the epiotics, which form the posterior corners of the cranium. The pterotics lie along the lateral borders of the parietals, forming the sides of the skull; they bear the lateral sensory canals for their full lengths. Behind each pterotic this canal enters an L-shaped extrascapular, which also receives the supratemporal canal from the posterolateral corners of the parietals.

This basic arrangement is also found in Saurida. The parietals of Saurida do not bear the supratemporal canals, and its pterotics bear the lateral canals between ridges of bone, instead of in closed tubes.

In Percopsis the parietals are separated anteriorly, and the supraoccipital meets the frontals. The shape of the skull is modified, the pterotics bowing outwards to form large posteroventral corners. The dermopterotics extend anteriorly over the sphenotics, each bearing a portion of the lateral canal in an open trough. The extrascapular in Percopsis is T-shaped.

The atheriniform cranial roof is variable. Parietals are present and separated in Menidia and Fundulus, but they are absent in Melanotaenia nigrans and Allanetta harringtonensis. In these fishes, the positions of the parietals are filled by the posterior portions of the frontals and the anterior portions of the epiotics. The supraoccipital is in contact with the frontals in all Atherinomorpha, and extends forward below them in a distinctive wedge-shaped process (Fig. C1). Rosen (1964) suggested this wedge-shaped process as a distinguishing characteristic of the superorder Atherinomorpha. The pterotics in Melanotaenia and Allanetta are elongated anteriorly, covering the posterior halves of the sphenotics. The extrascapulars are absent. Beryciform cranial roofs resemble those of Percopsis, but their pterotics are not bowed outward to the same degree (Zehren, 1979). The extrascapulars are present. In Holocentrus the frontals are expanded posteriorly, nearly reaching the end of the cranium.

In Scorpaeniformes some of the cranial roof characters found in Diplophos and Saurida are present. The parietals meet in the dorsal midline [illegible] the skull in Asterotheca (Fig. C2,A) and Prionotus, almost excluding the supraoccipitals from the cranial roof; in Sebastes and Cottus (Fig. C2,B), however, they are separated. The pterotics are expanded into posteroventral corners in Sebastes, but not in any of the other Scorpaeniformes I examined. They bear the lateral canal in all, but there are no extrascapulars.

In the perciforms I examined the supraoccipitals are relatively small, and they bear wedge-shaped anterior processes only in Perca. Parietals are present but do not meet in the midline. They partially cover the epiotics, which are simple limpet-shaped bones in Percalates, Perca, and Ammodytes but bear posterior processes in Plectroplites, Stizostedion , and Myctoperca . The frontals are expanded posteriorly, nearly reaching the posterior edge of the skull in Percalates and Plectroplites. The dermopterotics in Percalates, Perca, and Plectroplites overlap the posterior margins of the sphenotics and bear the lateral canals, which are continued posteriorly on T-shaped extrascapulars.

Gasterosteiformes

Gasterosteiformes have relatively large supraoccipitals with wedge-shaped anterior processes which lie under the frontals. The supraoccipitals are roughly diamond-shaped, their anterior margins bordered by the frontals and their lateral and posterior margins by the parietals and epiotics (Figs. C3-4). The parietals are relatively large and flat, their posterior borders meeting the epiotics and their lateral borders meeting the dermopterotics. In Gasterosteidae the dermopterotics do not bear any marked canals. In Aulorhynchidae, however, they bear the lateral canals in pronounced bony cylinders which extend anteriorly over the sphenotics, almost reaching the orbits (Fig. B7). I have already referred to these, in discussion of the orbital region, as fused dermopterotics and dermosphenotics.

Syngnathiformes

Syngnathiformes are distinguished by the absence of parietals, their positions being filled by either anterior extensions of the epiotics (Syngnathidae and *Solenostomus*; Fig. C5), by posterior expansion of the frontals (*Aulostomus* (Fig. C6,A) and *Fistularia*), or by both (*Macrorhamphosus*, and Centriscidae; Fig. C6,B and C).

The supraoccipital is relatively wide in Syngnathidae and *Solenostomus* (Fig. C5) and in *Macrorhamphosus* (Fig. C6,B), but narrow in other syngnathiforms. It bears a wedge-shaped anterior process in *Aulostomus*, *Fistularia*, *Solenostomus*, and Syngnathidae. The supraoccipital in *Solenostomus* also bears a rounded, platelike posterodorsal extension. In Centriscidae and *Macrorhamphosus* the supraoccipital is a thick sculptured bone, firmly sutured to the frontals and the epiotics.

The epiotics in *Aulostomus*, *Fistularia*, and Syngnathidae are limpet-shaped, their posterolateral corners overlain by the posttemporals. In my specimen of *Solenostomus paradoxus* they meet each other behind the supraoccipital, but this situation may vary, as Banister (1967) did not observe it in his specimen. Each of the epiotics in *Solenostomus* also bears an anterior process which runs along the lateral edge of the supraoccipital. The epiotics in *Macrorhamphosus* and Centriscidae appear dorsally as flat plates, square in the former and triangular in the latter, firmly sutured to the other cranial bones.

The dermopterotics are extended anteriorly in *Aulostomus*, *Fistularia*, and *Macrorhamphosus*, but only in the latter do they cover half or more of the sphenotics (Fig. A6,B). The dermopterotics of *Aulostomus*, *Fistularia*, and Centriscidae bear tubes for the lateral sensory canals; in the latter group the tubes are covered by and embedded in their strong, ornamented surfaces.

Indostomus

My observations of the neurocranium of *Indostomus* agree with Banister's (1970). Parietals are lacking in this species, their places being taken by the epiotics and frontals, as in Centriscoidei. The supraoccipital is roughly diamond-shaped, without any anterior process, and its spine and the flat dorsal plates of the epiotics together form a bony plate reaching posteriorly to the end of the first vertebra (Fig. A8). The epiotics are, otherwise, simple bones forming the posterolateral corners of the cranium. The pterotics form most of its sides but do not overlap the sphenotics, which are considerably reduced (see section B). Parallel ridges run along each dermopterotic to the frontal-borne anterior portion of the lateral sensory canal; I was unable to tell whether these ridges bounded the posterior portion of the lateral canal, but it seems reasonable to assume that they do so, since they are continuous with ridges on the frontal which obviously do form a tube.

Hypoptychus

In Hypoptychus the supraoccipital is overlain anteriorly by the frontals, which bear posteromedial processes extending towards its midpoint, and laterally by the parietals (Fig. A9). It bears an anterior wedge-like process extending below the frontals. The parietals are flat and extend posteriorly over the anterior borders of the epiotics. The epiotics are simple limpet-shaped bones forming much of the posterior face of the skull. The pterotics are elongate, overlapping the sphenotics, but the lateral canal on each side is borne in a separate tube lying above the dermopterotic (Fig. A10). The canal carried in this tube branches behind it to form the supratemporal canal, which runs dorsally in a vertical tube, and the posterior lateral canal, which passes through a second horizontal tubular bone on its way to the posttemporal. The anterior tubular bone is in a position which suggests that it is homologous to the dermopterotic, but the vertical tube and the posterior horizontal tube may be homologues either of the dermopterotic or the extrascapular. I incline to the latter view, as no other fishes examined had dermopterotics which bore the supratemporal canals in vertical tubes.

Pegasus

The supraoccipital in Pegasus (Fig. A11) is maple-leaf shaped with a thick, flat spine and no anterior process. The parietals, which are flat and sculptured, lie along its lateral edges. The supraoccipital is bordered posteriorly by the epiotics, which are small bones confined to the posterior surface of the skull and covered dorsolaterally by the posttemporals. The dermopterotics are heavy and bear the lateral canal; they do not extend anteriorly over the sphenotics.

Dactylopterus

The supraoccipital of Dactylopterus is confined to the mid-dorsal surface of the cranium, the large epiotics meeting behind it (Fig. A13). It extends anteriorly between the frontals but no anterior process beneath them is visible. Large flat parietals lie on either side of the supraoccipital, bordered posteriorly by the epiotics and small scale bones. The lateral canal extends posteriorly over the pterotic and onto the enlarged posttemporal. Extrascapulars are absent.

Table C1 : Characters from the cranium roof

(asterisks indicate those used in phenetic analyses)

*C1. Supraoccipital with large (1)/ small (0) dorsal plate

*C2. Supraoccipital crest present/ absent

*C3. Supraoccipital with/ without anterior wedge-like process

*C4. Parietals present/ absent

*C5. Epiotics bear/ do not bear posterior processes

*C6. Epiotics articulate with ossified ligaments/ ossified ligaments absent

*C7. Dermopterotics bear/ do not bear lateral canals

C8. Dermopterotics overlap over half/ less than half of sphenotics

*C9. Epiotics touch/ do not touch supraoccipital

C10. Extrascapulars present/ absent

*C11. Supraoccipital and frontals separated/ touching

C12. Supraoccipital length/head length (%)

Table C2 : Distributions of characters from the cranium roof among framework taxa

Taxon	12345	67890	1	2
Diplophos	01010	01011	1	20.6
Saurida	11011	01011	1	X
Percopsis	11010	01111	0	35.6
Fundulus	11111	00010	0	40.6
Melanotaenia	11100	0111X	0	29.7
Allanetta	11100	01110	0	33.2
Holocentrus	11011	01011	0	X
Asterotheca	00011	01010	1	10.4
Cottus	11111	01011	0	32.6
Sebastes	11011	01010	0	24.9
Prionotus	01011	01010	1	X
Percalates	11010	01111	0	37.2
Plectroplites	11011	01111	0	35.7
Perca	11110	01111	0	32.0
Ammodytes	10010	01011	0	27.7

Table C3 : Distributions of characters from the cranium roof among study groups

Taxon	12345	67890	1	2
Gasterosteus	11110	00010	0	30.6
Pungitius	11110	00010	0	31.0
Culaea	11110	00010	0	31.3
Apeltes	11110	00010	0	36.7
Spinachia	11110	00010	0	22.6
Aulichthys	11110	01110	0	18.5
Aulorhynchus	11110	01110	0	18.3
Syngnathus	11100	00010	0	19.6
Syngnathoides	11100	00010	0	18.6
Hippocampus	11100	00010	0	26.8
Solenostomus	11100	10010	0	10.5
Aulostomus	11100	11110	0	15.5
Fistularia	11100	11110	0	9.1
Macrorhamphosus	11000	00110	0	19.6
Aeoliscus	11000	01010	0	14.4
Indostomus	11000	01010	0	24.1
Hypoptychus	11110	01111	0	23.9
Pegasus	11010	01010	0	20.0
Dactylopterus	10010	01X10	0	40.9

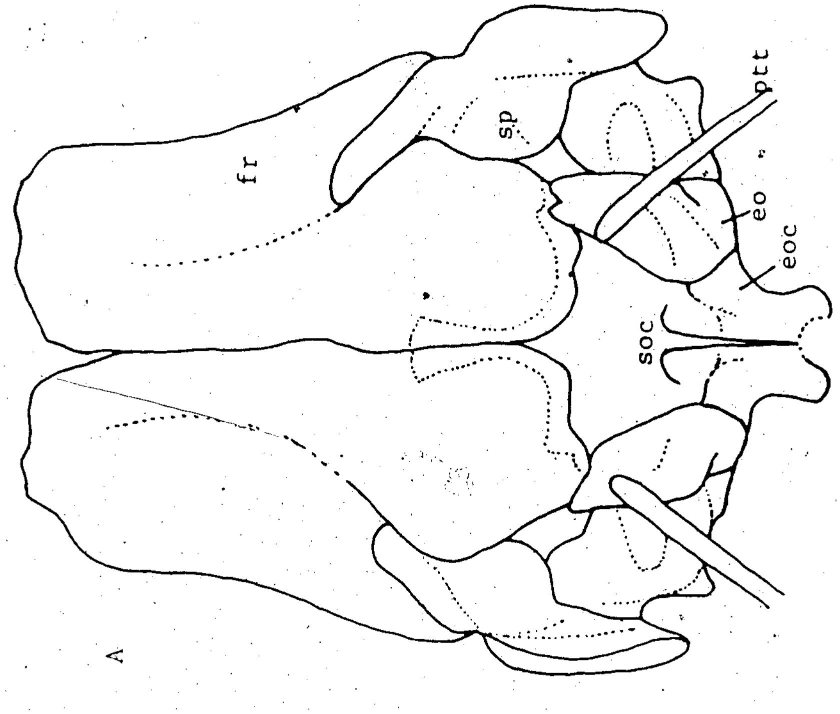
Figure C 1: Neurocrania of Atherinomorpha, dorsal views

A. Allanetta harringtonensis, X 11.5

B. Fundulus sp., X 23.5

(abbreviations are listed on pages xxv-xxvi)

A



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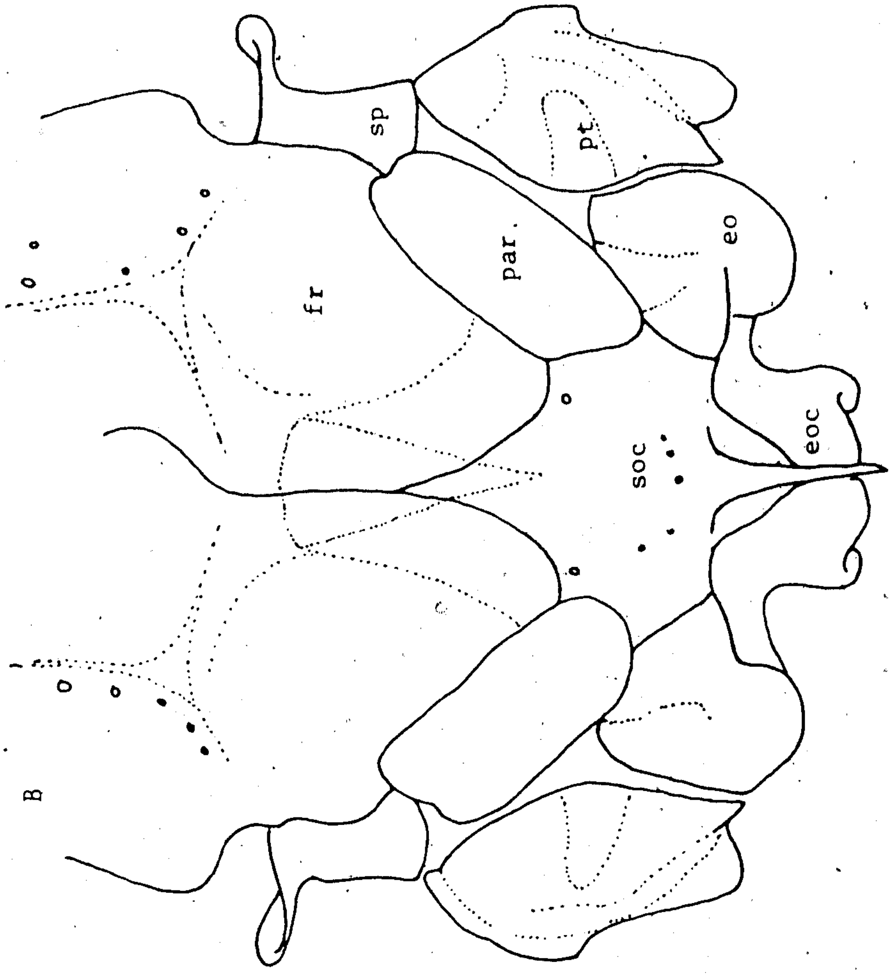

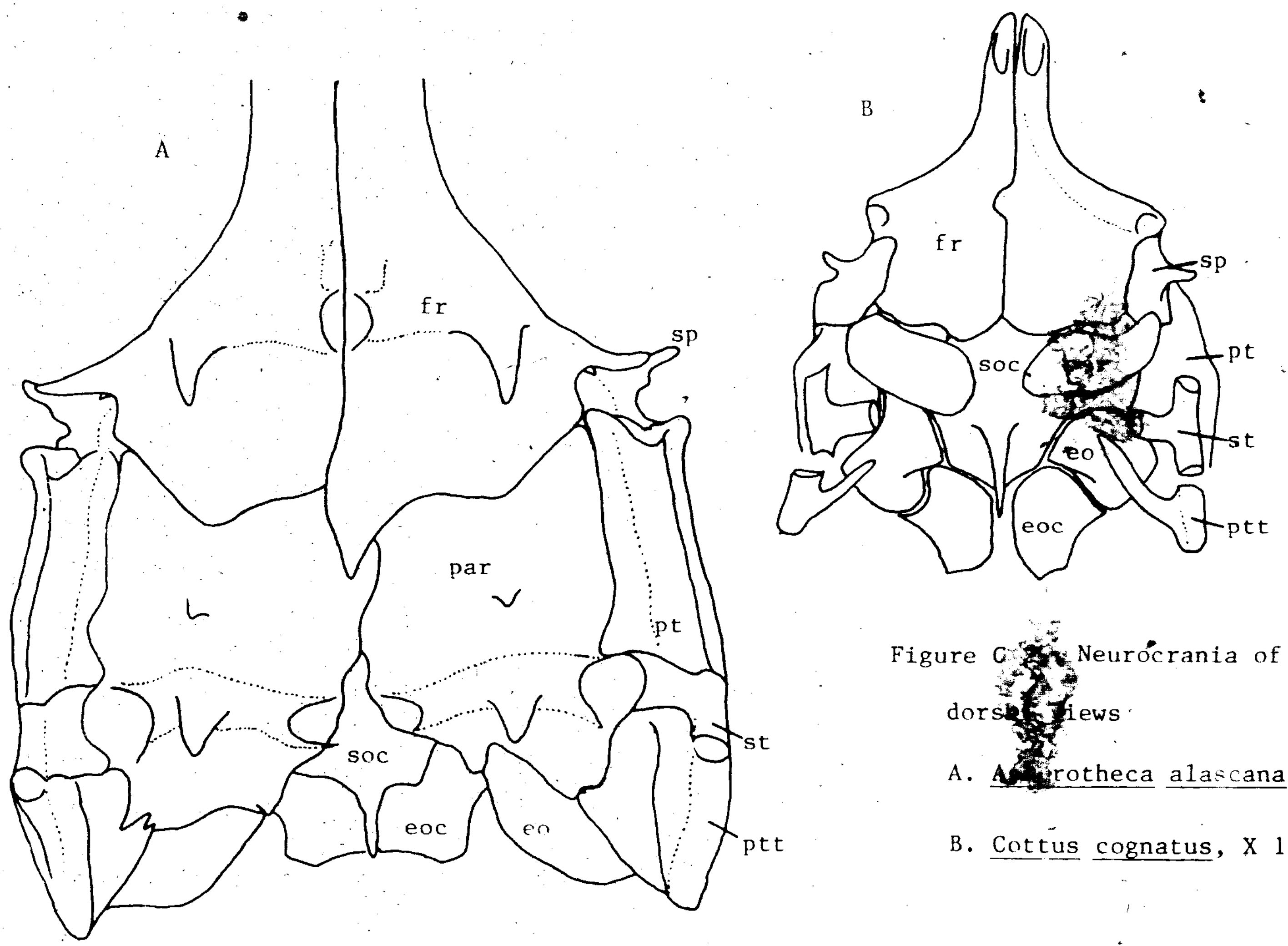

Figure C[illegible] Neurocrania of Cottoidei,
dors[illegible]iews

A. *A[illegible]rotheca alascana*, X 11.5

B. *Cottus cognatus*, X 11.5

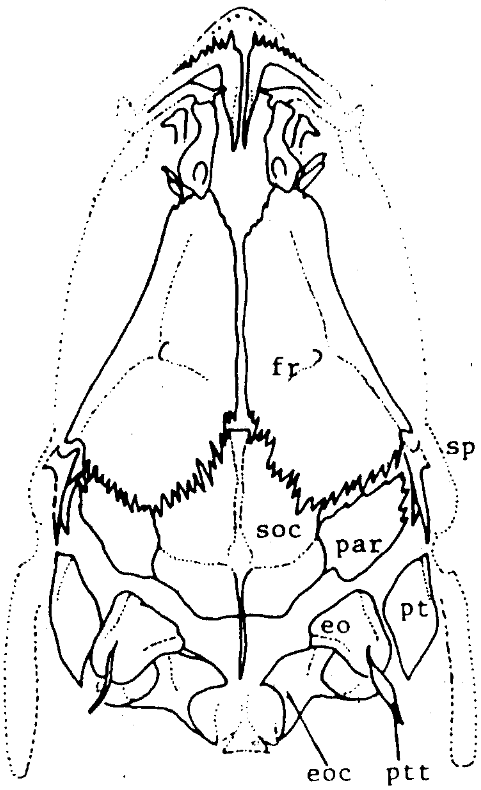

Figure C 3 : _Culaea_ _inconstans_ (immature), neurocranium, dorsal view, X 5.6

Figure C 4 : <u>Aulorhynchus</u> <u>flavidus</u>, neurocranium, dorsal view,

X 11.5 (UAMZ 1694)

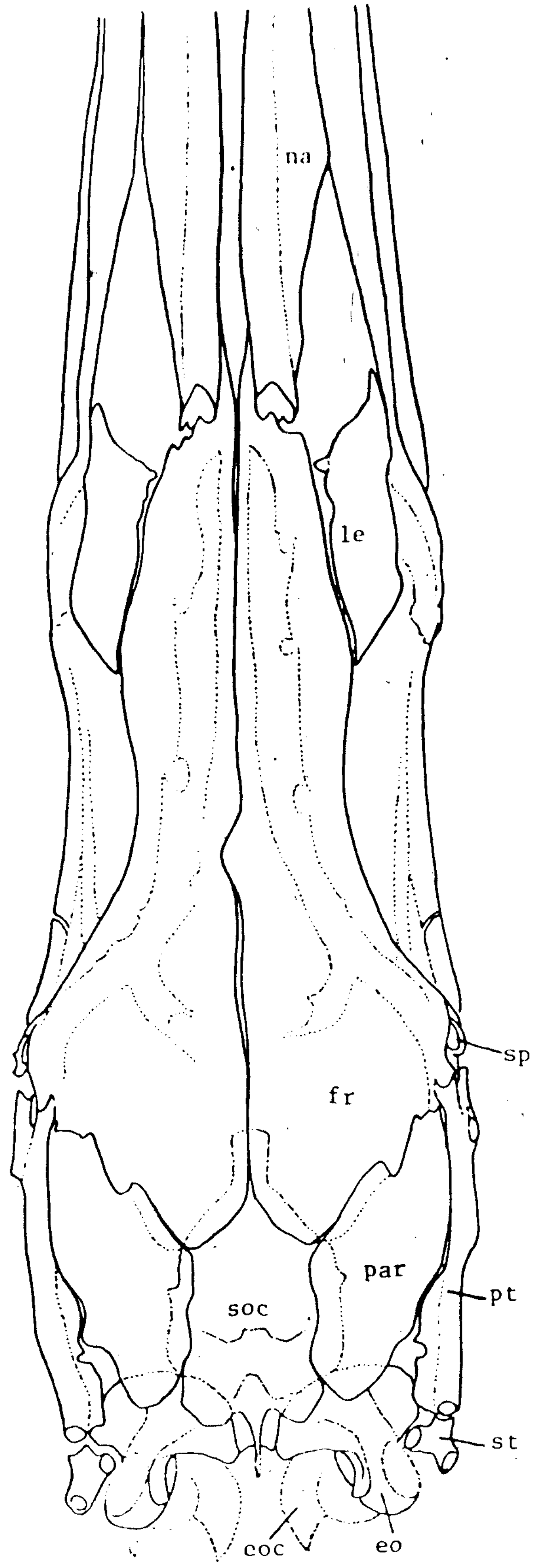
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Figure C 5 : Neurocrania of Syngnathiformes, dorsal views

A. _Syngnathus griseolineatus_, X 11.5

B. _Hippocampus hippocampus_, X 11.5

C. _Solenostomus paradoxus_, X 11.5

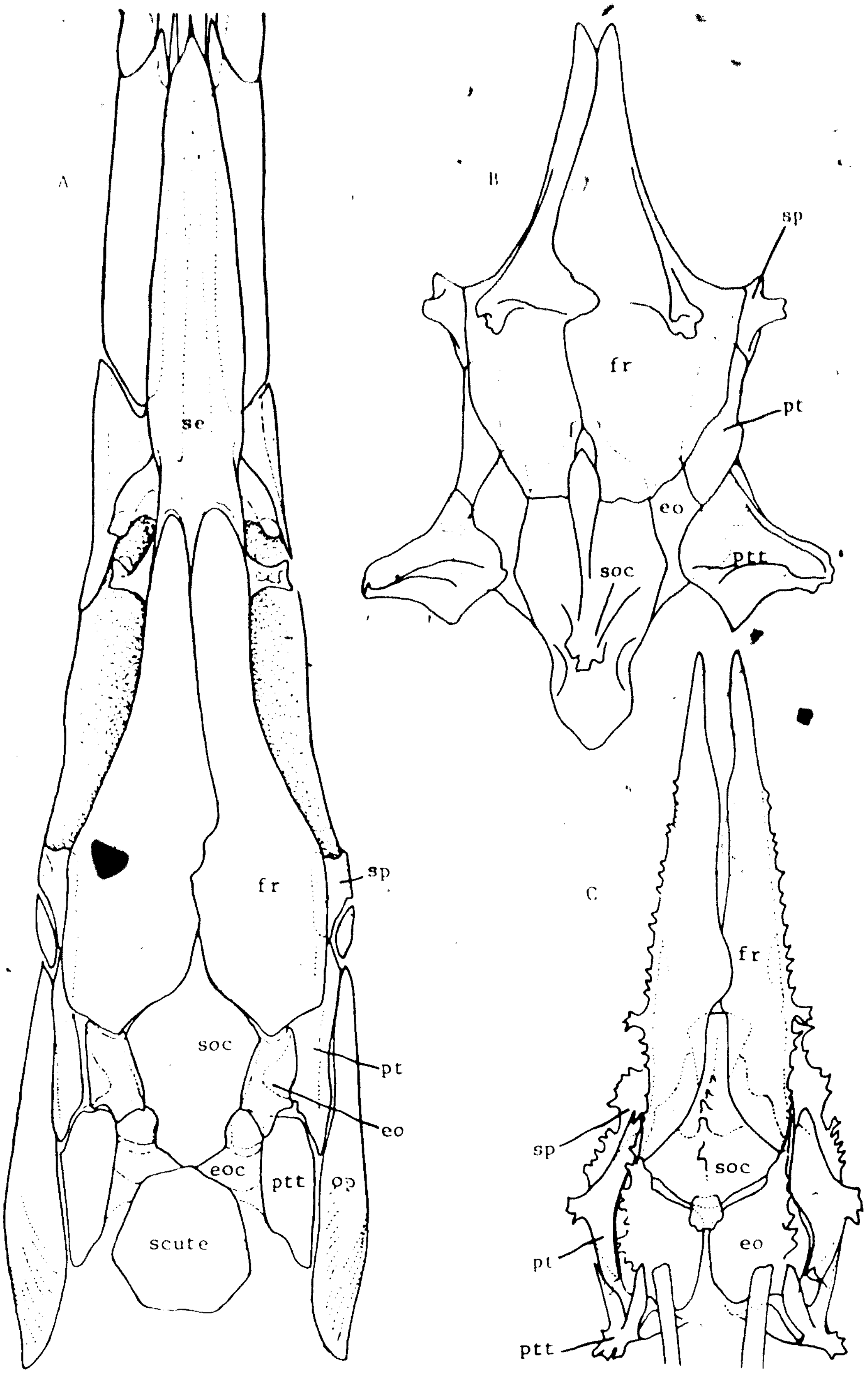
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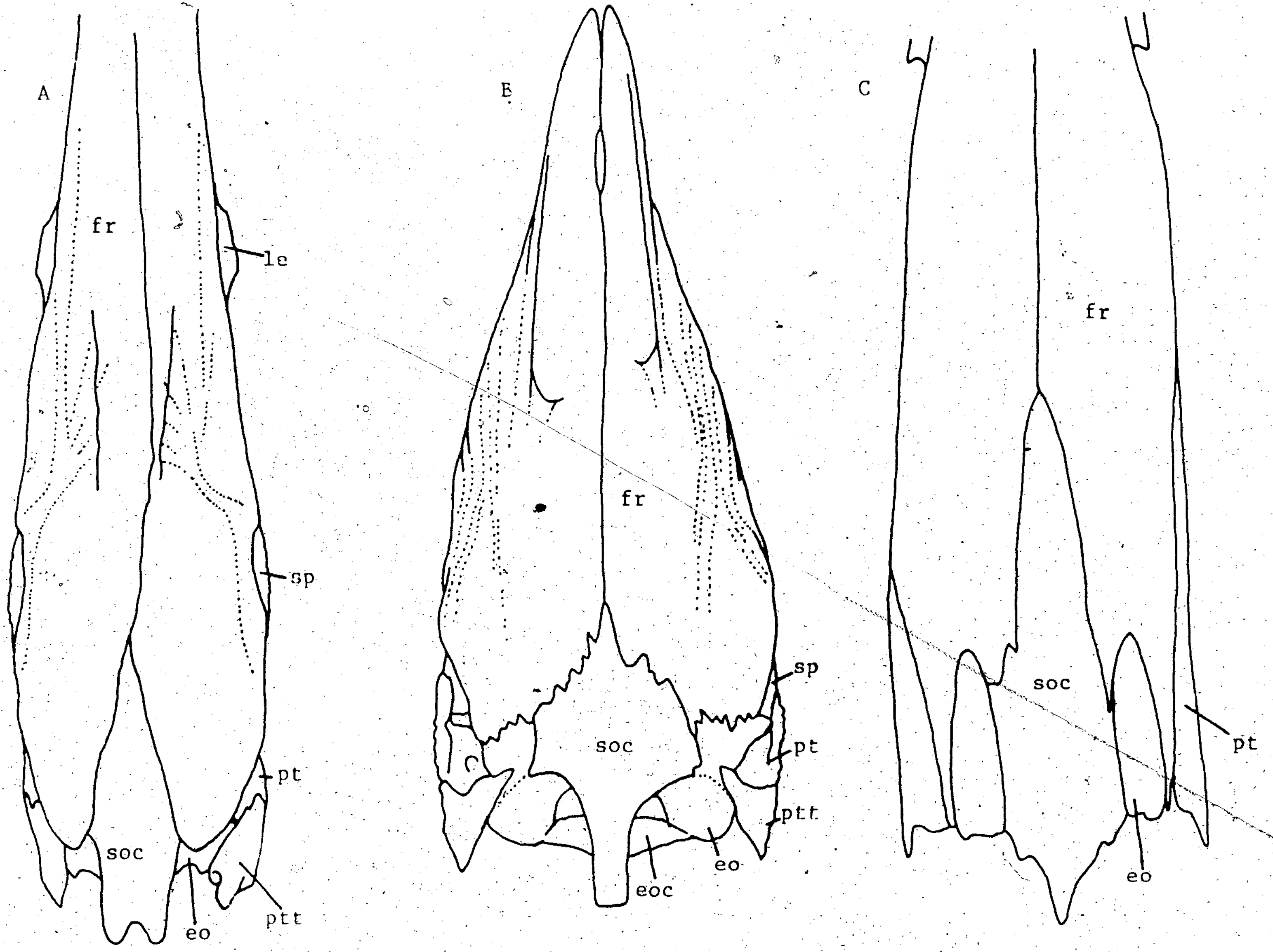
Figure C 6 : Neurocrania of Syngnathiformes, dorsal views

A. Aulostomus maculatus, X 11.5

B. Macrorhamphosus scolopax, X 5.6

C. Aeoliscus strigatus, X 11.5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D. The Cranium Floor

The bones forming the cranium floor are the unpaired parasphenoid and basioccipital, the prootics, the exoccipitals and the ventral faces of the endopterotics. The intercalaries (or opisthotics) may or may not be present. Characters from the cranium floor are listed in Table D1, their coded values for framework and study groups in Tables D2 and D3, respectively.

Framework

In Diplophos the parasphenoid anterior process is narrow and extends anteriorly almost to the vomer head. Its lateral processes are short and no carotid foramina are visible piercing them. The posterior process is broad and undivided. The anterior cranial floor is flat, formed by the prootics. Each prootic is a rounded bone bordered medially by the parasphenoid, posteriorly by the basioccipital and exoccipital, laterally by the pterotic and sphenotic, and anteriorly by the pterosphenoid and basisphenoid, which exclude it from the postorbital foramen. One foramen opens behind the prootic bridge, one in front of it.

The posterior cranial floor is ventrally convex; the basioccipital and exoccipitals bend downward on each side of the parasphenoid posterior process to form a deep otic bulla. (see Fig. 7 of Fink & Weitzman, 1982). The exoccipitals meet one another directly above the basioccipital condyle, their articular facets supplementing it dorsally. Each exoccipital is pierced laterally by a single foramen. The intercalaries are present but are confined to the posterior face of the cranium; each covers the junction of the pterotic, epiotic, and exoccipital.

In Saurida the parasphenoid is expanded between the lateral ethmoids and its short lateral processes are pierced by minute foramina. Its posterior process is very wide, almost covering the basioccipital, and is ventrally convex; posteriorly, it is divided into two lobes between which the basioccipital condyle emerges.

In this fish both the anterior and posterior portions of the cranial floor are ventrally convex. The prootics and exoccipitals extend dorsally from the parasphenoid-basioccipital strut and then turn abruptly laterally, so that the parasphenoid and basoccipital form a keel running the length of the neurocranium. The prootics bend dorsally at the prootic bridges, so that the anterior openings of the trigeminofacialis chambers open into the orbit. Each prootic has a single posterior foramen on its mid-ventral surface.

The exoccipitals do not form articular facets or condyles, but the vertical surface of each bears a triangular ventral process. A single lateral foramen opens at the base of this process. The horizontal face of the bone is pierced by a second, more anterior ventral foramen. Intercalaries lie on the posteroventral face of the cranium, over the exoccipital-epiotic suture.

In Percopsis the anterior process of the parasphenoid is narrow and the lateral processes are long, pierced by carotid foramina. The posterior process is slender and divided. The basioccipital and prootics are bowed ventrally to form the posterior and anterior portions of the otic bullae. The prootic bends dorsally at the prootic bridge; the trigeminofacialis chamber opens below the bridge via one divided foramen, and the anterior face of the prootic is pierced by three additional foramina.

The exoccipitals extend posteriorly to form large articular condyles; they are separated from the prootics anteriorly by the large intercalaries. Each exoccipital bears one foramen on its posterolateral surface, ventral to the base of the condyle, and one ventral foramen on the flat anterior portion of the bone.

Atherinomorpha have slender parasphenoids like those of Percopsis in most respects, although their lateral processes are short in Melanotaenia and Allanetta and double in Fundulus (one pair extending dorsally to the pterosphenoids and the second laterally to the prootics). A foramen appears on each side of the parasphenoid, its anterior and medial borders formed by the angle between the parasphenoid posterior and lateral processes. The prootics vary. In Melanotaenia and Allanetta (Fig. D1,A), which lack the anterior lateral process from the parasphenoid, the prootics participate in the postorbital foramina. The prootics of Fundulus (Fig. D1,B) are excluded from the postorbital foramina by the anterior parasphenoid processes, and each is pierced by two foramina behind the prootic bridge. Allanetta lacks the second posterior prootic foramina, but this may be because the prootics are only partially ossified in the specimens I examined.

The basioccipitals in Fundulus and Melanotaenia are nearly flat and are bounded anteriorly by the prootics and laterally by the exoccipitals; in Allanetta, however, the basioccipital is reduced to a small diamond-shaped bone whose lateral points are bent ventrally, forming the posteromedial corners of the otic bullae. A large unossified area separates the basioccipital from the prootics and pterotics.

The exoccipitals form medially-facing articular condyles. Each exoccipital is pierced by a lateral foramen (two in Allanetta and Fundulus) dorsal to the condyle and by a ventral foramen in the flat anterior portion of the bone. Intercalaries are absent.

In Holocentrus the parasphenoid bears lateral flanges in the orbital region and a short posterior process. It is not pierced by foramina. Each prootic has a large anterior face, pierced by two foramina , which is excluded from the postorbital foramen by the basi- and orbitosphenoids. The posterior portion of each prootic is pierced by a single foramen. The basioccipital is relatively flat. Its condyle is augmented by exoccipital condyles similar to those in Atherinomorpha. As in Diplophos, the exoccipitals meet above the basioccipital to form the ventral margin of the foramen magnum. They appear to have neither anterior nor lateral foramina and are firmly sutured to the prootics anteriorly. Intercalaries are located on the ventral surface of the skull over the pterotic-exoccipital sutures.

In the scorpaeniforms examined the parasphenoid is long, slightly expanded between the ethmoids (except in Cottus), and has a wide posterior process (Fig. D2). In Sebastes, Cottus, and Asterotheca there is a foramen in the angle between the lateral and posterior processes; in Prionotus the lateral and posterior processes are fused to form one wide plate, pierced on each side by a foramen. The anterior faces of the prootics reach the postorbital foramen in Sebastes and Prionotus, but are excluded from it by the parasphenoid and pterosphenoids in Asterotheca and Cottus (Fig. B2). Quast (1965) suggests that this characteristic be used to separate the scorpaenid fishes from the hexagrammids, zaniolepids, cottids, and agonids. The trigeminofacialis chambers open through a single large foramen beneath each prootic bridge; the ventral faces of the prootics bear some extremely small central foramina in all except Cottus, and similar tiny foramina pierce their anterior faces in Sebastes and Prionotus. The basioccipital is bowed ventrally and exoccipital condyles lie on either side of its condyle. A foramen opens on the base of each exoccipital condyle and another opens slightly anterior to it on the body of each bone. I observed intercalaries only in Cottus.

In the Perciformes examined the parasphenoids have lateral processes (pierced by foramina in Percalates and Plectroplites). Each trigeminofacialis chamber opens through two foramina, one before and one behind the prootic bridge, and a second small foramen is present in the anterior face of each prootic. In Ammodytes and Perca the ventral face of each prootic is pierced centrally by a second foramen. The exoccipitals are very similar to those of Sebastes, each with a condyle and two foramina. Ammodytes, Perca, and Plectroplites have intercalaries, but I could see none in the specimen of Percalates.

Gasterosteiformes

Gasterosteiform parasphenoids resemble those of the acanthopterygians examined (Fig. B3). A single foramen opens at the center of each prootic and each trigeminofacialis chamber opens anteriorly via a foramen between the anterior edge of the prootic and the posterior edge of the parasphenoid-frontal strut which bounds the postorbital foramen. I refer to this as an incomplete trigeminofacialis anterior foramen. The basioccipitals are roughly pentagonal or fan-shaped, and each forms the entire occipital condyle. The occipital condyle is flanked by flat posterior extensions from the exoccipitals, except in Aulorhynchus, which has exoccipital condyles (Fig. B3,B). Each extension is pierced by a lateral foramen. The exoccipitals of Gasterosteus, Pungitius, and Apeltes each have two ventral foramina.

Syngnathiformes

Syngnathiform parasphenoids are delicate compared to those of other fishes, their function in supporting the snout apparently being performed by the supraethmoids. The typical syngnathiform parasphenoid has a short, thin anterior process extending before the orbit for less than a third of the snout length (see Fig. D3,A). This process is expanded laterally between the lateral ethmoids. Behind the orbit it expands again to form short broad lateral processes, behind which it narrows gradually to form the posterior process. The carotid foramina, when visible, open in the angles between the lateral and posterior processes.

The prootics are distinguished by possession of wide prootic bridges so that each anterior trigeminofacialis foramen is separated from the ventral foramen by a wide flat space. In Syngnathoides and Solegnathus each anterior foramen opens between the anterior margin of the prootic and the frontal-parasphenoid strut (Fig. B8); in all other Syngnathiformes it is enclosed in the prootic, and in Aulostomus and Fistularia each prootic bears a second, more medial anterior foramen. Most Syngnathiformes are distinguished by a wide separation between their prootics and basioccipitals (Figs. D3-5). In Aulostomus and Fistularia the pterotics interpose between the two (Fig. D4,A) but in all others they are separated by a zone of cartilage. The basioccipitals are narrow in all Syngnathiformes except Macrorhamphosus (Fig. D4,B) and Solenostomus (Fig. D5), in which the basioccipital extends laterally to fill the area usually filled by the ventral surfaces of the exoccipitals. In all Syngnathiformes the basioccipitals form the occipital condyles. Jungersen (1910) found exoccipital condyles in Syngnathidae and posterolateral processes on the exoccipitals of Solenostomus; I saw neither. The exoccipitals in Syngnathidae and Macrorhamphosus have two ventrally opening foramina, but there are no foramina in those of Solenostomus and Fistularia. Intercalaries are absent in all Syngnathiformes.

Indostomus

The parasphenoid in Indostomus is simple, without lateral processes or foramina (Fig. B11). The prootics are confined to the ventral face of the skull. Banister (1970) states that each trigeminofacialis chamber opens through two ventral foramina, but I found only a single foramen in the center of each prootic and an incomplete anterior foramen whose anterior margin was formed by the pterosphenoid. The basioccipital is diamond-shaped, bordered anteriorly by the prootics and posteriorly by the exoccipitals, which extend posteriorly to form two rounded exoccipital condyles. No foramina are visible on the exoccipitals.

Hypoptychus

The parasphenoid of Hypoptychus is slightly expanded between the ethmoids (Fig. B12). Below the posterior portion of the orbit it is expanded into a plate which forms the posterior process. Its lateral processes are short, each pierced by a large foramen. The prootics are large and flattened and each has a single ventral foramen. The basioccipital is fan-shaped, its condyle flanked by well-developed exoccipital condyles. Each exoccipital is pierced by a single lateral foramen and a single ventral foramen.

Pegasus

The parasphenoid in Pegasus is short and robust (Fig. B13), its broad anterior process just reaching the anterior margin of the orbit. The lateral processes are short and stout with foramina located behind them. The prootics are roughly circular and each has one central foramen. The basioccipital is diamond-shaped, forming the entire occipital condyle; there are no exoccipital condyles. Each exoccipital is pierced by a lateral foramen opening on the posterior face of the skull and by a ventral foramen at its posterior margin. There are no intercalaries.

Dactylopterus

The parasphenoid is wide, with two short lateral processes behind the orbits (Fig. A14). The carotid foramina open in the angles behind these processes. Its posterior process is wide and not divided. Instead of lying on the ventral surface of the basiocciptal, it is sutured to the anterior margin of that bone. The prootics are large bones forming most of the posterior walls of the orbits, and each is pierced by a single ventral foramen and by two anterior foramina. They contact the pterosphenoids and pterotics. The lateral portion of each prootic bends dorsally to form the side of the neurocranium.

The basioccipital is narrow and flat. The exoccipitals bend sharply dorsally to form the walls of the otic bullae and then laterally beneath the lateral head shield. The lateral face of each exoccipital is pierced by three foramina, the anterior of which appears to be homologous with the ventral foramen of the exoccipital in other fishes. The central foramen appears homologous with the lateral exoccipital foramen.

Table D1 : Characters from the cranium floor

(asterisks indicate those used in phenetic analyses)

*D1. Parasphenoid pierced by carotid foramina (1)/ not surrounding carotid foramina (0)

*D2. Parasphenoid expanded/ not expanded between ethmoids

*D3. Parasphenoid with/ without distinct lateral processes

*D4. Parasphenoid posterior process divided/ not divided

*D5. Trigeminofacialis anterior foramina complete/ incomplete

D6. Prootics with/ without separate ventral foramina for VIII nerve

*D7. Prootics and exoccipitals meet/ do not meet

*D8. Prootics with/ without accessory anterior foramen(a)

*D9. Exoccipitals with/ without lateral foramina

*D10. Exoccipitals with/ without second ventral foramina

*D11. Exoccipital condyles present/ absent

D12. Basioccipital bowed ventrally to form otic bullae/ flat

*D13. Length of basioccipital greater than/ less than its width

D14. Intercalaries present/ absent

*D15. Prootics contact/ do not contact basioccipital

*D16. Exoccipitals separate/ do not separate pterotics and basioccipital

*D17. Prootics reach/ excluded from margin of postorbital foramen

D18. Parasphenoid length/head length (%)

D19. Neurocranium length/standard length (%)

Table D2 : Distributions of characters from the cranium floor among framework taxa

Taxon	12345	67890	12345	67	8	9
Diplophos	00101	01000	01010	10	48.1	18
Saurida	11111	01010	01111	10	X	18.3
Percopsis	10111	00110	11011	11	73.3	26.1
Fundulus	00111	11111	10001	10	58.5	30.2
Melanotaenia	01111	11011	1X001	11	X	23.0
Allanetta	01111	01110	11000	11	79.5	22.5
Holocentrus	00111	01100	10011	10	X	25.4
Asterotheca	01111	11010	11101	10	63.8	24.2
Cottus	00110	00010	11010	10	61.9	27.4
Sebastes	01111	11110	11101	11	68.3	34.4
Prionotus	11111	11110	11001	11	X	29.3
Percalates	10111	X1110	1X001	11	72.4	32.6
Plectroplites	10111	X1110	1X111	11	71.9	31.4
Perca	00111	11110	11010	11	70.0	30.1
Ammodytes	00111	11110	11010	11	76.0	16.1

Table D3 : Distributions of characters from the cranium floor among study groups

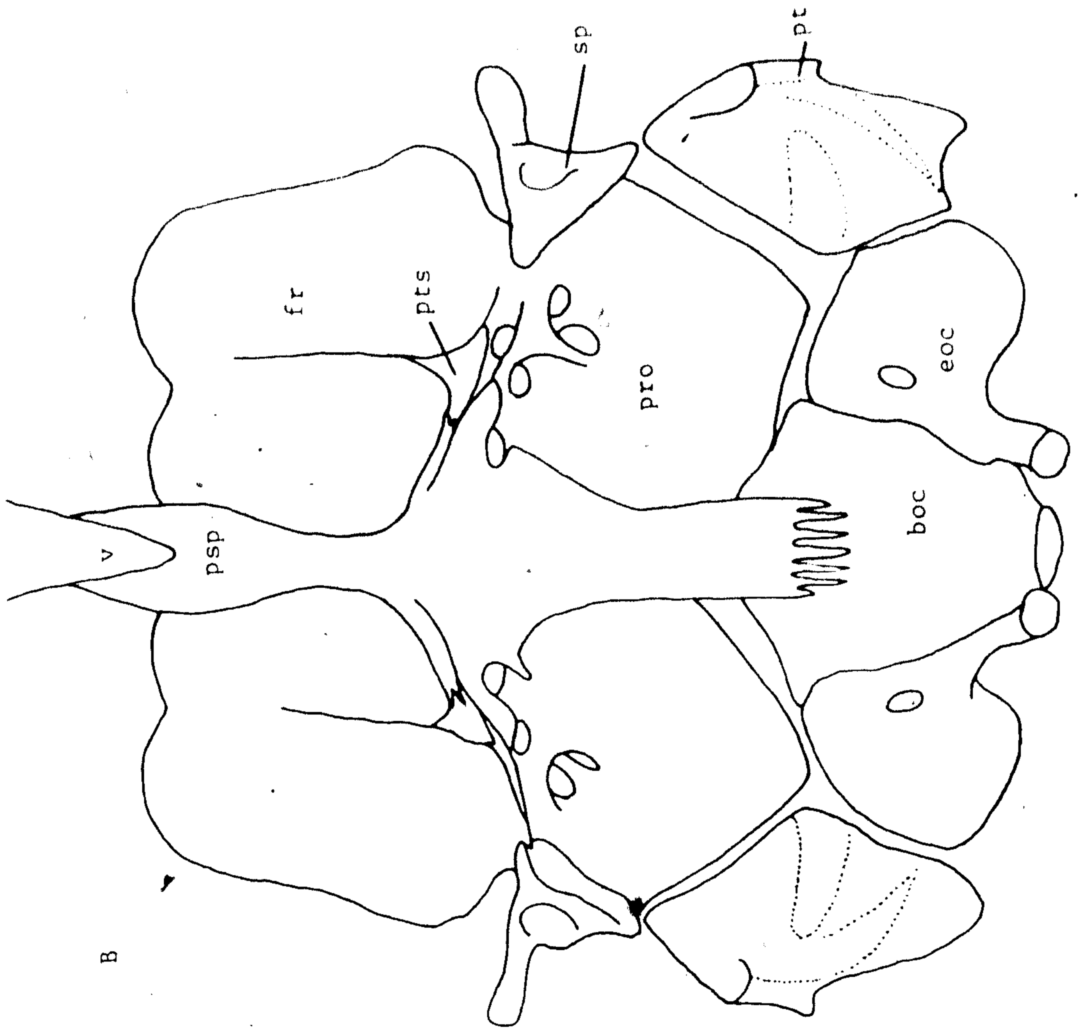
Taxon	12345	67890	12345	67	8	9
Gasterosteus	10110	01011	00111	10	73.4	28.8
Pungitius	00110	01011	00111	10	72.1	27.1
Culaea	00110	01011	00111	10	64.3	29.9
Apeltes	10110	01010	00111	10	71.1	25.0
Spinachia	10110	01010	00111	10	67.3	26.1
Aulichthys	00110	01010	00111	10	61.2	25.1
Aulorhynchus	10100	01010	10111	10	76.7	25.3
Syngnathus	01101	10001	10100	00	54.3	12.0
Syngnathoides	01100	10001	10100	00	53.1	18.0
Hippocampus	01101	10001	10100	00	58.6	19.4
Solenostomus	01101	10000	10000	01	86.1	42.4
Aulostomus	01111	10010	10100	01	50.0	31.5
Fistularia	01011	10001	10100	00	30.0	33.9
Macrorhamphosus	01111	10001	10100	01	66.8	45.7
Aeoliscus	01111	10000	00100	01	50.0	39.2
Indostomus	00000	11000	10001	10	42.6	20.2
Hypoptychus	11010	01010	11111	11	70.5	18.5
Pegasus	01110	01010	00001	11	27.6	30.8
Dactylopterus	01101	01110	00101	11	66.5	32.0

Figure D 1 : Neurocrania of Atherinomorpha, ventral views

A. Allanetta harringtonensis, X 11.5

B. Fundulus sp., X 23.5

(abbreviations are listed on pages xxv-xxvi)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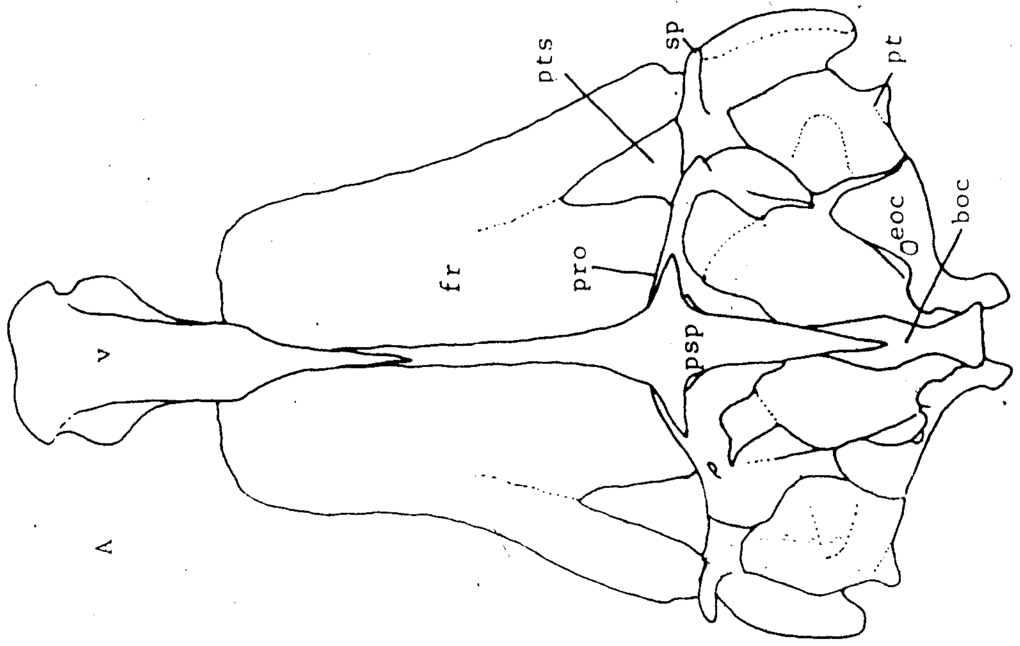
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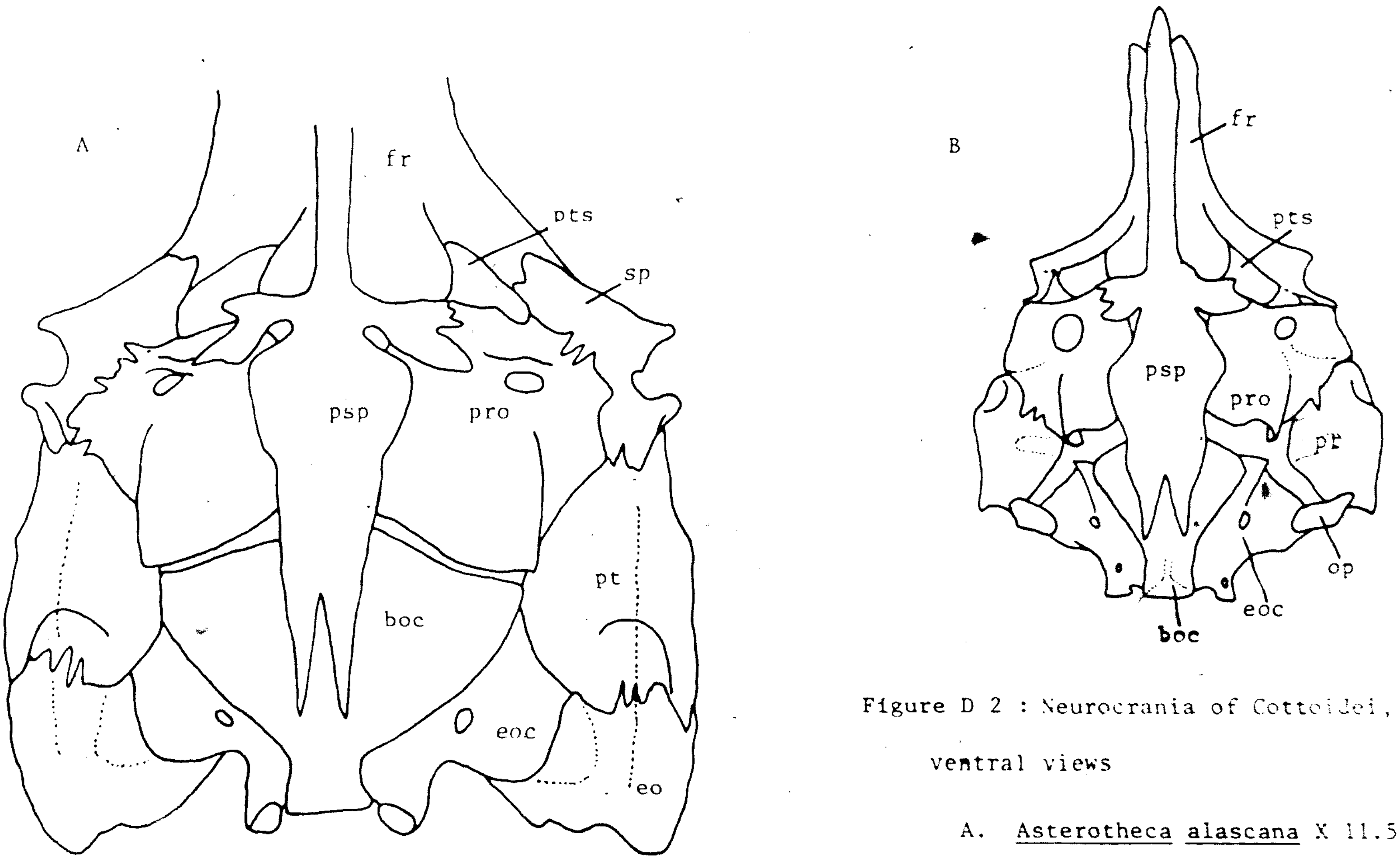


Figure D 2 : Neurocrania of Cottoidei, ventral views

A. <u>Asterotheca</u> <u>alascana</u> X 11.5

B. <u>Cottus</u> <u>cognatus</u> X 11.5

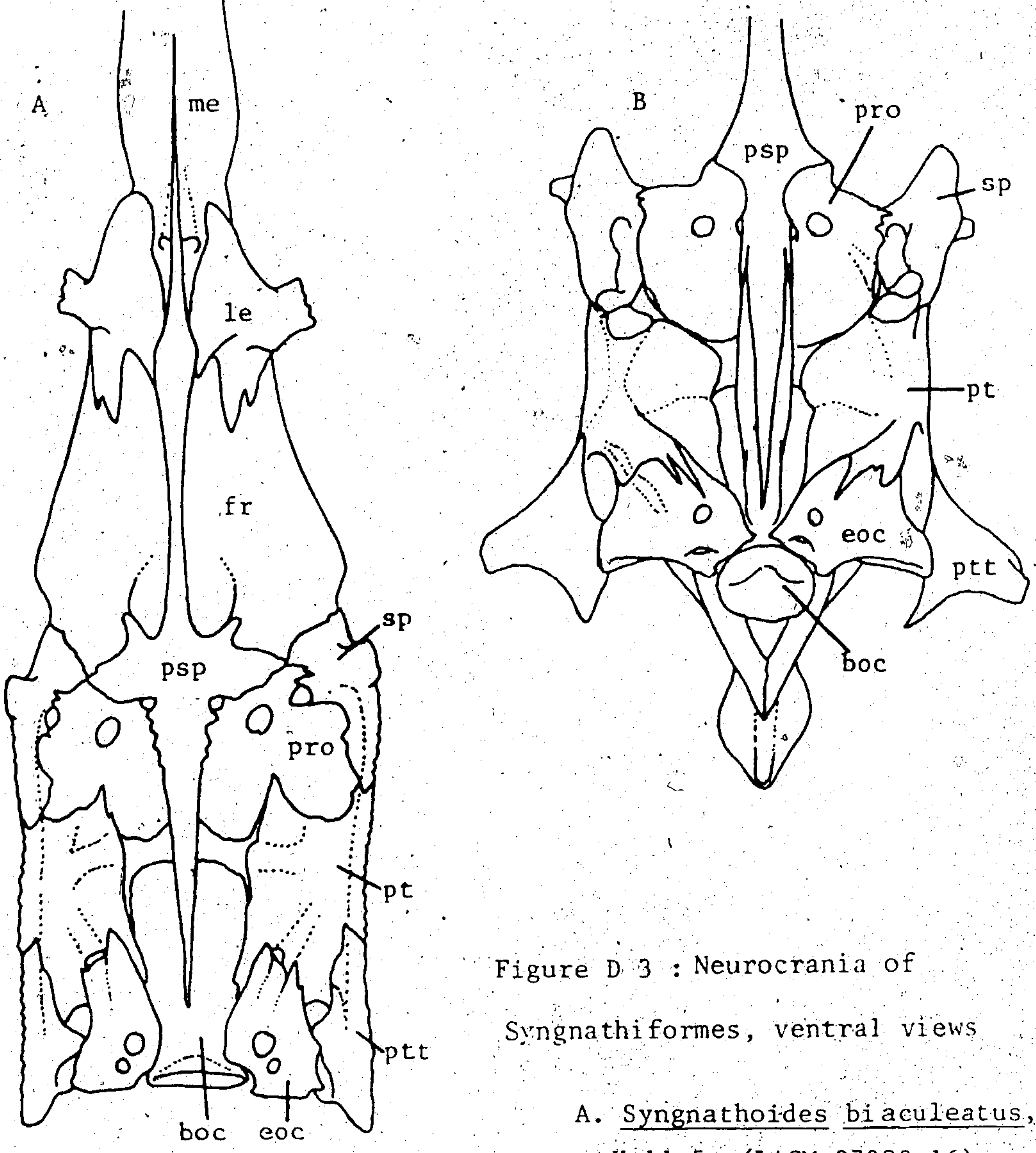


Figure D 3 : Neurocrania of Syngnathiformes, ventral views

A. Syngnathoides biaculeatus, X 11.5 (LACM 37398-16)

B. Hippocampus hippocampus, X 11.5

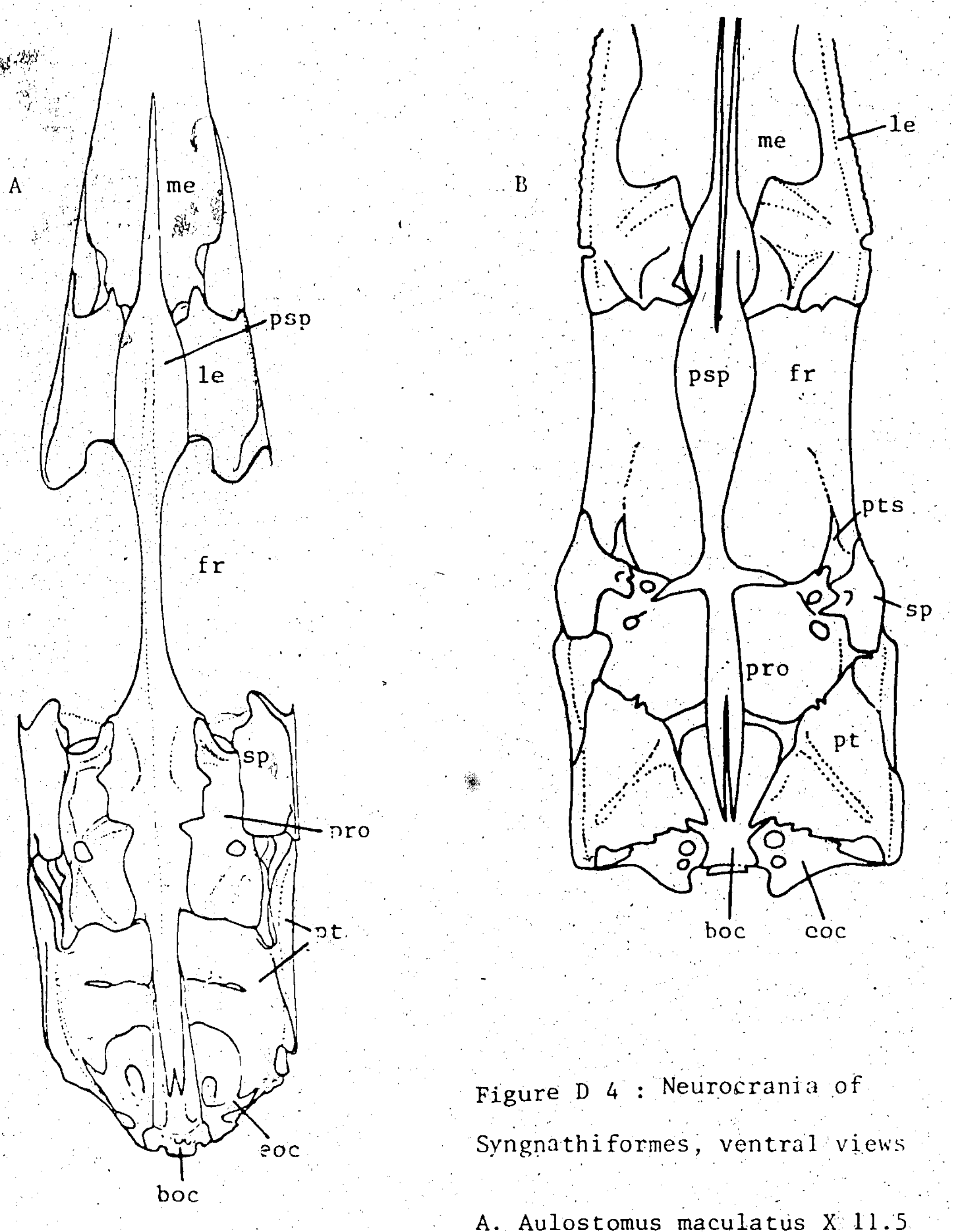


Figure D 4 : Neurocrania of Syngnathiformes, ventral views

A. Aulostomus maculatus X 11.5

B. Macrorhamphosus gracilis X 11.5

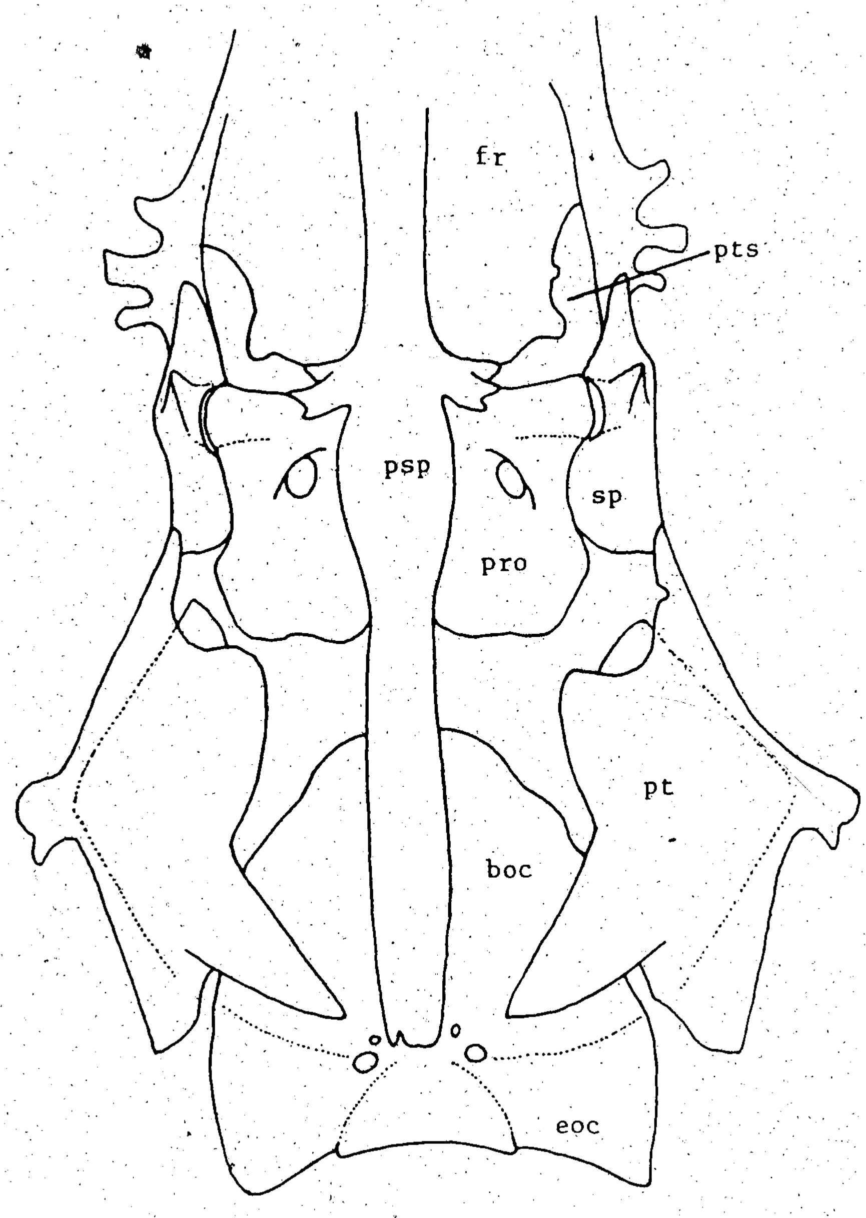


Figure D 5 : Solenostomus paradoxus, neurocranium, ventral view, X 23.5

E. The Upper Jaw and Palatine Arches

The upper jaw is composed of the paired premaxillae and maxillae. The palatine arches contain the palatine bones, and the ecto-, endo-, and metapterygoids. The characters used from this region are listed in Table E1, and the coded data for framework and study taxa are in Tables E2 and E3, respectively.

Framework

The premaxillae of Diplophos are toothed and each bears a single posterior process beginning slightly lateral to the symphysis. Fink and Weitzman (1982) identify these as articular processes; the maxillae articulate with their ventral surfaces. The maxillae are elongate, forming over half of the toothed margins of the upper jaw. The dorsal end of each bends medially to form a single spatulate process which slides under the articular process of the premaxilla. The maxilla shaft has no distinct palatine process. Its ventral end is flattened, toothed for almost its entire length; its posterior border is covered by two supramaxillae.

The palatines are relatively short and stout, with condylar heads and dorsomedial flanges. Teeth run along their ventral edges. The ectopterygoids are elongate, connecting with the palatines behind the lateral ethmoids and running the full length of the orbits before giving rise to ventral processes which lie along the anterior margins of the quadrates. The endo- and ectopterygoids lie above the dorsal borders of the quadrates. The endopterygoids are connected to the palatine flanges anteriorly and bend medially to form most of the orbit floors and interorbital septum. They have small teeth scattered along their anterior borders. The metapterygoids lie directly posterior to them, each giving rise to a posterolateral flange which lies over the hyomandibula shaft.

In S[illegible]da the premaxillae are the major bones forming the gape. Each is heavily toothed, with a short articular process. The maxillae are very thin and closely applied to the premaxillae. The anterior end of each curves ventrally to pass under the articular process of the premaxilla. Immediately lateral to this process the lateral edge of the maxilla bends dorsally to form a facet for articulation with the palatine head. The palatines are short and toothed, their medial edges turned up into flanges bearing facets which lie along the borders of the lateral ethmoids. The posterior end of each palatine is overlain by the ectopterygoid, another flat toothed bone which runs straight from the palatine to the middle of the anterior edge of the quadrate. The medial edge of each ectopterygoid lies along the border of the endopterygoid, a toothed oval bone which extends medially under the orbit. The metapterygoids are flat and toothless, their posterior portions expanded to fill the space between the dorsal margins of the quadrates and the anterior hyomandibular laminae.

Percopsis has toothed premaxillae, each with a short ascending process and a slightly shorter articular process, both laterally compressed. Rosen and Patterson (1969) recorded post-maxillary processes in Percopsis and Aphredoderus, but I did not see these in my specimens. The dorsal and ventral articular heads of each maxilla are connected posteriorly by a bony flange. This flange is extended posteriorly into a large process and a similar posterior process extends from a point on the maxilla shaft directly lateral to the articular heads. Each palatine has a conical head extending anterolaterally and bearing a vertical flange on its dorsal surface. The palatines are expanded posteriorly into flat vertical plates, each with an accessory medial flange forming a cone-shaped fossa on its anterior end. The palatines are attached to both the endo- and ecto-pterygoids. The former are smaller than the palatines, their posterior ends extending ventrally along the anterior borders of the quadrates; the latter are large ovoid bones, bowed medially to extend under the orbits. Both ecto- and endo-pterygoids are toothless in Percopsis omiscomaycus; Rosen and Patterson (1969) report that the ectopterygoid is toothed in P. transmontana and that both are toothed in Aphredoderidae. The metapterygoid is a roughly rectangular plate, bilaminar at its posterior end. It fills the space between the quadrate, endopterygoid, and hyomandibula.

The premaxillae of the athinomorphs examined each bear a single posteromedial process in the form of a wide vertical flange (Fig. E1). Rosen and Patterson (1969) suggest that these are homologous to articular processes. They resemble more, however, the ascending processes of fishes which have both ascending and articular processes (see Fig. E2). In these maxillary-articular process articulations, the maxillary heads fold around the posterior edges of the articular processes and can exert anteriorly directed forces on the premaxillae through them. The ascending processes, on the other hand, lie freely over the ventral articular heads of the maxillae, as do the single processes of Atherinomorpha.

Atherinomorph maxillae bend ventrally at their medial ends to form the maxillary hooks (Rosen, 1974). The dorsolateral portions of these hooks are not developed into distinct dorsal articular heads in *Fundulus* or *Allanetta*, but are so developed in *Melanotaenia*.

The palatines are relatively small, wide cylindrical bones. In all the species examined they bear ventral flanges; in *Melanotaenia*, the flanges are toothed. The ectopterygoids are small. The metapterygoids are reduced to small bones lying over the symplectic-hyomandibular connections in *Melanotaenia* and *Allanetta*; they are absent in *Fundulus*.

The premaxillae in *Holocentrus* have ascending and articular processes, postmaxillary processes, and teeth. The maxillae have both dorsal and ventral articular heads, connected by posterior flanges. *Holocentrus* lacks supramaxillae, but Zehren (1979) found them in many beryciform groups. The palatines have conical heads and toothed ventral laminae. They are attached ventrally to both the ecto- and endo-pterygoids. The ectopterygoids run along almost the full lengths of the palatine flanges and the anterior margins of the quadrates. They are toothless in *Holocentrus*. Endopterygoids are large, their anterior tips attached to the palatines and their antero-ventral borders to the ectopterygoids. They also are toothless. The metapterygoids are wide flat bones filling the gaps between the quadrates and hyomandibulae.

Scorpaeniformes have toothed premaxillae with both ascending and articular processes, although in *Prionotus* the ascending processes are reduced. The ventral ends of the premaxillae are expanded in all; the postmaxillary processes are distinct in all except *Asterotheca*. The maxillary heads resemble those of *Holocentrus*. They do not have marked palatine facets and are not greatly expanded laterally. The palatines are toothed in *Asterotheca*, *Sebastes*, and *Prionotus*. They have large cylindrical heads and ventral laminae attached to the pterygoids. In *Cottus* and *Asterotheca* a lateral process extends from each palatine head to the lachrymal (Fig. E2,A and E3).

In *Cottus* the pterygoids are fused into a single bone (Fig. E2,B); in *Sebastes*, *Asterotheca* (Fig. E3), and *Prionotus* they are separate, the ectopterygoids lying along the anterior borders of the quadrates. The endopterygoids extend medially in all three species but only in *Sebastes* are they large enough to form the floors of the orbits. The metapterygoids are relatively large, running from the quadrate fans to the hyomandibula shafts.

The perciformes examined all have toothed premaxillae with ascending, articular, and postmaxillary processes. Their maxillae resemble those of Scorpaeniformes; in Ammodytes their dorsal articular heads give rise to dorsally-projecting spurs. Ammodytes is also distinguished by the presence of incompressible ligaments attaching the ventral maxillary heads to the articular processes. Percalates and Plectroplites have a single supramaxilla above each maxilla. No special palatine facets are present, the palatines usually articulating with the lateral sides of the dorsal articular heads of the maxillae. The palatines have cylindrical heads and vertical flanges, as in Scorpaeniformes; they are toothed in Perca, Stizostedion , Percalates, and Plectroplites and bear medial processes to the vomers in Stizostedion and Myctoperca . In Ammodytes their ventral flanges are extremely large and reach posteriorly to the quadrates. The ectopterygoids in Ammodytes are reduced and lie along the dorsal margins of the quadrates behind the point at which the palatines and the quadrates meet. In other Percifomes the ectopterygoids occupy their normal position along the anterior margins of the quadrates, and they are toothed in Percalates and Plectroplites. The endopterygoids are oval toothless bones extending under the orbits in all the Perciformes examined and the metapterygoids are wide flat bones similar to those of Sebastes.

Gasterosteiformes

All Gasterosteiformes (Figs. E4-5) have premaxillae with long ascending processes, toothed in all except female Aulichthys. There are no articular processes, and postmaxillary processes are present only in Aulichthys (Fig. B6,B). The maxillary articular heads lie along the dorsal and ventral sides of the ascending processes (Fig. A4); slight palatine facets are present on the posterior margins of the maxillae directly lateral to the dorsal articular heads. The posterior tips of the flanges connecting the dorsal and ventral articular heads are developed into distinct posterior processes. The palatines are slender bones, each with a conical head which gives rise to a lateral process (Fig. E4,B). Posteroventrally each palatine is attached to a triradiate bone which occupies the positions of the ecto- and endo-pterygoids (Figs. E4-5); a ventral spur from this bone runs down the anterior margin of the quadrate and a wide vertical flange extends along the dorsal margin of the quadrate. The metapterygoids are reduced to small splints of bone over the symplectic-hyomandibular connections.

Syngnathiformes

In Syngnathiformes the gapes are bordered by toothless, spike-shaped premaxillae (Fig. E6) which may bear short posterodorsal processes (Fig. E6,B). Since these processes lie over the articular heads of the maxillae without being surrounded by them, I feel they are homologous to the ascending processes; in a case of such reduction, however, homologies are hard to determine. The maxilla heads are shortened and the dorsal articular heads tilted ventrally. The 'dorsal' heads articulate with the vomers. The palatines lie against ridges along the dorsal surfaces of the maxillae, directly lateral to the maxillary articular heads. The maxilla shafts are widely expanded into triangular or rectangular plates. In Syngnathidae and Macrorhamphosus (Fig. E6,B) the ventral edges of these plates may curve forward below the ventral tips of the premaxillae.

The palatines in all except Centriscidae have distinct conical heads lying directly lateral to the vomer heads and, in Aulostomus and Fistularia, tightly sutured to them. In Aulostomus separate dorsal and ventral shafts appear to run posteriorly from the palatine heads, the ventral shafts fusing to the vomer and the dorsal shafts lying above the anterior end of the parasphenoid (Fig. E7). In Fistularia the palatines run along the lateral edges of the vomer and are spurlike in shape and toothed ventrally. In both genera the palatines lie in grooves on the dorsolateral surfaces of the ectopterygoids. The ecto- and endopterygoids of Aulostomoidei are fused into a single flat bone lying along the dorsal and anterior borders of each quadrate ; the metapterygoids are large flat bones lying along the posterior and posterodorsal margins of the quadrates (Fig. E7).

In other syngnathiforms the palatines are not sutured to the vomers. The syngnathid palatines are short peg-shaped bones fitting into grooves on the dorsal surfaces of the ectopterygoids. These fishes have separate ecto- and endopterygoids (Fig. E8,A). The ectopterygoids lie along the anterior edges of the quadrates. The endopterygoids are reduced to thin bones and only touch the anterodorsal borders of the quadrates; the metapterygoids are absent. The palatine arches of Solenostomus resemble those of Syngnathidae.

Macrorhamphosus and Centriscidae are distinguished by their possession of palatines which lie free on the lateral surfaces of the ectopterygoids (Fig. E6). In Macrorhamphosus the palatines have conical heads and long, ventrally curving shafts, while in centriscids they are small oval bones. In both the ecto- and endopterygoids are separate, the ectopterygoids resembling those of Syngnathidae and the endopterygoids lying along the dorsal margins of the quadrates (Fig. E8,B). The metapterygoids in Macrorhamphosus resemble those of Aulostomus, but those of Centriscidae are apparently partially fused to the preopercula.

Indostomus

The premaxillae of Indostomus are heavily toothed. They lack distinct articular and ascending processes and are attached firmly to the ethmovomerine block by a narrow band of cartilage. The maxillae are very small thin bones lying along the medial edges of the premaxillae, as illustrated in Banister (1970).

A ridge runs along each side of the ventral surface of the median ethmoid, beginning directly behind the maxilla ; these ridges occupy the positions of the palatines and may represent fusion of the palatines and median ethmoid. Their posterior edges meet the pterygoids, which run the length of the orbits before reaching the anterior borders of the quadrates (Fig. E9). These bones are probably homologous to the ectopterygoids, but whether they also contain elements of the endopterygoids is not clear from my material. The posterior borders of the quadrates touch the metapterygoids, which are flat bones lying over the symplectic-hyomandibular connections.

Hypoptychus

Ida (1976) reports sexual dimorphism in premaxillary dentition in Hypoptychus, males having toothed premaxillae and females toothless premaxillae. The premaxillary ascending processes are extremely long and slender. Articular processses are absent but postmaxillary processes are present. The maxillae have articular heads similar to those in Fistularia; each maxilla bends ventrally to extend under the ascending process of the premaxilla. The dorsal surface of each maxilla head gives rise to a short spurlike process (Fig. A9). There are no palatine articular facets. The maxillary shafts are expanded but narrow again at their ventral ends.

The palatines are slender cylindrical bones whose dorsal portions bend toward the dorsal midline to lie along the margins of the vomer (Fig. B12). Their posterior ends bend laterally to meet the pterygoids. Gosline (1963) illustrates the 'ectopterygoid' as a strut of bone between the palatine and quadrate; in my specimens the pterygoids cover the entire medial surfaces of the quadrates (Fig. E10), extending behind them along the symplectics. Their homologies are uncertain; since they overlap the anterior edges of the quadrates, they can be homologized with the ectopterygoids, but whether or not they contain elements of the endopterygoids is not obvious from adult material. The metapterygoids are thin cylinders lying along the symplectic-hyomandibular connections.

Pegasus

The premaxillae in Pegasus have flat ventral portions and styliform processes extending anteriorly. These processes might be homologous with either ascending or articulating processes; they appear to have developed their anterior orientation along with elongation of the anterior processes of the maxillae and an increased antero-posterior tilt of the premaxillae. The maxillae articulate with the premaxillae via ossified ligaments extending from the premaxilla heads to articular facets on the medial sides of the maxillary shafts (Fig. E11). The maxillae bear short posterior processes and long, anteriorly directed processes. In Pegasus volitans the medial sides of the maxillary articular heads bear oblique ledges ending in posterior condyles which articulate with the 'palatines' (maxillovomerine ligaments of Pietsch, 1978). Jungerson (1915) felt that these were fused palatines and ectopterygoids, but they show no evidence of compound origins. There are no separate pterygoids in Pegasus.

Dactylopterus

The premaxillae of Dactylopterus are shortened and bear noticeable postmaxillary processes (Fig. E12,A). Each bears a long laterally compressed ascending process and a shorter articular process. The ascending processes are connected by a vertical flange of cartilage. The premaxillae are toothed.

The maxillae have dorsal and ventral articular heads connected posteriorly by flanges simialr to those in Scorpaeniformes. They lack palatine articular facets. The entire upper jaw apparatus, as in Pegasus, slides in and out of a deep cavity between the vomer and the median ethmoid / nasal complex.

The palatines are relatively short bones, their heads bent ventromedially like those of Sebastes. They are toothless.

Each pterygoid arch is composed of three bones (Fig. E12,B). The ectopterygoids extend ventrally from the palatine flanges to the quadrate condyles. The endopterygoids are flat and thin, lying along the dorsal margins of the ectopterygoids and bending medially to form part of each orbit floor. The remainder of each orbit floor is formed by a large flat bone extending medially from the suborbitals. Although these bones resemble the endopterygoids of Sebastes and Allanetta, I was unable to separate them from the suborbitals and therefore regard them as enlarged suborbital shelves. The metapterygoids are flattened bones lying along the dorsal edges of the symplectics.

Table E1 : Charactérs from the upper jaw and palatine arches (asterisks indicate those used in phenetic analyses)

*E1. Premaxillae toothed (1)/ toothless (0)

E2. Premaxillae bear/ lack ascending processes

E3. Premaxillae bear/ lack articular processes

*E4. Premaxillae bear/ lack postmaxillary processes

*E5. Maxillae with forked/ single dorsal articular heads

*E6. Ventral articular heads of maxillae elongated/ short

*E7. Maxillae with/ without palatine articular facets

*E8. Maxilla shafts greatly/ slightly expanded

*E9. Maxillary hooks present/ absent

*E10. Dorsal and ventral maxilla heads connected/ not connected posteriorly

*E11. Palatine heads cylindrical/ laterally compressed

E12. Premaxillae with/ without anterior processes

E13. Palatine shafts lie over the lateral surfaces of the pterygoids/ attached to dorsal surfaces of pterygoids

*E14. Palatines toothed/ toothless

E15. Palatines larger than/ not larger than ectopterygoids

*E16. Palatines fused to/ separate from ectopterygoids

*E17. Palatine heads bear/ lack lateral projections

*E18. Palatines fused to/ separate from median ethmoid

E19. Ectopterygoids lie along/ do not lie along the anterior margins of the quadrates

E20. Ectopterygoids lie along/ do not lie along the dorsal margins of the quadrates

E21. Ectopterygoids toothed/ toothless

E22. Ectopterygoids with/ without long anterior processes

*E23. Separate endopterygoids present/ absent

*E24. Separate metapterygoids present/ absent

*E25. Supramaxillae present/ absent

E26. Palatine length/head length (%)

Table E2 : Distributions of characters from the upper jaw and palatine arches among framework taxa

Taxon	12345	67890	12345	67890	12345	6
Diplophos	10100	00100	10010	00011	01111	21.4
Saurida	10100	01000	10010	00010	10110	X
Percopsis	11100	00001	10001	00010	00110	22.4
Fundulus	11000	10010	10000	10010	00110	11.5
Melanotaenia	11000	00000	1X010	00010	00110	13.6
Allanetta	11000	00010	10000	00010	00110	27.2
Holocentrus	11110	01001	10010	00010	01110	X
Asterotheca	11100	00001	10011	00010	00110	27.8
Cottus	11111	00001	10001	01011	01010	25.6
Sebastes	11110	00101	10011	00011	01110	22.0
Prionotus	11110	10001	10010	00010	00110	X
Percalates	11110	00001	1X010	00010	10111	31.0
Plectroplites	11110	00001	1X010	00010	10111	30.1
Perca	11110	00001	10010	00010	00110	21.6
Ammodytes	11110	00001	10001	00001	00110	40.0

Table E3 : Distributions of characters from the upper jaw and palatine arches among study groups

Taxon	12345	67890	12345	67890	12345	6
Gasterosteus	11000	01000	10000	01011	00010	13.6
Pungitius	11000	01000	10000	01010	00010	12.5
Culaea	11000	01000	10000	01011	00010	11.2
Apeltes	11000	01000	10000	01010	00010	12.2
Spinachia	11000	01000	10000	01011	00010	9.7
Aulichthys	11010	01000	10000	01011	00010	19.9
Aulorhynchus	11010	01000	10000	01011	00010	25.4
Syngnathus	01000	01100	10000	00010	00100	4.3
Syngnathoides	01000	01100	10000	00010	00100	3.9
Hippocampus	01000	01100	10000	00010	00100	7.0
Solenostomus	01000	01100	10000	00010	00100	3.6
Aulostomus	01000	01100	10000	00011	00010	5.3
Fistularia	01000	01100	10010	00011	00010	3.7
Macrorhamphosus	01000	01100	10100	00010	00110	7.1
Aeoliscus	01000	01100	00100	00010	00100	1.9
Indostomus	10000	00000	00000	00100	01010	X
Hypoptychus	11010	00010	10000	00010	01010	11.5
Pegasus	0XX00	11000	0XX0X	X00XX	XX000	X
Dactylopterus	11110	10001	10000	00010	01110	21.8

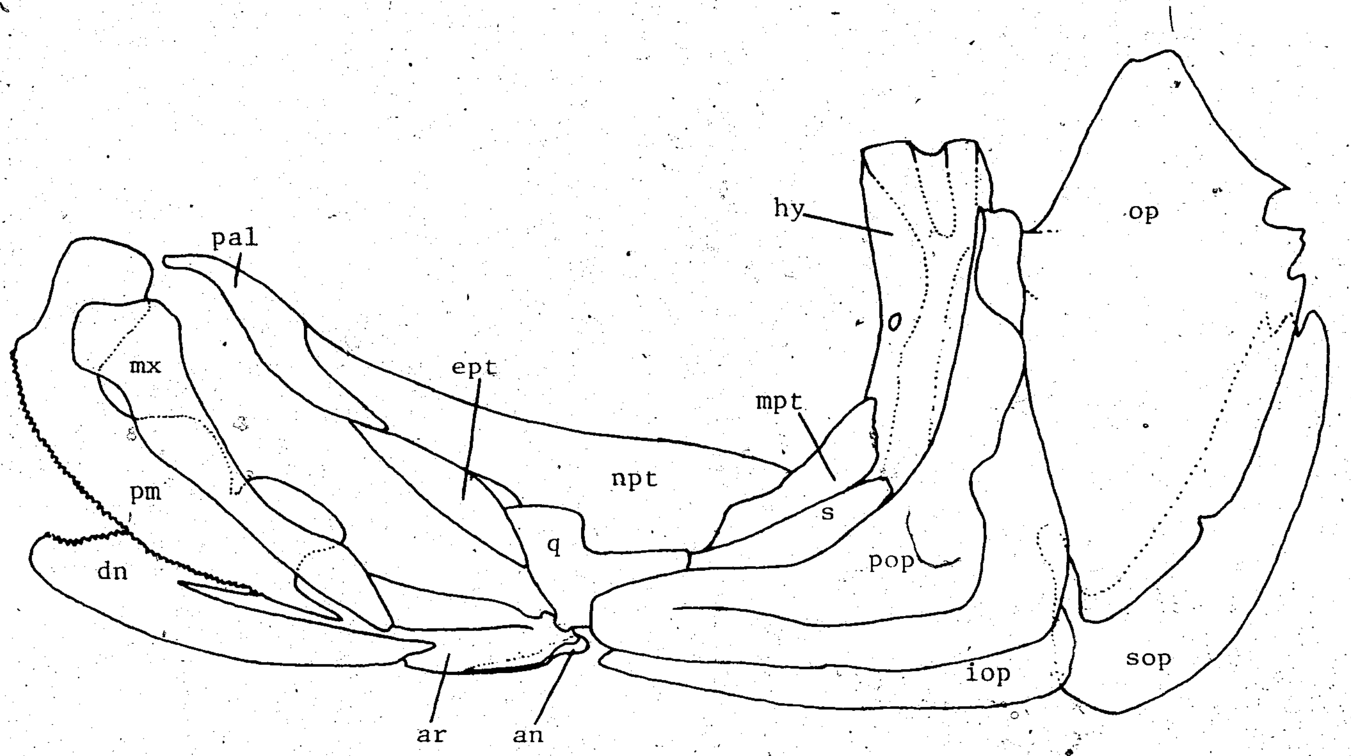


Figure E 1 : Allanetta harringtonensis, left suspensorium and pterygoid arch, lateral view with suborbital series removed. X 11.5

(abbreviations are listed on pages xxv-xxvi)

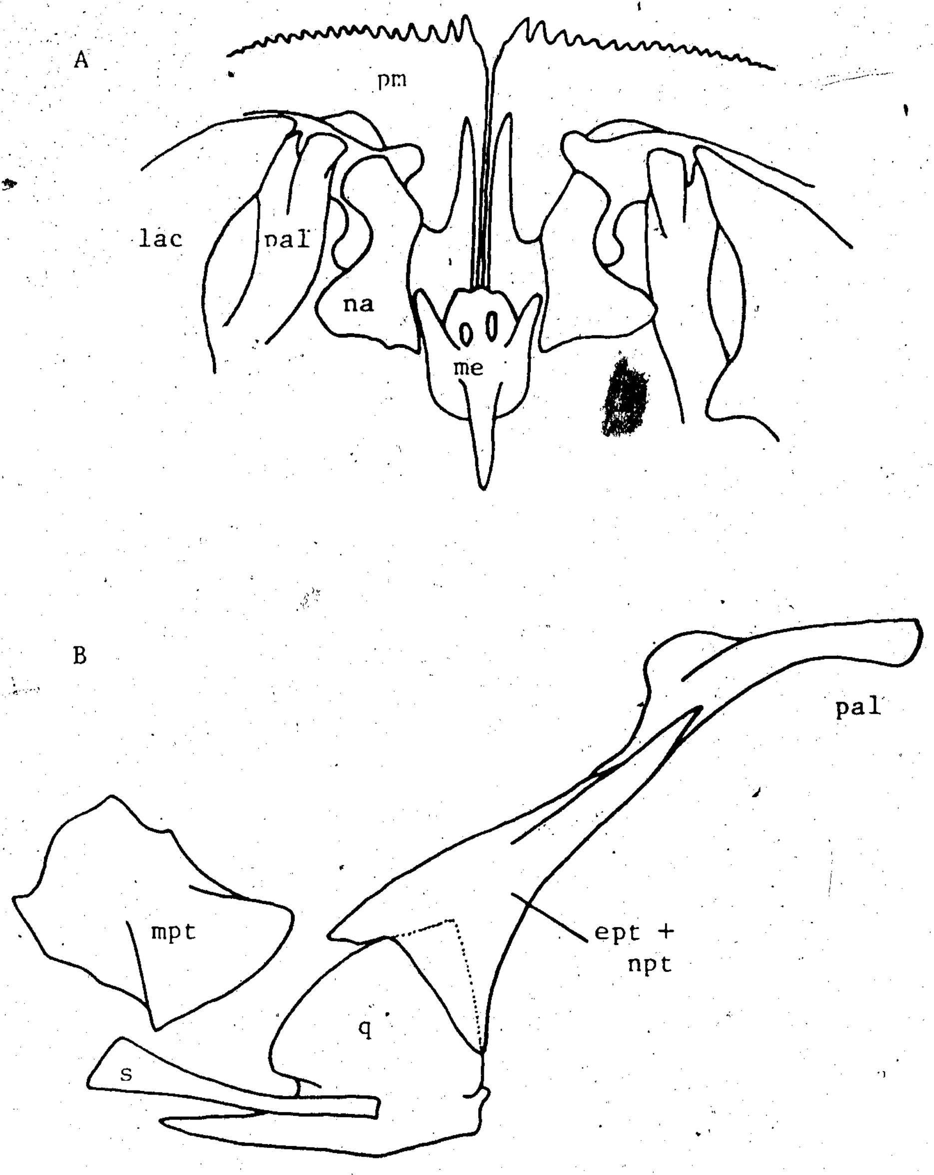


Figure E 2 : Cottus cognatus

A. Premaxillae and palatines, dorsal view X 23.5

B. Left palatine-pterygioid arch, medial view. X 23.5

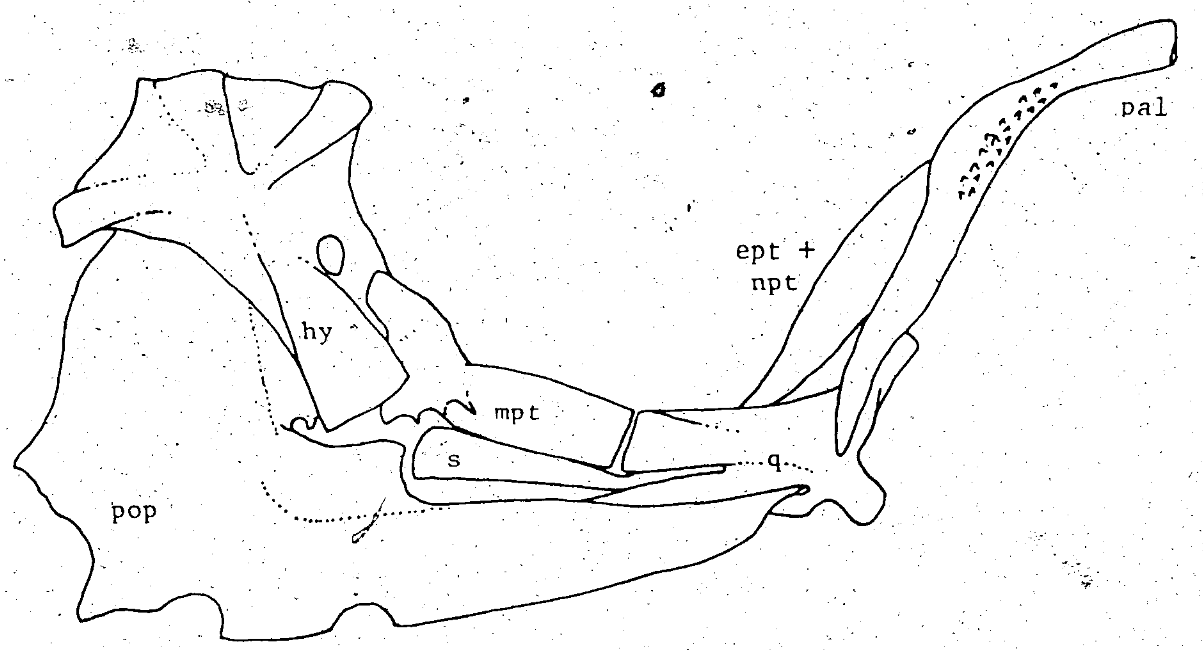
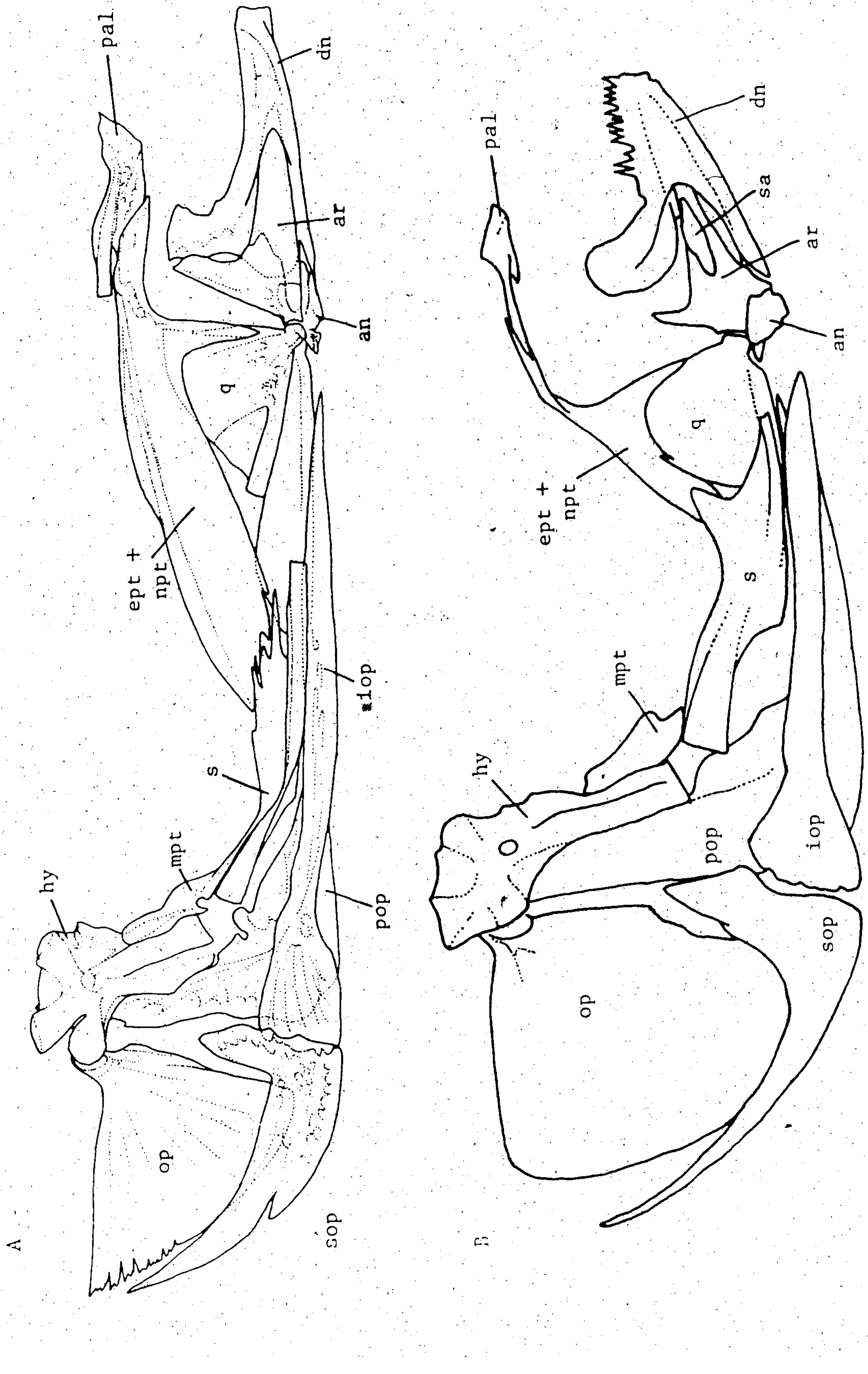


Figure E 3: Asterotheca alascana left suspensorium, medial view. X 11.5

Figure E 4 : Left suspensoria of Gasterosteiformes, medial views

A. *Spinachia spinachia*, X 15

B. *Gasterosteus aculeatus*, X 11.5 (UAMZ 5512)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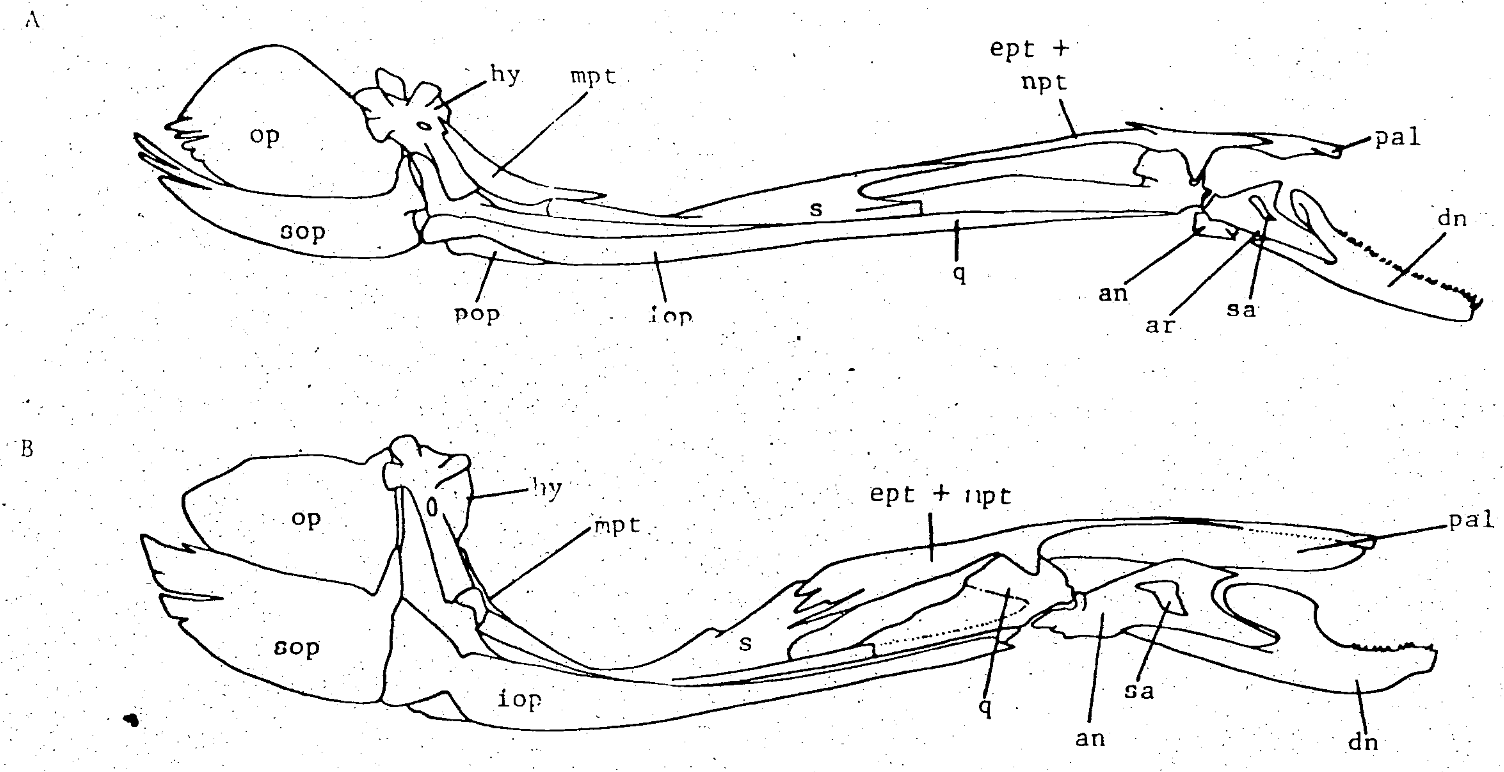

Figure E 5 : Left suspensoria of Aulorhynchidae, medial views.

A. Aulichthys japonicus, X 7.2

B. Aulorhynchus flavidus, X 6.5 (UAMZ 1694)

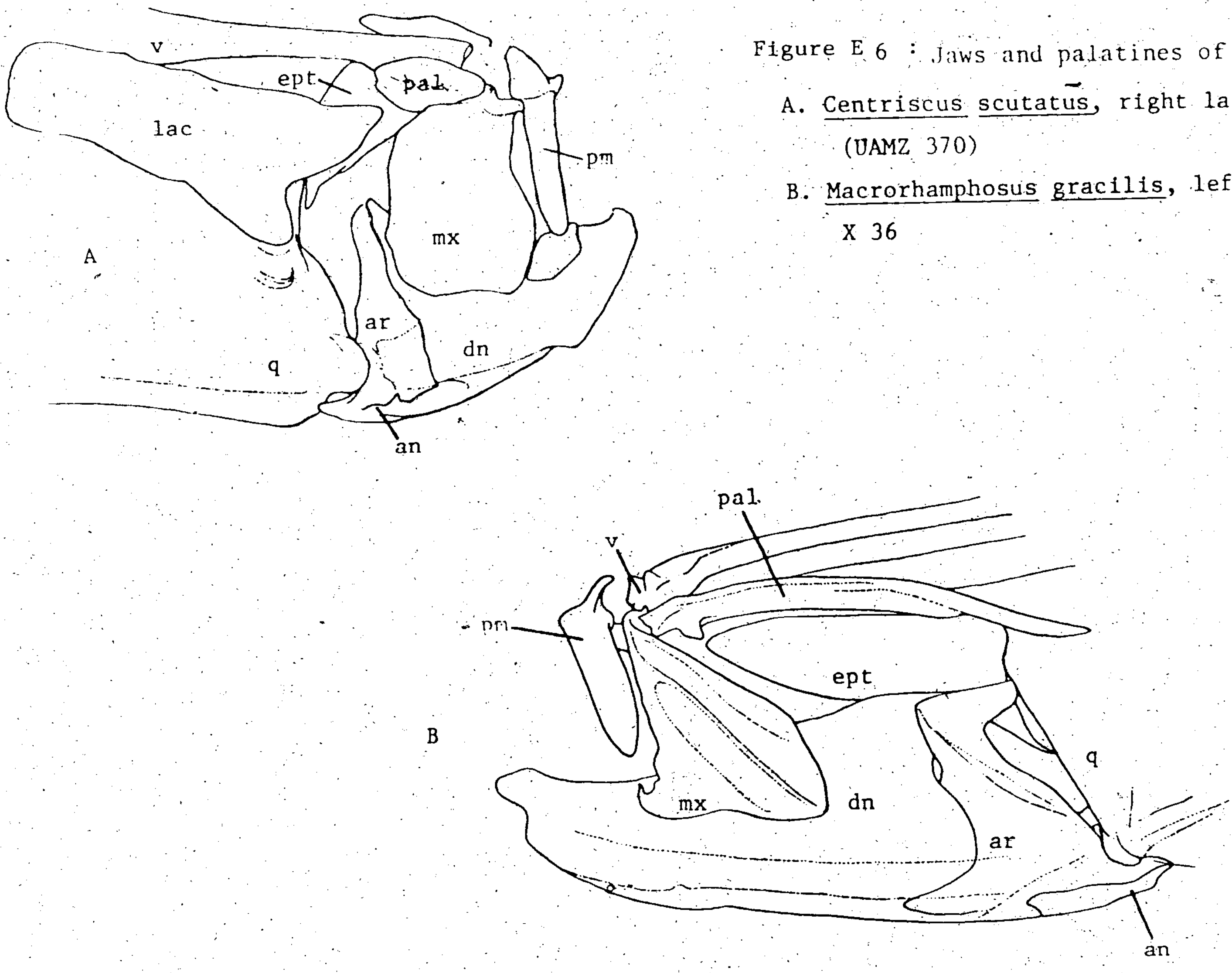

Figure E 6 : Jaws and palatines of Syngnathiformes

A. Centriscus scutatus, right lateral view X 36
(UAMZ 370)

B. Macrorhamphosus gracilis, left lateral view,
X 36

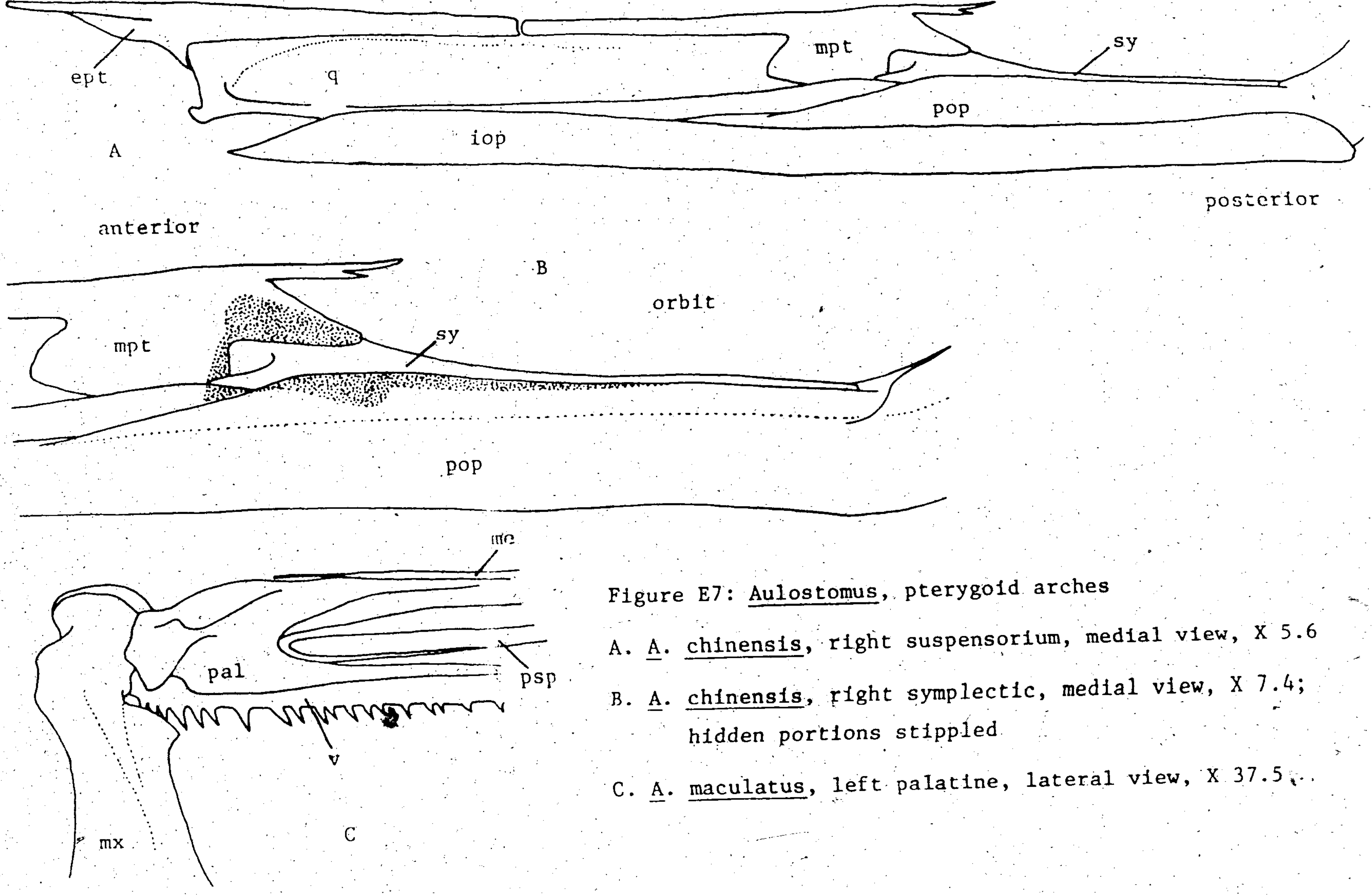

Figure E7: Aulostomus, pterygoid arches

A. A. chinensis, right suspensorium, medial view, X 5.6

B. A. chinensis, right symplectic, medial view, X 7.4; hidden portions stippled

C. A. maculatus, left palatine, lateral view, X 37.5

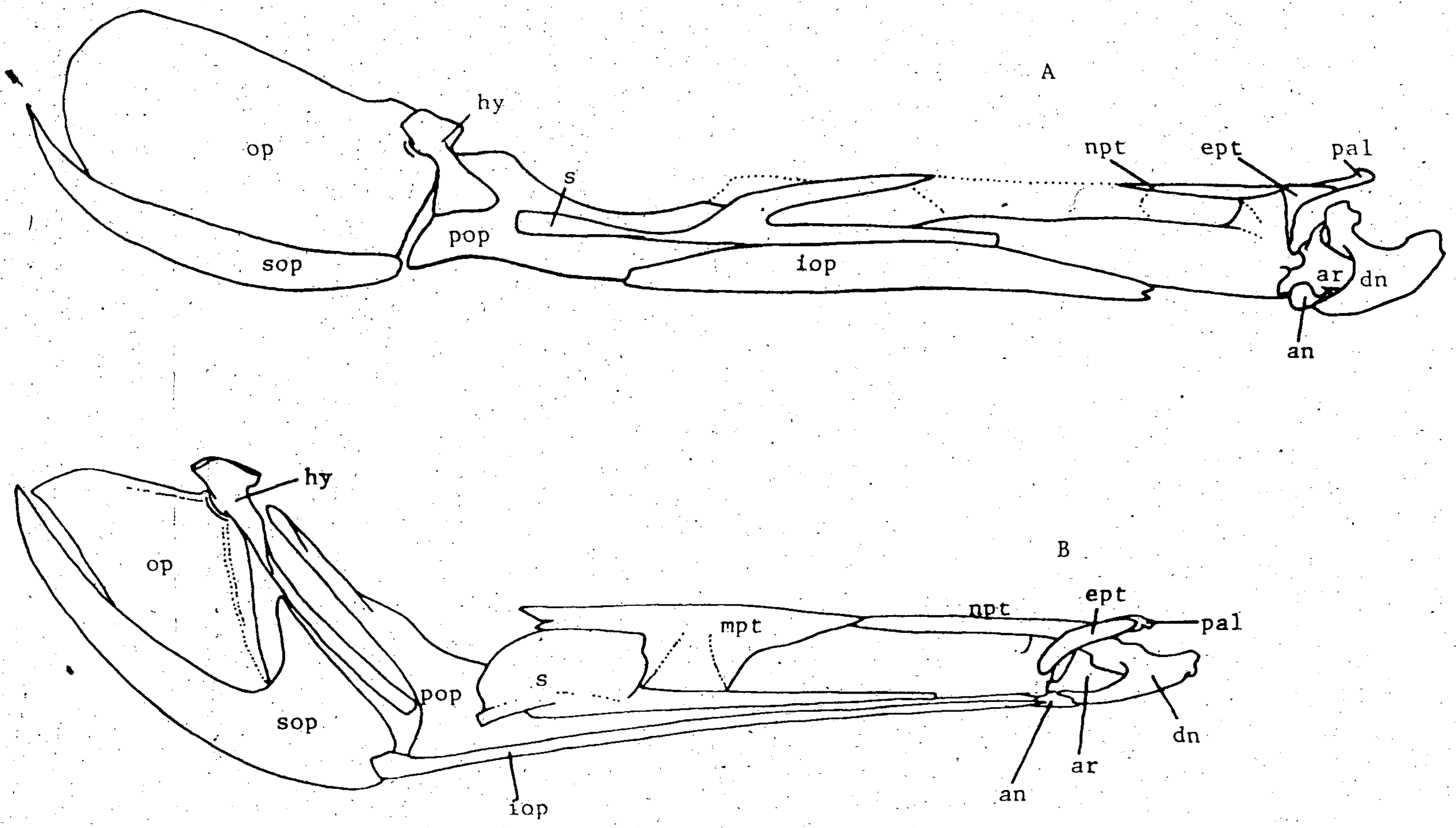

Figure E8 : Left suspensoria of Syngnathiformes, medial views

A. <u>Syngnathus griseolineatus</u>, X 9

B. <u>Macrorhamphosus gracilis</u>, X 6.5

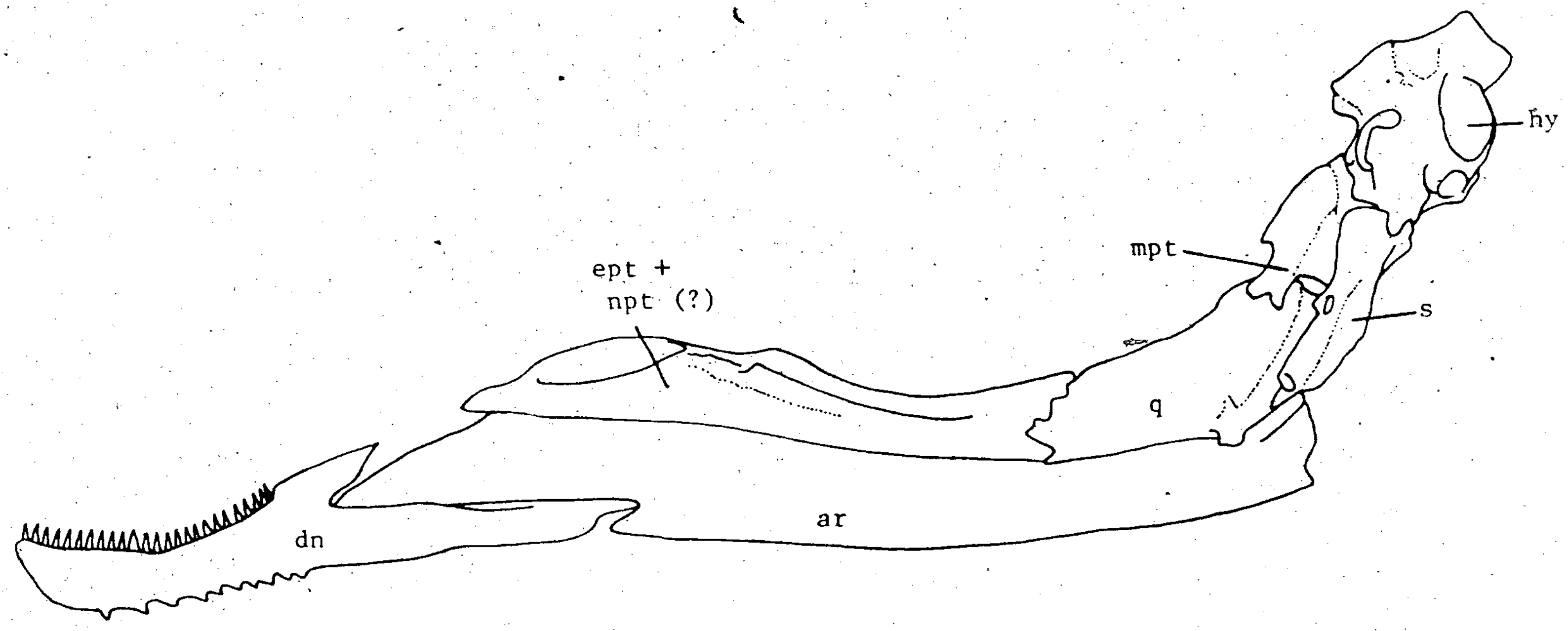

Figure E 9 : *Indostomus paradoxus*, right suspensorium, medial view, X 48

(composite drawing of USNM 203888 and UAMZ, uncatalogued)

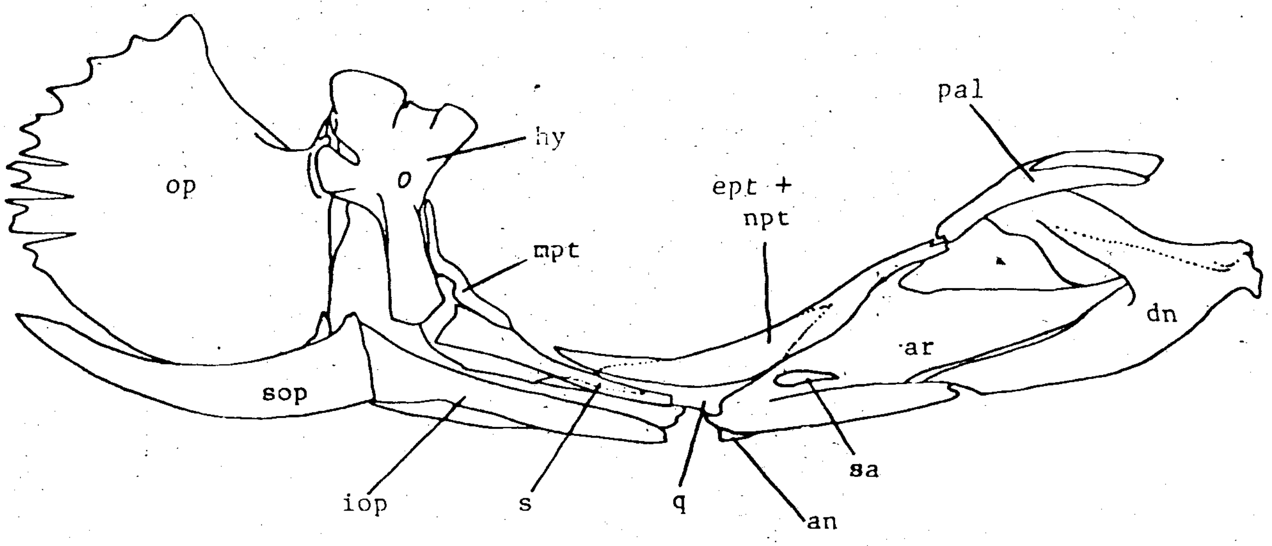

Figure E 10 : *Hypopt[illegible]chus dybowski*, left suspensorium, medial view, X 8

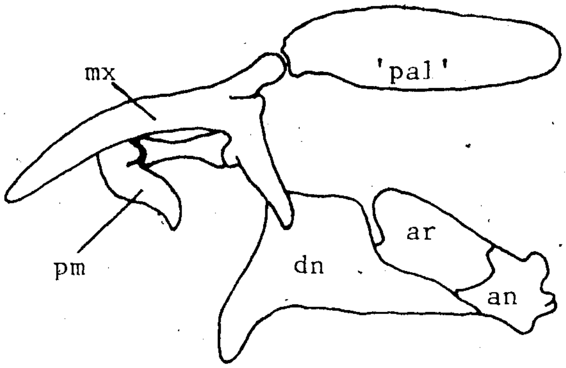

Figure E 11 : Pegasus volitans, jaws and 'palatine', left lateral view, X 11.5

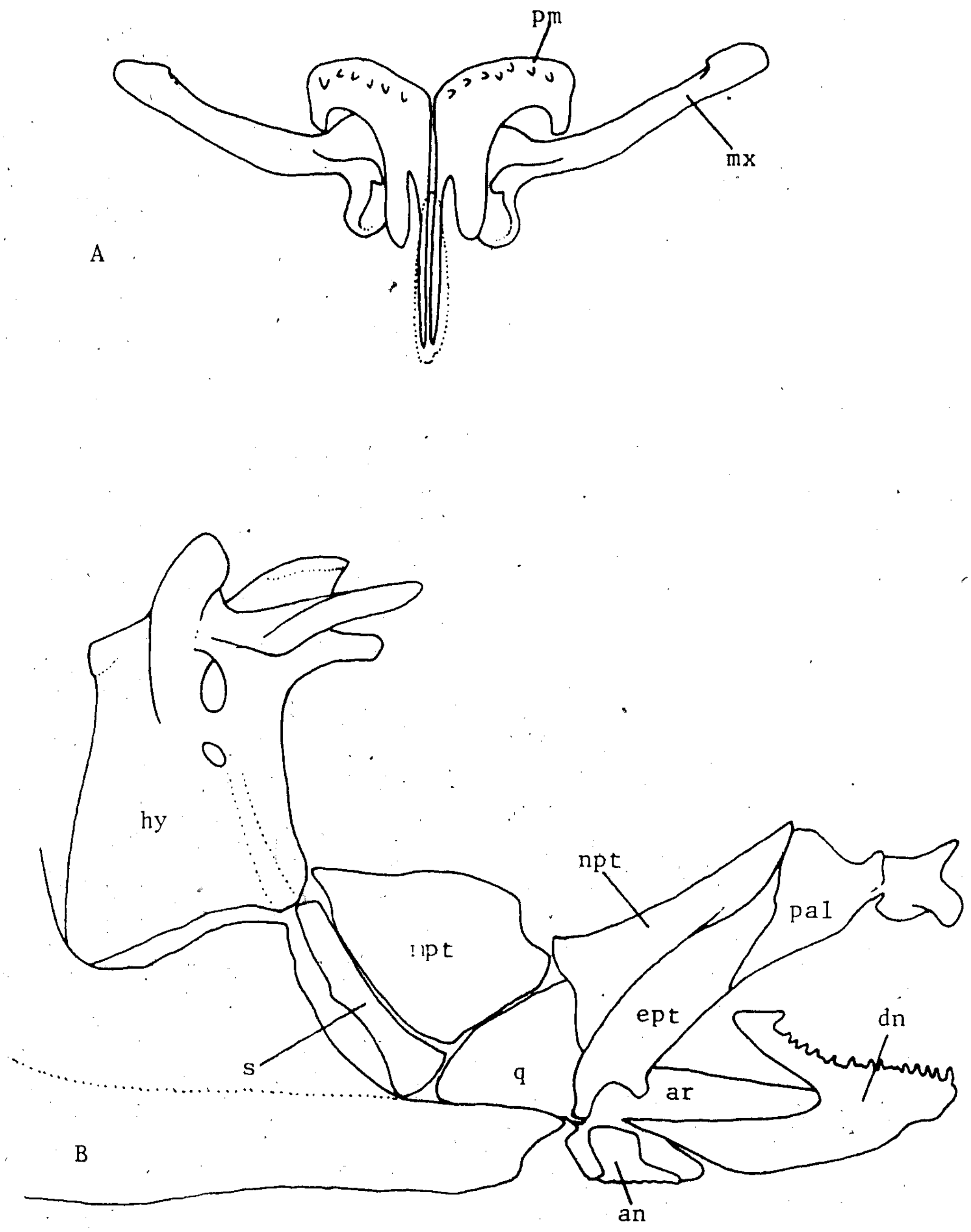

Figure E12: *Dactylopterus volitans*

A. Premaxillae and maxillae, ventral view, X11.6

B. Left suspensorium, medial view, X11.6

F. The Lower Jaw and Suspensoria

The lower jaws are formed of the dentaries, articulars, angulars, and the sesamoid articulars, if present. The suspensoria contain the quadrates, symplectics, and hyomandibulae. Characters used from this region are listed in Table F1 and the coded data for framework groups and study groups in Tables F2 and F3, respectively.

Framework

The dentaries in Diplophos are toothed for almost their full lengths, with no elevated coronoid processes. Each is composed of a posteriorly concave lateral lamina and a more deeply concave medial lamina. A narrow lateral ridge runs along the lower side of each dentary; it continues along the articular to near the quadrate condyle.

Each articular extends forward between the lateral and medial laminae of each dentary. Articulars in Diplophos lack coronoid processes but have small subdentary processes. The angulars are small caps of bone on the posteroventral corners of the articulars.

Each quadrate is shaped like an acute isosceles triangle, its apex at the quadrate condyle. A narrow flange extends laterally from its posterior border and the symplectic, a narrow cylindrical bone, lies along the medial side of its border directly opposite to this flange. The symplectics do not extend past the quadrates. The hyomandibulae, therefore, are more closely attached to the metapterygoids than to the symplectics. The hyomandibula shafts have narrow lateral flanges and wide anterodorsal laminae. The cranial condyles of each are fused, their bases separated by a foramen, and the opercular condyles are elongate and extend posteroventrally.

The dentaries of Saurida resemble those of Diplophos in shape and in tooth position, although Saurida has many more teeth than does Diplophos. Narrow bony tubes run along their ventral sides; these probably carry the anterior ends of the preoperculomandibular canals. There are no sesamoid articulars. The angulars are cones whose wide ends are attached to the ventral surfaces of the articulars below and behind the quadrate condyles; each is covered laterally by a flat plate.

The quadrates are not fan-shaped, but are cylindrical bones extending anterodorsally toward the pterygoids. The bases of these cylinders bear anterior and posterior flanges and, behind the posterior flanges, small posterior shafts originating near the quadrate articular condyles. These processes are probably formed by the fusion of the quadrates and symplectics, for no separate symplectics are visible. The hyomandibulae are long, curved bones whose anterior and posterior cranial condyles are short and widely separated. Their anterior laminae are very large.

In *Percopsis* the bony troughs bearing the preoperculomandibular canals are so large that they form most of the dentaries and the toothed dentary shafts lying above them are comparatively small. Coronoid processes are developed. The subdentary processes of the articulars are similar to and continuous with the ventral portions of the dentaries. Articular coronoid processes are present. The angulars, whose structures are similar to those of *Saurida*, lie along the medial of the two laminae forming the subdentary processes. The symplectics are widened posteriorly, bearing both posterodorsal and posteroventral laminae. The hyomandibulae are large, their cranial and opercular condyles elongate and distinct from each other, but connected by laminae. Each hyomandibula shaft bears a large medial foramen and a wide anterior lamina whose ventral border is attached to the metapterygoid.

The Atherinomorpha I examined have toothed dentaries; all except *Melanotaenia* have marked coronoid processes. In *Fundulus* and *Allanetta*, the dentary posterior margins are deeply cleft. The preoperculomandibular canals run along the articulars and dentaries in *Allanetta* and *Melanotaenia*. The articulars have coronoid processes only in *Fundulus*, but have subdentary processes in all the atherinomorphs examined. *Melanotaenia* has sesamoid articulars. The angulars of *Fundulus* and *Melanotaenia* are composed of vertical cones with anteroventral processes running under the articulars. In *Allanetta* their conical portions are not distinct. The quadrates have distinct fans and posterior processes and the symplectics lie medially along their ventral margins (Fig. E-1). The cranial condyles of the hyomandibulae are separated in *Fundulus* and *Allanetta* but fused in *Melanotaenia*. The hyomandibulae of all three have anterior laminae.

The suspensoria of *Holocentrus* differ from those of *Percopsis* in only a few points. The dentaries have anterolateral foramina and the preoperculomandibular canals are borne along them in complete, narrow tubes rather than wide open ones. The articulars in *Holocentrus* have no subdentary processes. The symplectics bear only central laminae, and the hyomandibular cranial condyles are fused.

The dentaries of Sebastes, Asterotheca, and Prionotus resemble those of Holocentrus. Their articulars have subdentary processes and sensory canals (Fig. A3). The angulars in Sebastes and Prionotus resemble those of Holocentrus in structure and position. Prionotus, Sebastes, and Cottus (Fig. E2,B) have wide fan-shaped quadrates with short posteroventral processes; the quadrates of Asterotheca are cylindrical rather than fan-shaped and reach anteriorly to the palatines (Fig. E3). The symplectics in all are cylindrical with no noticeable flanges. The hyomandibular cranial condyles are separated in all, and anterior laminae are present; their medial foramina are absent in Prionotus.

The dentaries in most of the perciforms examined lack anterolateral foramina and elevated coronoid processes. Ammodytes has very unusual dentaries; they are toothless and their coronoid processes bend anteriorly to form hooks. The dentaries are very deeply cleft posteriorly, the cleft extending anteriorly to separate the coronoid processes and ventral shafts. A large long foramen pierces each dentary anteriorly, leaving only a delicate bony strut between the coronoid process and the symphyseal knob. The articulars in all the perciforms examined lack noticeable subdentary processes and both dentaries and articulars bear the preoperculomandibular canals. Ammodytes has sesamoid articulars. The angulars are constructed like those of Holocentrus in Percalates, Plectroplites, and Perca, but they have no apparent conical portions in Ammodytes.

The quadrates in all except Ammodytes are composed of wide fans and short posterior processes. In Ammodytes the quadrates are cylindrical rather than fanlike, and bear anterior processes to the pterygoids; their posterior processes are elongate. The symplectics have small central laminae or none. The hyomandibulae have separate cranial condyles in Percalates, Plectroplites, and Ammodytes, but fused condyles in Perca, Stizostedion , and Myctoperca . The hyomandibulae in Ammodytes are almost cross-shaped, their shafts and anterior cranial condyles displaced anteriorly. Foramina for the 9th nerves are present; in Ammodytes many foramina pierce the laminae between hyomandibular cranial heads.

Gasterosteiformes

All Gasterosteiformes except female Aulichthys have toothed dentaries. In all the dentaries have well-developed coronoid processes and deeply-cleft posterior margins. Their articulars also have coronoid processes (Figs. E4-5). Sesamoid articulars are present in Gasterosteus, Pungitius, Culaea, and Aulorhynchidae; short subdentary processes are present in Culaea. The preoperculomandibular canals extend along the articulars and dentaries in Aulorhynchidae but only along the dentaries in Gasterosteidae. Gasterosteus is the only gasterosteid in which these canals are apparent, although they may be present among the sculpturing on the dentaries of the other species. The angulars consist of vertical cones and anteroventral processes, as in most of the other fishes examined. The quadrates are expanded into fans with posteroventral processes, which are longer in the longer-snouted forms (see Fig. E4). The symplectics are cylindrical with anterodorsal flanges lying along the borders of the pterygoids (Figs. E4-5). The symplectics of some Gasterosteiformes are shown in Fig. F1. In all Gasterosteidae except some specimens of Gasterosteus a small ventral flange is present at the midpoints of the symplectics. The symplectics of Culaea have small posteroventral laminae.

The hyomandibular cranial condyles are separate (Figs. E4-5). Their shafts be[illegible] anterior laminae and medial foramina.

Syngnathiformes

Most of the elongation in syngnathiform suspensoria appears in the quadrates and symplectics. The development of tubular snouts also involves some dorsal expansion of the quadrates and symplectics to form their walls (Figs. E7-8) except in those species (Syngnathidae) in which the antorbitals fill this position (Fig. E8,A).

The dentaries in all Syngnathiformes have coronoid processes. A sequence of dentary shapes can be observed (Fig. F2); those of Fistularia are the least shortened, have the most deeply cleft posterior margins, and are toothed. The dentaries in Aulostomus are also toothed, but the teeth are small. The dentary posterior laminae are cleft and the coronoid processes expanded. Macrorhamphosus gracilis has slender dentaries with relatively low coronoid processes, but in M. scolopax the dentaries are shortened until they approach the shape of equilateral triangles with one face deeply excavated. The dentaries in Syngnathidae and Centriscidae are triangular. Those in Solenostomus resemble syngnathid dentaries but have more deeply cleft posterior laminae.

The articulars in Syngnathiformes are strongly attached to the dentaries, both by dentary processes and by coronoid processes (Fig. E6). Subdentary processes are present. In Macrorhamphosus, Aulostomus, and Fistularia the articular coronoid processes bear marked posterior hooks. The preoperculomandibular canals extend along the articulars and dentaries of Aulostomus and Macrorhamphosus and along the dentaries of Aeoliscus. The angulars have conical structure only in Macrorhamphosus. The quadrates have relatively narrow bodies in Syngnathidae and Solenostomus and, in all except Syngnathidae, are connected to their long posterior processes by wide sheets of bone. In Syngnathidae their bodies and posterior processes are separated by deep notches (Fig. E8,A).

The symplectics are narrow cylinders, augmented by various flanges (Fig. F3). In Solenostomus a large anterodorsal flange extends from each symplectic to the posterior edge of the quadrate, forming the snout wall for almost half its length. Syngnathus and Syngnathoides have similar anterior flanges, but they are attached to the antorbitals as well as to the quadrates. In Macrorhamphosus the symplectics bear posterodorsal flanges to the posterior edges of the metapterygoids. In Aulostomus and Fistularia the symplectics are attached to the metapterygoids via anterior flanges. The symplectics in Centriscidae are not easily separable from the quadrates, and bear anterodorsal flanges similar to those found in Syngnathus. The hyomandibulae have fused cranial condyles and simple shafts with anterior laminae.

Indostomus

The dentaries are elongate in Indostomus, extending almost to the orbits (Fig. E9). The coronoid processes are small and the dentaries are not deeply cleft posteriorly. The articulars lack coronoid processes but have subdentary processes. They extend the full length of the orbits and form their ventral borders. Angulars are small and without apparent conical structure. The quadrates are elongated anteriorly, extending as far anteriorly as they do posteriorly. Their dorsal margins are concave and their anteroventral margins thickened into cylindrical shafts. The symplectics are simple, resembling squat cylinders constricted centrally. They bear narrow posterior flanges. The hyomandibulae have separate cranial condyles and medial foramina. Banister (1970) identified sesamoid articulars lying in the tendons of the adductor mandibulae, but I did not see them in my specimens.

Hypoptychus

The dentaries in Hypoptychus are cleft posteriorly (Fig. E10) and are toothed in males. Both they and the articulars have coronoid processes and bear the preoperculomandibular canals. The articulars have subdentary processes and sesamoid articulars are present. The angulars have conical bodies and anteroventral processes.

The quadrates are shaped like those of Indostomus, extending both anteriorly and posteriorly from their articular condyles. Their posterior margins are cylindrical and each is augmented by a posterior process extending from the condyle along the dorsal edge of the preoperculum. The cylindrical symplectics lie along the dorsal surfaces of these processes. Each symplectic has small dorsal and ventral flanges in its central portion. Each hyomandibula articulates with the skull via two long condyles and with the operculum by a similarly elongate condyle. There are no distinct anterior laminae on the hyomandibulae, but medial foramina are present.

Pegasus

Pegasus has toothless dentaries with wide coronoid processes and slightly cleft posterior borders. The ventral portion of each dentary runs along the full length of the articular to meet the angular; there are therefore no subdentary processes on the articulars. The articulars do, however, bear marked coronoid processes. There are no sensory canals on either bone. The angulars have conical posterodorsal portions and flat anteroventral flanges (Fig. F4).

The quadrates show no cylindrical structure. They are short leaf-shaped bones without elongate ventral processes. The symplectics are wide, stout cylinders, reinforced centrally by dorsal and ventral flanges. The hyomandibulae have short, stout shafts. They extend posteriorly at a sharp angle, so that their anterior cranial condyles extend forward at a similar angle. Small anterior laminae connect these condyles with the quadrate shafts.

The cranial condyles are widely separated. There are no medial foramina on the hyomandibula shafts.

Dactylopterus

The dentaries of Dactylopterus are toothed, with elevated coronoid processes (Fig. E12,B), and bear wide preoperculomandibular canals. The articulars lack both coronoid processes and preoperculomandibular canals. The angulars, which lie along their medial surfaces, resemble vertical cones with anteroventral flanges.

The quadrates are fan-shaped without anterior extensions. The symplectics are flattened cylinders bearing very small central laminae.

The hyomandibulae of Dactylopterus are unique in having not three but five dorsal articular heads. Two anterior condyles articulate with the sphenotics, the central condyle articulates with the pterotic, and the posterior condyle articulates with the opercula. An additional elongate condyle extends medially to attach to the prootic bridge. Each hyomandibula bears a narrow anterior lamina and a very large posterior lamina.

Table F1 : Characters from the lower jaw and suspensoria (asterisks indicate those used in phenetic analyses)

*F1. Dentaries toothed (1)/ toothless (0)

*F2. Dentaries with/ without anterolateral foramina

*F3. Dentaries have/ lack elevated coronoid processes

F4. Dentaries touch/ do not touch angulars

*F5. Posterior borders of dentaries are deeply/ slightly cleft

*F6. Dentaries with/ without anterodorsal struts

*F7. Dentaries bear/ do not bear preoperculomandibular canals

*F8. Articulars have/ lack subdentary processes

*F9. Articulars have/ lack elevated coronoid processes

*F10. Sesamoid articulars are present/ absent

*F11. Articulars bear/ do not bear preoperculomandibular canals

*F12. Angulars are cylindrical/ noncylindrical

*F13. Angulars bear/ lack anterior processes

*F14. Angulars form/ do not form quadrate articulations

*F15. Quadrates have fanlike/ cylindrical bodies

*F16. Quadrate shafts make up over half/ less than half of quadrate lengths

*F17. Quadrates extend/ do not extend anterodorsally

*F18. Quadrate shafts are distictly demarcated/ are confluent with quadrate bodies

*F19. Symplectics bear/ lack central laminae

*F20. Symplectics bear/ lack anterodorsal laminae

*F21. Symplectics bear/ lack anteroventral laminae

*F22. Symplectics bear/ lack posterodorsal laminae

*F23 Symplectics bear/ lack posteroventral laminae

*F24. Cranial condyles of hyomandibulae are separate/ fused

*F25. Hyomandibulae have/ lack medial foramina on shafts

*F26. Hyomandibulae have/ lack anterior laminae

*F27. Quadrates articulate with lower jaws behind/ anterior to the orbits

Table F2 : Distributions of characters from the lower jaw and suspensoria among framework taxa

Taxon	12345	67890	12345	67890	12345	67
Diplophos	10001	00100	01001	00000	00001	11
Saurida	10001	01110	11100	01000	00011	11
Percopsis	10101	01110	11101	00100	01111	10
Fundulus	11101	01110	01101	00110	00011	10
Melanotaenia	100X0	01101	11101	00100	01101	10
Allanetta	10101	01100	10101	00110	00011	10
Holocentrus	11101	01010	11101	00110	00001	10
Asterotheca	11101	01111	11100	01100	00011	10
Cottus	10101	01111	10101	00110	00011	10
Sebastes	11001	01110	11101	00100	00001	10
Prionotus	11101	01111	11101	00100	00010	10
Percalates	100X1	01000	11101	00100	00011	10
Plectroplites	100X1	01000	11101	00100	00011	10
Perca	10101	01000	11101	00110	00001	10
Ammodytes	01111	11001	10100	11110	00011	10

Table F3 : Distributions of characters from the lower jaw and suspensoria among study groups

Taxon	12345	67890	12345	67890	12345	67
Gasterosteus	11111	01011	01101	00111	00011	10
Pungitius	10111	00011	01101	10111	00011	10
Culaea	11111	00111	01101	10111	00111	10
Apeltes	10111	00010	01101	00111	01011	10
Spinachia	11111	00010	01101	10010	01010	00
Aulichthys	10111	01011	11101	10001	00011	10
Aulorhynchus	11101	01011	11101	00101	00011	10
Syngnathus	01110	00010	00100	10101	00001	10
Syngnathoides	00110	00010	00100	10101	00001	10
Hippocampus	00110	00010	00100	10101	00000	10
Solenostomus	00111	00110	00100	10001	00001	10
Aulostomus	10101	01110	10101	10001	00001	10
Fistularia	10101	00110	00101	10001	00001	10
Macrorhamphosus	00100	01110	11101	10000	01001	10
Aeoliscus	00100	01110	00101	10001	00001	10
Indostomus	10001	00100	00000	01000	01111	11
Hypoptychus	10101	01111	11100	01110	00011	00
Pegasus	00111	00010	01100	00010	00010	10
Dactylopterus	11101	01100	01101	00110	00011	10

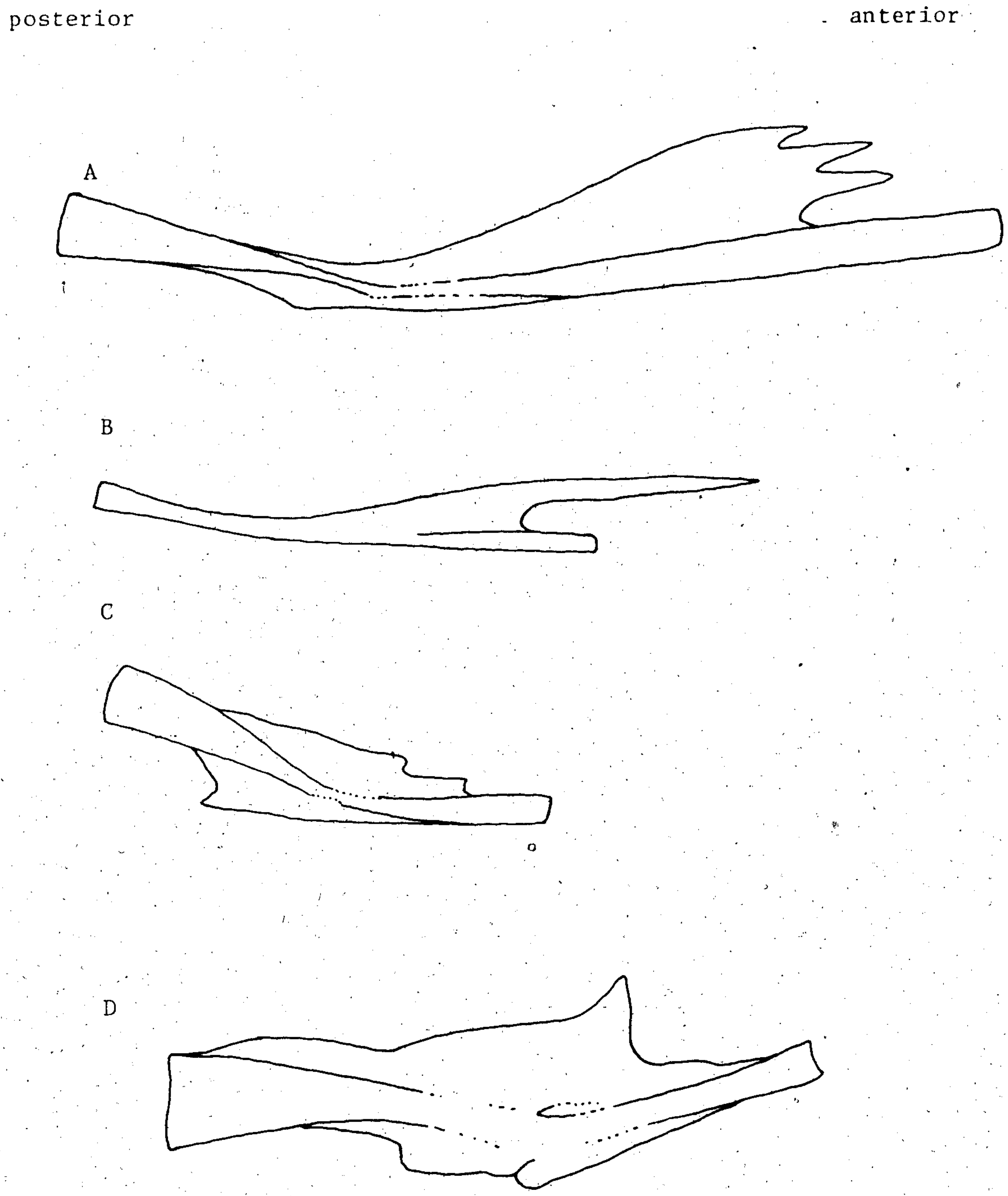

Figure F 1 : Left symplectics of Gasterosteiformes, medial views

A. Spinachia spinachia, X 23.5

B. Aulorhynchus flavidus, X 11.5 (UAMZ 1694)

C. Pungitius pungitius, X 23.5 (UAMZ 4754)

D. Apeltes quadracus, X 23.5

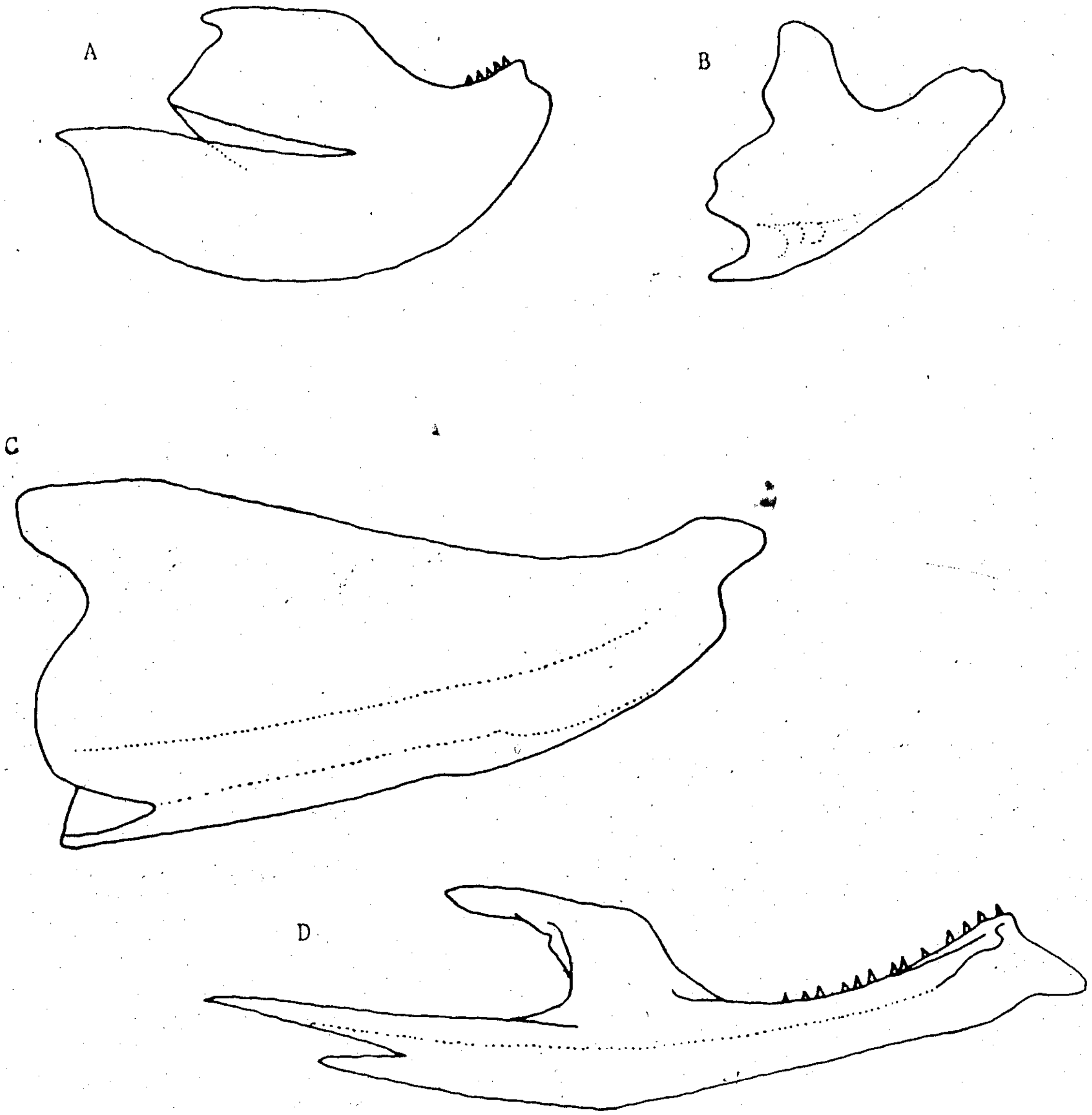

Figure F 2 : Dentaries of Syngnathiformes

A. Aulostomus maculatus, left dentary, medial view, X 7.5

B. Syngnathus griseolineatus, right dentary, lateral view, X 36

C. Macrorhamphosus gracilis, right dentary, lateral view, X 48

D. Fistularia tabacaria, right dentary, lateral view, X 11.6

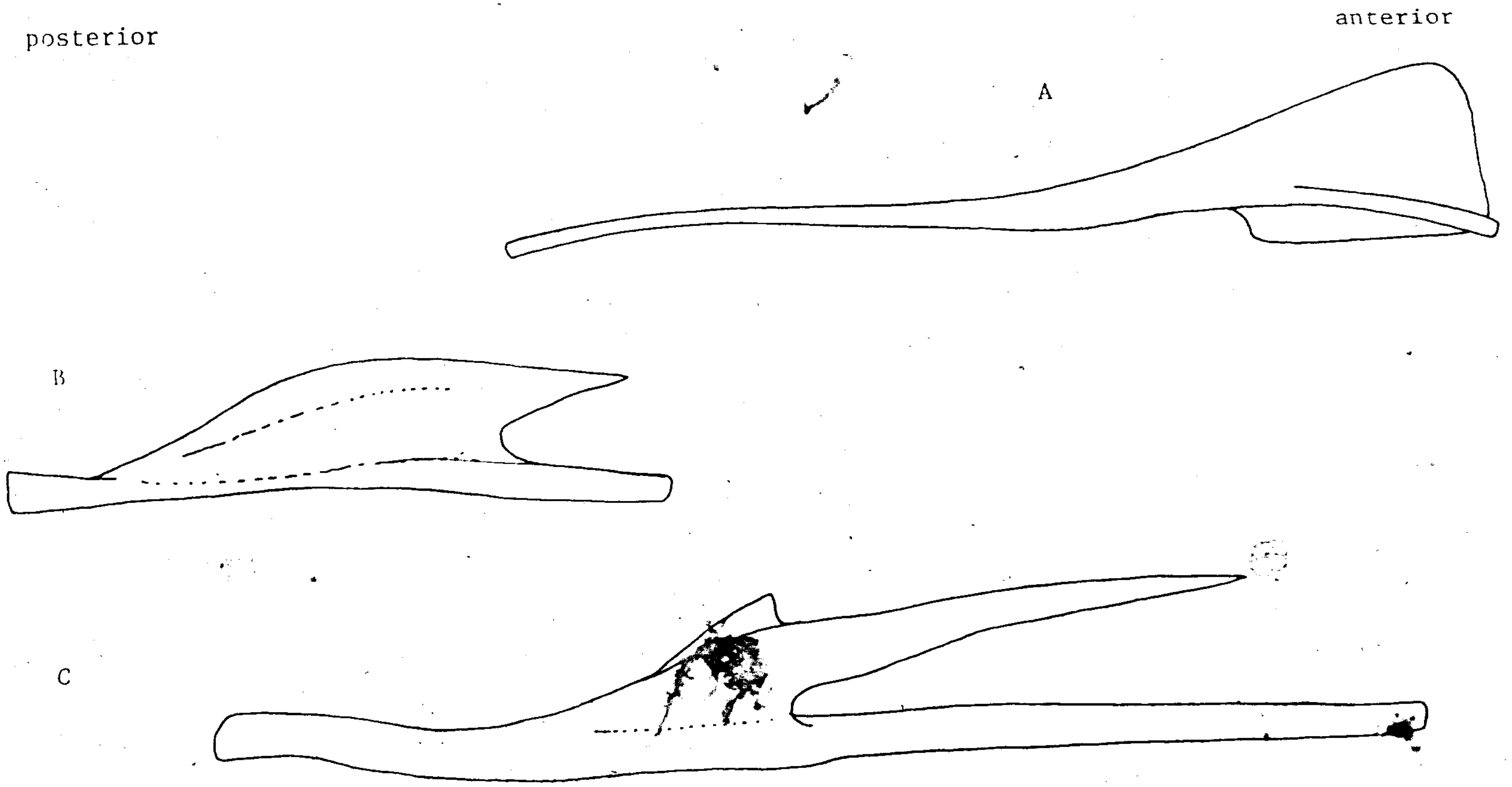

Figure F 3 : Left symplectics of Syngnathiformes, medial views

A. *Aulostomus maculatus*, X 11.5

B. *Syngnathoides biaculeatus*, X 11.5 (LACM 37398-16)

C. *Syngnathus griseolineatus*, X 23.5

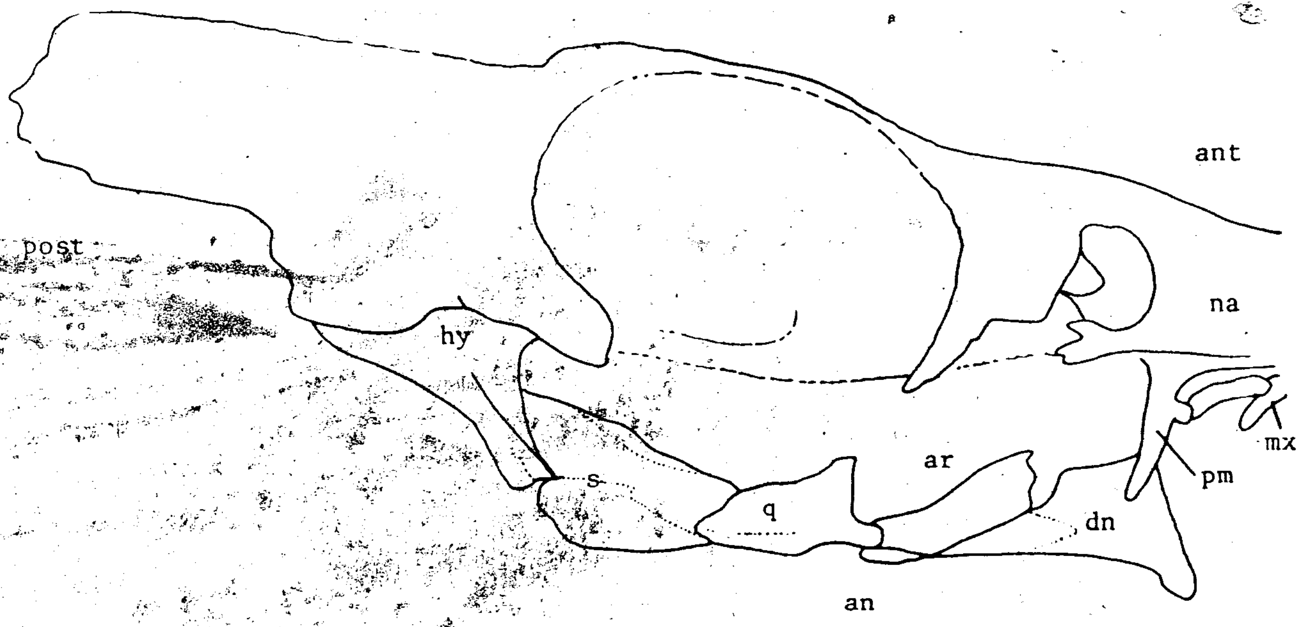

Figure F 4 : *Pegasus volitans* right lateral view with suborbital and opercular series removed, to show suspensoria. X 11.5

G. The Opercular Region

The opercular region contains the opercula, the subopercula, the interopercula, and the preopercula. Characters from this region are listed in Table G1, coded values for framework groups in Table G2, and values for study groups in Table G3.

Framework

The preopercula in Diplophos are almost straight. They bear the posterior portions of the preoperculomandibular canals in open troughs. The interopercula are elongated oval bones, the dorsal one-half to two-thirds of each covered by the preopercula. The opercula are triangular, their apices formed by pointed laminae above the 'condylar struts', which are thickened ridges extending from the opercular condyle to the posterior margin of each operculum. The subopercula are wide flat bones without ascending limbs. They lie along the ventral borders of the opercula.

The preopercula in Saurida are narrow, nearly straight, and bear open sensory canals. The interopercula have narrow anterior portions and wide posterior ends. The opercula have triangular laminae below their condylar struts and square laminae above them, so that each operculum is shaped like a triangle with its apex pointed downwards. The subopercula have marked ascending limbs and wide ventral flanges which follow the posterior margins of the opercula to the condylar struts.

Percopsis has L-shaped preopercula with wide, posteriorly incomplete canals. Their posteroventral corners are widened and weakly serrated, with spines in Aphredoderidae (Rosen & Patterson, 1969). The interopercula are flat, their posterior ends a little deeper than their anterior ends and their ventral margins serrated; they are approximately the same length as the ventral limbs of the preopercula.

The opercular condylar struts in Percopsis extend posteroventrally rather than directly posteriorly like those of Diplophos and Saurida. The flanges above and below them are both triangular, giving the operculum a roughly diamond-shaped outline. Its anterodorsal and posteroventral borders are concave. Distinct vertical struts run along the anteroventral margins of the opercula. The subopercula have short ascending processes and long posterior processes which follow the opercula to the condylar struts.

Atherinomorpha have L-shaped canal-bearing preopercula without any serrations or spines on their posterior borders (Fig. G1); Rosen (1964) gives the absence of serrations and spines as a characteristic of the Atherinomorpha. The interopercula are relatively deep at their posterior ends, but become slender and pointed anteriorly. Condylar struts are not distinct on the opercula, which are unarmed. The subopercula have both ascending and posterior limbs, the latter slightly expanded ventrally and closely following the borders of the opercula.

Holocentrus has L-shaped canal-bearing preopercula with many small posterior spines. In some other Beryciformes (Zehren, 1979) the preopercula bear long spines at their posteroventral corners. The interopercula are oval plates, slightly pointed at their anterior ends, and they also bear posterior spines. The opercula are armed, with long ventral laminae and reduced condylar struts; they are expanded into square laminae above the condylar struts and bear distinct vertical struts along their anterior edges. The subopercula have short ascending and posterior limbs and spines along their ventral margins.

The preopercula in Scorpaeniformes are L-shaped, but in Asterotheca, Peristedion , and Prionotus their anterior limbs are bent medially to lie on the ventral surfaces of their heads; the expanded posterior corners of the preopercula form wide ventral shelves in Peristedion . All Scorpaeniformes examined have canals along the preopercula and all have preopercular spines. The interopercula vary; those of Sebastes are ovoid, those of Cottus and Asterotheca narrow anteriorly, and those of Prionotus narrow posteriorly. The opercula have marked condylar struts which extend posteriorly to end as opercular spines (Fig. A3). The laminae above these struts are relatively small.

Sebastes, Cottus, and Asterotheca have subopercula with ascending and posterior limbs. The angles between the two limbs are acute. In Prionotus the ascending limbs are reduced and the anteroventral corners of the bones are extended. The posterior limbs are slender. In Asterotheca the posterior limbs of the subopercula lie along the medial sides of the opercula, rather than along their margins (Fig. A3,A).

The Perciformes I examined have L-shaped canal-bearing preopercula; in Percalates, Plectroplites, Perca, and Stizostedion the preopercula have small spines along their posterior margins. In Ammodytes their margins are serrated but the serrations are weak and soft. The interopercula are ovoid, slightly wider posteriorly in all except Ammodytes. The opercula have strong condylar struts and thickened anterior margins; they are armed [illegible] except Ammodytes and, in all, have small laminae above the struts. The suboperc[illegible]ll have small ascending limbs and long posterior limbs which closely follow the opercular margins; in Ammodytes the ventral edges of the subopercula are deeply incised, forming long slender lobes.

Gasterosteiformes

In Gasterosteiformes the preopercula are L-shaped (Figs. B4-5). They bear the preoperculomandibular canals. The interopercula are slender and their posterior ends are enlarged. The opercula of Gasterosteidae are shaped roughly like quarter-circles, with their dorsal margins horizontal and their anterior margins almost vertical. They have neither distinct condylar struts nor obviously thickened anterior margins. In Aulorhynchidae the opercula are ovoid or rectangular in shape (Fig. B6) and, again, lack well-developed condylar and anteromarginal struts. The sub-opercula in all Gasterosteiformes have ascending and posterior processes, the anterior ends of the posterior processes closely following the opercular margins. In Aulichthys the posterior processes of the subopercula are expanded to form about one-third of the area of each gill cover.

Syngnathiformes

The inter- and pre-opercula in Syngnathiformes are elongated to help form the snout walls and floors (Figs. A6, B10, E7-8). The preopercula have elongate ventral limbs which extend for over half of the snout length in Syngnathidae (Fig. B10) and Solenostomus and for the full length of the snout in Aulostomus, Macrorhamphosus, and Centriscidae (Fig. A6); only in Fistularia are the preopercula confined to the posterior portions of the snout. The posteroventral corners of the preopercula are extended into short spurs in Syngnathidae, Solenostomus, and Macrorhamphosus and into wide lobes in Centriscidae. Their ascending limbs are truncated in Syngnathidae and relatively small in all other Syngnathiformes except Macrorhamphosus. The preoperculomandibular canals are borne in tubes on the preopercula of Macrorhamphosus and Centriscidae; in Aulostomus and Fistularia only shallow lateral grooves are apparent.

In Macrorhamphosus and Centriscidae the interopercula are slender shafts of bone running along the full lengths of the preopercular anterior limbs. In Macrorhamphosus (Fig. E8,B) the interopercula are enlarged posteriorly. The interopercula of other Syngnathiformes are elongate flat plates; in Aulostomus (Fig. E7,A) and Fistularia they extend almost the full length of the snout, but in Syngnathidae (Fig. E8,A) and Solenostomus they are restricted to the central portion of the snout. Most Syngnathiform opercula are oval to rectangular, with the exceptions of Macrorhamphosus, in which they are triangular (Fig. E8,B), and Centriscidae (Fig. A6,A), in which they are irregularly rounded. Condylar and anteromarginal struts are not apparent in any syngnathid or centriscid opercula, but are present in the other syngnathiforms examined.

The subopercula in Macrorhamphosus have slender ascending and posterior limbs (Fig. A6,B). In Centriscidae both limbs are enlarged and the subopercula form over half of the gill covers (Fig. A6,A). In Aulostomus and Fistularia only the ascending limbs of the subopercula are enlarged, forming triangular plates between the interopercula and the opercula. In Syngnathidae (Fig. E8,A) and Solenostomus the anterior processes are lost and the posterior limbs are narrow, varying from sabre-shaped in Syngnathoides to threadlike in Solenostomus.

Indostomus

The preopercula in Indostomus lie above the posterior ends of the articulars and form the posterior margins of the orbits. They have very short ventral limbs and serrated posterior margins. There are no canals along the preopercula. The interopercula are square and lie behind the preopercula and the posterior margins of the articulars. The opercula are rounded, with large spines on their posterior margins. No condylar struts are present, but a set of lateral ridges radiate outwards from the condyle to the spines. The subopercula are represented only by thin rods lying along the posterodorsal corners of the opercula.

Hypoptychus

The preopercula in Hypoptychus are L-shaped, their ventral limbs reaching almost to the quadrate condyles (Fig. A10). Both limbs bear the preoperculomandibular canal. The posterior laminae are neither expanded, serrated, nor armed. The interopercula are slender and expanded posteriorly (Fig. E10). The opercula are unarmed, but their posterior margins are scalloped. No condylar struts are present. The subopercula have short ascending limbs and sabre-shaped posterior limbs which lie along the ventral margins of the opercula.

Pegasus

In Pegasus the preopercula lie on the ventral surface of the head except for their ascending limbs, which bend dorsally onto the sides of the head (Fig. A12). Almost half of the length of each preoperculum is made up of its expanded posterior lamina, which forms most of the gill cover. The preoperculomandibular canals run along the anterior margins of the preopercula. Each gives rise to three radial canals which extend onto these enlarged flanges.

The interopercula in P. papilio are apparently reduced to long thin cylindrical bones lying between the articulars and the interhyoids; in P. volitans they are flat and slightly expanded posteriorly. The opercula are extremely small palmate bones with thickened 'anterior' edges (Fig. A12). The subopercula are curved rods lying posteroventrally to the opercula.

Dactylopterus

The interopercula of Dactylopterus are reduced to thin bony splints. The preopercula are enlarged, their posterior borders being expanded into long spines (Fig. G2). They bear large anterior flanges reaching to the symplectics and posterodorsal processes which lie over the lateral sides of the opercula.

The opercula are relatively small and have no struts. The subopercula have no ascending limbs. They are small bones whose expanded posterior ends touch the posteroventral corners of the opercula, their anterior ends extending ventrally beneath the preopercula.

Table G1 : Characters from the opercular region
(asterisks indicate those used in phenetic analyses)

*G1. Preopercula have dorsal and ventral arms (1) / lack distinct dorsal and ventral arms (0)

*G2. Preopercula bear / do not bear preoperculomandibular canals

*G3. Opercula have / lack distinct condylar struts

*G4. Posterior borders of preopercula are expanded / not expanded

*G5. Posterior borders of preopercula are incised or serrated / entire

*G6. Preopercula are armed / unarmed

*G7. Interopercula extend full length of preopercula / are shorter than preopercula

*G8. Anterior ends of interopercula are expanded / not expanded

*G9. Posterior ends of interopercula are expanded / not expanded

*G10. Posterior margins of opercula are pointed / rounded

*G11. Opercula form most of the gill covers / less than 2/3 of the gill covers

*G12. Opercula are armed / unarmed

*G13. Subopercula have ascending and posterior limbs / lack distinct ascending and posterior limbs

*G14. Ventral laminae of subopercula are expanded / not expanded

*G15. Ventral laminae of subopercula are lobed / entire

*G16. Posterior limbs of subopercula reach / do not reach the posterior margins of the opercula

*G17. Posterior limbs of subopercula closely follow / do not closely follow margins of the opercula

G18. Opercula have / lack distinct anteromarginal struts

*G19. Preopercula bend medially to form the floors of the branchial chambers / do not bend medially

Table G2 : Distributions of characters from the opercular regions among framework taxa

Taxon	12345	67890	12345	6789
Diplophos	01100	01110	10000	0010
Saurida	01100	01011	10110	1100
Percopsis	11101	01011	10100	1110
Fundulus	11000	01010	10110	0100
Melanotaenia	11000	01010	10110	01X0
Allanetta	11000	00010	10110	1100
Holocentrus	11101	11110	11100	0110
Asterotheca	11101	11011	11100	1011
Cottus	11100	11011	10100	1010
Sebastes	11101	10111	11100	1110
Prionotus	11100	10101	11100	1011
Percalates	11101	11011	11100	1110
Plectroplites	11101	11011	11100	1110
Perca	11101	11011	11100	1110
Ammodytes	11101	01110	10111	1110

Table G3 : Distributions of characters from the opercular regions among study groups

Taxon	12345	67890	12345	6789
Gasterosteus	11000	01010	10100	1100
Pungitius	11000	01010	10100	1100
Culaea	11000	01010	10100	0100
Apeltes	11000	01010	10100	1100
Spinachia	11000	01010	10100	1100
Aulichthys	11000	01010	10110	0100
Aulorhynchus	11000	01010	10100	0100
Syngnathus	10010	00110	10000	0100
Syngnathoides	10010	00110	10000	0100
Hippocampus	10010	00110	10000	1100
Solenostomus	10110	00111	10000	1010
Aulostomus	11100	01110	10100	0110
Fistularia	11100	01110	10100	0110
Macrorhamphosus	11110	01010	10100	1110
Aeoliscus	11010	01000	00110	0100
Indostomus	00001	00110	11000	0000
Hypoptychus	11000	01010	10100	0100
Pegasus	11010	00010	00000	0011
Dactylopterus	11010	10000	00000	0000

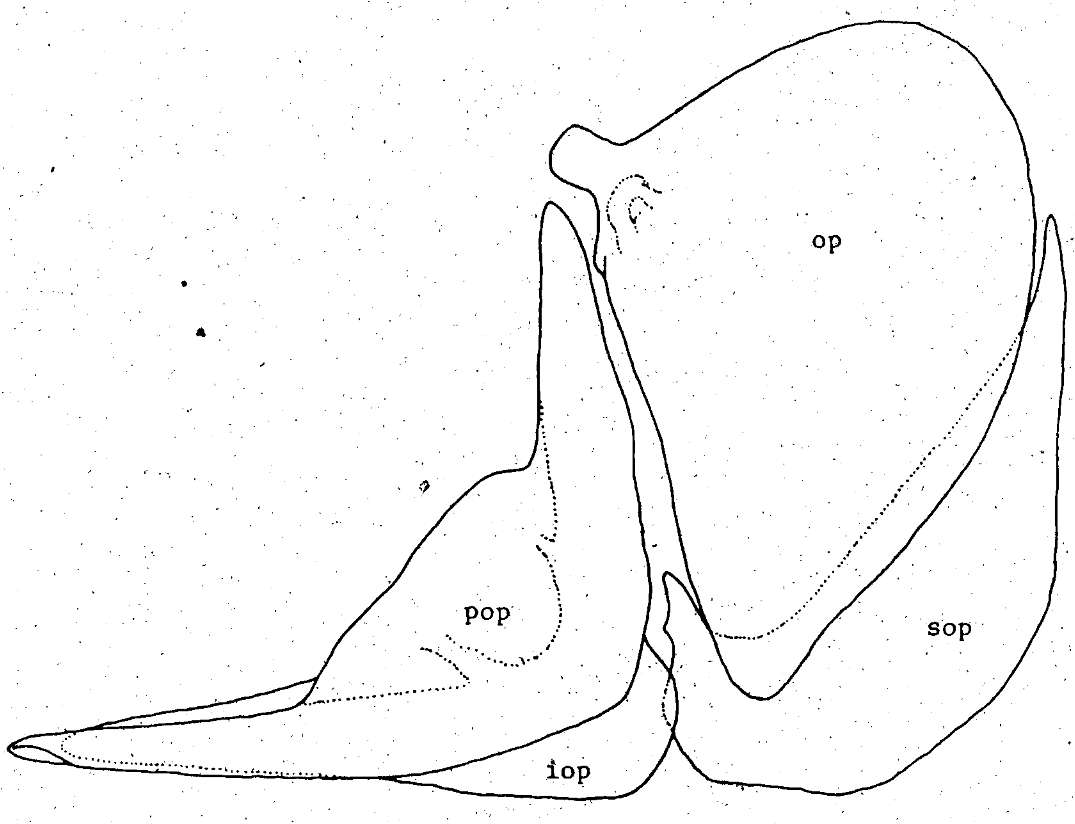

Figure G 1: Fundulus sp., left opercular series, lateral view, X 23.5

(abbreviations are listed on pages xxv-xxvi)

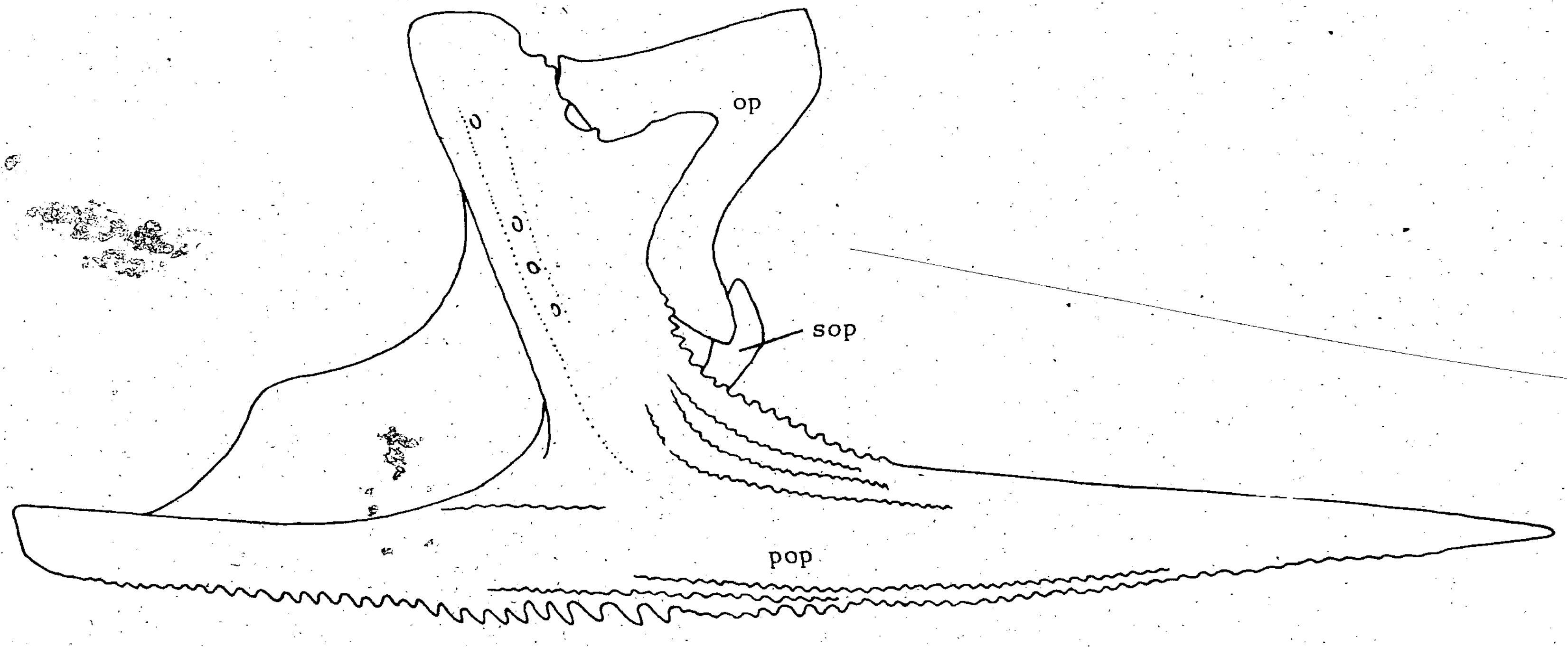

Figure G2: Dactylopterus volitans, left opercular series, lateral view, X11.6

H. The Hyoid Arch

The hyoid arches are comprised of the unpaired urohyal and glossohyal, two pairs of hypohyals, and one pair each of ceratohyals, epihyals, and interhyals. Characters from this region appear in Table H1 and their coded values for framework and study groups (respectively) in Tables H2 and H3.

Framework

In Diplophos the small toothed glossohyal is shaped like a broad cone lying over the anterior symphysis of the hyoid arches. Two hypohyals are present in each arch, one lying above the other at the medial end of the ceratohyal. The ceratohyals are flat rectangular bones, their anterior borders slightly convex and their posterior borders slightly concave. They are attached to the epihyals by simple, almost straight borders. The epihyals are likewise rectangular with convex anterior borders, their posterodorsal corners excavated to receive the ventral ends of the rod-shaped interhyals. Fifteen branchiostegal rays are present on each arch, the first inserted on the ventral hypohyal and the rest at equal intervals along the arch, ten on the ceratohyal and four on the epihyal. The penultimate branchiostegal is sabre-shaped, the ultimate expanded into a broad plate. The urohyal is a thin vertical blade of bone bearing dorsolateral flanges in large specimens, according to Fink and Weitzman (1982).

Saurida also has a toothed glossohyal; its base is conical but its dorsal surface extends anteriorly as a ventrally concave flange. The hypohyals and ceratohyals resemble those of Diplophos, but the ceratohyal is slightly narrower in its centre than at its ends. The epihyals are flat and rectangular; a ridge runs along the lateral sides of both cerato- and epihyals. The interhyals are cylindrical. Each arch bears sixteen branchiostegals, five of which articulate with the narrow central portion of the ceratohyal, five with its posterior portion, and six with the epihyal. The urohyal is a plain vertical blade of bone.

Percopsis has a short conical glossohyal and two pairs of hypohyals. The ventral hypohyals lie along the anteroventral margins of the ceratohyals. The ceratohyals are shaped like flattened hourglasses with dorsal and ventral flanges augmenting their central constrictions. Their enlarged posterior margins are attached to the triangular epihyals; wide grooves run along the dorsal edges of the cerato- and epihyals and a series of toothplates runs along their ventromedial edges. The interhyals are cylindrical. Six branchiostegals are present on each hyoid arch, two articulating with the the ceratohyal shaft, three with its posterior expansion, and one with the epihyal. The urohyals are simple vertical blades.

Atherinomorphs have conical glossohyals, toothless in Fundulus and Melanotaenia but toothed in Allanetta. Two pairs of hypohyals are present (Fig. H1), the dorsal hypohyals lying along the anterodorsal borders of the ceratohyals in Melanotaenia and Allanetta. The ceratohyals have relatively narrow anterior shafts and wide posterior heads, a shape which Rosen (1964) described as characteristic of the Atherinomorpha. In the atherinomorphs I examined, the ceratohyals are attached to the epihyals by dorsal struts originating on the epihyals. Rosen (1964; Fig. 14) illustrates such struts from several other atherinomorphs, but does not indicate from which bones they arise. The epihyals are triangular, their posterior corners articulating with cylindrical interhyals. Rosen (1964) and Rosen and Parenti (1981) have discussed the atherinomorph branchiostegals in detail. They are divided into two series; the anterior branchiostegals are thin and delicate and insert on the shafts of the ceratohyals, while The posterior ones are bladelike and insert on the expanded posterior heads of the ceratohyals and on the epihyals. The urohyals of the atherinomorphs I examined had ventrolateral flanges, narrow in Fundulus and Allanetta and wide in Melanotaenia. These ventral flanges appear to be characteristic of atherinomorpha, appearing in almost all the atherinomorph urohyals figured by Kusaka (1974).

Zehren (1979) describes the beryciform glossohyals as variable both in presence and, when present, in morphology. The glossohyal of Holocentrus is long and flattened, without teeth. Two pairs of hypohyals are present, neither overlapping the ceratohyals. The ceratohyals are usually rectangular, according to Zehren, but in Holocentrus they are centrally constricted, like those of Percopsis, and have large posterior heads attached to the triangular epihyals. Vertical flanges, often pierced by oval foramina, arise from the ceratohyal dorsal margins (Zehren, 1979). The interhyals are cylindrical. Branchiostegals arise from the shafts and heads of the ceratohyals and from the epihyals. As a rule more than two branchiostegals insert on the shafts and they are similar in size to those inserting on the ceratohyal heads and the epihyals The urohyal is a deep blade, posteriorly concave and with a slightly thickened ventral border. The concave posterior border is evident in all the beryciform urohyals figured in Kusaka (1974).

The glossohyals vary in structure among the scorpaeniforms examined. In Prionotus and Sebastes they are flattened, but the glossohyal of Sebastes retains some conical structure. Asterotheca and Cottus have no glossohyals. All have two pairs of hypohyals, the dorsal pair overlapping the ceratohyals (Fig. H2). The ceratohyals have slightly constricted shafts and simple connections with the triangular epihyals. The interhyals are cylindrical. Branchiostegals articulate with the shafts and heads of the ceratohyals and with the epihyals; those articulating with the ceratohyal shafts are slender. The urohyals are posteriorly concave with narrow dorsolateral flanges, in Sebastes and Prionotus, and with wide posteriorly incised ventrolateral flanges in Asterotheca.

The glossohyals of the perciforms examined are cylindrical, those of Perca and Stizostedion slightly flattened. All have two pairs of hypohyals and in Ammodytes and Perca the dorsal pair overlap the ceratohyal. The ceratohyals of Percalates and Plectroplites resemble those of Holocentrus, their dorsal laminae pierced by elongate foramina. In Perca, Stizostedion , and Ammodytes neither the dorsal laminae nor the dorsal foramina are apparent. The ceratohyals are attached to the eiphyals by lateral struts in Percalates, Plectroplites, Lipogramma , Mugil , and Aequidens ; in Centropomus they are connected by medial struts and in Stizostedion by complex sutures. The connections are simple in Perca and Ammodytes, and Blennius and Chaenopsis have dorsal struts like those found in Atherinomorpha. The epihyals are triangular and the interhyals cylindrical. Branchiostegals are arranged like those of Scorpaeniformes. The urohyals are vertical plates, posteriorly concave in Perca but entire in Percalates, Plectroplites, and Ammodytes; in Percalates and Plectroplites they bear narrow ventrolateral flanges.

Gasterosteiformes

Gasterosteiform glossohyals are simple rods, slightly flattened posteriorly. Two pairs of hypohyals are present, the dorsal pair (and the ventral pair, in Aulichthys) overlapping the ceratohyals (Fig. H3). The ceratohyals have narrow shafts and wide heads and in all Gasterosteiforms except Aulichthys they bear dorsal struts extending to the epihyals. The epihyals are triangular and the interhyals hourglass-shaped. The urohyals are divided into a ventral blade and a dorsal, posteriorly directed spur in Spinachia, Culaea and

Aulorhynchidae, and in my small specimens of Pungitius, but not in Kusaka's (1974) slightly larger specimens. All have ventrolateral flanges, which are posteriorly incised in Spinachia, Aulorhynchidae, and my Pungitius (but not in Kusaka's). Branchiostegals articulate only with the widened heads of the ceratohyals.

Syngnathiformes

Most of my observations of syngnathiform hyoid arches agree with Jungersen's (1908, 1910). Their glossohyals are cylindrical. They are short, thin, and fragile in Syngnathidae, and hardly extend anteriorly before the hypohyals. They are elongate and slender in Aulostomus and Fistularia and are augmented by lateral flanges in Macrorhamphosus and Centriscidae. Solenostomus has no glossohyal. The other elements of the hyoid arches are extensively overlapped so that the connections between them involve their lateral and medial surfaces rather than their anterior and posterior edges. There are two pairs of hypohyals, the ventral by far the largest; in all except Solenostomus they are almost entirely confined to the ventromedial sides of the ceratohyals. In Macrorhamphosus and Centriscidae the dorsal hypohyals are reduced to small plates tipping the posterodorsal processes of the ventral hypohyals (Fig. H4); in Aulostomus, Fistularia, and Syngnathidae their positions are more anterior (Fig. H5). Solenostomus is unusual in that its hypohyals are of equal size, occupying the dorsal and ventral positions seen in most fishes.

The ceratohyals in Solenostomus and Macrorhamphosus are shaped like flattened rods, slightly constricted centrally. In Syngnathidae, Aulostomus, and Fistularia they are almost triangular, their apices anterior and their lateral sides almost completely covered by the hypo- and epihyals. The epihyals are triangular in Solenostomus, Aulostomus, and Fistularia. They extend anteriorly along the lateral sides of the ceratohyals in Syngnathidae, along both sides in Aulostomus and Fistularia, and along their medial sides in Macrorhamphosus and Centriscidae. In Aulostomus and Fistularia an anterodorsal process from each epihyal meets a dorsal process from the ceratohyal to form the rim of a dorsal foramen.

The interhyals articulate with the sphenotics by rounded condyles. In Centriscidae they are simply rounded knobs of bone on the posterodorsal corners of the epihyals. In

Macrorhamphosus they are enlarged into irregularly rounded bones. In Solenostomus and Syngnathidae they bear medial flanges, and in Aulostomus and Fistularia are enlarged into bony fans with expanded dorsal articular surfaces.

The urohyals of Syngnathidae, Aulostomus, and Fistularia are simple, slightly flattened rods; those of Solenostomus and Centriscidae bear deeply incised dorsolateral flanges, and Macrorhamphosus has a deep urohyal with slightly incised dorsolateral flanges. The branchiostegals in Syngnathiformes are reduced in number and, in most, insert on the epihyals. In Aulostomus and Fistularia the first ray on each side inserts on the ceratohyal; in Centriscidae the last ray inserts on the interhyal.

Indostomus

The glossohyal of Indostomus (basihyal of Banister, 1970) is the largest element of the hyoid arch, a stout cylindrical bone reaching almost the entire length of the snout. There are two pairs of hypohyals, the dorsal lying along the dorsal border of the ceratohyal (fig. H6,A). The ceratohyals are almost hourglass-shaped. The epihyals are triangular; Banister (1970) reports dorsal connections between the cerato- and epihyals, but in the specimens I examined the connections between them were simple (Fig. H6,A). The interhyals are flattened, broadened cylinders, constricted centrally. The urohyal bears ventrolateral flanges; its blade is incised posteriorly. The branchiostegals articulate with the narrowest portions of the ceratohyals, with their expanded posterior heads, and with the cartilage between the cerato- and epihyals.

Hypoptychus

The glossohyal of Hypoptychus is long and cylindrical with a slight ventral flange. There are two pairs of hypohyals, the ventral curving over the anterior ends of the ceratohyals and the dorsal pair lying in notches on the anterodorsal edges of the ceratohyals (Fig. H6,B). The ceratohyals expand posteriorly to simple connections with the epihyals. The interhyals are short wide cylinders and the urohyal bears posteriorly incised ventrolateral flanges. Two branchiostegals articulate with the head [illegible] each ceratohyals and two with each epihyal.

Pegasus

Pegasus volitans has a very short stout cylindrical glossohyal, P. papilio a longer conical one. Both have two pairs of hypohyals; in P. papilio (Fig. H6,C) both lie along the anterior margins of the ceratohyals, while in P. volitans the dorsal hypohyals lie along their dorsal margins. The ceratohyals and epihyals are depressed, but an hourglass-shaped structure is visible in the ceratohyals. Pietsch (1978) noted dorsal spurs between the epi- and ceratohyals, but I saw none; rather, the two are connected by medial struts in P. papilio and by complex sutures in P. volitans . The interhyals are cylindrical. The urohyal of P. papilio is a simple vertical blade, while that of P. volitans has both dorso- and ventrolateral flanges. Both species have one thin branchiostegal inserting on the shaft of each ceratohyal, one on each ceratohyal head, and three on each epihyal.

Dactylopterus

The glossohyal of Dactylopterus is cylindrical and toothless. Two pairs of hypohyals are present, the dorsal pair lying along the dorsal margins of the ceratohyals (Fig. H7). The ceratohyals are centrally constricted, and each bears a small dorsal projection on its posterodorsal corner. The ceratohyals and epihyals are connected by simple straight borders. The epihyals are triangular, each bearing a small dorsal process on its anterodorsal corner which is bound to the dorsal process of the ceratohyal. The interhyals are simple cylindrical bones. Two small branchiostegal rays articulate with each ceratohyal shaft and four broader ones articulate with each epihyal. The urohyal blade is deeply incised posteriorly and bears narrow dorsolateral flanges and wider ventrolateral flanges. The latter are slightly incised posteriorly.

Table H1 : Characters from the hyoid arches
(asterisks indicate those used in phenetic analyses)

H1. Glossohyal cylindrical (1) / flattened (0)
H2. Glossohyal toothed / toothless
*H3. Dorsal hyophals overlap ceratohyals / lie anterior to ceratohyals
*H4. Ventral hypohyals overlap ceratohyals / lie anterior to ceratohyals
*H5. Ceratohyals expanded / not expanded at anterior end
*H6. Ceratohyals constricted / not constricted centrally
*H7. Ceratohyals attached to epihyals by dorsal struts originating on epihyals / no dorsal struts originate on epihyals
*H8. Ceratohyals attached to epihyals by medial or lateral struts / no medial or lateral struts
*H9. Ceratohyal shafts bear / do not bear branchiostegals
*H10. Ceratohyal posterior heads bear / do not bear branchiostegals
*H11. Ceratohyals with / without toothplates
*H12. Epihyals triangular / quadrangular
*H13. Epihyals with / without toothplates
*H14. Interhyals cylindrical / rounded
*H15. Posterior branchiostegals expanded into plates / not expanded
*H16. Urohyal with / without dorsolateral flanges
*H17. Urohyal with / without ventrolateral flanges
H18. Urohyal flanges posteriorly incised / entire
*H19. Urohyal blade posteriorly incised / entire
*H20. Hypohyals bear / do not bear branchiostegals

Table H2 : Distributions of characters from the hyoid arches among framework taxa

Taxon	12345	67890	12345	67890
Diplophos	11001	00011	00011	10001
Saurida	11001	10011	00010	00000
Percopsis	10011	10011	11110	00000
Fundulus	10000	11011	01010	01000
Melanotaenia	10100	11011	01010	01000
Allanetta	11100	11011	01010	01000
Holocentrus	00001	10011	01010	01010
Asterotheca	XX100	10011	01010	01010
Cottus	XX100	10011	01010	00X00
Sebastes	00100	00011	01010	01000
Prionotus	00100	10011	01010	10010
Percalates	10000	10111	01010	01000
Plectroplites	10000	10111	01010	01000
Perca	10100	10011	01010	00010
Ammodytes	10100	10011	01010	00000

Table H3 : Distributions of characters from the hyoid arches among study groups

Taxon	12345	67890	12345	67890
Gasterosteus	10100	10001	01010	01000
Pungitius	10100	10001	01010	01010
Culaea	10100	10001	01010	01010
Apeltes	10100	10001	01010	01000
Spinachia	10100	10001	01010	01110
Aulichthys	10110	10001	01010	01110
Aulorhynchus	10100	10001	01010	01110
Syngnathus	10110	00100	00000	00000
Syngnathoides	10110	00100	00000	00000
Hippocampus	10110	00100	00000	00000
Solenostomus	XX000	10000	01000	10100
Aulostomus	10110	00101	01000	00000
Fistularia	10110	00101	01000	00000
Macrorhamphosus	10110	10100	00000	10110
Aeoliscus	10110	00100	00000	10110
Indostomus	10101	10011	01010	10010
Hypoptychus	10110	10001	01010	01110
Pegasus	101*0	10111	00010	11110
Dactylopterus	10101	10010	01010	11110

* - both states are found

Figure H 1 : Hyoid arches of Atherinomorpha, left lateral views

A. <u>Melanotaenia nigrans</u>, X 11.5

B. <u>Allanetta harringtonensis</u>, X 23.5

C. <u>Fundulus</u> sp., X 48

(abbreviations are listed on pages xxv-xxvi)

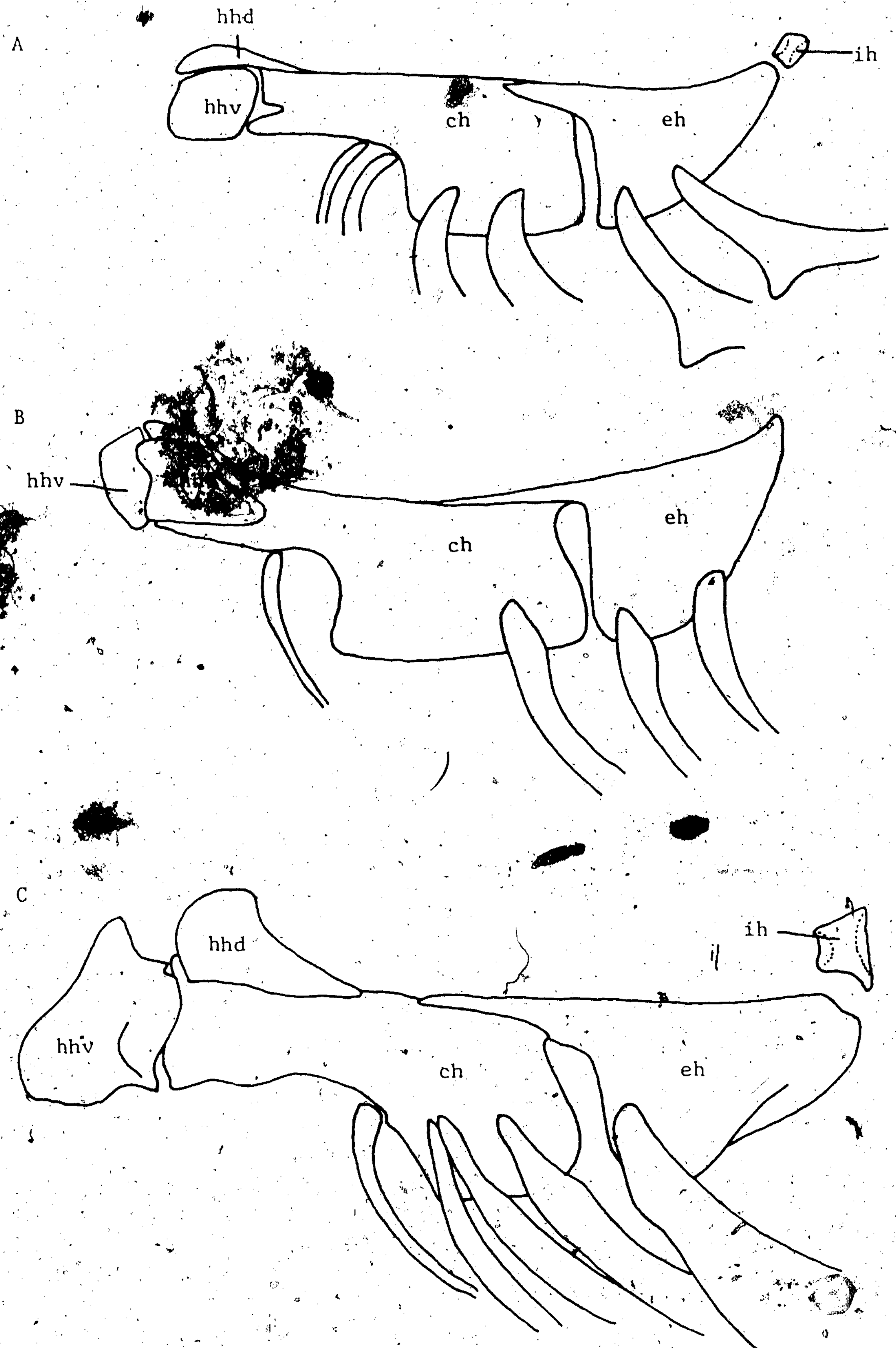
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Figure H 2 : Hyoid arches of Scorpaeniformes, left lateral views.

A. *Sebastes flavidus*, X 11.5

B. *Prionotus carolinus*, X 5.6

C. *Asterotheca alascana*, X 11.5

D. *Cottus cognatus*, X 23.5

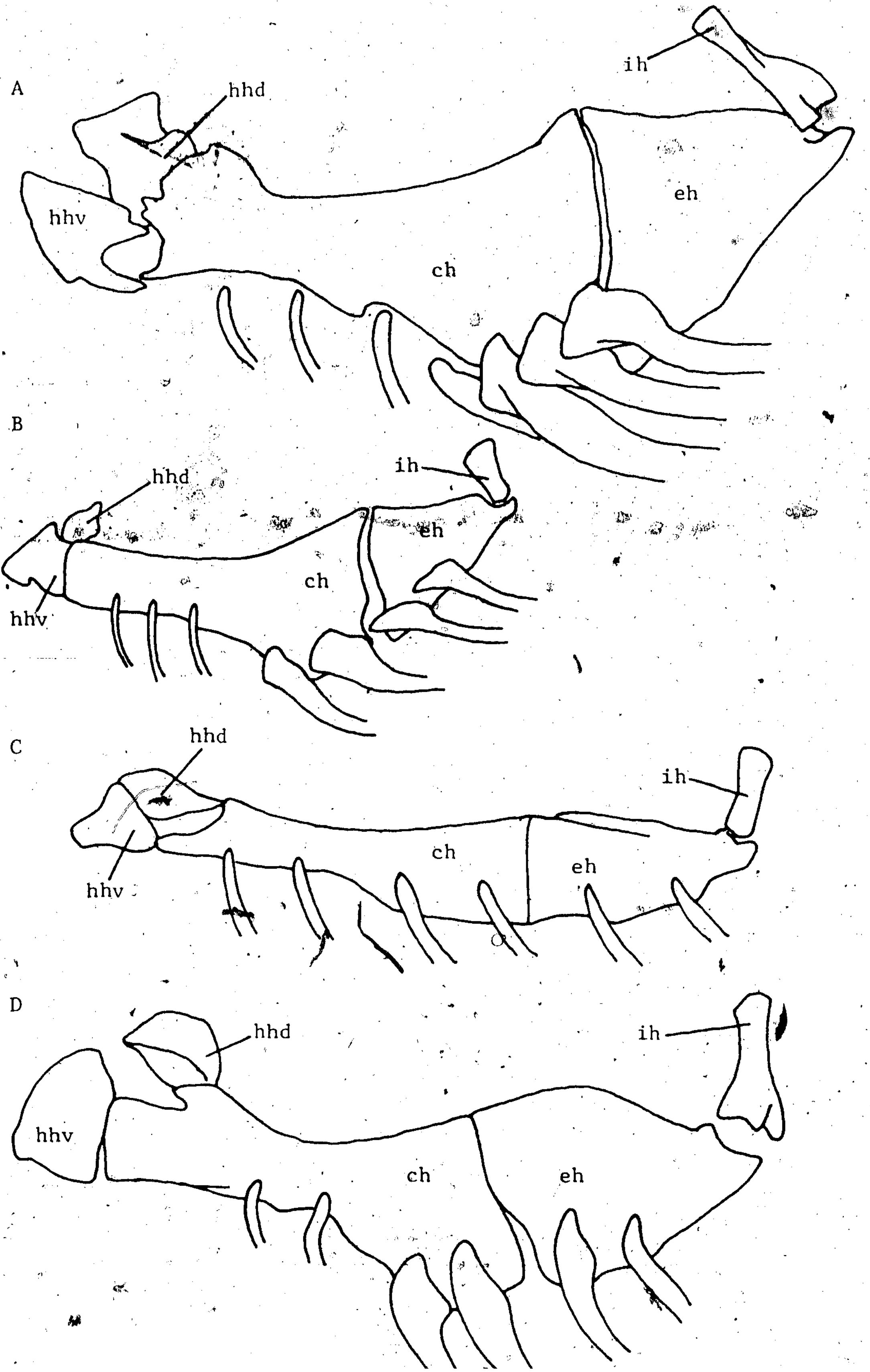
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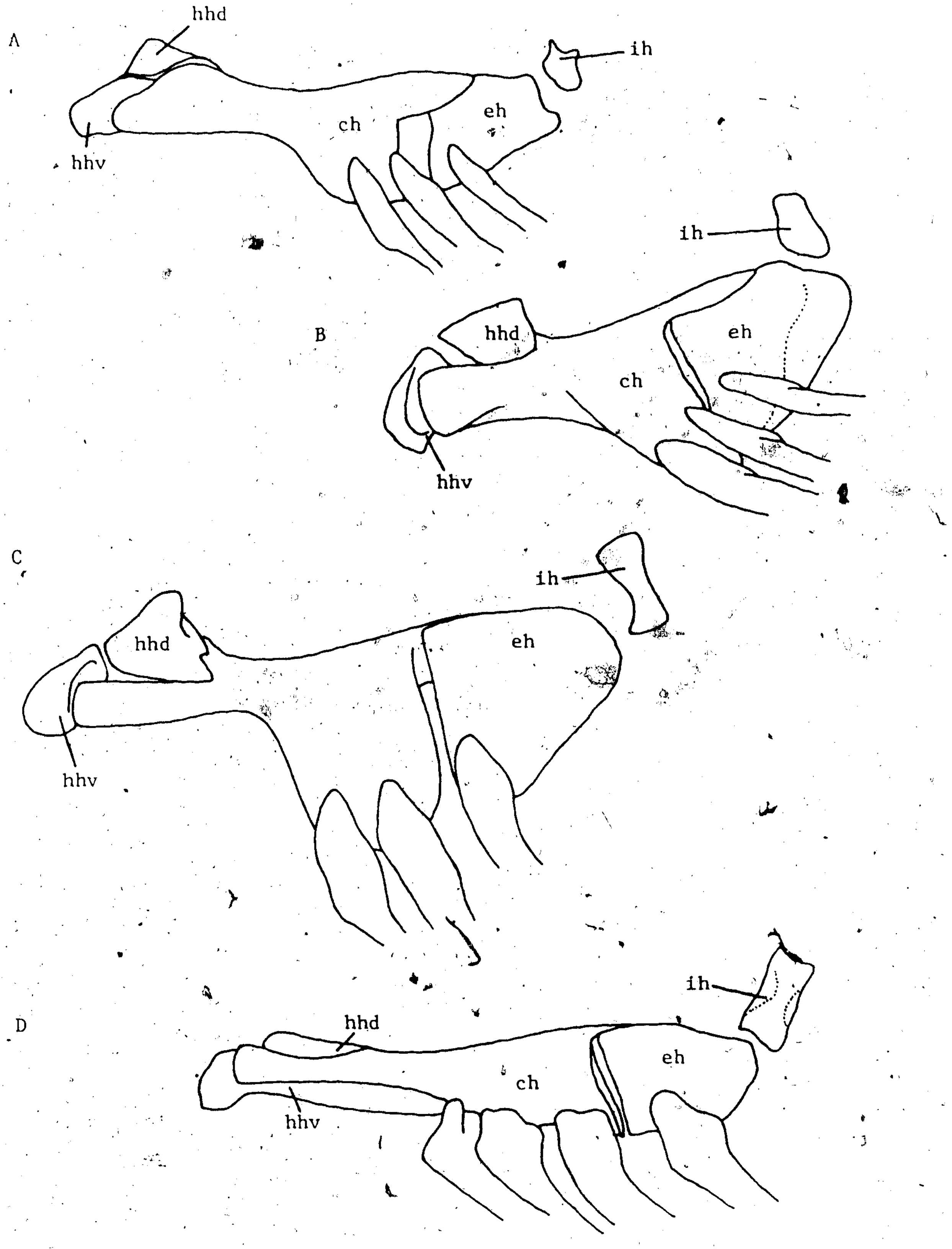
Figure H 3 : Hyoid arches of Gasterosteiformes, left lateral views

A. *Spinachia spinachia*, X 23.5

B. *Apeltes quadracus*, X 48

C. *Gasterosteus aculeatus*, X 23.5 (UAMZ 5512)

D. *Aulichthys japonicus*, X 23.5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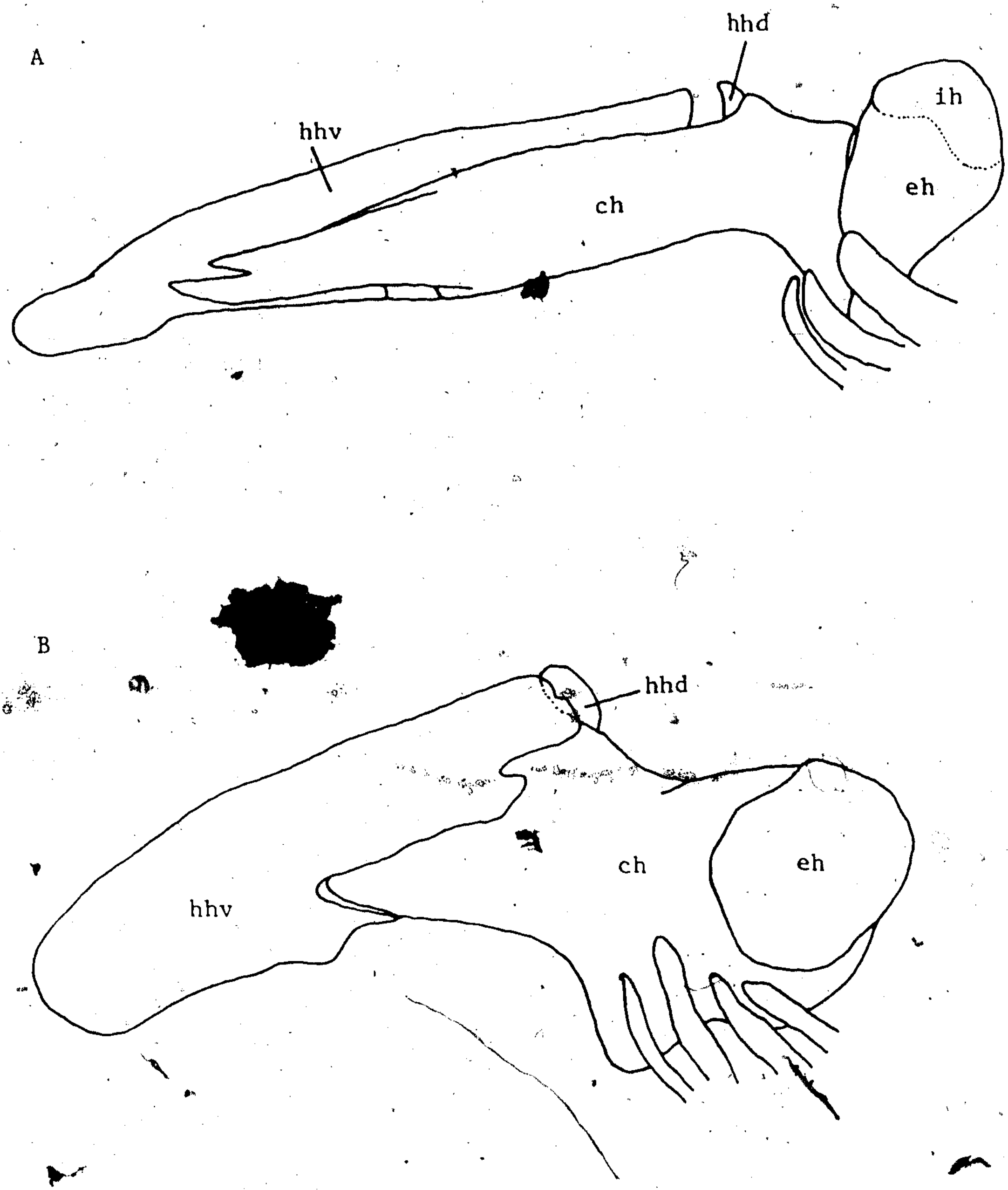


Figure H 4 : Hyoid arches of Syngnathiformes, left lateral views

A. <u>Macrorhamphosus gracilis</u>, X 48

B. <u>Centriscus scutatus</u>, X 48 (UAMZ 370)

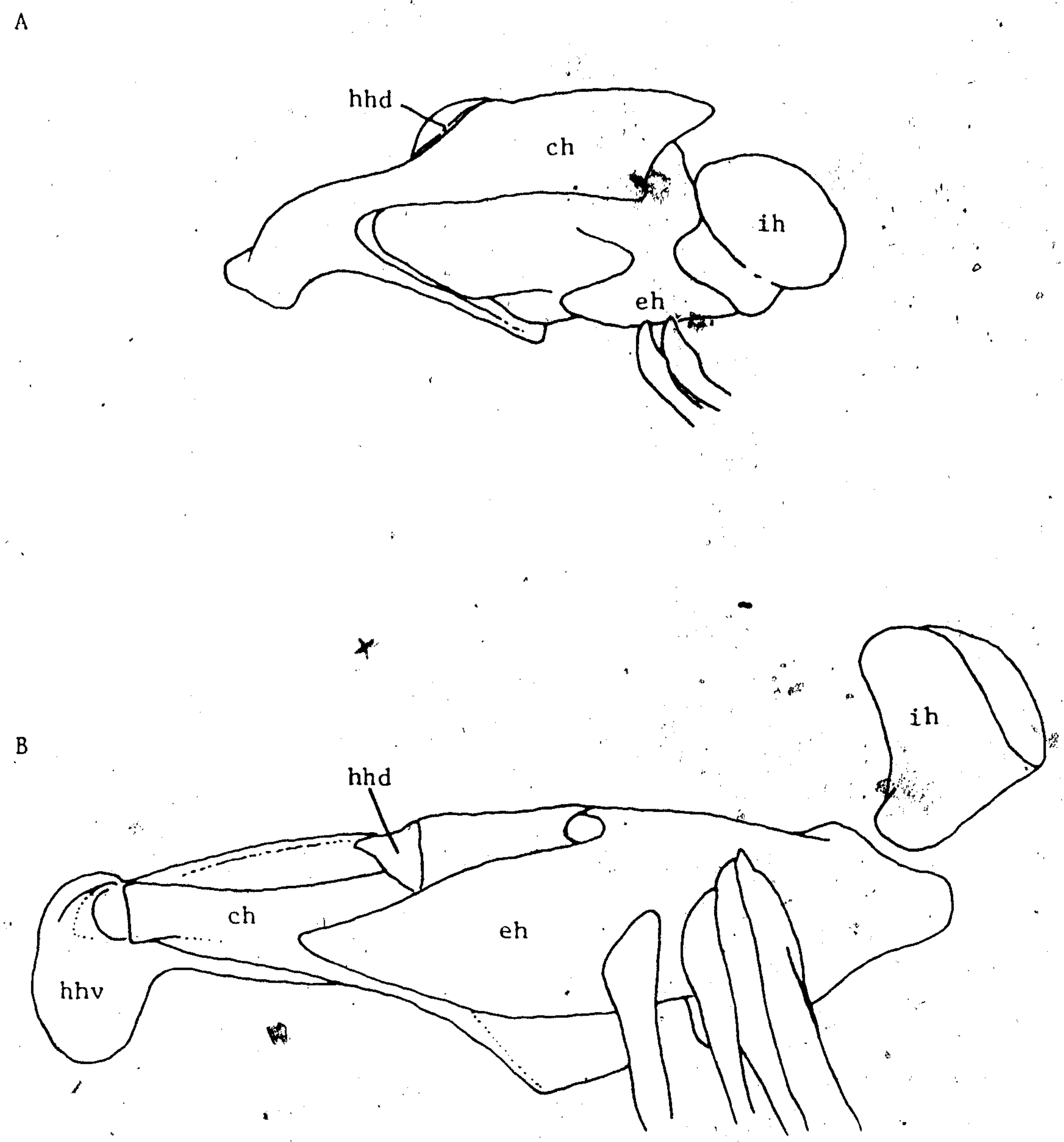


Figure H 5 : Hyoid arches of Syngnathiformes, left lateral views

A. *Syngnathus griseolineatus*, X 48

B. *Aulostomus chinensis*, X 23.5

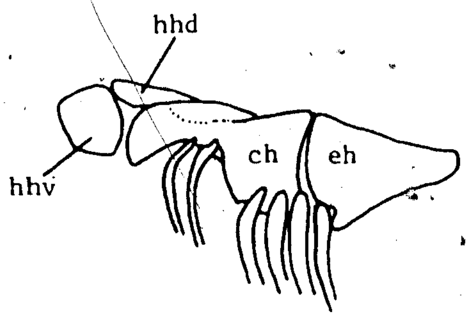
Figure H 6 : Hyoid arches of study groups, left lateral view~~s~~

A. *Indostomus paradoxus*, X 48 (USNM 203888)

B. *Hypoptychus dybowski*, X 23.5

C. *Pegasus papilio*, X 23.5

A



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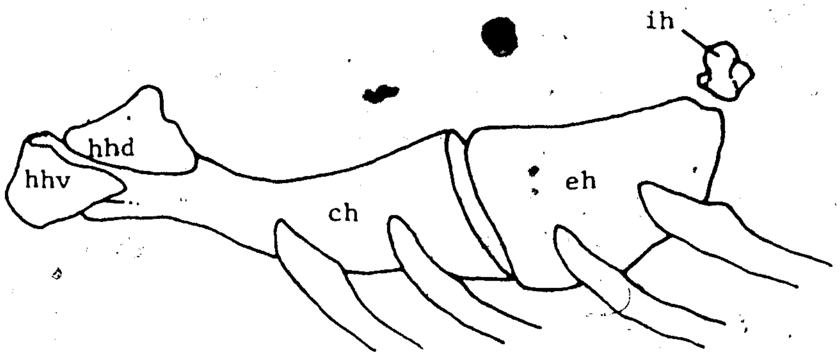

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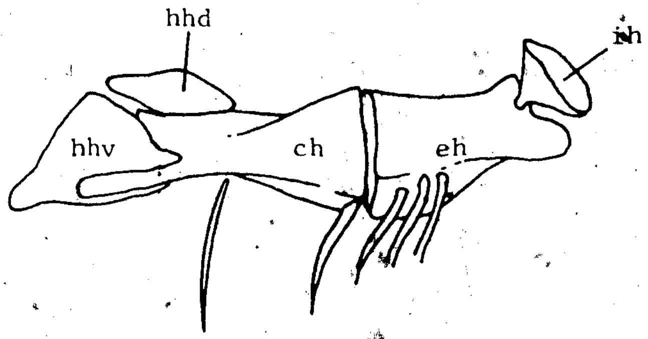


M27. Number of vertebrae

M28. Precaudal vertebrae / total vertebrae (%)

M29. Number of epipleural ribs

M30. Number of pleural ribs

M31. Body depth / standard length (%)

M32. Body width / standard length (%)

M33. Length of first four vertebrae / standard length (%)

M34. Average length of first vertebrae / length of central vertebrae

M35. Average length of last caudal vertebrae / length of first caudal vertebrae

** - used only in binary character analyses (including phenetic analyses)

Table M2 : Distributions of binary characters from the axial skeleton among framework taxa

Taxon	12345	67890	12345	67890	12345	6
Diplophos	00010	11001	10011	11101	01110	0
Saurida	01000	00100	10011	11010	01110	0
Percopsis	11000	01111	10010	11001	01110	0
Fundulus	00001	01111	10010	11001	01110	0
Melanotaenia	11001	00111	10010	11001	11110	0
Allanetta	11001	00111	10010	11001	01110	0
Holocentrus	11000	11111	10010	11011	11110	0
Asterotheca	10000	00111	10000	11001	01110	0
Cottus	10000	00111	10010	11001	01110	0
Sebastes	11000	10111	10010	11001	00010	0
Prionotus	11000	00111	10000	11001	01110	0
Percalates	01000	00111	10010	11001	01110	0
Plectroplites	01000	00111	10010	11001	01110	0
Perca	01000	00111	10010	11000	01100	0
Ammodytes	11000	00111	10010	11011	01110	0

Table M3 : Distributions of numerical characters from the axial skeleton among framework taxa

Taxon	27	28	29	30	31	32	33	34	35
Diplophos	63-87	40.0	21	38	9.2	1.8	3.4	.79	.80
Saurida	54	80.0	41	31	15.0	11.1	5.7	.80	.80
Percopsis	33	48.5	2	16	20.1	13.4	7.3	.84	.67
Fundulus	30-33	45.3	11-12	12-13	24.7	17.8	9.5	1.01	.85
Melanotaenia	36	58.3	26	19	29.6	10.0	10.0	.92	.73
Allanetta	43	54.6	23-24	21-22	17.3	10.0	6.3	1.2	.75
Holocentrus	23	34.5	13	8	39.0	19.5	X	.80	.70
Asterotheca	39-40	29.1	0	10-11	12.9	5.5	5.1	.73	1.06
Cottus	32	34.4	0	13	21.3	21.7	7.9	.84	.80
Sebastes	25-27	39.8	8-9	9-10	18.8	19.2	8.8	.79	.87
Prionotus	X	X	X	X	19.6	19.3	X	X	X
Percalates	34	X	6	7	34.3	19.0	10.2	.96	.94
Plectroplites	35	X	6	7	31.8	17.6	11.3	1.0	.87
Perca	39-41	52.5	13-14	17-18	14.7	13.3	6.6	1.14	.67
Ammodytes	65-68	67.7	45	40	9.9	4.0	4.7	.96	.73

Table M4 : Distributions of binary characters from the axial skeleton among study groups

Taxon	12345	67890	12345	67890	12345	67
Gasterosteus	01000	00111	00010	11001	10010	0
Pungitius	01000	00111	10010	11000	11110	0
Culaea	01000	00111	10010	11001	11110	0
Apeltes	01000	00111	00010	11001	11010	0
Spinachia	01000	00011	00010	11000	01110	0
Aulichthys	01000	00011	00010	11000	11010	0
Aulorhynchus	01000	00011	00010	01000	11010	1
Syngnathus	01000	00110	00100	01000	00000	1
Syngnathoides	01000	00110	00100	01000	00000	1
Hippocampus	01000	00110	00100	01000	10000	1
Solenostomus	01000	01111	10000	00000	01000	0
Aulostomus	01100	00111	11000	01011	00110	0
Fistularia	01100	00011	10000	01010	11111	0
Macrorhamphosus	01000	01111	10000	01011	01101	1
Aeoliscus	01100	00101	10100	01011	00101	1
Indostomus	01000	00110	01100	01001	10011	0
Hypoptychus	01000	00110	00000	11011	01110	0
Pegasus	01100	00110	00100	11101	10000	0
Dactylopterus	11100	00101	10100	10101	00110	0

Table M5 : Distributions of numerical characters from the axial skeleton among study groups

Taxon	27	28	29	30	31	32	33	34	35
Gasterosteus	32-33	46.3	11-12	9-10	X	X	11.3	1.5	0.9
Pungitius	31-33	44.7	11	9	X	X	7.9	1.2	1.3
Culaea	29-33	48.5	16	11-12	19.5	11.7	9.6	1.0	0.98
Apeltes	28-31	35.8	9-10	8-9	X	X	9.6	1.1	1.1
Spinachia	39-43	46.0	18-19	14-15	X	X	6.3	0.96	0.7
Aulichthys	49-53	47.0	0	0	X	X	6.7	1.4	1.1
Aulorhynchus	52-62	48.6	1-2	22-23	X	X	6.3	1.2	1.1
Syngnathus	55-64	33.4	0	0	X	X	5.6	0.99	0.75
Syngnathoides	67	26.9	0	0	X	X	10.4	1.98	0.3
Hippocampus	54	24.1	0	0	14.4	7	10.6	1.3	0.5
Solenostomus	32	25.0	0	0	19.3	3.3	13.6	1.5	0.6
Aulostomus	58-60	39.5	0	0	4.7	3.8	12.5	2.4	0.8
Fistularia	78-83	61.9	0	0	X	X	13.4	6.1	0.9
Macrorhamphosus	23-24	36.5	0	0	X	X	14.9	1.5	0.9
Aeoliscus	19-20	35.6	0	0	14.4	4.1	37.5	7.6	0.55
Indostomus	20-21	43.5	0	0	X	X	10.9	0.6	0.8
Hypoptychus	54-55	54.6	0	28-29	X	X	5.9	0.95	0.8
Pegasus	18-24	39.5	0	0	15.9	31.3	13.6	0.97	1.06
Dactylopterus	21	42.9	0	9	25.3	24.3	11.7	0.84	1.24

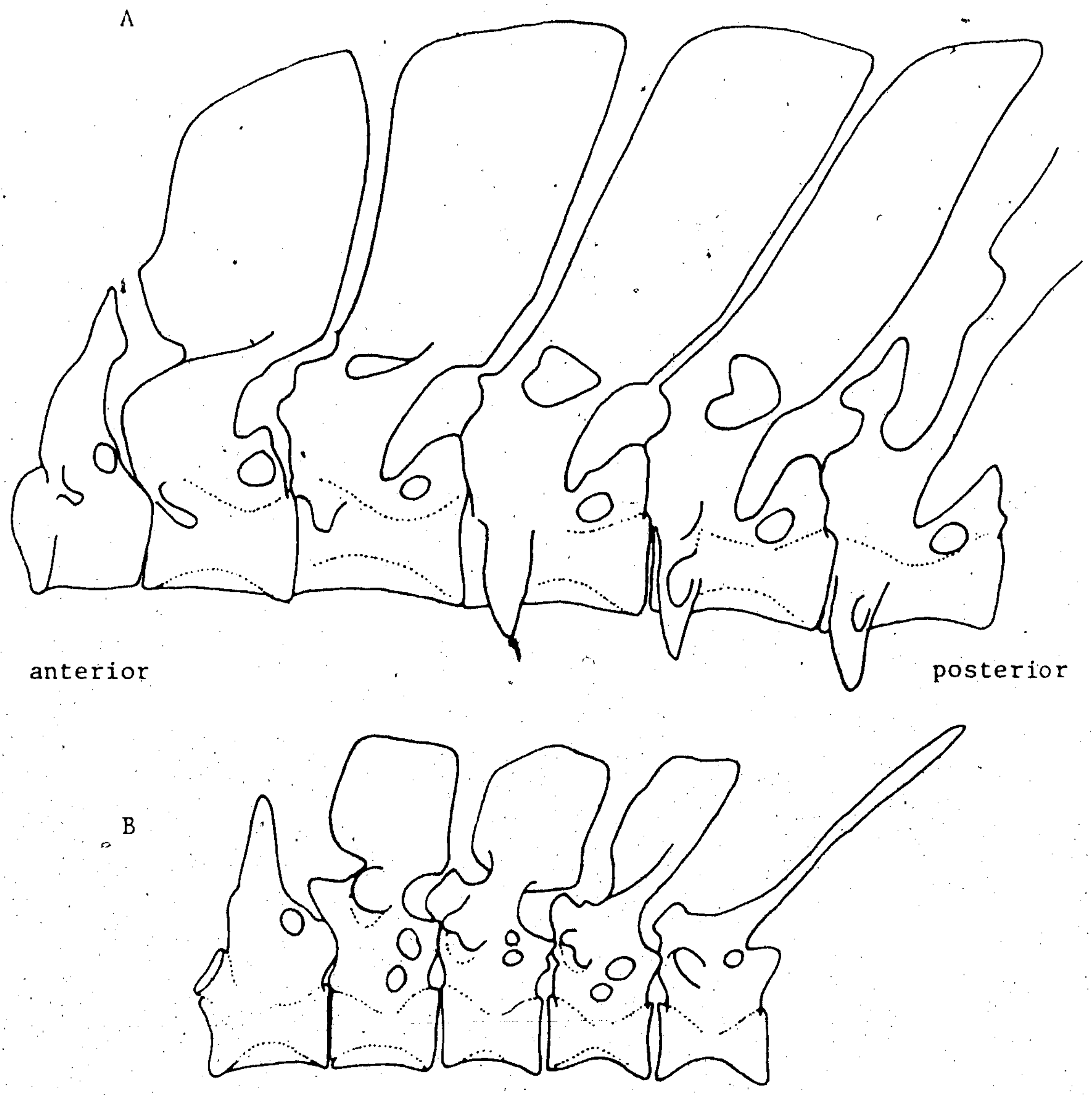


Figure M 1 : Vertebrae of Atherinomorpha, left lateral views

A. Allanetta harringtonensis vertebra 1 - 6, X 23.5

B. Fundulus sp., vertebra 1 - 5, X 23.5

(abbreviations are listed on pages xxv-xxvi)

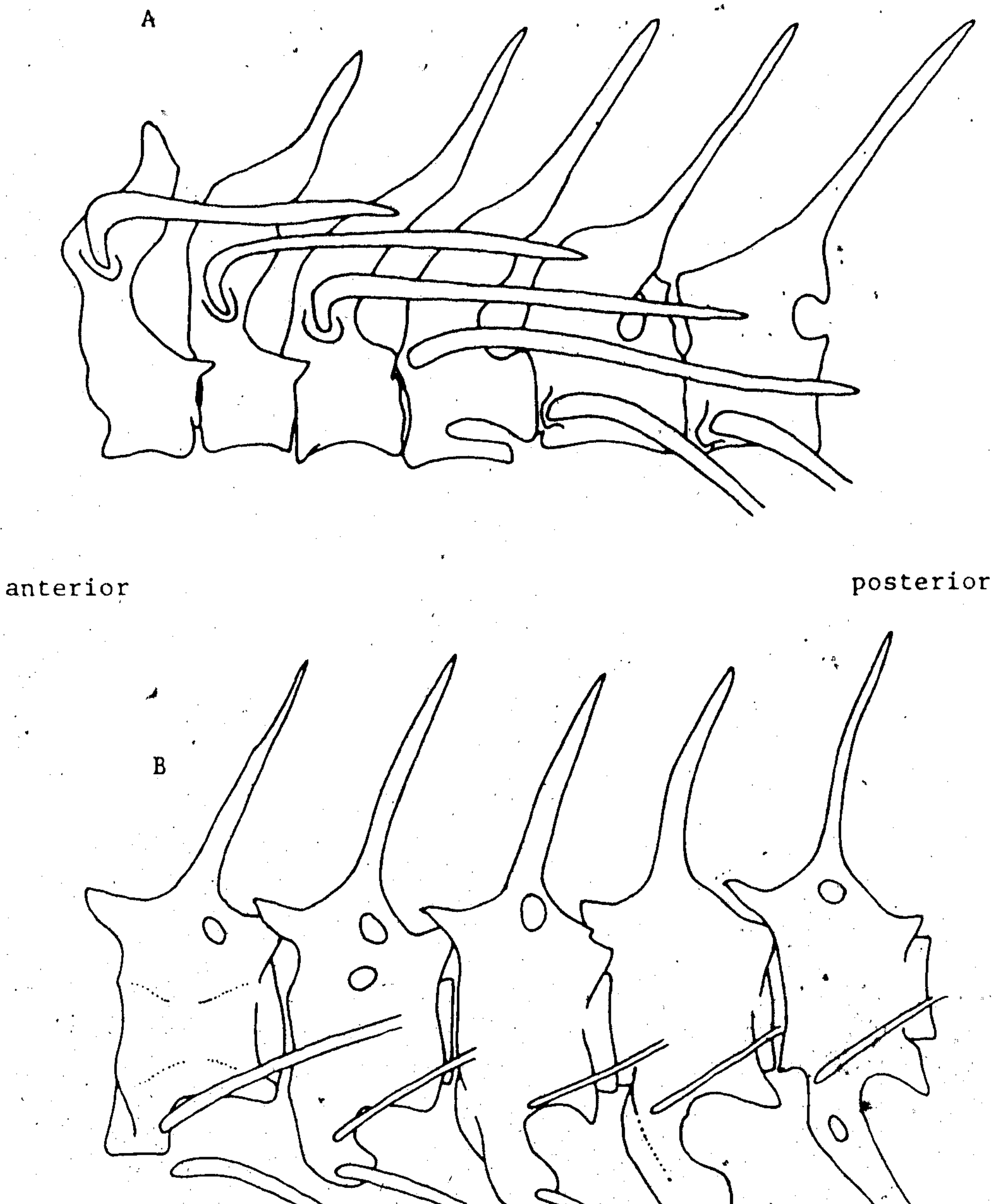


Figure M2 : Cottus cognatus vertebrae, left lateral views, X23.5

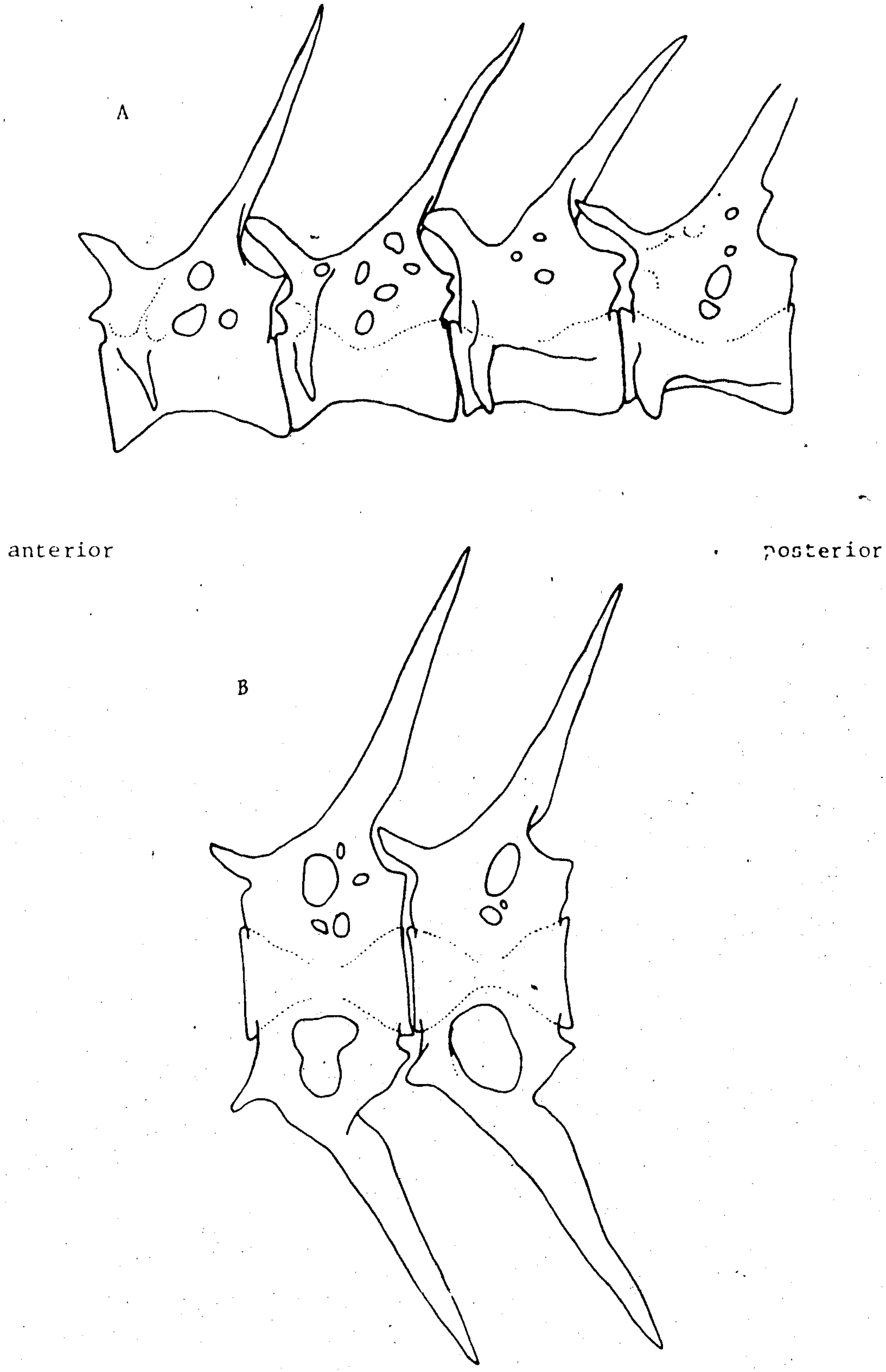
A. Vertebrae 1 - 6

B. Vertebrae 10-17

Figure M 3 : *Culaea inconstans*, vertebrae, left lateral views

A. Vertebrae 1-4, X 23.5

B. Caudal vertebrae 6-7, X 23.5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B

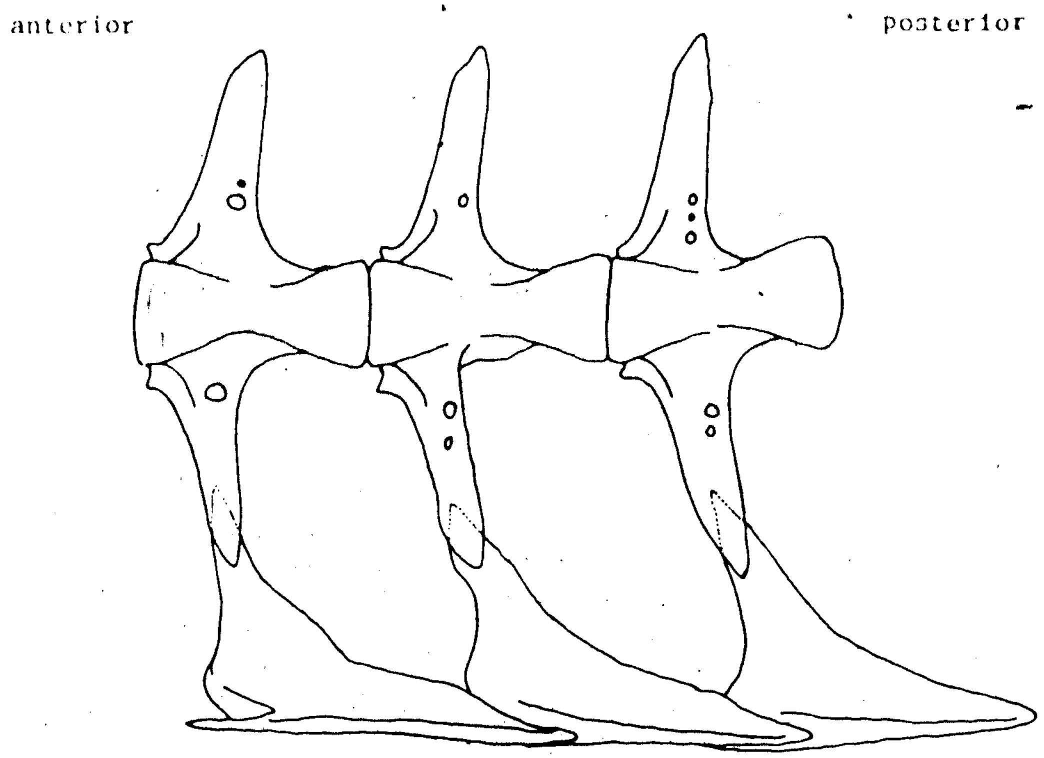


Figure M 4: Aulorhynchus flavidus, vertebrae 9 - 11 and associated right scutes, ventral view. X 23.5 (UAMZ 1694)

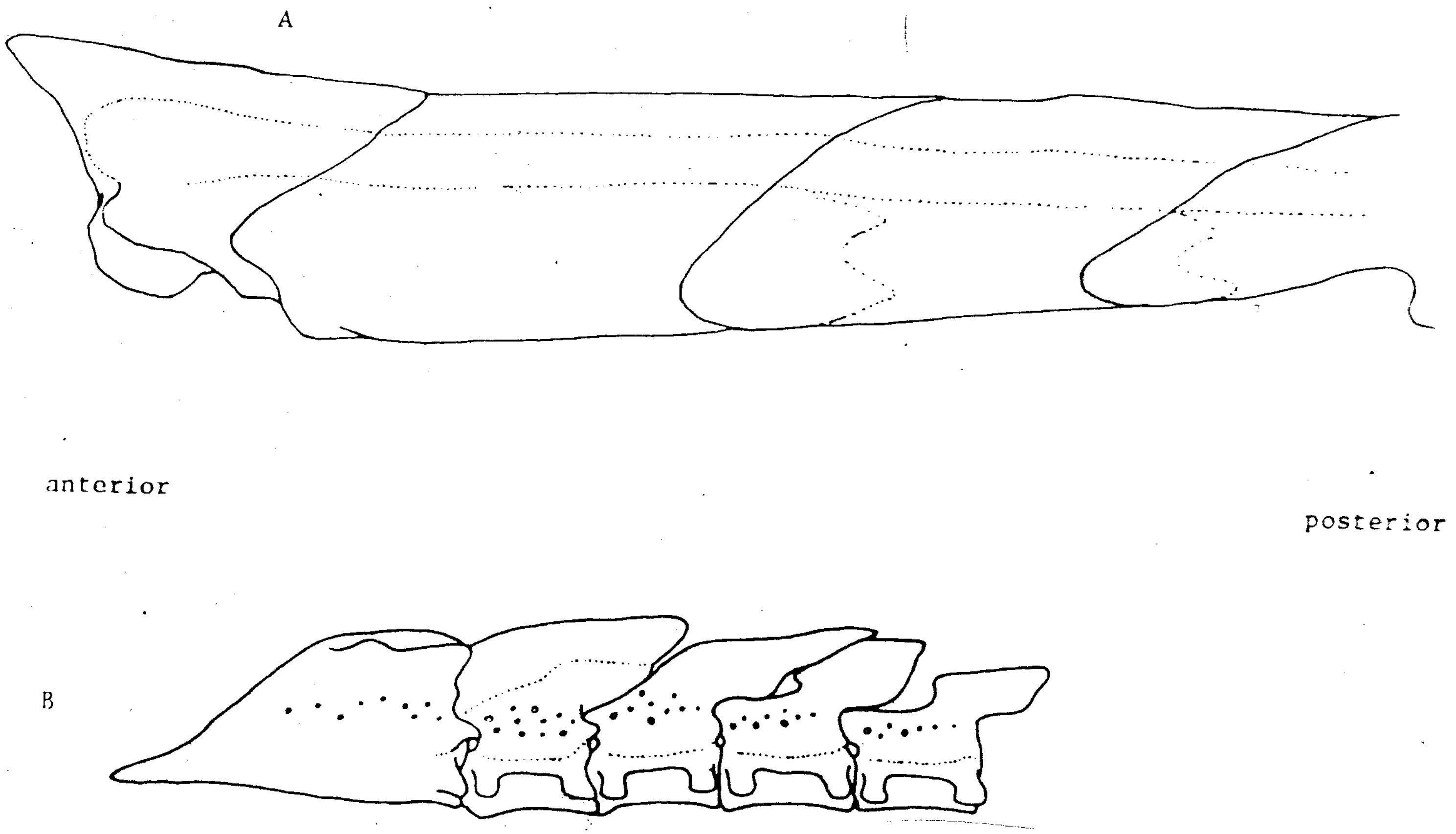
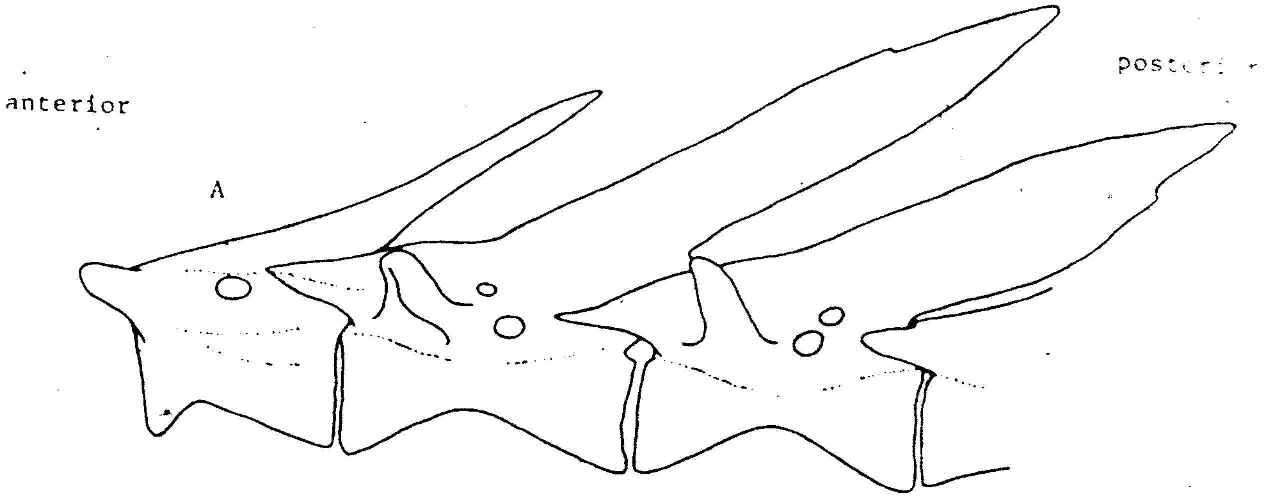


Figure M 5: *Aulostomus maculatus*, vertebrae, left lateral views.

A. Vertebrae 1 - 3, X 23.5

B. Vertebrae 4 - 8, X 11.5



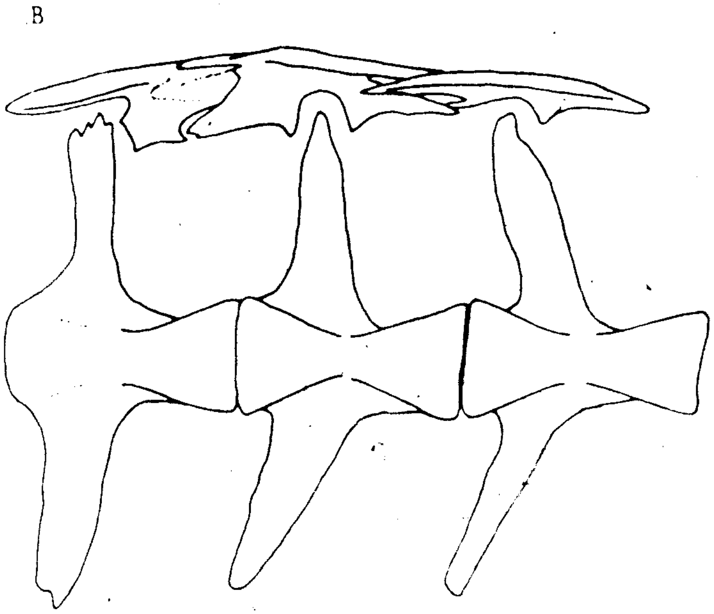
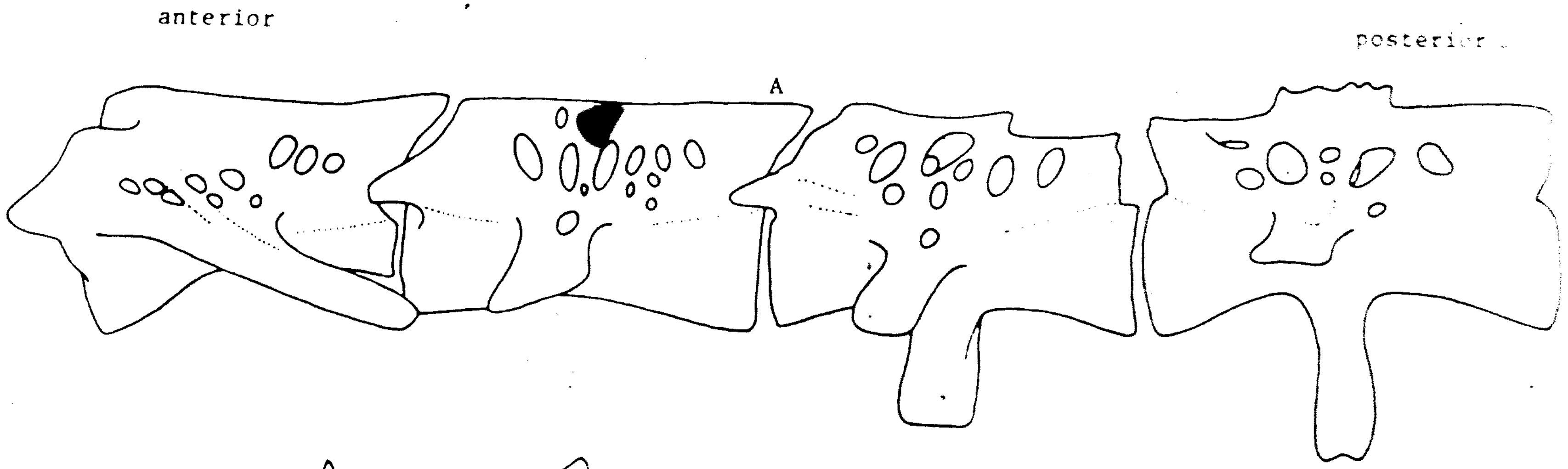


Figure M 6 : Macrorhamphosus gracilis, vertebrae 1-3

A. Left lateral view, X 11.5

B. Ventral view with associated left scutes, X23.5



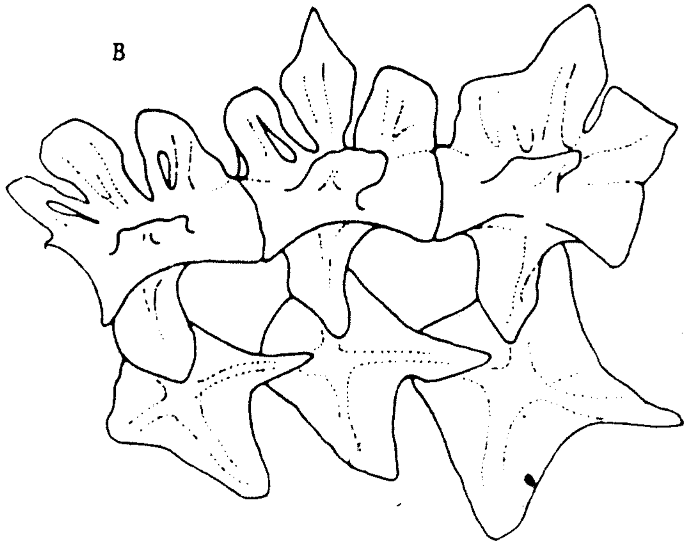


Figure M 7 : Vertebrae of Syngnathidae, left ventrolateral views

A. Syngnathus griseolineatus. vertebrae 1-4, X23.5

B. Hippocampus hippocampus, vertebrae 4-6 and associated right scutes, X 11.5

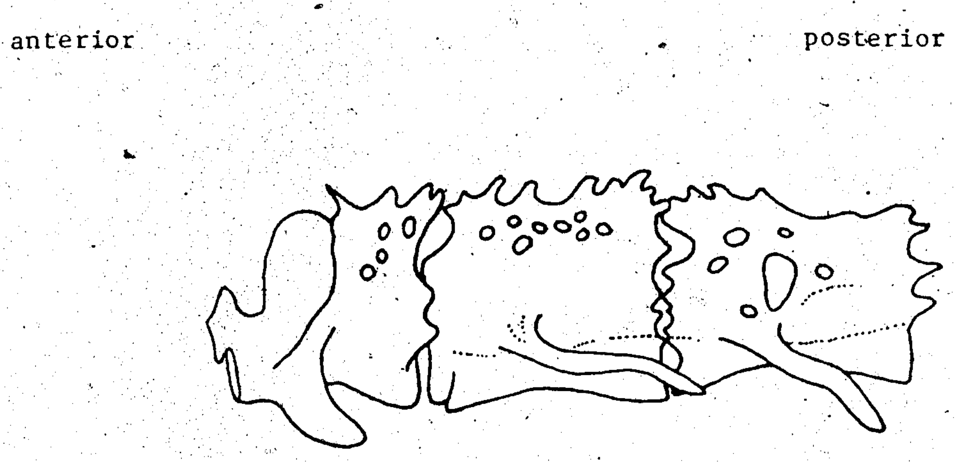


Figure M 8 : Indostomus paradoxus, vertebrae 1-3, left lateral view,
X 48 (USNM 203888)

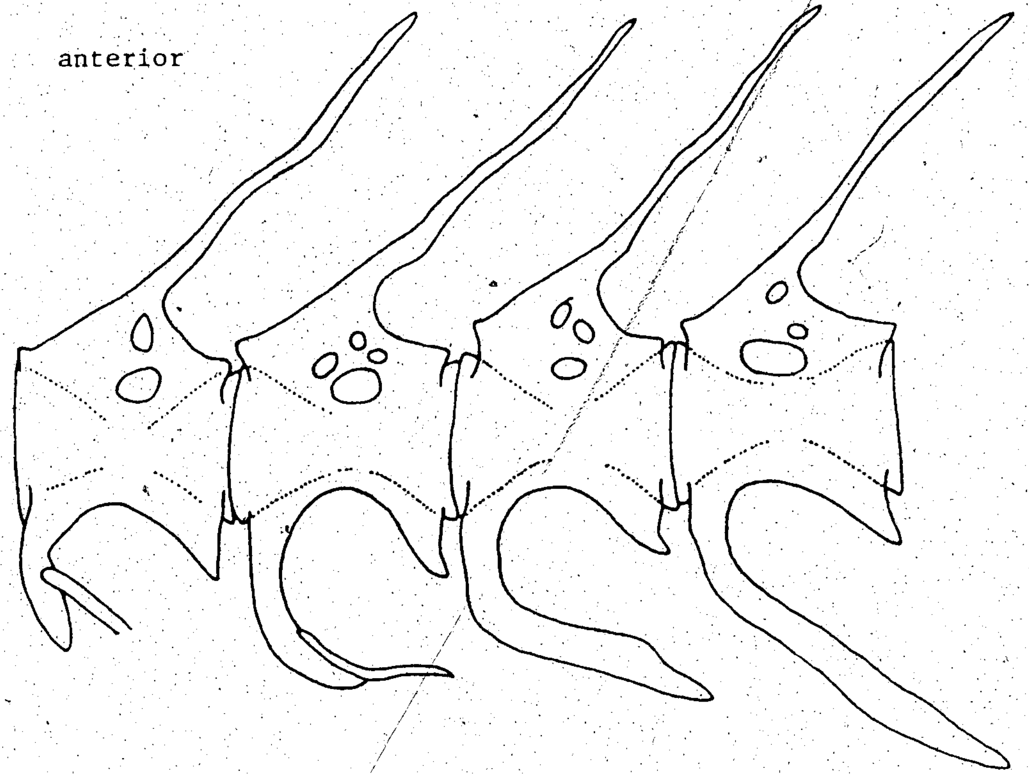


Figure M 9 : <u>Hypoptychus dybowski</u>, last precaudal and first three caudal vertebrae, left lateral view, X 23.5

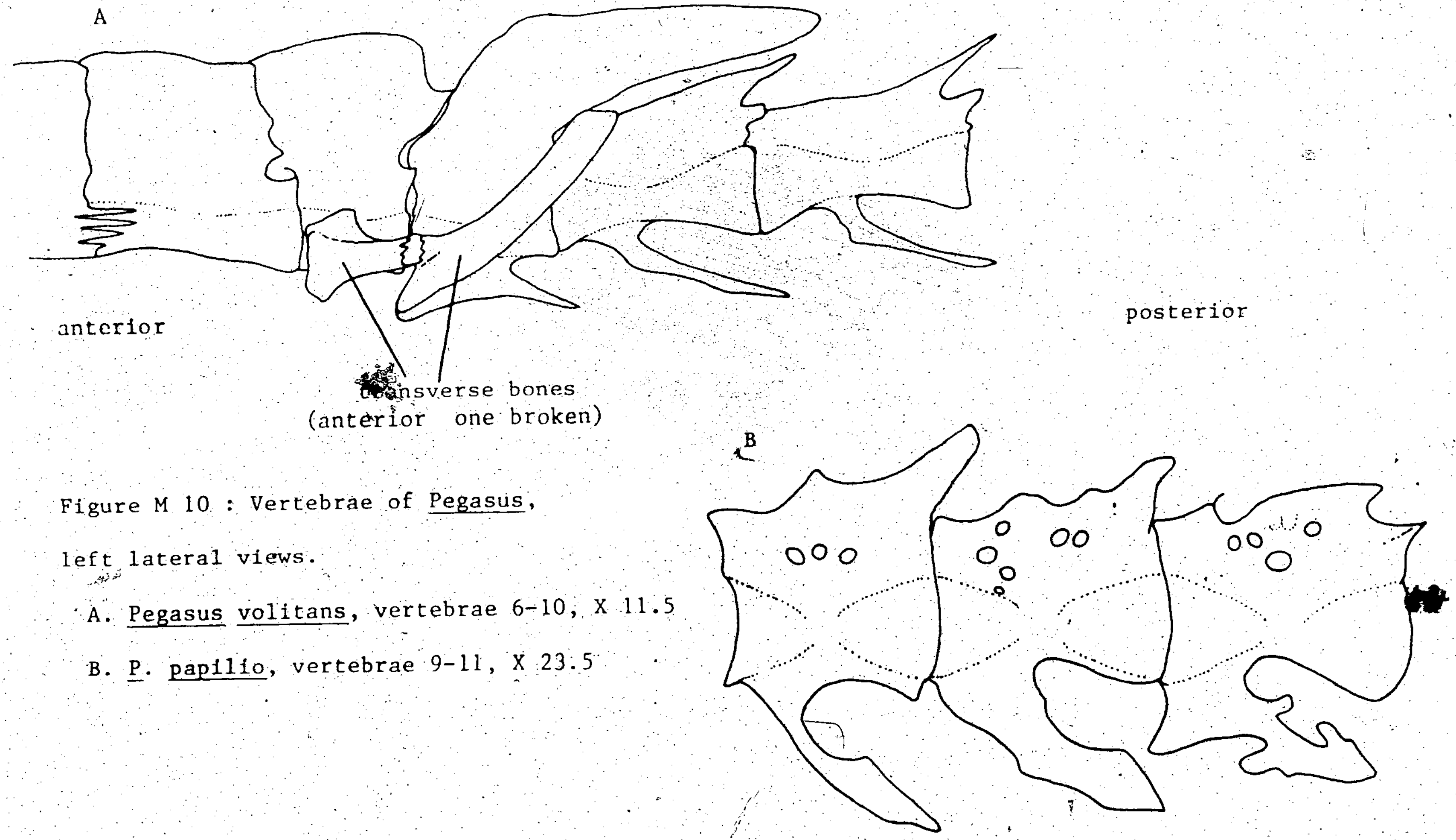


Figure M 10 : Vertebrae of Pegasus, left lateral views.

A. Pegasus volitans, vertebrae 6-10, X 11.5

B. P. papilio, vertebrae 9-11, X 23.5

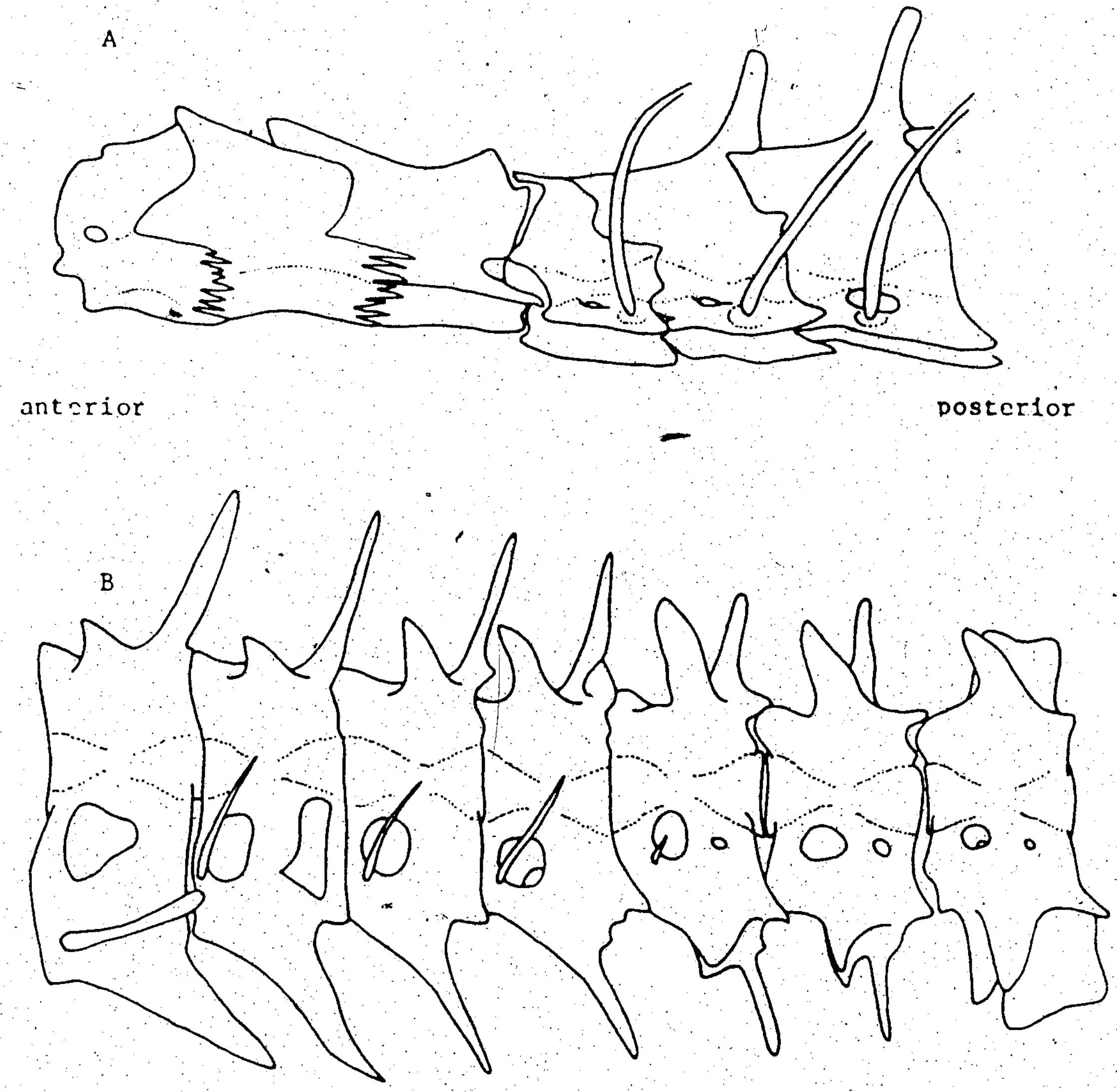


Figure M 11 : Dactylopterus volitans, vertebrae, left lateral views

A. Vertebrae 1-6, X 11.6

B. Caudal vertebrae 1-7, X 11.6

N. The Caudal Skeleton

The caudal skeleton is made up of the posterior preural vertebrae, the ural centra, the bones supported by or arising from them (the hypurals, the epurals, the uroneural and the parhypural), and the rays supported by these bones. Characters from this region are listed in Table N1 and their coded values for framework and study groups are in Tables N2 and N3, respectively.

Framework

The hypurals in Diplophos are supported by a compound centrum composed of the first preural and first ural centra and by a separate second ural centrum. Hypurals 1 and 2 are supported by the compound centrum; these, along with the parhypural, form the ventral hypural complex. Hypurals 3-6 form the dorsal hypural complex based on the second ural centrum. This complex is supplemented dorsally by two uroneurals and three epurals. The second preural centrum bears a short autogenous neural spine which touches the third epural. In two of the three specimens examined, it also bears a complete neural spine on its anterior end. A full autogenous haemal spine is present, its ventral end supporting a principal ray; in one specimen an accessory anterior haemal spine is present.

Saurida has a deeply forked caudal fin supported by six hypurals similar to those of Diplophos in their position. There is only one obvious ural centrum. The parhypural and two uroneurals are autogenous and separated from the hypurals. Two epurals are present. The second preural centrum bears an incomplete neural spine and a full haemal spine, both autogenous. The haemal spine supports principal rays.

In Percopsis the hypurals are supported by a compound centrum and a free second ural centrum. Only four separate hypurals are present; hypurals 1 and 2 appear to be fused. Hypurals 3 - 5 are supported by the second ural centrum. Two uroneurals and two epurals are present and the second preural centrum bears both a full neural spine and a full haemal spine, the latter supporting a principal ray.

Rosen (1964) thoroughly reviewed the atherinomorph caudal skeleton; my observations agree with his. Melanotaenia shows the least caudal fusion. It has five hypurals, four forming the dorsal hypural plate and all arising from a single compound centrum. A single uroneural is present, as are two epurals. The parhypural is almost completely fused to the lower hypural plate. Both the uroneural and parhypural support principal rays. The second preural centrum bears an incomplete neural spine. Allanetta (Fig. N1,B) differs from Melanotaenia in hypural number; all of its upper hypurals are fused to one another, leaving it with two separate hypural plates. Its parhypural is entirely separated from the hypurals. Fundulus (Fig. N1,A) has an almost completely symmetrical caudal skeleton, its hypurals fused into a single fan flanked dorsally by an autogenous uroneural and ventrally by an autogenous parhypural. Epurals are absent. The second preural centrum bears complete neural and haemal spines, both of which support principal rays.

The beryciform Holocentrus has five hypurals, two forming the ventral hypural plate and three forming the dorsal plate. Two dorsal hypurals are supported by the second ural centrum, which is autogenous in a small specimen but fused to the compound centrum in a larger one. One or two uroneurals and three epurals are present. The second preural centrum bears an autogenous haemal spine, which supports principal rays, and a low neural arch.

Fusion of the caudal skeleton appears in both subgroups of Scorpaeniformes examined. Sebastes has four free hypurals, two forming the ventral hypural plate and two the dorsal plate, supplemented dorsally by two uroneurals and three epurals. In Cottus(Fig. N2,A), Asterotheca(Fig. N2,B), and Prionotus, however, the hypurals are fused into two plates. A single uroneural is present in each of these three, fused to the hypurals in Cottus and Prionotus, but autogenous in Asterotheca; Prionotus and Cottus have in addition three epurals. Both Prionotus and Asterotheca have complete neural spines on the second preural centra. The number of caudal rays is reduced in Asterotheca and procurrent rays are almost absent. In both cottoids the caudal rays extend slightly laterally in an alternating pattern.

Plectroplites and Percalates have four hypurals, arranged as in Sebastes; Perca has five, three forming the dorsal hypural plate. Percalates and Plectroplites have a second uroneural. All three species have three epurals. Ammodytes has a more highly fused caudal skeleton with only three hypurals; two form the dorsal hypural plate and one forms the ventral plate. All Perciformes examined have separate uroneurals and parhypurals which support principal rays, and their second preural centra bear non-autogenous incomplete neural spines.

Gasterosteiformes

All Gasterosteiformes (e.g. Figs. N3-4) have highly fused caudal skeletons. Each of the upper and lower hypural plates is a single element, with the uroneural fused to the upper and the parhypural fused to the lower. In adults of all except Gasterosteus the two hypural plates are fused with one another. Juvenile Gasterosteus and adult Spinachia (Fig. N3,A) have two epurals; in adult Gasterosteus (Fig. N3,B) only one is separate, while the second epural in adult Spinachia is closely applied to the upper hypural plate. The second preural centra bear full non-autogenous neural spines in all.

Syngnathiformes

Syngnathiformes also have highly fused caudal skeletons; the entire caudal plate and fin are lost in many Syngathidae. In those Syngnathiformes with a caudal skeleton all the major elements are fused, though they may still be distinguishable. In all except Syngnathus and Solenostomus the hypurals are arranged into dorsal and ventral hypural plates fused at their bases and the uroneural is fused to the dorsal hypural plate in all except Solenostomus. In Centriscidae (Fig. N5,A) and Macrorhamphosus (Fig. N5,B) a remnant of the second ural centrum is visible at the base of the upper hypural plate. A single epural lies along the dorsal border of the dorsal hypural plate and in Aeoliscus an autogenous parhypural lies along its ventral border. Both support principal rays. The second preural centrum bears complete non-autogenous neural and haemal spines. Aulostomus (Fig. N6,A) and Fistularia lack the second ural centrum; their parhypurals are separate but not autogenous and their epurals are supplemented by tiny splints along their anteroventral borders.

Solenostomus (Fig. N6,B) has a wide anteriorly extending uroneural and a similar parhypural; the uroneural is partially separate but the parhypural is fused to the hypurals. The second preural centrum has no neural spine and a small haemal spine. Syngnathus (Fig. N6,C) has an even more reduced caudal skeleton with the uroneural and parhypural completely fused to the hypural fan. Its second preural centrum, however, bears a complete neural spine, a normal haemal arch, and lateral processes. The other Syngnathidae examined have no caudal fins or skeletons.

Indostomus

The caudal skeleton of Indostomus (Fig. N7,A) is fused into a single plate apparently containing the hypurals, parhypural and uroneural. No epurals are present. The second preural centrum is fused to the scutes surrounding it. The caudal is symmetrical, each half containing two procurrent rays and five to six principal rays.

Hypoptychus

Hypoptychus (Fig. N7,B) has two distinct hypural plates, the lower fused to the parhypural. The uroneural lies along the dorsal edge of the upper plate. Two epurals are present. The second preural centrum has a full neural spine. Neither uroneural nor parhypural completely support a principal ray.

Pegasus

The entire caudal skeleton of Pegasus (Fig. N7,C) is fused into a small, heavy bony plate which supports eight principal rays. Procurrent rays are absent. The second preural centrum apparently bears a full neural spine but this character is unclear, since the spines on all posterior caudal vertebrae are merely low crests.

Dactylopterus

The dorsal hypurals in Dactylopterus are fused into a single plate (Fig. N8) which is supported by the fused preural and ural centra. Three epurals lie along the dorsal margin of this complex. The first extends anteriorly along the dorsal margin of the second preural centrum. The ventral hypural plate contains one separate hypural and a large ventral complex apparently formed of the ventral hypurals and the parhypural. The haemal spine on the second preural centrum extends almost to the posterior end of the hypural plate. The parhypural and the haemal spines of the second and third preural centra are autogenous. The second preural centrum does not bear a full neural spine.

Table N1 : Characters from the caudal skeleton
(asterisks indicate those used in phenetic analyses)

*N1. Caudal present (1)/ absent (0)
N2. Second ural centrum present/ absent
N3. Second uroneural present/ absent
N4. First uroneural separate from/ fused to the hypurals
N5. Uroneural autogenous/ attached to preural vertebra
N6. Uroneural supports/ does not support principal caudal rays
N7. Parhypural separate from/ fused to hypurals
N8. Parhypural autogenous/ attached to preural vertebra
N9. Parhypural supports/ does not support principal caudal rays
N10. Epural #3 present/ absent
N11. Preural centrum #2 bears a full/ partial neural spine
N12. Preural centrum #2 bears an autogenous/ attached neural spine
N13. Upper hypurals are separate from/ fused to one another
N14. Lower hypurals are separate from/ fused to one another
N15. Hypurals are organized into dorsal and ventral plates/ fused into a single plate
N16. Number of dorsal caudal rays
N17. Number of ventral caudal rays
N18. Length of longest caudal ray/standard length (%)
N19. Depth of caudal peduncle/standard length (%)
N20. Length of hypural complex/standard length (%)
N21. Length of hypural complex/average length of central vertebrae

Table N2 : Distributions of characters from the caudal skeleton among framework taxa

Taxon	12345	67890	12345	6	7	8	9	0	1
Diplophos	11111	01111	11111	10	9	X	[illegible].7	1.7	1.5
Saurida	10111	01110	01111	11	10	20.1	6.6	4.3	3.1
Percopsis	11111	01110	10101	9	9	13.6	7.9	5.1	2.3
Fundulus	10011	11110	10000	10	9-10	25.1	14.2	4.8	2.0
Melanotaenia	10010	10010	00101	9	8	X	11.3	4.1	2.0
Allanetta	10010	11010	00001	9	9-10	X	7.2	4.1	2.2
Holocentrus	11110	11111	00111	10	9	20.4	9.0	X	2.2
Asterotheca	10011	00000	10001	6	5	10.5	2.7	3.2	1.5
Cottus	10000	00011	00001	6	6	26.0	8.6	3.4	1.7
Sebastes	10111	X11X1	00111	X	X	15.4	5.5	1.9	X
Prionotus	10010	01001	10001	6	6	29.9	6	X	X
Percalates	10111	11111	00111	9	7	14.1	X	6.7	2.3
Plectroplites	10111	11111	00111	9	7	14.4	X	4.7	2.2
Perca	10011	11111	00111	9	8	19.3	7.9	4.6	2.4
Ammodytes	10011	11010	00101	7-8	7-8	9.6	3.0	1.6	1.2

Table N3 : Distributions of characters from the caudal skeleton among study groups

Taxon	12345	67890	12345	6	7	8	9	0	1
Gasterosteus	10101	00010	10001	6	6	12.7	X	4.2	2.15
Pungitius	10001	00000	10000	6	6	7.9	X	3.7	2.17
Culaea	10001	00000	10000	6	6	13.3	5.7	5.7	2.4
Apeltes	10001	00000	10000	6	6	17.3	X	4.9	2.06
Spinachia	10101	00000	10000	6	6	9.9	X	2.7	1.0
Aulichthys	10001	00000	10000	6-7	6-7	7.4	X	1.8	1.4
Aulorhynchus	10001	00000	00000	6-7	6-7	9.3	X	2.3	1.8
Syngnathus	10000	10010	10000	5	5	3.0	0.7	1	0.7
Syngnathoides	0XXXX	XXXXX	XXXXX	na	na	na	na	na	na
Hippocampus	0XXXX	XXXXX	XXXXX	na	na	na	na	na	na
Solenostomus	10010	10010	00000	6	6	23.3	2.3	3.8	3
Aulostomus	10000	11010	10001	6	6	7.3	2.05	1.5	1.7
Fistularia	10000	11010	10001	5	5-6	45.9	0.8	0.7	1.5
Macrorhamphosus	11000	10010	10001	4-5	4-5	11.8	3.6	3.4	1.4
Aeoliscus	11000	11110	10001	3-4	3	6.9	2.6	1.8	1.4
Indostomus	10000	10010	10000	6	5-6	4.9	X	X	X
Hypoptychus	10010	00000	10001	7-8	6	8.1	X	3	1.9
Pegasus	10000	10010	10000	4	3-4	11-21	1.1	1.1-3.6	.25-1.2
Dactylopterus	10000	10111	00011	5	5	25	5.8	6.2	1.8

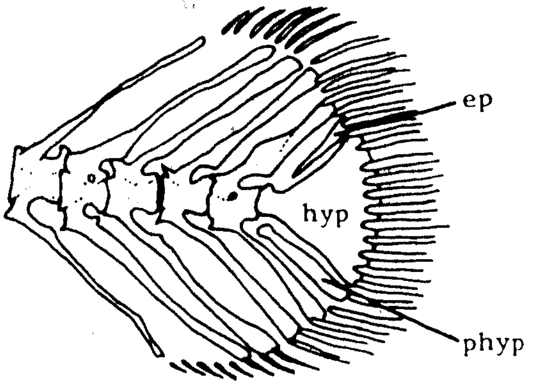
Figure N 1 : Caudal skeletons of Atherinomorpha,
left lateral views

A. *Fundulus* sp., X 11.5

B. *Allanetta harringtonensis*, X 23.5

(abbreviations are listed on pages xxv-xxvi)

A



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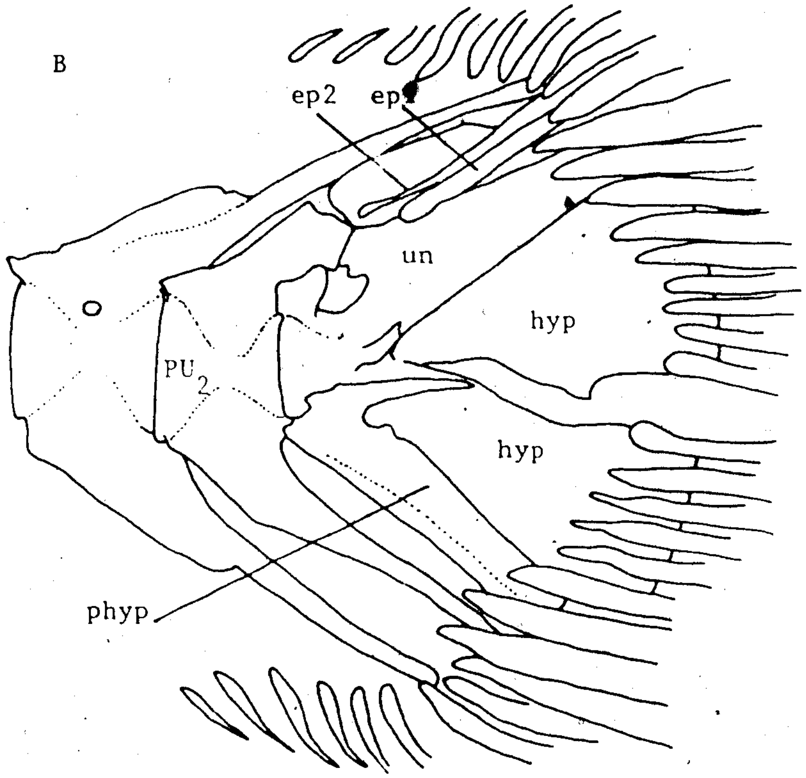
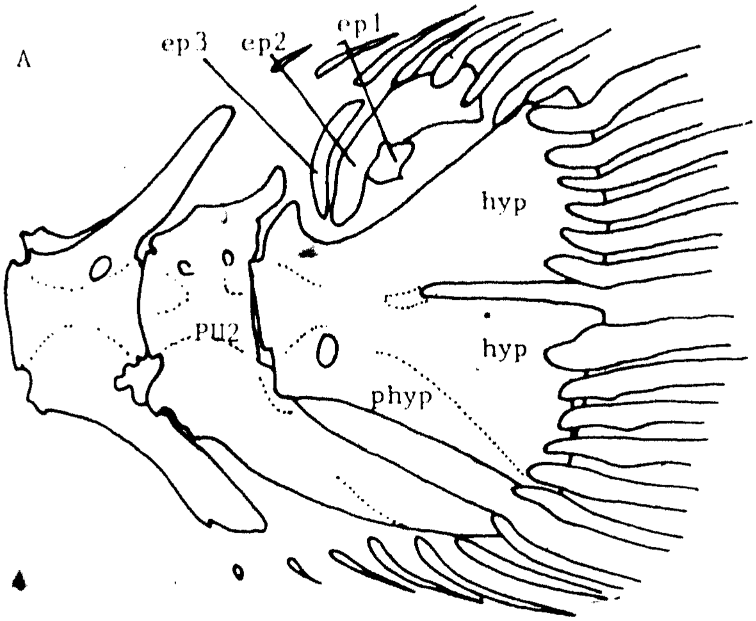




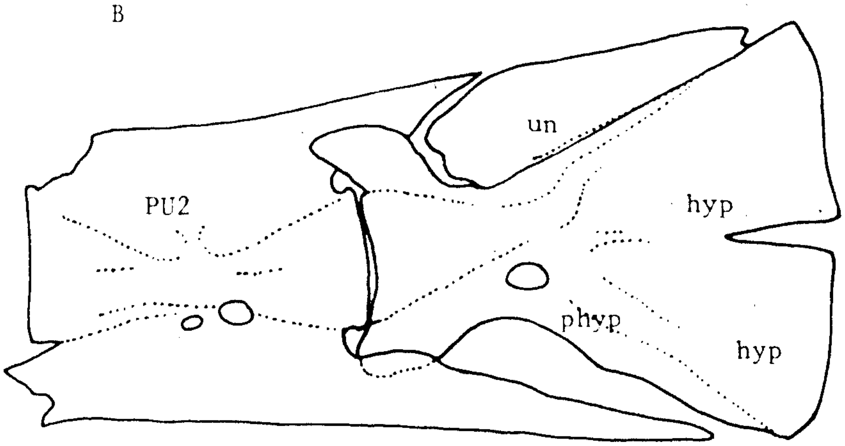


Figure N 2 : Caudal skeletons of Cottoidei, left lateral views

A. Cottus cognatus, X 23.5

B. Asterotheca alascana, X 23.5

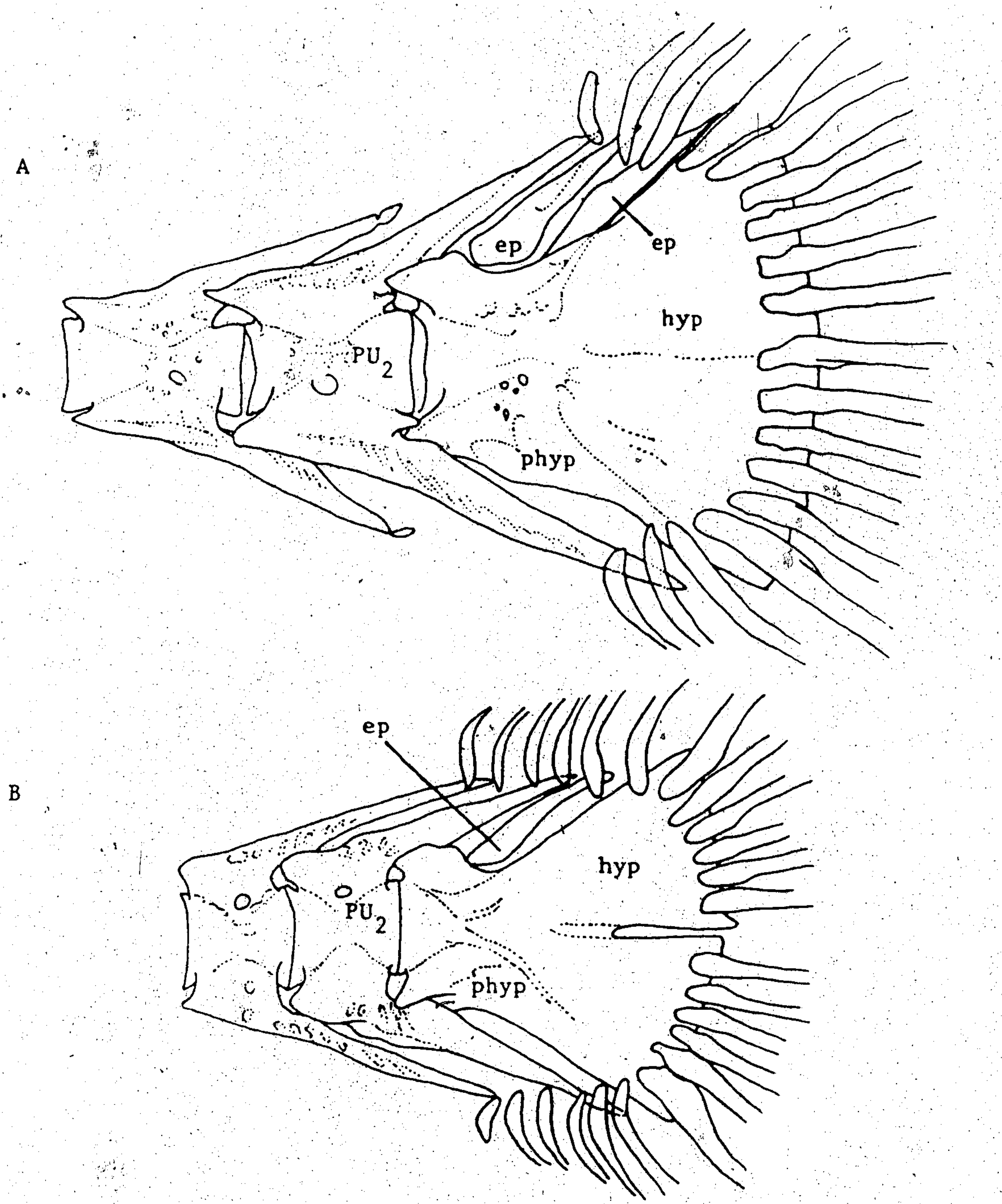


Figure N 3 : Caudal skeletons of Gasterosteidae, left lateral views

A. Spinachia spinachia, X 23.5

B. Gasterosteus aculeatus, X 23.5 (UAMZ 5512)

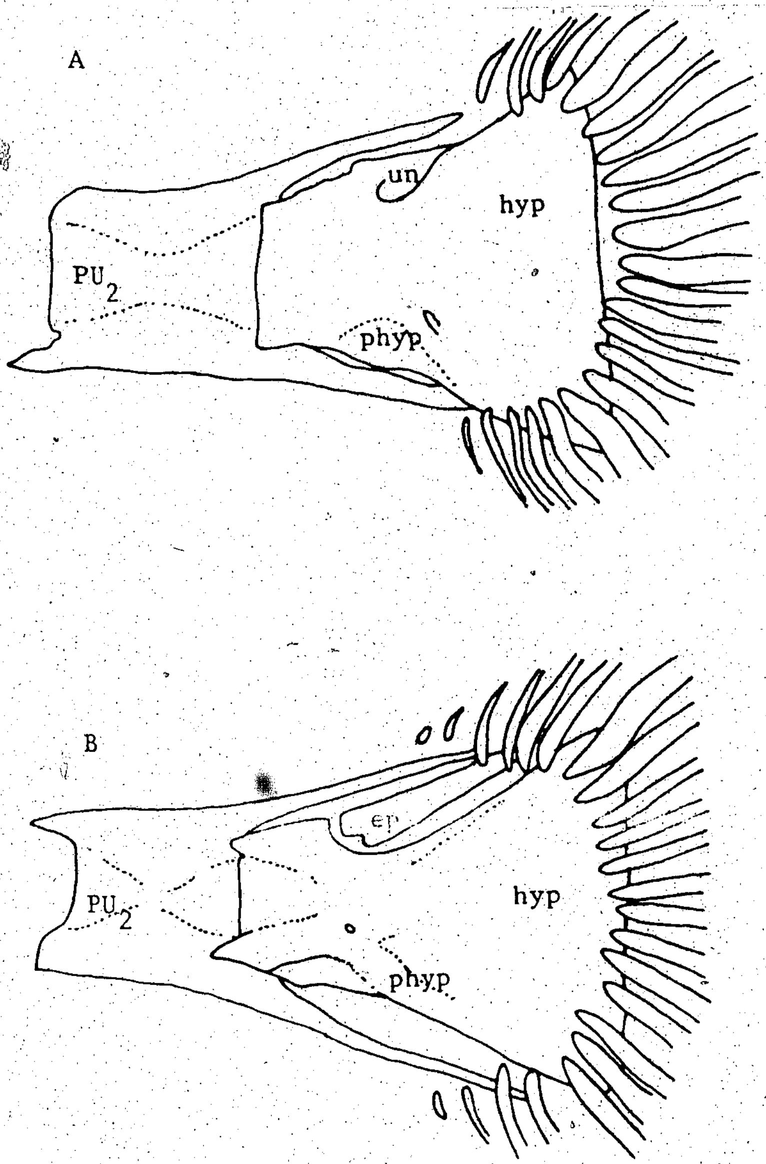


Figure N 4 : Caudal skeletons of Aulorhynchidae, left lateral views

A. Aulorhynchus flavidus, X 23.5 (UAMZ 1694)

B. Aulichthys japonicus, X 23.5

Figure N 5 : Caudal skeletons of Syngnathiformes,
left lateral views

A. Aeoliscus strigatus, X 48

B. Macrorhamphosus gracilis, X 48

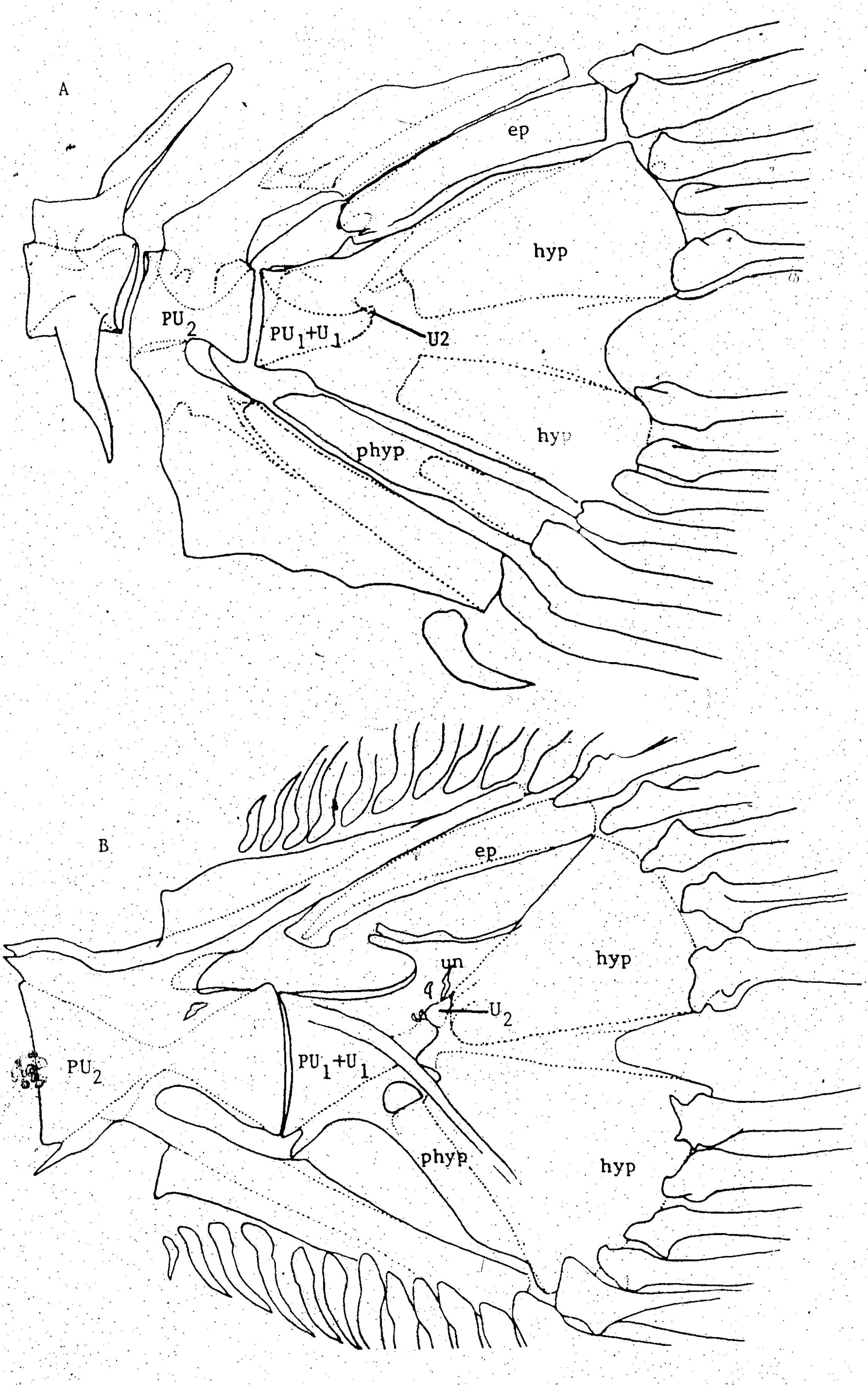

A
ep
hyp
PU2
PU1+U1
U2
hyp
phyp
B
ep
hyp
un
U2
PU2
PU1+U1
phyp
hyp

Figure N 6 : Caudal skeletons of Syngnathiformes, left lateral views

A. *Aulostomus chinensis*, X 23.5

B. *Solenostomus paradoxus*, X 23.5

C. *Syngnathus griseolineatus*, X 48

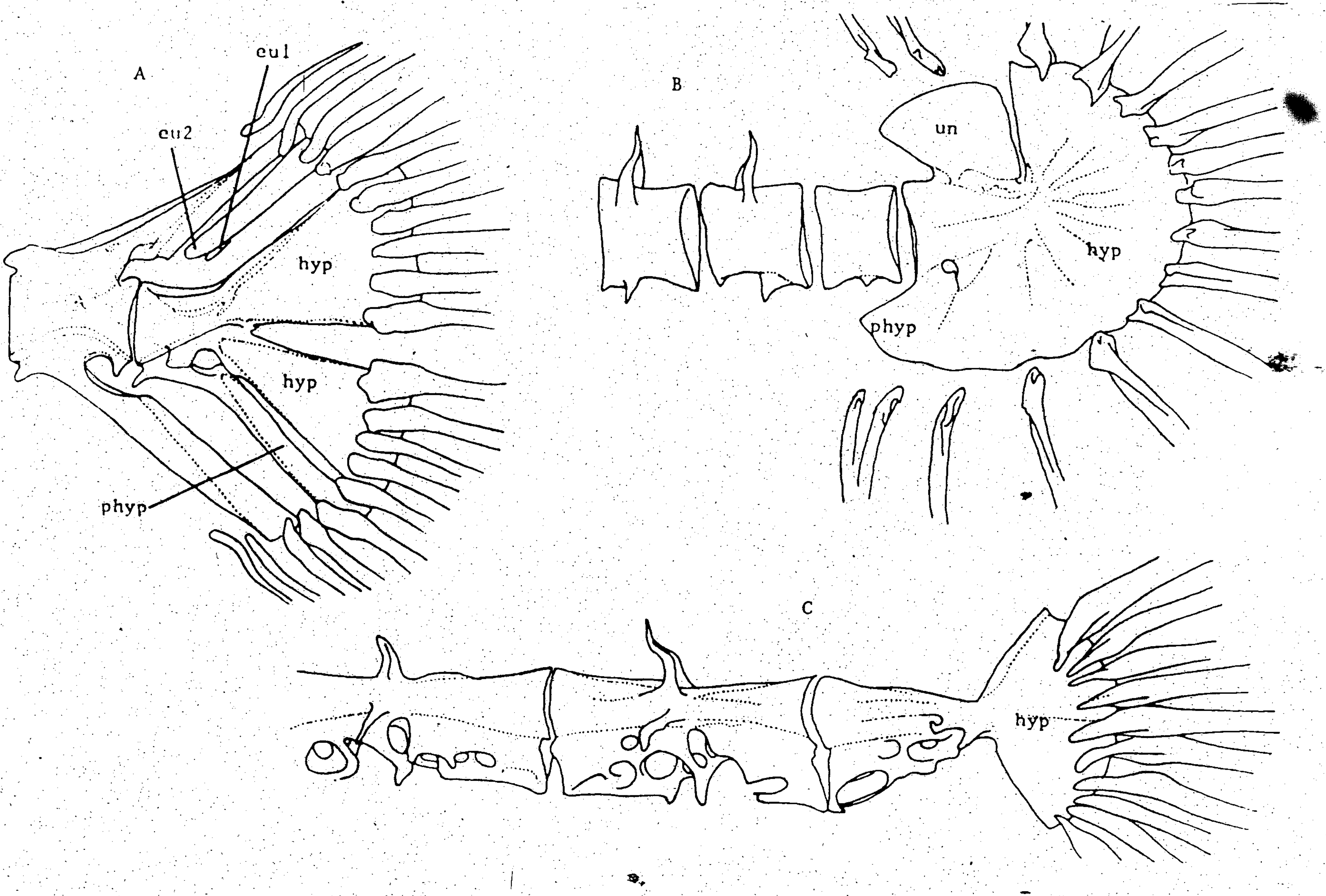
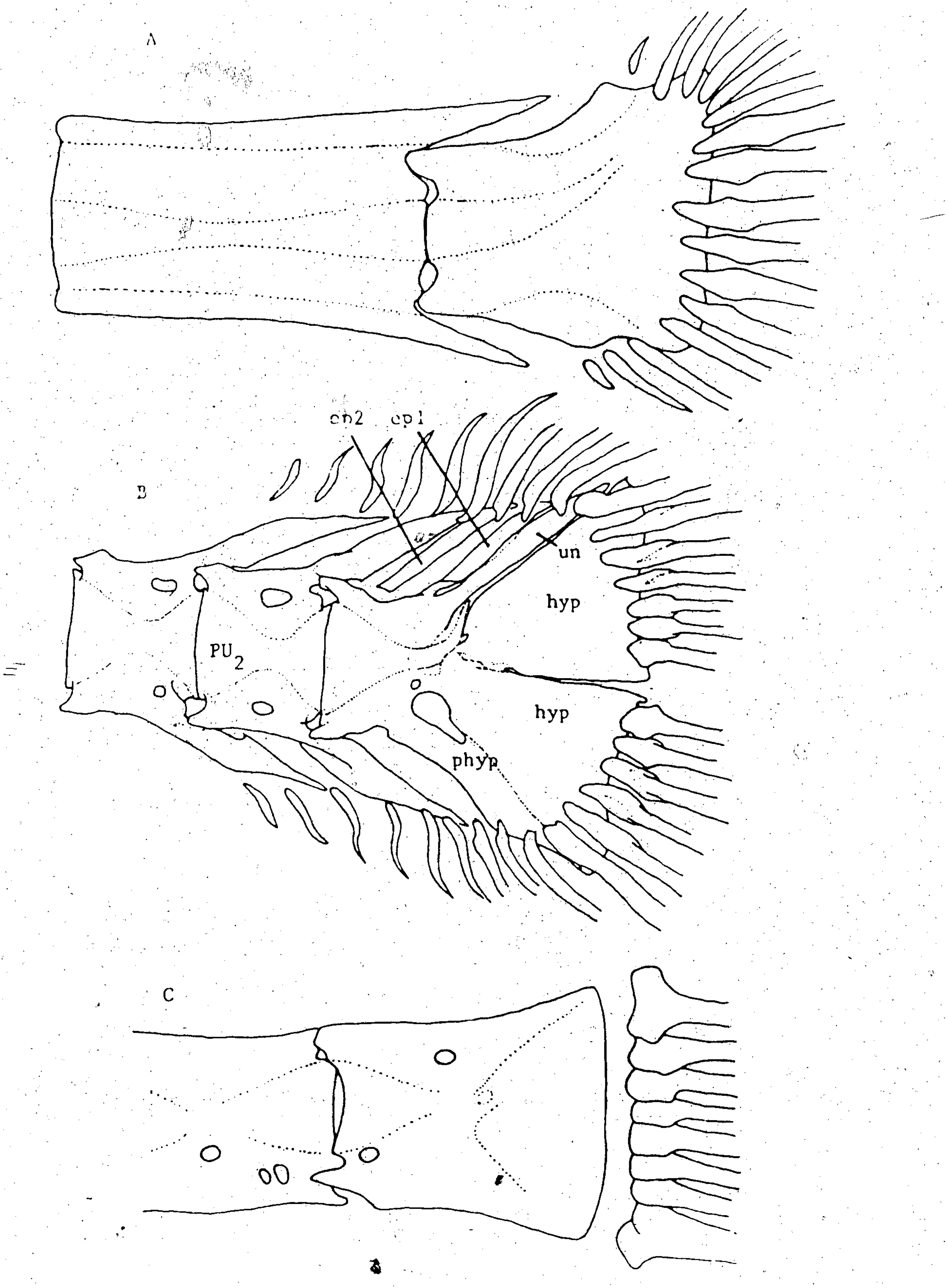

A
eu1
eu2
hyp
hyp
phyp
B
un
hyp
phyp
C
hyp

Figure N 7 : Caudal skeletons of study groups, left lateral views

A. Indostomus paradoxus (after Banister, 1970)

B. Hypoptychus dybowski, X 23.5

C. Pegasus papilio, X 23.5


A
B
ep2
ep1
un
hyp
PU$_2$
hyp
phyp
C

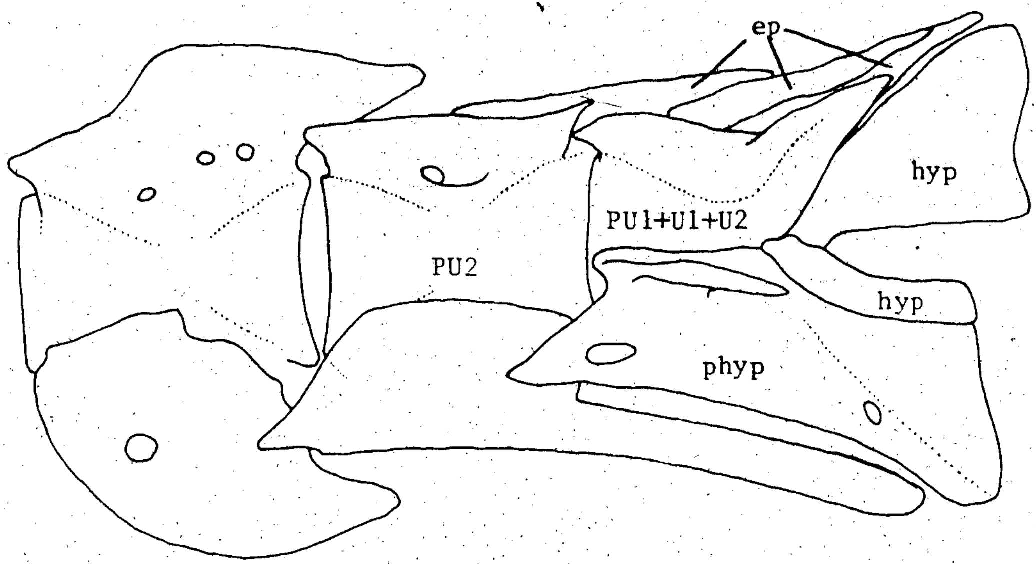


Figure N8: Dactylopterus volitans, caudal skeleton, left lateral view, X 23.5

IV. Systematic Analyses

A. Introduction

The three schools of systematics as I have applied them form a sequence of analyses incorporating increasingly stringent character weighting criteria. In phenetics all characters and all character states are weighted equally. In unweighted numerical phylogenetics the derived states of all characters are given equal weight, but their primitive states are given no weight. In weighted numerical phylogenetics derived states which seem to appear independently in two or more taxa are given no weight. Finally, in evolutionary systematics *a priori* weighting is applied, with derived states involving loss or reduction being given less weight than those involving the gain of a structure.

The analyses may therefore be viewed not only as a comparison of the three different schools of systematics but also as an investigation of the effects of the application of weighting techniques, regardless of the schools of systematics with which they are associated in this study.

B. Phenetic Systematics

Introduction

Phenetic systematics views taxa as groups of phenotypically similar organisms and views classification as a process of summarizing the characteristics of organisms; phylogenetic relationships are of interest only insofar as they coincide with similarity relationships. Phenetics, therefore, ignores most of the criteria of relationship used by phylogenetic and evolutionary systematists, replacing them with the criterion of overall similarity. This is the theoretical similarity between two individuals if they are compared in every respect. It is approximated by taking an average of their similarities over a large number of individual characters. The results of these measurements are then presented as a resemblance matrix (Rohlf and Sokal, 1981) and a separate process of clustering is used to find groups of similar organisms. This is the approach used in this thesis. Alternatively, the calculations of similarities and clustering may be avoided by presenting the organisms as points on a scatter plot each of whose axes represents a combination of characters. In this type of analysis (e.g. principal components analysis) the organisms' similarities are represented by their relative positions on the graph and they are grouped visually by the investigator.

Phenetic methods, like all systematic methods, can be viewed as progressive simplification of a data set in order to represent it within the relatively inflexible framework of a hierarchical classification. Since phenetics admits no theoretical rationale for de-emphasizing certain character states or characters, it simplifies data through averaging and approximation.

The first step in a phenetic analysis is the reduction of a data matrix (e.g. Tables A2, A3, B2, etc.) to a resemblance matrix which displays the similarities or dissimilarities between each pair of organisms or taxa (Operational Taxonomic Units, OTUs). Many different resemblance coefficients exist for phenetic analysis, but since each represents a definition of resemblance there is no independent criterion of resemblance against which to measure their efficiencies.

The overall similarities or overall dissimilarities of the OTUs having been calculated, an attempt is made to find the one grouping of the OTUs which best expresses all of them. This may be done by expressing the OTUs as points on a scatter plot (ordination), by constructing minimum length trees linking them, or by segregating them into clusters by any one of several algorithms. The last of these is the more commonly used, for binary data, and results in a hierarchical arrangement of OTUs which can readily be transformed into a classification. It is at this level that different methods can be tested, both for the faithfulness of their results to the orginal resemblance matrix and for the extent to which they express the data. In every type of phenetic anaylsis, however, final groups are defined on their overall similarity rather than on possession of particular characters or character states (i.e., groups are based on the number of shared character states, rather than on the specific character states shared).

The tree produced in a phenetic analysis is not necessarily incompatible with the construction of evolutionary or phylogenetic hypotheses. Its proponents suggest that members of phenetic groups will usually also be phylogenetically related to one another, relationships being indicated by similarity (Sneath and Sokal, 1973). Phenetic analysis has been suggested as a superior method for the recognition of phylogenetic lineages which may have undergone large amounts of divergence and reversal, obscuring their distinguishing synapomorphies (Gauld and Mound, 1982; Davies, 1983). Such authors suggest the use of phenetics to delineate groups which are then interpreted with reference to phylogenetic analyses, the characteristics shared within each phenetic group being evaluated for probable apomorphies which can be used in constructing taxon definitions.

Methods

All analyses are performed by the computer packages CLUSTAN and NEW:CLUSTAN (Wishart, 1978; 1982), with the exceptions of Gower's W, which is calculated manually from character distribution data provided by CLUSTAN.

Two different clustering algorithms and seven resemblance coefficients are tested against one another on a preliminary data set of 169 binary characters. The clustering algorithms used are the commonly used Unweighted Pair-Group Mean Average (UPGMA), which sequentially unites those clusters of OTUs whose mean positions are closest to one another, and a nearest-neighbor single linkage algorithm which unites clusters that contain each other's nearest neighbors. Each clustering method is used on similarity matrices generated by the simple matching coefficient (SMC), Rogers-Tanimoto coefficient, Yule coefficient, product-moment correlation coefficient, and Farris' special similarity coefficient, and on dissimilarity matrices expressing squared euclidean distance (=average distance, =manhattan metric) and error sum of squares (see Wishart, 1978 and Farris, 1979b for calculation of coefficients). Each analysis is tested for faithfulness to the resemblance matrix by calculation of the cophenetic correlation coefficient (Sneath and Sokal, 1973) between resemblances in the original matrix and those expressed in the final dendrogram. Each is also tested for expression of the data (or 'predictivity') by the calculation of Gower's W (Gower, 1974; Fig. P 1), the number of correct predictions about the members of a cluster which will be made if the cluster is 'described' as having the character states appearing in the majority of its members, at the eight-cluster to three-cluster levels. The stability of each analysis as data are added is calculated by performing repeated analyses on randomly selected 60-character subsets of the data and measuring their similarity to the resemblance matrices derived from the full data set by the cophenetic correlation coefficient. A close correlation between the classifications based on 60 characters and one based on 169 (a high average subset correlation, Table P 1) indicates a method which is relatively unaffected by the introduction of new data and will yield a stable classification. The results of these tests appear in Table P 1. Those methods which show the highest cophenetic correlations and subset correlations and the highest W-values are used for analysis of a more complete binary data set including all the 231 binary characters for which values are available from all members of both study groups and framework groups. This data set is dictated by the restraints on the clustering program, which will neither combine binary and numerical data nor use characters which are not measured for all OTUs.

Each final analysis consists of construction of a resemblance matrix and a dendrogram followed by calculation of cophenetic correlation between the two and of Gower's W for the ten to two-cluster levels. Each final dendrogram is then tested by subjection to two iterative relocation procedures in which the OTUs are randomly assigned to clusters and then shifted between them until they are arranged into clusters whose members most closely resemble one another.

Results

Comparison of Phenetic Methods

The highest cophenetic correlation, 0.945, is that between a matrix of squared euclidean distances and the dendrogram constructed from it by nearest-neighbor clustering (Table P 1). This is the only case in which a nearest-neighbor clustering is preferable to UPGMA. Cophenetic correlations over 0.9 are obtained for UPGMA analyses based on simple matching coefficient, Rogers and Tanimoto's coefficient, product-moment correlation coefficient, and Farris' special similarity. In all analyses except those using squared euclidean distances UPGMA clustering yields a higher cophenetic correlation than does nearest-neighbor clustering.

Average subset correlation coefficients are relatively high, all exceeding 0.8. Squared euclidean distance, simple matching coefficient, and Rogers and Tanimoto's coefficient yield average subset correlations above 0.9 with both clustering algorithms, and product-moment correlations yield a correlation over 0.9 with UPGMA clustering. Again, UPGMA clustering gives consistently higher correlations than does nearest-neighbor clustering.

Gower's W values are higher for all UPGMA analyses than for nearest-neighbor analyses, and are highest for analyses based on squared euclidean distances and simple matching coefficients. Farris' special similarity has unusually low W-values with both clustering methods.

Of the methods tested, UPGMA clustering shows general superiority over nearest-neighbor clustering. The squared euclidean distance and simple matching coefficients give best results in terms of predictivity (Gower's W) and stability (average subgroup correlation) of the final results, although Rogers and Tanimoto's coefficient and Farris' special similarity give higher cophenetic correlations. My final analyses were performed using UPGMA clustering with squared euclidean distance, simple matching coefficient, and Rogers and Tanimoto's coefficient.

Phenetic relationships of study and framework groups

All of the phenetic clustering methods applied to the complete data set yielded the same dendrogram, as did all iterative relocation procedures (Figs. P2-5). The differences in cophenetic correlation coefficients, then, only indicate differences in the resemblance matrices. All three resemblance coefficients yield matrices which agree closely with the dendrogram. This dendrogram does not express the data particularly well, however, as evident from the values of Gower's W from the nine- to two-cluster levels; out of 7,854 character state predictions made at each cluster level, an average of 86% are correct (Table P2).

The between-framework group phenetic relationships (Fig. P2) differ greatly from the phylogenetic relationships hypothesized for these groups (Fig. Cl. 1), although some of the same groups are recognized. Atherinomorpha is recognized at the 0.85 simple matching coefficient (SMC) level and Scorpaeniformes at the 0.79 SMC level, but the two scorpaeniform suborders are not separated. The order Perciformes is not recognized, Percopsis and Holocentrus being more similar to Perca, Plectroplites, and Percalates than is Ammodytes. The taxonomic levels of the different framework groups are not correlated with fixed levels of similarity, but all of the presently accepted orders have been separated by the 0.72 SMC level; this may, then, be regarded as the minimum similarity level at which two OTUs may be placed in the same order.

The study groups do not resemble any framework group sufficiently to be firmly placed in the same order by this criterion. Gasterosteiformes are linked to the united framework groups by a Pungitius-Cottus similarity at the 0.723 SMC level, if either of the similarity coefficients is used, and by Pungitius-Cottus, Culaea-Fundulus, and Culaea-Allanetta similarities at the 0.723 SMC level in all analyses. Hypoptychus is linked to Ammodytes above the 0.72 SMC level. Syngnathiformes resembles Perciformes most closely, with a Macrorhamphosus-Perca similarity in the analyses using squared euclidean distance (distance coefficient of 0.329) and Macrorhamphosus-Percopsis and Macrorhamphosus-Perca similarities of 0.671 SMC. Dactylopterus resembles Prionotus more than any other OTU in all analyses (SMC 0.723), and is also similar to Asterotheca (SMC 0.701). Gasterosteiformes might therefore be placed in either Scorpaeniformes or Atherinomorpha, Hypoptychus placed in Perciformes, and Dactylopterus might be placed in Scorpaeniformes, all cases falling on the borderline of the required similarity level.

Three order-level groupings appear among the study groups (Figs. P3-5). Hypoptychus is linked to Gasterosteiformes by a Hypoptychus-Culaea similarity of 0.766 SMC; it resembles all members of Gasterosteiformes at SMC levels above 0.72. Gasterosteiformes (Fig. P4) is itself defined at the 0.88 SMC level, its two subgroups being united by an 0.896 SMC link between Aulichthys and Pungitius.

Syngnathiformes may be viewed as one very diverse order or as two orders; it is united at the 0.71 SMC level (Fig. P5). Its subgroups, (Syngnathidae + Solenostomus) and (Aulostomoidei + Centriscoidei), being distinguished at the 0.72 - 0.73 SMC level and linked to one another by a Macrorhamphosus-Solenostomus link at the 0.775 SMC level.

Dactylopterus, Pegasus, and Indostomus form a separate group on the final dendrogram (Fig. P3) but it is poorly defined, being distinguished at the 0.68 SMC level. Indostomus resembles Pegasus more than it does any other OTUs, but that is only at the 0.662 level; and Pegasus resembles Dactylopterus most closely, at the

0.714 level. Only *Pegasus* and *Dactylopterus*, therefore, can be regarded as belonging in the same order.

Discussion

Phenetic methods seem to reflect the data gathering technique in their segregation of the framework groups. The data for study groups were selected before the framework taxa were examined, and therefore many character states uniting some study groups but absent from all framework taxa were noted. In phylogenetic and evolutionary systematics these would be interpreted as apomorphies, only conveying information about the study groups possessing them. Phenetics, however, views both states of these characters as equally important, and they therefore provide a block of data supporting the amalgamation of all the framework groups. It appears, then, that data for phenetic analyses should be collected over the entire set of OTUs at one time, with an attempt made to concentrate upon all of them equally.

If some of the segregation of framework groups is due to data collection methods, then the similarities between study groups and framework taxa may have been underestimated. This leaves open the possibility that Gasterosteiformes, *Hypoptychus*, and *Dactylopterus* are linked with framework groups at the order level. Placing them with those taxa, however, would distort their similarities with other framework groups as portrayed on the dendrogram. It is necessary to remember that the dendrogram is, like a hierarchical phenetic classification, simply a two-dimensional representation of the complex similarities among the OTUs. The best way to include in a classification the possibilities of Gasterosteiformes-Atherinomorpha, Gasterosteiformes-Scorpaeniformes, and *Dactylopterus*-Scorpaeniformes links would be by "phenetic sequencing" of the separate orders, leading to a classification in which each order is near its nearest neighbors, as follows:

Order Atheriniformes
Order Gasterosteiformes
Order Scorpaeniformes
Order *Dactylopterus*
Order *Pegasus*

Order Indostomus

Order Syngnathiformes

Order Perciformes

There is a limit to the extent to which such resemblances can be expressed. It is impossible to place Hypoptychus in this sequence, for example, in a position which will indicate its similarities to both Gasterosteiformes and Ammodytes.

The practice of applying set levels of similarity to the complete dendrogram in order to define taxon levels does not seem applicable to this analysis, unless I were prepared to completely re-evaluate neoteleost classification. It would also, as pointed out above, ignore those similarities which cannot be well expressed in the dendrogram. I have therefore subdivided the orders Gasterosteiformes and Syngnathiformes without reference to the rest of the dendrogram. This may also be more valid because data on these two groups were gathered together and similarities within them may be more comparable.

Syngnathiformes (Fig. P5) can be divided into suborders at the 0.75 - 0.77 SMC level, resulting in the suborders Syngnathoidei and Aulostomoidei. Division of Gasterosteiformes at this level (Fig. P4) forms the suborders Gasterosteoidei and Hypoptychoidei.

Families within the suborders may be separated at the 0.85 - 0.9 SMC level, dividing Gasterosteoidei into Gasterosteidae and Aulorhynchidae, Syngnathoidei into Syngnathidae and Solenostomidae, and Aulostomoidei into Aulostomidae and Macrorhamphosidae. The last two families might be further divided into subfamilies at the 0.95 SMC level, but such division would not be suitable for Gasterosteidae, which dissolves into a cluster of OTUs all resembling one another at the 0.88 - 0.95 SMC level.

Conclusion

The study groups cannot be placed together in one order, or indeed in any separate taxon, according to phenetic results. They do form three separate clusters, (Gasterosteiformes + Hypoptychus), (Dactylopterus + Pegasus + Indostomus), and Syngnathiformes, but only the first and last of these are defined at or near the level at which the framework orders are defined. All three of these clusters contain members which resemble framework OTUs more than they resemble members of the other two clusters, and in the cases of (Gasterosteiformes + Hypoptychus) and (Dactylopterus + Pegasus + Indostomus) the similarities with framework groups are at the order level. (Gasterosteiformes + Hypoptychus) may be linked with either Atherinomorpha or Scorpaeniformes, (Dactylopterus + Pegasus + Indostomus) may be linked with Scorpaeniformes.

A classification reached by applying flexible similarity levels to define orders (0.72 SMC), suborders (0.75 - 0.77 SMC), families (0.85 - 0.9 SMC), and subfamilies (0.95 SMC) to the study groups (but not the framework groups), and by attempting to place each order between the two to which it is most similar, results in the following classification;

- Order Atherinomorpha
- Order Gasterosteiformes
  - Suborder Hypoptychoidei
  - Suborder Gasterosteoidei
    - Family Gasterosteidae
    - Family Aulorhynchidae
- Order Scorpaeniformes
- Order Dactyl[illegible]iformes
- Order Pegasif[illegible]es
- Order Indostomiformes
- Order Syngnathiformes
  - Suborder Syngnathoidei
    - Family Syngnathidae
    - Family Solenostomidae
  - Suborder Aulostomoidei
    - Family Aulostomidae
      - Subfamily Aulostominae
      - Subfamily Fistulariinae
    - Family Macrorhamphosidae
      - Subfamily Macrorhamphosinae
      - Subfamily Centriscinae

Order Perciformes

The within-study group phenetic classification is internally consistent, subgroups being delineated clearly and at set levels. Its relationship to neoteleost classification as a whole is obscure, however, since framework groups are separated at widely different levels. This restricts the usefulness of the phenetic classification.

Table P1 : Comparison of different phenetic similarity and clustering methods

Resemblance Coefficient	Cophenetic Correlation	W-VALUES								average
		Number of clusters								subset
		8	7	6	5	4	3	TOTAL	N	correlation
NEAREST NEIGHBOR CLUSTERING										
Squared euclidean distance	.94529	3147	3102	2985	2884	2785	2723	17626	8	.91608
Simple matching coefficient	.86300	"	"	"	"	"	"	"	8	.91674
Yule similarity coefficient	.74758	"	"	"	"	2780	"	17621	8	.85057
Rogers and Tanimoto similarity coefficient	.89308	"	"	"	"	2777	"	17618	8	.91459
Error sum of squares distance coefficient	.74758	"	"	"	"	2780	"	17621	8	.85057
Product-moment correlation	.85123	"	"	"	"	"	"	"	8	.85123
Farris' special similarity	.89434	2964	2915	2913	2897	2835	2723	17247	9	.86209
UPGMA CLUSTERING										
Squared euclidean distance	.88547	3147	3090	3028	2965	2901	2827	17958	8	.93145
Simple matching coefficient	.90542	"	"	"	"	"	"	"	8	.93157
Yule similarity coefficient	.82863	"	"	3038	2974	2866	2803	17918	8	.88572
Rogers and Tanimoto similarity coefficient	.92721	"	"	3028	2965	2901	2803	17934	5	.93797
Error sum of squares distance coefficient	.82863	"	"	3038	2974	2866	"	17918	8	.88572
Product-moment correlation	.90296	"	"	"	"	"	2822	17937	8	.92614
Farris' special similarity	.91434	3131	3077	2969	2897	2866	2788	17728	8	.89493

Table P2 : Gower's W values for the final dendrogram, 10- to 2-cluster levels

10-cluster level	7155
9-cluster level	7099
8-cluster level	7027
7-cluster level	6961
6-cluster level	6839
5-cluster level	6827
4-cluster level	6536
3-cluster level	6426
2-cluster level	6305
TOTAL	61,179

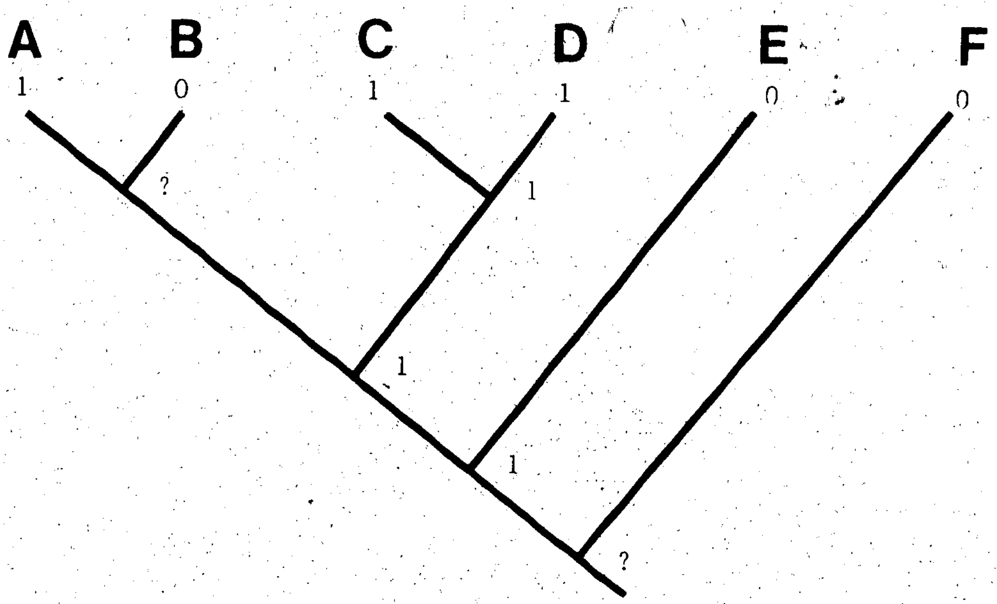


Figure P1: Calculating Gower's W

four-cluster level:

the majority character state for cluster AB is unknown; either state will give one wrong prediction. All other predictions are correct. W = 5 (out of 6 possible predictions).

three-cluster level:

the majority character state for cluster A-D is (1). It predicts the character states for A, C, and D correctly, but errs in predicting B's state. All other predictions are correct : W = 5 out of 6

two-cluster level:

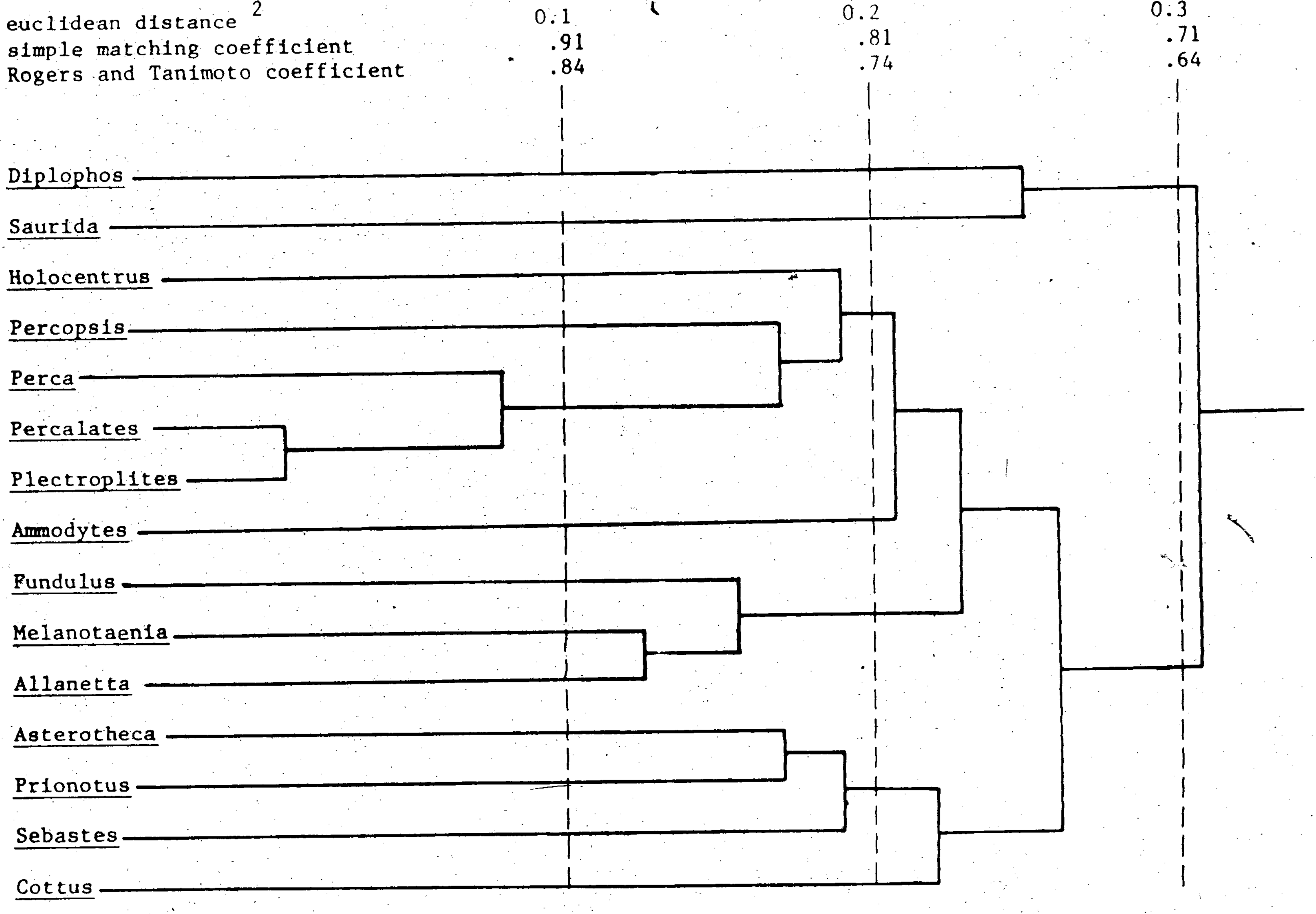
the majority character state for A-E is (1); it predicts the states of B and E incorrectly. All other predictions are correct : W = 4 out of 6

one-cluster level:

the majority character state for A-F is unknown; either state will lead to 3 correct and 3 incorrect predictions. W = 3 out of 6

TOTAL GOWER'S W = 17 out of a possible 24 predictions are correct

Figure P2: Phenetic dendrogram of framework taxa


euclidean distance 2
simple matching coefficient
Rogers and Tanimoto coefficient
0.1
.91
.84
0.2
.81
.74
0.3
.71
.64
Diplophos
Saurida
Holocentrus
Percopsis
Perca
Percalates
Plectroplites
Ammodytes
Fundulus
Melanotaenia
Allanetta
Asterotheca
Prionotus
Sebastes
Cottus

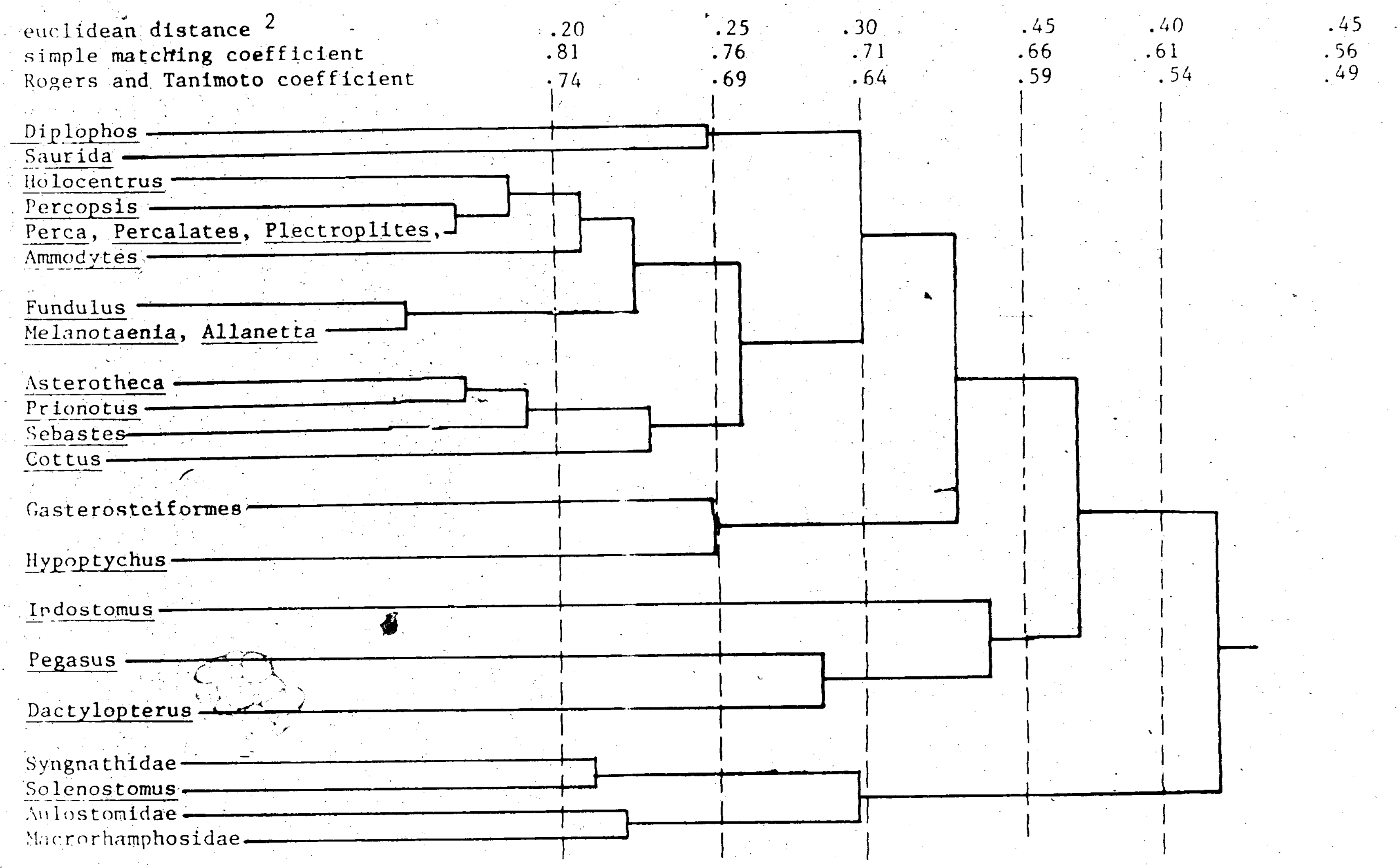


Figure P 3 : Phenetic dendrogram of framework and study groups

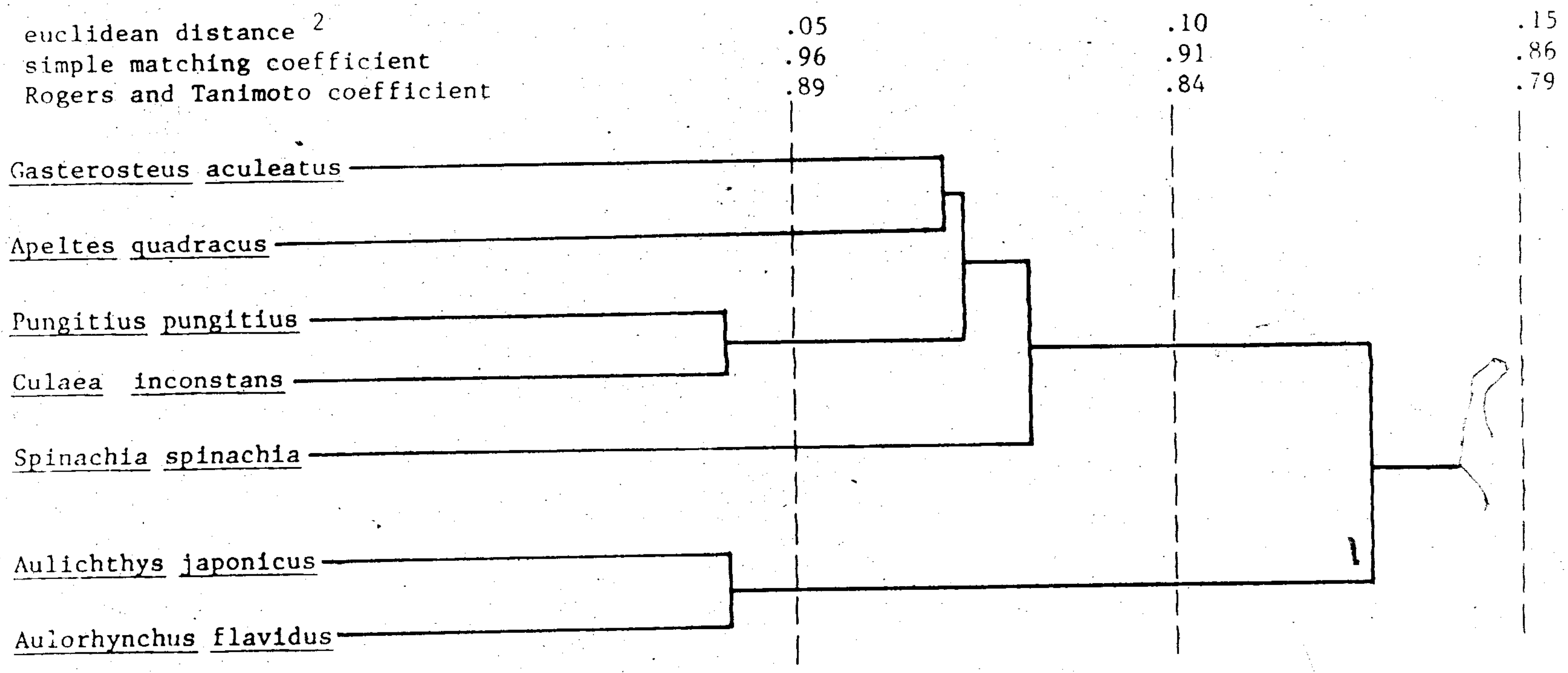


Figure P 4 : Phenetic dendrogram of Gasterosteiformes

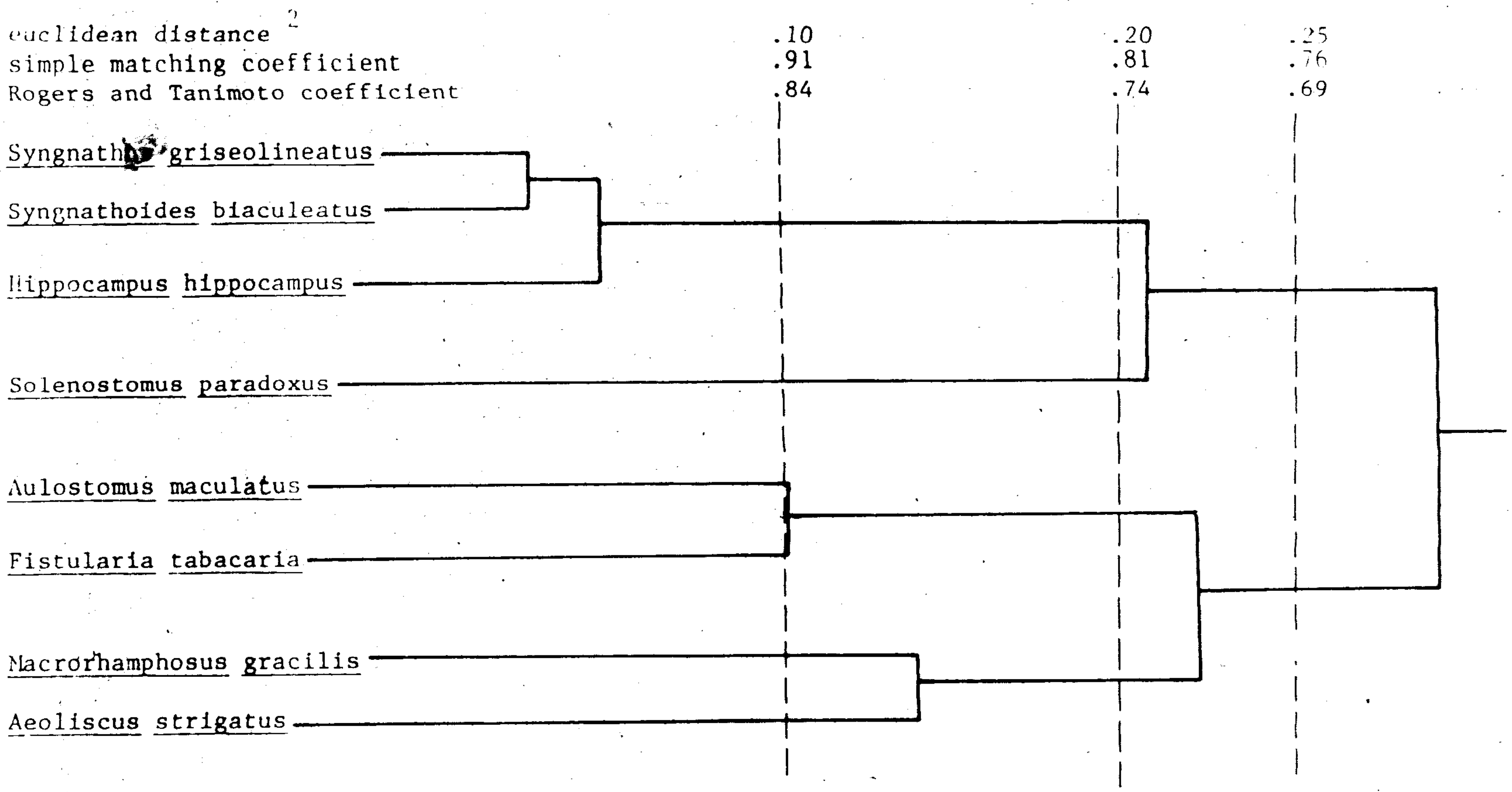


Figure P 5 : Phenetic dendrogram of Syngnathiformes

C. Phylogenetic or Cladistic Analysis

Introduction

Phylogenetic systematics is an attempt to determine the genealogical history of organisms and to represent this history exactly in a hierarchical classification. The genealogical history is reconstructed by identifying those subgroups of the group being studied which share a common ancestor; such a subgroup is referred to as a clade. The members of a clade are recognized by their joint possession of shared derived characters, or synapomorphies, which are presumed to have arisen in their common ancestor. Only synapomorphies can provide information about common ancestry. The terms 'resemblance' and 'similarity' are used in this chapter, accordingly, to indicate resemblance in derived character states.

Derived character states, or apomorphies, can be recognized by several criteria, including comparison with fossil relatives of the group being investigated and analysis of the embryonic development of the individual characters. The most commonly used criterion, however, is comparison with extant relatives, or outgroups; a character state that appears both in members of the group being studied and in the outgroup is regarded as primitive.

Clades are not regarded as groups defined by the possession of particular synapomorphies, but as lineages, historical individuals recognized by the possession of these synapomorphies. Since each lineage is ultimately based on a speciation event, the synapomorphies distinguishing large clades will not necessarily be more noticeable or more stable than those distinguishing species (E. O. Wiley, pers. comm.). As Cracraft (1982) has pointed out, since clades are not defined by their characters, phylogenetic analysis can only indicate relationships; neither the lack of synapomorphies nor the presence of autapomorphies can conclusively demonstrate that a given organism does not belong to a particular taxon. A hypothesis of monophyly can only be disputed, in phylogenetics, by the introduction of a better-supported hypothesis.

In order to determine whether Gasterosteiformes, Syngnathiformes, Indostomus, Hypoptychus, Pegasus, and Dactylopterus should be recognized as a clade, therefore, it is necessary to compare the hypothesis that they do comprise a clade with the alternative hypotheses that have been outlined in the general introduction.

Lauder and Liem (1983) (Fig. CI.1) provide an overview of the proposed phylogenetic relationships between the different framework groups with which the study groups have been affiliated. The various hypotheses of relationships between framework and study groups can be compared by investigating the synapomorphy distributions supporting the placement of study groups in different positions on this framework cladogram. Figure CI.2 shows the framework cladogram composed of the particular representatives of framework groups which I have investigated. This is the actual framework cladogram on which the study groups were placed; I have performed the phylogenetic analyses as though it provided an adequate representation of Figure CI.1, which is a gross oversimplification. This must be borne in mind when evaluating the results.

The analyses in this section are based on the school of phylogenetic systematics outlined by Farris (1979a, 1979b), Wiley (1981), Eldredge and Cracraft (1980), Brooks et al. (1984), and Maddison et al. (1984), among others. This school interpretes phylogenetic analyses in terms of parsimony, attempting to find those hypotheses of relationship that require the fewest hypothesized character state changes. Computer algorithms are often used to construct minimum-length trees, the shortest tree (i.e. the one with the fewest hypothesized character state changes or evolutionary steps) being preferred. Also based on the concept of parsimony are the methods of character state optimization onto an existing cladogram. Optimization procedures infer the character states at the internal nodes of a cladogram from the character states at its terminal nodes, minimizing the number of hypothesized evolutionary steps along the cladogram.

Methods

Throughout this section I use the terminology of Maddison et al. (1984) to describe the components of a cladogram, using the term 'node' to refer both to branch points within a cladogram and to terminal taxa and the term 'internode' to refer to any segment of the cladogram lying between two nodes.

Comparisons between study groups and framework groups

Unweighted Numerical Phylogenetics

The positions of the study groups on the framework cladogram are assessed by a series of comparisons between each study group and the framework groups. The apomorphies associated with each framework group are identified by mapping the states of each character onto the framework cladogram in Fig. Cl.2 and using the Farris optimization procedure (Brooks et al., 1984) to find the most probable character states for the internal nodes of the cladogram. A character state that appears along the internode attaching a framework group to the main stem of the cladogram is accepted as an apomorphy of that framework group. The appearance of one of these apomorphies in a study group provides evidence supporting the hypothesis that the study group and framework group in question shared a common ancestor.

For the study groups Indostomus, Hypoptychus, Pegasus, and Dactylopterus, this can be determined directly from an examination of the coded data. In the two groups Gasterosteiformes and Syngnathiformes, however, some of the apomorphies are present in only a few of the species examined. Only those apomorphies that appear in the hypothetical common ancestor of the study group can represent synapomorphies with a framework taxon. These ancestral character states can be determined by applying an optimization procedure to cladograms of the study groups.

Within-study group cladograms are generated by the computerized Wagner tree procedure PHYLIP (Felsenstein, 1982), using data sets of the 44 characters varying within Gasterosteiformes and the 109 varying within Syngnathiformes.

This computer package generates unrooted trees. To apply optimization and make hypotheses about ancestral character states, the trees must be rooted; the position of the root depends on which suite of character states is regarded as primitive. My study involves hypothesizing many different positions on the framework cladogram for these study groups, and each position on the framework represents a different supposed origin for the study group and therefore a different suite of primitive character states. A separate Wagner analysis is therefore performed for each comparison that involves placing the study group in a different position. The character states at the node directly below the point at which the study group is supposed to have originated on the framework cladogram (the rooting node, Fig. CI.3) are included in the analysis as an additional species. The position of this rooting node on the resulting within study group Wagner tree defines the root of that tree, and the point at which the rooting node attaches to the other members of the study group is the node representing the common ancestor of the study group.

For example, within-Gasterosteiformes trees intended for comparison with Saurida are rooted at NODE A on Fig. CI.2, those compared with Percopsis at NODE B, those compared with Atherinomorpha and Percomorpha at NODE C, those compared with Holocentrus and (Perciformes + Scorpaeniformes) at NODE D, those compared with Scorpaeniformes and Perciformes at NODE E, and those compared [illegible] scorpaeniform subgroups at NODE SC.

Since the order of species introduction affects the resu[illegible]gner analyses, three standard orders were used for each rooting. First, species were introduced in order of increasing advancement index (number of apomorphies with reference to the rooting node), the rooting node being introduced first; second, the rooting node, 'most advanced' and 'least advanced' species were introduced, followed by the others in order of increasing advancement index; last, species were introduced in the sequence which yielded the shortest unrooted within-Gasterosteiformes or within-Syngnathiformes tree, and the rooting node introduced last. Character states at the bases of the within-study group Wagner trees were determined by downward optimization. Since the trees are all of similar lengths, only those states recognized as ancestral in all of the trees generated using a given rooting node are regarded as unambiguous.

The numbers of apomorphies shared by the study groups with each framework group appear in the tables as 'synapomorphies' (S). Some of the framework groups include others; for example, study groups are compared to both (Percopsis + Acanthopterygii) and its subgroup, Scorpaeniformes. A synapomorphy uniting a study group with (Percopsis + Acanthopterygii) is also **consistent** with its relationship to any members of that group (e.g. Scorpaeniformes), unless the synapomorphy has been reversed along an intervening internode. In Fig. Cl.4, for example, the character state (1) arises along the internode leading to (Percopsis + Acanthopterygii), and its presence in a study group would be a synapomorphy uniting the two. This synapomorphy would also be consistent with the study group's placement with Percopsis, Acanthopterygii, Atherinomorpha, and Percomorpha, for the study group could be placed as a sister group of any of these without hypothesizing any additional evolutionary steps. It would not be consistent with the study group's placement within Percomorpha, because members of Percomorpha have lost state (1), and [illegible] presence in a study group placed within Percomorpha would involve hypothesizing its reappearance in the study group. The numbers of synapomorphies consistent with different placements of the study groups, or 'consistent synapomorphies', are indicated by 'C' in the tables.

The second method of comparison used is a parsimony criterion approximating that used in a distance-based Wagner analysis (e.g. Wiley, 1981). The numbers of hypothesized evolutionary steps added to the overall cladogram by placing a study group in different positions are determined by counting the numbers of characters in which the ancestral state of the study group differs from the state present over the internode to which it is being attached. The numbers of evolutionary steps are indicated by 'L' in the tables, and the numbers of steps in the within-study group cladograms rooted at the various positions are indicated by 'W'.

Weighting-based methods

Character weighting is an attempt to separate a data set into characters that are more likely to appear independently in unrelated species and those whose independent appearance is unlikely, the latter being regarded as containing more important phylogenetic information. In the school of phylogenetics that I am following, weighting is based primarily on observation of the distribution of an apomorphy among outgroup taxa or within the study group; particular types of apomorphies are not regarded as being intrinsically more likely to evolve in parallel, but particular apomorphies may be observed to have done so, and may therefore be given lower weight (for comparison of this method and *a priori* weighting, see the evolutionary systematics section). This weighting may be applied either by analysis of each apomorphy with reference to some already established relationships, like those in the framework cladogram used in this study, or by the use of algorithms to identify characters that undergo many state changes along the tree being constructed and de-emphasize their contribution to the total length of the tree (Felsenstein, 1981). I use the former method, applying weighting criteria in three steps.

Primary weighting

Primary weighting is the removal from the data set of those apomorphies which arise independently along the internodes leading to two or more different framework groups. These are regarded both as homoplasies and as uninformative for discriminating between framework groups. The remaining apomorphies are those which arise along the internode leading to only one framework group; they are referred to in the text as apomorphies **distinguishing** that taxon.

Secondary weighting

In secondary weighting, not only those apomorphies which appear as apomorphies characterizing two or more of the framework groups are removed from the data set, but those appearing in any framework species outside the framework group they distinguish. The application of this criterion removes any apomorphies that have arisen by reversal, since these character states appear in more primitive framework groups. It also removes any apomorphies that have apparently arisen in parallel both along the internode leading to one framework group and in a terminal taxon of another framework group.

Tertiary weighting

Tertiary weighting is an extension of secondary weighting, using the literature as a supplementary source of information about the distribution of the apomorphies being weighted.

Comparisons between Study Groups

Unweighted Numerical Phylogenetics

After each study group is examined, it is assigned its best-supported position(s) on the framework, and subsequent study groups are compared with it. For example, Gasterosteiformes might belong with either Cottus or Ammodytes. To test the affinities of other study groups with Gasterosteiformes in the former position, Gasterosteiformes is placed with Cottus as the 'primary study group' (Fig. CI.5). The apomorphies distinguishing Gasterosteiformes within the cottoid lineage are determined by comparing the basal states of Gasterosteiformes with the character states along the internode to which it has been attached. Other study groups, the 'secondary study groups', are then examined for possession of these apomorphies.

Characters for which Gasterosteiformes and Cottoidei share the same state are constant along the internode leading to Gasterosteiformes. Differences between the character states along this internode and the states in the secondary study group represent evolutionary steps added to the overall cladogram if the secondary study group is attached to that internode.

The data set relevant for comparisons among study groups is small enough to allow analysis by the PHYLIP program mentioned above. Wagner trees are generated by the same procedures described for within-study group

Wagner trees, using the character states along the internodes leading to Cottus and Ammodytes as alternative rooting nodes.

Weighting-based methods

Primary Weighting

Primary weighting removes from consideration those synapomorphies that can support a study group's placement in two different, incompatible positions. Since the relationships among the study groups are unknown, the distribution of apomorphies among the study groups themselves cannot be used for weighting. If the study groups are assumed to belong together, however, any character state appearing as an apomorphy both in a study group and along the internode leading to a framework group may be regarded as having arisen independently in these positions. In primary weighting, these apomorphies are removed from the data set used to assess relationships between study groups.

Secondary and Tertiary Weighting

These weighting steps, like the scondary and tertiary weighting in the previous analyses, remove apomorphies that appear in any fishes outside the study groups from the data set. Tertiary weighting is, again, based on a literature search.

Clique Methods

Felsenstein (1981) has suggested a different approach to character weighting, based on the likelihood of a given cladogram. This method uses the number of state changes in a character along the tree being constructed as an index of the probability of change in the character. Characters with more state changes than states will be less reliable indicators of monophyletic groups, having undergone reversal or parallelism, and cladograms which require many such characters will be less likely. Both the number of steps in the cladogram and the number of uninformative characters which must be hypothesized to accept the cladogram are minimized in this weighting model. The most stringent application of this criterion is that in which only one state change is allowed in a character and any character for which homoplasies must be hypothesized is discarded as uninformative. This is clique analysis or strict compatibility analysis. It generates the tree which is supported by the largest set of completely compatible characters. Clique analysis was performed by Felsenstein's PHYLIP program.

Results

Within-Gasterosteiformes and -Syngnathiformes Wagner Trees

The repeated Wagner analyses of Gasterosteiformes were inconclusive, since different trees were generated for most rooting nodes and orders of ETU introduction (Figs. CI.6-7).

For trees rooted at NODES A and B Gasterosteus had the lowest advancement index; for those rooted at NODE C Aulichthys had the lowest advancement index, and for all succeeding nodes Apeltes had the lowest advancement index. In all of the trees except two of those rooted at NODE D the two families Aulorhynchidae and Gasterosteidae were separated at the root. Within-Gasterosteiformes Wagner analysis, then, supports the division of this order into the two groups currently named Family Aulorhynchidae and Family Gasterosteidae (Nelson, 1976). The synapomorphies distinguishing these families appear in Table CI.1.

Relationships within Gasterosteidae remain ambiguous, since no subgroups within this family appear in all cladograms. Eight of the twelve cladograms support a (Culaea +Pungitius) grouping, but this group is distinguished by only one character state (presence of postneurapophyses) and this state is plesiomorphic with respect to all the positions for Gasterosteiformes on the framework cladogram. There is no consensus on the interrelationships of other gasterosteids.

Only one unrooted within-Syngnathiformes tree was generated, and rooting nodes attached to it in only two places (Fig. CI.8). In all rooted analyses, Aulostomus had the lowest advancement index. Both rootings divided Syngnathiformes into three groups corresponding to the currently accepted superfamilies Aulostomoidea (Aulostomus +Fistularia) and Centriscoidea (Macrorhamphosus +Aeoliscus) and suborder Syngnathoidei (Syngnathus +Syngnathoides +Hippocampus +Solenostomus); they disagreed only in the order in which the first two groups were affixed to the main branch of the tree, one separating the macrorhamphosid lineage from all other syngnathiforms and one separating the aulostomid lineage. In no case were these two groups segregated together, so my data do not justify the currently accepted Suborder Aulostomoidei, containing Aulostomoidae and Centriscoidae (Nelson, 1976). The synapomorphies supporting the subgroups of Syngnathiformes appear in Table Cl.2.

Study Group Positions on the Framework Cladogram

Unweighted Numerical Phylogenetics

Table Cl.3 contains the list of apomorphies distinguishing framework groups and the study groups which share them. The numbers of apomorphies shared by framework groups and study groups are presented in Table Cl.4, as are the numbers of synapomorphies consistent with each grouping.

The numbers of synapomorphies directly supporting different study group positions are highest when Gasterosteiformes and Dactylopterus are placed with (Percopsis + Acanthopterygii) and when Syngnathiformes, Indostomus, and Hypoptychus are placed with Ammodytes. Pegasus could be placed in either position. The synapomorphies uniting study groups with (Percopsis + Acanthopterygii), while supporting study group positions along the NODE A-NODE B internode, also support their placements within (Percopsis + Acanthopterygii) and are included in the numbers of synapomorphies consistent with these positions.

Within (Percopsis + Acanthopterygii) all of the study groups except Gasterosteiformes and Dactylopterus share the most apomorphies with Ammodytes. Dactylopterus is also strongly linked to Scorpaeniformes, and Gasterosteiformes might be placed with either Atherinomorpha or

Ammodytes.

Consistent synapomorphy counts give a different picture of relationships between study groups and framework groups. All of the study groups, with the exceptions of Hypoptychus and Pegasus, are placed with or within Scorpaeniformes by this criterion. Both Hypoptychus and Pegasus are placed with Ammodytes.

Distance data (Table CI.5) show that Gasterosteiformes, Syngnathiformes, Indostomus, and Hypoptychus are attached to the framework cladogram by the shortest internode when they are placed with Ammodytes, while Pegasus and Dactylopterus are closest to Cottus. None of the study groups are linked to Atherinomorpha by this criterion. The difference in rooting internode lengths, or total lengths added in the cases of Gasterosteiformes and Syngnathiformes, associated with placing study groups with Ammodytes and scorpaeniforms are relatively small for all study groups except Syngnathiformes and Hypoptychus.

Unweighted phylogenetic analyses all agree in placing Hypoptychus as a sister group of Ammodytes and in placing Dactylopterus with or within Scorpaeniformes, but disagree in their placement of the other study groups. Since raw numbers of synapomorphies and evolutionary steps do not give unambiguous results, more detailed examination of the synapomorphies supporting the different positions is necessary. This is accomplished by weighting.

Weighting-based Methods

Primary Weighting

Within (Percopsis + Acanthopterygii), all study groups share many apomorphies with Ammodytes, Atherinomorpha, and Scorpaeniformes (or scorpaeniform subgroups). This is partly due to the presence of a suite of apomorphies which appear independently in these three framework groups. Ammodytes and members of Atherinomorpha and Scorpaeniformes share incomplete suborbital rings, ceratohyals overlain by the dorsal hypohyals, cleithra expanded ventrally into symphyseal plates, absence of supraneurals before the first dorsal element, and non-autogenous parhypurals. Members of Atherinomorpha and Scorpaeniformes both have lateral ethmoids with fused medial projections, parasphenoids extending for 60-70% of the head length and expanded between the lateral ethmoids, median ethmoids without lateral faces and supraoccipitals with anterior wedge-like processes; members of both lack intercalaries and have only one uroneural. Ammodytes and members of Scorpaeniformes share lateral ethmoids extending posteriorly onto the orbit roof, supraoccipitals without posterior crests or spines, large palatines, ectopterygoids lying along the dorsal borders of the quadrates, flattened angulars, quadrates without fanlike bodies and with anterodorsal extensions, first epibranchials without toothplates, soft dorsals and anals without anterior spines, relatively short caudal fins and hypural complexes, and fewer than three epurals. All of these apomorphies are found in one or more of the study groups, contributing to the ambiguity surrounding their placement. All of them are removed by the application of primary weigting.

The apomorphies remaining after primary weighting, or distinguishing apomorphies, are identified by asterisks in Table CI.3; the numbers of them shared by study groups appear in Table CI.6.

All study groups show a higher affinity for (Percopsis + Acanthopterygii) than for any other framework group. Within (Percopsis + Acanthopterygii), Gasterosteiformes, Indostomus, Pegasus, and Dactylopterus share more distinguishing apomorphies with Scorpaeniformes or members thereof than with any other framework groups. Syngnathiformes share more with Atherinomorpha and Hypoptychus shares most with Ammodytes. For all study groups except Hypoptychus, more weighted synapomorphies are consostent with placement within Scorpaeniformes than with any other placement.

Secondary and Tertiary Weighting

Since these weighting steps differ only in the sources from which the information used are gathered, I apply them together. Both remove apomorphies which appear in more than one position on the framework cladogram, or appear in fishes not on the framework, from the data set. The apomorphies which remain after secondary weighting, which is based on the framework groups examined, are listed in Table CI.7. Those which are removed from the list because of their appearance in other fish groups in the literature are listed in Table CI.8, along with the groups from which they are recorded and the relevant reference(s). Table CI.9 contains the numbers of synapomorphies linking study and framework groups after secondary and tertiary weighting have been applied.

Gasterosteiformes, <u>Indostomus</u>, <u>Pegasus</u>, and <u>Dactylopterus</u> share the most apomorpies with Scorpaeniformes or members thereof, although more apomorphies are consistent with a relationship between <u>Indostomus</u> and <u>Ammodytes</u>. Syngnathiformes share more apomorphies with <u>Ammodytes</u> than with any other framework taxa, but consistent synapomorphy counts support their placement with either Atherinomorpha or <u>Cottus</u>. <u>Hypoptychus</u> shares the most apomorphies with Atherinomorpha and consistent synapomorphy counts support its placement with either Atherinomorpha or <u>Cottus</u>.

Summary

All of the synapomorphy counts applied place the study groups with or within (<u>Percopsis</u> + Acanthopterygii). Within (<u>Percopsis</u> + Acanthopterygii), unweighted synapomorphy counts support both Atherinomorpha, Scorpaeniformes, and <u>Ammodytes</u> as sister groups for the study groups. The numbers of evolutionary steps added to the cladogram are minimized when <u>Pegasus</u> and <u>Dactylopterus</u> are placed within Scorpaeniformes and the other study groups are placed with <u>Ammodytes</u>.

The application of primary weighting removes much of the support for placing the study groups with Atherinomorpha and *Ammodytes*, and the application of secondary and tertiary weighting leaves Scorpaeniformes and scorpaeniform subgroups as the best-supported sister groups for all study groups except *Hypoptychus* and Syngnathiformes. This leaves open the possibility that the study groups form a monophyletic group arising near or within Scorpaeniformes, with *Hypoptychus* and Syngnathiformes having independently acquired some of the apomorphies distinguishing *Ammodytes* and Atherinomorpha.

Comparison of the Study Groups

Unweighted Numerical Phylogenetics

Since their positions on the framework cladogram are ambiguous, study groups are compared to one another with reference to both positions, within Scorpaeniformes and with *Ammodytes*. The apomorphies distinguishing each study group when affixed to the NODE CD-*Cottus* internode and NODE E-*Ammodytes* internode (see Fig. CI.2) are used for identification of synapomorphies. The numbers of apomorphies shared by different pairs of study groups, when placed in these positions, are listed in Table CI.10. Study groups share more apomorphies with one another than with framework groups, and more synapomorphies are consistent with study groups' placement with one another than with their placements with framework groups.

The same study group relationships are supported by synapomorphy counts and by numbers of consistent synapomorphies. If study groups are placed with *Cottus*, Gasterosteiformes share more apomorphies with *Hypoptychus* than with any other study groups, and *Indostomus* and *Dactylopterus* share more with *Pegasus*; all other groups are most closely allied with *Indostomus*. The relationships indicated when study groups are placed with *Ammodytes* are the same except for those of Syngnathiformes, which share more synapomorphies with *Pegasus* than with *Indostomus* in this position, and *Hypoptychus*, which shares more with Gasterosteiformes than with *Indostomus*.

When a primary study group has been affixed to an internode on the framework cladogram, how many evolutionary steps will be added to the cladogram if another, secondary study group is attached to the primary study group? Table Cl.11 contains these figures. If Gasterosteiformes is the primary study group, for example, and Syngnathiformes the secondary study group (see Fig. Cl.5), the length of the internode between Syngnathiformes and the hypothesized common ancestor of Syngnathiformes and Gasterosteiformes is 45 steps if they are placed with *Cottus*, 53 if they are placed with *Ammodytes*. The length of the internode between Gasterosteiformes and the common ancestor is found by considering Syngnathiformes to be the primary study group and Gasterosteiformes to be the secondary study group; it is 35 steps if they are placed with *Cottus* and 29 if they are placed with *Ammodytes*.

Every study group is closer to the internode leading to at least one other study group than it is to any position on the framework (compare Tables Cl.5 and Cl.11). When the study groups are placed in either framework position, all of them except *Indostomus* are closer [illegible] Gasterosteiformes than to other study groups. *Indostomus* is closer to Syngnathiformes.

Both synapomorphy counts and distance measurements, then, support the hypothesis that the study groups belong together. They do not provide clear indications of the relationships among the study groups, however. Wagner tree analysis performed on the characters which vary among study groups (156 characters when study groups are rooted at Atherinomorpha, 92 when they are rooted at Cottoidei) yields the trees in Figures Cl.9 and 10. The shortest trees generated are those rooted at Cottoidei. There is little consensus among these trees, however. Four of the five group Gasterosteiformes and *Hypoptychus* together, and three place *Pegasus* with *Indostomus*. Of the three trees rooted at *Ammodytes*, two contain the (Gasterosteiformes + *Hypoptychus*) group and two contain the (*Indostomus* +

Pegasus) group.

Unweighted analyses, then, indicate closer relationships among study groups than between study groups and framework taxa, but do not provide clear definitions of these relationships.

Weighting-Based Methods

Primary Weighting

For primary weighting, those apomorphies which appear both in study groups and along the internodes leading to framework groups are removed from the data set. The numbers of synapomorphies uniting pairs of study groups after primary weighting are listed in Table Cl. 12.

Most pairs of study groups are united by more synapomorphies when placed with Ammodytes than when placed with Cottus. In both positions, Indostomus, Pegasus, and Dactylopterus are more similar to one another than to other study groups. Syngnathiformes resemble Indostomus, Hypoptychus, and Pegasus equally if they are placed with Cottus, but are most similar to Pegasus when placed with Ammodytes. In both positions, Gasterosteiformes resemble Hypoptychus, but when they are placed with Ammodytes Gasterosteiformes resemble Pegasus and Hypoptychus equally.

Secondary and Tertiary Weighting

These weighting procedures reduce the data set to those character states which appear to be present only in the study groups. Some of these are not characters which seem likely to be so restricted in distribution (for example, the lack of ceratobranchial dentition), but I did not find papers recording their occurrence in other fishes. The counts of these synapomorphies appear in Table Cl. 13. According to them, Gasterosteiformes and Hypoptychus are each other's closest relatives, united by five synapomorphies. These are:

1. Ceratohyal shafts do not bear branchiostegal rays
2. Second ceratobranchials lack toothplates

3. Coracoid shafts are incised anteriorly
4. Fourth actinosts bear anteroventral spike-like processes, and
5. Postneurapophyses are absent.

Indostomus, Pegasus, and Dactylopterus are likewise linked together, Pegasus sharing five apomorphies with each of the others. All three possess the synapomorphies:

1. Second ceratobranchials lack toothplates, and
2. Neural arches are closed for their full lengths.

In addition, Indostomus and Pegasus share:

1. Palatines lack cylindrical heads
2. Third epibranchials lack uncinate processes, and
3. Postneurapophyses are absent.

Pegasus and Dactylopterus share in addition the apomorphies:

1. Posterior borders of the preopercula are expanded
2. Posttemporals are co-ossified with the cranium, and
3. The first four vertebrae are fused.

Syngnathiformes share three apomorphies with Gasterosteiformes, and three with Indostomus. The three shared with Gasterosteiformes are:

1. Symplectics with anterodorsal laminae
2. Ceratohyal shafts do not bear branchiostegal rays, and
3. Second ceratobranchials lack toothplates.

Syngnathiformes and Indostomus share:

1. Lachrymals do not bear infraorbital canals
2. Second ceratobranchials lack toothplates, and
3. Pleural ribs are absent.

Clique Analysis

Clique analysis weights characters not on their distributions among framework groups, but on the congruence with one another of their distributions among the study groups.

Clique analysis performed on the same data yielded 11 trees rooted at Cottoidei (Fig. Cl. 11) and six rooted at Ammodytidae (Fig. Cl. 12). The trees rooted at Cottoidei agree only in the formation of a (Pegasus + Dactylopterus) grouping and in retaining Indostomus and Hypoptychus on a single lineage, although Gasterosteiformes and Syngnathiformes are often included with the latter two groups. In two of the cladograms Gasterosteiformes are separated from all other groups, and in two Syngnathiformes are separated.

If the study groups are placed with Ammodytes, there is even less consensus among clique-based trees. A lineage containing Gasterosteiformes, Hypoptychus, and Indostomus appears in all, but the interrelationships of these three vary. Relationships among the other three study groups are also unclear. Either Pegasus is placed with Syngnathiformes and Dactylopterus remains separate from all the others, or Pegasus is placed with Dactylopterus and Syngnathiformes is separated from all the others.

Discussion

The positions of study groups on the framework cladogram are clear only for Pegasus and Dactylopterus, which are placed with Cottoidei by all criteria except unweighted synapomorphy counts. Since different criteria give different placements for the other four study groups, it is necessary to consider which aspects of the data will be emphasized by the different criteria.

The first criterion used, numbers of synapomorphies supporting a given grouping (Table Cl.4), has the disadvantage of ignoring the extent to which synapomorphies characterize subgroups of the taxon in which they first arise; it identifies apomorphies only at their first appearance, which allows it to indicate higher cladistic similarity between (Percopsis + Acanthopterygii) and study groups than between Percopsis and the study groups, even though all apomorphies present in (Percopsis + Acanthopterygii) (i.e. at NODE B in Fig. Cl.2) must necessarily have been present in Percopsis. This criterion may therefore be expected to place study groups **with** taxa rather than **within** them. This tendency may explain the fact that all study groups except Indostomus and Hypoptychus are placed with (Percopsis + Acanthopterygii) by unweighted synapomorphy counts. It may also explain the fact that Ammodytes shares more direct synapomorphies with study groups than do cottoid species; the apomorphies in which Ammodytes resembles study groups are considered under the five categories (Percopsis + Acanthopterygii), Acanthopterygii, Percomorpha, (Perciformes + Scorpaeniformes), and Perciformes, while those present in Cottus or Asterotheca may appear as apomorphies of six other groups: (Percopsis + Acanthopterygii), Acanthopterygii, Percomorpha, (Perciformes + Scorpaeniformes), Scorpaeniformes, and Cottoidei.

The criterion of consistent synapomorphies is used to avoid this problem. This count mimics the method usually used to place an organism in a known framework, that of fitting it into successively smaller groups within one another. It can be misleading, however, when reversals occur within a group. In Fig. CI.4, for example, the presence in a study group of state (1) is a synapomorphy directly supporting a study group-(Percopsis + Acanthopterygii) link and is consistent with sister-group relations between the study group and Percopsis, Acanthopterygii, Atherinomorpha, and Percomorpha **even though it is not present in Percomorpha.** With respect to Percomorpha, which has undergone reversal in this character, state (1) is plesiomorphic. The consistent synapomorphy criterion is therefore open to the criticism that it uses plesiomorphies as indicative of relationships with taxa in which they are not present!

The same problem appears in the distance measurements between study groups and framework groups. Figure CI.13 illustrates such a situation. The apomorphic character states found in taxa C and D are plesiomorphic with respect to the very derived taxon E. Therefore, a study group identical to taxon C is completely plesiomorphic with respect to taxon E. It can be placed at any of internodes one to five with an equally short rooting internode, and an equal number of synapomorphies will be consistent with each placement.

In this manner, the inclusion of Ammodytes on my framework cladogram reclassifies many of the synapomorphies which unite study groups with (Percopsis + Acanthopterygii), Acanthopterygii, and Percomorpha as symplesiomorphies. These apomorphies are, however, still included in the numbers of synapomorphies consistent with study group - Ammodytes relationships, and are not regarded as evolutionary steps separating the study groups from the NODE E - Ammodytes internode. Accordingly, the criterion of consistent synapomorphies unites Gasterosteiformes with Ammodytes by 70 synapomorphies, 11 of which are reversed in Ammodytes and six of which are ambiguous in Ammodytes. Only two of the 72 synapomorphies consistent with the placement of Gasterosteiformes with Cottus are reversed or ambiguous in Cottus, and only three of the 68 consistent with a Gasterosteiformes - Asterotheca link are reversed or ambiguous in Asterotheca. Hypoptychus is more firmly placed with Ammodytes, only two of the synapomorphies consistent with their linkage being reversed in Ammodytes.

When the consistent synapomorphy counts are revised to contain only those synapomorphies which are actually present in both groups being compared, the figures in Table Cl.14 remain. These support the placement of Hypoptychus with Ammodytes and of all other study groups within Cottoidei. While this revised criterion can be classified as similarity-based, emphasizing the shared character states found in study groups and Cottoidei even though, with respect to Ammodytes, they may be plesiomorphic, I believe it to be superior to the original consistent synapomorphy counts. The original criterion used the same 'plesiomorphic' character states as evidence for positioning study groups, but regarded their possession as evidence not only for relationship with framework groups which shared them but with those which had lost them. The revised consistent synapomorphy criterion attempts to find groups which are not only well-supported by synapomorphies but do not contain members which lack those synapomorphies.

The question of the effect of highly apomorphic taxa on distance-based phylogenetic methods has not been discussed in detail. A situation like that in Fig. Cl.13, in which a species can be as parsimoniously placed with one (E) with which it shares no character states as with one (C) to which it is identical, seems unsatisfactory. At the root of this problem, again, is the question of whether the character states in question are apomorphic or plesiomorphic. The problem only arises, in my study, with respect to characters which have undergone state change followed by reversal on the framework cladogram. The best strategy for dealing with such characters may be to regard them as impossible to polarize and remove them from the data set; the presence of reversals in them classifies them as homoplasious, and they are removed from the data set by secondary weighting criteria.

Primary weighting removes apomorphies which have evolved in parallel among the framework groups, but does not affect those which have only undergone reversal. The synapomorphy counts after this weighting is applied agree with unweighted synapomorphy counts in placing Gasterosteiformes, and *Dactylopterus* with (*Percopsis* + Acanthopterygii). They also place Syngnathiformes, *Indostomus*, *Pegasus*, and *Hypoptychus* with (*Percopsis* + Acanthopterygii), greatly reducing the numbers of synapomorphies linking these study groups with *Ammodytes*. Within (*Percopsis* + Acanthopterygii), the largest numbers of synapomorphies after primary weighting are consistent with the placement of all study groups except *Hypoptychus* within Cottoidei and the placement of *Hypoptychus* with *Ammodytes*.

In secondary and tertiary weighting, characters which have undergone reversal among framework groups and character states which have evolved in parallel in terminal members of framework groups and/or in fishes not examined in this study are removed. The application of these weighting criteria greatly reduces the size of the data set. The relationships supported by these synapomorphy counts (Tab. CI.9) support the placement of all study groups except Syngnathiformes and *Hypoptychus* with or within Scorpaeniformes. In all cases except that of *Dactylopterus*, however, only one or two more synapomorphies support the scorpaeniform placement than support placement with *Ammodytes* or Atherinomorpha.

For all the study groups except *Hypoptychus*, a majority of the phylogenetic criteria support positions on the framework cladogram in the cottoid region. Only *Dactylopterus* is placed here by all criteria. The two criteria which most strongly support *Ammodytes* as sister group to the study groups, consistent synapomorphy counts and distance measurements, are those most affected by the presence of reversals or ambiguous characters. Analyses which attempt to remove these characters tend to move the study groups into the cottoid region.

The tendency of all criteria to place the study groups in one of the same two positions on the framework cladogram leaves open the possibility that they form a monophyletic clade in one of these positions. That hypothesis is strongly supported by the fact that, by all criteria except a few of the weighted analyses, the study groups resemble one another more than they resemble any framework taxa. The only cases in which study groups appear better allied with framework groups are in the primary weighted analyses of Gasterosteiformes and Hypoptychus (compare Tables Cl.6 and Cl. 12) and in the tertiary weighted analyses of all study groups (compare Tables Cl.9 and Cl. 13). All of these are cases in which the study groups share more apomorphies with (Percopsis + Acanthopterygii) than with other study groups; but as discussed above, many of the synapomorphies uniting study groups with (Percopsis + Acanthopterygii) are also found in other study groups. The disagreement between the relationships implied by numbers of consistent synapomorphies (Table Cl. 10) and by weighted synapomorphy counts (Tables Cl. 12-13) raise the question of whether some of the consistent synapomorphies uniting study groups are in fact, as discussed above, character states which are not actually present in both of the groups they unite. When these numbers are corrected to remove reversals and ambiguous characters, however (Table Cl. 15), they still strongly support the study groups' placements with one another rather than with any framework groups.

Two subgroups appear in a majority of the analyses comparing study groups with one another; these are (Gasterosteiformes + Hypoptychus) and (Indostomus + Pegasus + Dactylopterus). The position of Syngnathiformes is highly ambiguous; some criteria place it with Gasterosteiformes, some place it with Indostomus, and some place it with Hypoptychus.

Wagner analyses do not unambiguously support any given groupings of study groups, even though the distance measurements in Table Cl. 11 support the groups (Gasterosteiformes + Hypoptychus) and (Indostomus +Syngnathiformes). This disagreement probably arises because of differences between my measurement of the distances between study groups and the measurements made in the Wagner algorithm.

In my use of the distance criterion for comparison of study groups I treated each pair of study groups individually. Rather than affixing the best-supported secondary study group to the internode leading to the primary study group and comparing subsequent study groups to the three resulting internodes (Fig. Cl. 14,A) I compared all secondary study groups to the characters along the internode connecting the primary study group to the framework cladogram (Fig. Cl. 14,B). This [illegible] element of approximation into my results, for characters which might be homoplasies in a fully resolved study group cladogram may not appear in distances calculated by this method. For example, if Syngnathiformes were affixed to the Gasterosteiformes - Cottoidei internode as in Fig. Cl. 14,A two of the three internodes resulting would have state 0 for the character 'suborbital stay'. Attaching Pegasus or Dactylopterus to either of these internodes would involve hypothesizing a reacquisition of the suborbital stay. When Pegasus and Dactylopterus are compared with the rooting internodes of Gasterosteiformes and Syngnathiformes as in Fig. Cl. 14,B, however, the suborbital stay is not a distance-informative character.

My method, therefore, is less sensitive to homoplasies within a tree containing several study groups than is a traditional Wagner method. This insensitivity may be regarded as a weighting criterion, since it does not include character states found in the supposed common ancestor and secondarily lost in the distance counts. While my method is adequate for comparison of two study groups, it cannot be expected to clearly indicate relationships among three or more. At that level the Wagner tree algorithm is more precise, since it takes previously hypothesized relationships between study groups into account when adding a new study group to the tree. The Wagner trees were very susceptible to changes in the order of ETU introduction, however, and the differences in tree lengths were minor, indicating that the data are highly incongruent.

Weighting methods are based on the reasoning that such incongruence is due to the presence of homoplasious characters and that these can be identified and removed from the data set. Synapomorphy counts based on weighted data (Tables Cl. 12-13) support the formation of an (Indostomus + Pegasus + Dactylopterus) group and a (Gasterosteiformes + Hypoptychus) group. The position of Syngnathiformes among study groups remains ambiguous.

Clique methods support the (Pegasus + Dactylopterus) group but give different resolutions for the other study groups. None of the trees generated by the clique program are supported by more than a small subset of the characters. I see no reason to accept the basic assumption of the clique analysis that character state distribution among the study groups is unrelated to character state distribution outside them, and so I prefer the primary to tertiary weighting criteria. My preference is of little importance in this case, since the clique analyses do not agree among themselves on any groupings which contradict the other weighted analyses.

My majority consensus tree for the study groups (Fig. Cl. 15) is an unresolved trichotomy containing the groups (Gasterosteiformes + Hypoptychus), Syngnathiformes, and (Indostomus + Pegasus + Dactylopterus). The latter group is also an unresolved trichotomy, since synapomorphy counts indicate that Dactylopterus shares the most apomorphies with Pegasus, but Pegasus shares more with Indostomus than with Dactylopterus.

The position of this composite taxon on the framework cladogram is unclear, because many of the synapomorphies which unite it to Cottoidei are plesiomorphies with respect to Ammodytes, its alternative sister group. I therefore regard it as a percomorph order whose position cannot be precisely determined in the absence of more detailed and thorough investigation of Scorpaeniformes and Perciformes.

Conclusion

Gasterosteiformes, Syngnathiformes, Indostomus, Hypoptychus, Pegasus, and Dactylopterus form a polythetic monophyletic percomorph group which can be defined only by one relatively minor synapomorphy, the absence of dentition on the first three pairs of ceratobranchials, relative to character states along the internodes leading to either Cottus or Ammodytes. Study groups, with the exception of Gasterosteiformes, have third actinosts attached to the coracoids and lack epipleural ribs. With the exception of Syngnathiformes, they have opercula without condylar struts. All except Indostomus have fourth ceratobranchials without toothplates and all except Hypoptychus have basioccipitals which are not bowed ventrally. All except Dactylopterus have maxillae with separated dorsal and ventral articular heads and a full neural spine on the second preural centrum.

I propose retaining the name **Gasterosteiformes** for this taxon, and dividing it into three suborders:

Order Gasterosteiformes

  Suborder Gasterosteoidei

    Superfamily Gasterosteoidae

        Family Aulorhynchidae
        Family Gasterosteidae
    Superfamily Hypoptychoidae
        Family Hypoptychidae
Suborder Syngnathoidei
    Superfamily Centriscoidae
        Family Macrorhamphosidae
        Family Centriscidae
    Superfamily Aulostomoidae
        Family Aulostomidae
        Family Fistulariidae
    Superfamily Syngnathoidae
        Family Solenostomidae
        Family Syngnathidae
            Subfamily Syngnathinae
            Subfamily Hippocampinae
Suborder Dactylopteroidei
        Family Dactylopteridae
        Family Pegasidae
        Family Indostomidae

I have retained existing nomenclature as much as possible. The suborder containing <u>Dactylopterus</u>, <u>Pegasus</u>, and <u>Indostomus</u> is named for its (apparently) most plesiomorphic member, and superfamilies are not specified within it because my data do not support the segregation of either (<u>Pegasus</u> + <u>Dactylopterus</u>) or (<u>Pegasus</u> + <u>Indostomus</u>) as a monophyletic group.

The new suborder **Gasterosteoidei** is characterized by the following synapomorphies:

1. Sesamoid articulars are present
2. Epibranchials 3 and 4 articulate
3. Coracoid shafts are incised anteriorly
4. Coracoids have posterior extensions past actinosts

5. Scapular foramina are not circular
6. Fourth actinosts have anteroventral spikes to coracoids
7. Urohyal lacks dorsolateral flanges.

Within this suborder, Superfamily **Gasterosteoidae** is characterized by:

1. Nasals have ventromedial flanges
2. Frontals touch parasphenoids
3. Pterosphenoids are absent
4. Frontals have distinct medial postorbital processes
5. Exoccipital condyles are absent
6. Prootics are excluded from the postorbital foramen
7. Palatine heads bear lateral projections
8. Ectopterygoids extend along the dorsal borders of the quadrates
9. Symplectics bear anterodorsal laminae
10. Ceratohyals and epihyals are connected by a dorsal strut
11. Ectocoracoids are present
12. Fourth actinosts are not connected to coracoids by anteroventral flanges
13. Pelvic plates lack anteromedial flanges
14. Pelvic plates bear ascending processes
15. Soft dorsal fin has anterior spines
16. Separated spines are present before the soft dorsal
17. Supraneurals are present behind the soft dorsal
18. Anal fin has anterior spines
19. Central dorsal pterygiophores are flattened
20. Epipleural ribs are present
21. Haemal arches are pierced by lateral foramina
22. Uroneural is autogenous.

My analysis of this superfamily separates it into the two families listed, whose apomorphies appear in Table Cl. 1, but does not give any resolution below the family level.

The superfamily **Hypoptychoidae** is characterized by:

1. Lateral ethmoids have narrow lateral faces
2. Ventromedial projections of lateral ethmoids have posterior processes

3. Medial plate of median ethmoid is reduced
4. Extrascapulars are present
5. Parasphenoid does not have distinct lateral processes
6. Maxillary hooks are present
7. Quadrates do not have fanlike bodies
8. Quadrates extend anterdorsally
9. Hyomandibulae lack anterior laminae
10. Hypobranchials are straight
11. Fifth ceratobranchials are toothless
12. Fifth ceratobranchials are not expanded laterally
13. Fourth actinosts are fused to coracoids
14. Pelvic fins and plates are absent
15. First anal pterygiophore extends between ribs
16. First uroneural is separate from the hypurals
17. More than 7 dorsal soft rays are present
18. Preneurapophyses are absent.

The suborder **Syngnathoidei** shares synapomorphies with both Gasterosteoidei and Dactylopteroidei; in addition, several apomorphies appear both in Syngnathoidei and in one of the members of Dactylopteroidei. This would tend to indicate a closer relationship between the latter two suborders, but is insufficient to place Syngnathoidei firmly with either *Dactylopterus*, *Pegasus*, or *Indostomus*; if a relationship between the two suborders is postulated, it must be on the basis of a shared **tendency to develop** certain apomorphies (see discussion under Evolutionary Systematics).

Syngnathoidei and superfamilies within Gasterosteoidei share:

1. Incomplete suborbital series
2. Basisphenoid is absent
3. Supraoccipital bears anterior wedge-like process
4. Ventral hypohyals overlap ceratohyals
5. Ceratohyal shaft does not support branchiostegal rays
6. Pelvic plates do not bear anteromedial spurs.

Syngnathoidei and members of Dactylopteroidei share:

1. Premaxillae lack postmaxillary processes
2. Dentaries and articulars do not bear preoperculo-mandibular canals
3. Quadrates do not have distinct shafts
4. Cranial condyles of each hyomandibula are connected
5. Postcleithra are present
6. Pleural ribs are absent.

Syngnathoidei itself is characterized by:

1. Lateral ethmoids have anterolateral extensions
2. Median ethmoid is ossified ventrally
3. Median ethmoid bears ventrolateral ridges
4. Vomer shaft is exposed dorsally
5. Frontals reach near posterior end of the skull
6. Prootics do not meet exoccipitals or basioccipital
7. Exoccipitals do not separate pterotics and basioccipital
8. Maxilla shafts are greatly expanded
9. Palatine length is less than 10% of head length
10. Ceratohyals are not constricted centrally
11. Interhyals are not cylindrical
12. Basibranchials are absent
13. Posttemporals lack median struts
14. Actinosts are constricted centrally and bear lateral flanges on their distal ends
15. 4 pelvic rays are present
16. Snout-pelvic fin distance is more than 50% of standard length
17. Anterior vertebrae are elongated and fused
18. Soft dorsal lies above caudal vertebrae
19. Posterior dorsal pterygiophores are fused .

The synapomorphies characterizing the subgroups of Syngnathoidei have been described in Table CI.5. Since both of the alternative rootings for this group (see Fig. CI.8) appear among Wagner trees rooted at NODE E, the three superfamilies within Syngnathoidei are presented as an unresolved trichotomy.

The suborder **Dactylopteroidei** is characterized by many synapomorphies, but the vast majority of these occur in only two of the three families within the suborder. The only synapomorphies shared by all three families are:

1. Lateral ethmoids extend posteriorly onto orbit roof
2. Medial projections of each lateral ethmoid are fused
3. Posterior myodome is absent
4. Dermosphenotics bear infraorbital canals
5. Ectopterygoids have long anterior processes
6. Interopercula are short
7. Subopercula lack ascending limbs
8. Subopercula do not lie along the margins of the opercula
9. Ceratohyal shafts bear branchiostegal rays
10. Urohyal bears dorsolateral flanges
11. Posttemporals lack anteroventral processes
12. Neural arches are closed for their full lengths.

Within Dactylopteroidei, Dactylopteridae and Pegasidae share the apomorphies:

1. Vomer head connects lateral ethmoids
2. Suborbitals extend to touch preopercula
3. Basisphenoid is present
4. Prootics lack separate ventral foramina
5. Exoccipital condyles are absent
6. Ventral articular heads of maxillae are elongated
7. Posterior borders of preopercula are expanded to form most of the gill covers; opercula are reduced
8. Third pharyngobranchials lack anterior cylindrical processes
9. Posttemporals are co-ossified with the cranium
10. Pelvic plates bear anteromedial spurs
11. Transverse bones are present
12. First four vertebrae are fused.

Dactylopteridae and Indostomidae share:

1. Posterior process of the parasphenoid is not divided

2. Articulars lack elevated coronoid processes
3. Ceratohyals are expanded anteriorly
4. Nasals are either absent or completely fused to median ethmoid.

and Indostomidae and Pegasidae share:

1. Palatines are poorly developed, without cylindrical heads
2. Basioccipital is wider than long
3. Scapulae are fused to first actinosts
4. Preneurapophyses, prehaemapophyses, and posthaemapophyses are absent
5. Bodies are encased in bony plates.

<u>Dactylopterus</u> is further characterized by:

1. Sclerotic rings are present
2. Supraoccipital crest is absent
3. Supraoccipital length is more than 40% of head length
4. Prootics have accessory anterior trigeminofacialis foramina
5. Premaxillae have articular processes
6. Dorsal and ventral articular heads of each maxilla are connected by a posterior flange
7. Hyomandibulae have complex heads, with five articular surfaces
8. Hyomandibulae bear large posterior flanges
9. Interopercula are not expanded posteriorly
10. Preopercula are armed
11. Posterior heads of ceratohyals do not support branchiostegals
12. Basibranchials have lateral flanges
13. Cleithra do not have distinct "head" and "shaft" regions
14. First actinosts are pierced by foramina
15. Pelvic and pectoral girdles touch each other
16. Pelvic plates bear dorsomedial struts reaching to the cleithrum
17. Pelvic plates are pierced by lateral foramina
18. Anterior spinous dorsal is present
19. First vertebra is shortened
20. Precaudal neural arches are nonperforate

21. Anterior transverse processes are absent
22. Vertebrae bear dorsolateral spines
23. Parhypural is autogenous
24. Third epural is present
25. Second preural centrum bears an incomplete neural spine
26. Lower hypurals are separate from each other
27. Hypural plate length is more than 5% of standard length.

<u>Pegasus</u> is characterized by:

1. Nasals are fused into a rostrum
2. Median ethmoid bears a ventral transverse flange
3. Medial projections of lateral ethmoids extend posteriorly into the orbits
4. Median ethmoid lacks lateral faces
5. Median ethmoid touches lateral ethmoids
6. Vomer shaft is short, not extending posteriorly past lateral ethmoids
7. Dermosphenotics bear lateral canals
8. Frontals bear distinct ventromedial processes
9. Parasphenoid length is 27-28% of head length
10. Premaxillae and dentaries are toothless
11. Endopterygoids are absent
12. Dentaries touch angulars
13. Hyomandibulae lack medial foramina
14. Preopercula bend medially to form the floors of the branchial chambers
15. Ceratohyals are attached to epihyals by complex lateral sutures
16. Third basibranchial is absent
17. Second and third hypobranchials are absent
18. Hypobranchials lack anterior processes
19. Cleithra bear posteromedial extensions to coracoids
20. Coracoid shafts do not touch cleithra
21. Scapular foramina are incomplete
22. Actinosts are sutured together, and to scapulae and coracoids
23. Haemal laminae do not extend the full length of each caudal. vertebrum

Indostomus is characterized by:

1. Median ethmoid, palatines, and vomer are fused
2. Lachrymals do not bear infraorbital canals
3. All suborbital bones except lachrymals are absent
4. Parietals are absent
5. Parasphenoid lacks lateral processes
6. Prootics have separate ventral foramina
7. Exoccipital lateral foramina are absent
8. Prootics do not reach the margin of the postorbital foramen
9. Premaxillae lack ascending processes
10. Ectopterygoids do not lie along the anterior margins of the quadrates
11. Dentaries lack elevated coronoid processes
12. Angulars are flat, without anterior processes
13. Symplectics bear posterodorsal and posteroventral laminae
14. Quadrates articulate with lower jaws behind the orbits
15. Preopercula lack distinct dorsal and ventral arms
16. Preopercula lack preoperculomandibular canals
17. Posterior borders of preopercula are incised
18. Opercula are armed
19. Hypobranchials bear anterior processes
20. Fourth ceratobranchials are toothed
21. Posttemporals do not bear lateral canals
22. Cleithra lack anterior symphysis
23. Cleithra bear posterolateral laminae covering scapular foramina
24. Coracoids bear posterior extensions past the actinosts
25. Actinosts are elongate and fourth actinosts bear anteroventral extensions
26. Pelvic fins are spineless
27. Pelvic plates lack medial processes and sutures
28. Separate spines precede soft dorsal
29. Ossified tendons are present in the axial musculature
30. Haemal canals are closed for their full lengths.

Many of the apomorphies distinguishing members of this suborder also appear within Syngnathoidei, suggesting that these study groups share a common genome with the propensity to develop such apomorphies. The effect of considering these possible 'parallel apomorphies' as indicators of relationship is discussed in the section on Evolutionary Systematics. The trichotomies in my cladogram may be impossible to resolve by numerical phylogenetic methods until such methods are refined to take parallel apomorphies into account.

Table CI.1: Apomorphies characterizing subgroups of Gasterosteiformes

Gasterosteidae

B9(0) Suborbital rings incomplete
B10(1) Suborbital stays present
B18(0) Sclerotic rings absent
C7(0) Dermopterotics do not bear lateral canals
E4(0) Premaxillae lack postmaxillary processes
F7(0) Dentaries do not bear preoperculomandibular canals
F11(0) Articulars do not bear preoperculomandibular canals
F19(1) Symplectics bear central laminae
I37(0) Fourth pharyngobranchials absent
J1(1) Posttemporals bear cylindrical median struts
J12(0) Cleithra shafts without ventral expansion into symphyseal plate
J29(1) Fourth actinosts enlarged
L4(1) Supraneurals before dorsal

Aulorhynchidae

A8(1) Ventromedial projections with posterior processes
B9(1) Suborbital rings complete
B10(0) Suborbital stays absent
B18(1) Sclerotic rings present
C8(1) Dermopterotics overlap over half of sphenotics
G16(0) Subopercula posterior limbs do not reach the dorsal borders of the opercula
I6(0) Basibranchial #1 similar to succeeding basibranchials
I37(1) Fourth pharyngobranchials present
J1(0) Posttemporals lack cylindrical median struts
J3(1) Posttemporals resemble lateral scutes or scales
J12(1) Cleithra shafts with ventral expansion into symphyseal plate
J31(1) Actinosts attached to one another via sutures
L18(0) Soft dorsal not supported anteriorly by precaudal vertebrae
M20(0) Haemal spines do not originate anteriorly

Table Cl.2 : Apomorphies characterizing subgroups of Syngnathiformes

(Macrorhamphosus + Aeol[illegible]cus)

C3(0) Supraoccipital lacks anterior wedge-like process
E13(1) Palatine shafts lie over lateral surfaces of pterygoids
H1(0) Glossohyal not cylindrical
H3(0) Dorsal hyophals do not overlap ceratohyals
H16(1) Urohyal with dorsolateral flanges
H18(1) Urohyal flanges posteriorly incised
H19(1) Urohyal blade posteriorly incised
I2(1) Basibranchial #2 present
I3(1) Basibranchial #3 present
I11(0) Hypobranchials not cylindrical
I12(1) Hypobranchials with [illegible]erior processes
I27(1) Third epibranchials with uncinate processes
I28(1) Third and fourth epibranchials articulate
J20(0) Scapu[illegible]d to the size of actinosts
J22(1) Scapu[illegible]rders notched to receive actinosts
J28(1) Fourth a[illegible]s with anteroventral spikes
J29(1) Fourth actinosts enlarged
L6(1) First dorsal element supported by pterygiophore complex
N2(1) Second ural centrum present

(Aulostomus + Fistularia)

A10(1) Vomer with dorsal projections over parasphenoids
A17(1) Vomer head tightly attached to palatines
C6(1) Epiotics articulate with ossified ligaments
C8(1) Dermopterotics overlap over half of sphenotics
E20(1) Ectopterygoids lie along dorsal borders of quadrates
E23(0) Separate endopterygoids absent
E24([illegible]) Separate metapterygoids present
F1(1) Dentaries toothed
F5(1) Posterior borders of dentaries are deeply cleft
F8(1) Articulars have subdentary processes
G4(0) Posterior borders of preopercula are not expanded
H10(1) Ceratohyal posterior heads bear branchiostegal rays
J18(1) Ectocoracoids present
J25(1) Actinosts elongate
J26(0) Actinosts without lateral distal flanges
M12(1) Ossified tendons are present in the axial musculature
M24(1) Haemal laminae extend the full lengths of centra
M26(0) Vertebrae do not bear lateral processes to scutes
N7(1) Parhypural separate from hypurals

Syngnathidae + Solenostomus

A1(0) nasals absent
B1(0) Frontals lack supraorbital canals
D4(0) Parasphenoid posterior process not divided
F4(1) Dentaries touch angulars
F15(0) Quadrates lack fanlike bodies
G2(0) Preopercula lack preoperculomandibular canals

Table Cl.2 continued
G7(0) Interopercula do not extend full length of preopercula
G13(0) Subopercula lack ascending limbs
I10(0) Third hypobranchials absent
I23(0) Fifth ceratobranchials lack teeth
I24(0) Fifth ceratobranchials are not laterally
I25(0) First epibranchials lack uncinate processes
I37(0) Fourth pharyngobranchials absent
J17(0) Coracoid fans not incised
J32(0) First postcleithra absent
K6(0) Pelvic plates lack medial processes
K12(1) Pelvics are thoracic
L14(0) Proximal dorsal pterygiophores lack flanges
L15(0) Proximal anal pterygiophores lack flanges
M3(0) First four vertebra are not fused
M19(0) Posterior transverse processes are absent
M20(0) Haemal spines do not originate anteriorly
M23(0) Posthaemapophyses are absent
M25(0) Haemal canal is not closed over its full length

Table C1.3 : Apomorphies characterizing framework subgroups with the study groups in which they appear and the character numbers, states, and descriptions. Asterisks indicate apomorphies which do not appear on the internode leading to any other framework group.

G = Gasterosteiformes
S = Syngnathiformes
I = *Indostomus*
H = *Hypoptychus*
P = *Pegasus*
D = *Dactylopterus*

Saurida (Aulopiformes)

P	A 1 1(0)Median ethmoids lack lateral faces
	*A17(1)Vomer head tightly attached to palatines
S P	*A20(0)Vomer shaft does not extend posteriorly past lateral ethmoids
P	A25 Vomer less than 15% of head length
I PD	B13(0)Posterior myodome absent
S HPD	D 2(1)Parasphenoid expanded between ethmoids
I P	D13(0)Length of basioccipital not greater than its width
GS P	E 7(1)Maxillae with palatine articular facets
	*E21(1)Ectopterygoids toothed
IHP	F15(0)Quadrates lack fanlike bodies
IH	F17(1)Quadrates extend anterodorsally
	G14(1)Ventral laminae of subopercula are expanded
G IH D	G18(0)Opercula lack distinct anteromarginal struts
P	*I 3(0)Basibranchial #3 absent
SI P	*I16(0)First ceratobranchials lack gill rakers
	I31(1)Interarcual cartilages present
G H	J21(0)Scapular foramina ovoid
IHP	*M10(0)Preneurapophyses absent
S H	M19(1)Posterior transverse processes are present
	*M20(0)Haemal spines do not originate anteriorly

(*Percopsis* + Acanthopterygii)

S H	*A 3(0)Lateral ethmoids do not extend posteriorly onto orbit roof
GSIHPD	A16(0)Vomer head toothless
GSIHP	*A23 Snout length more than 25% of head length
G D	A25 Vomer length 17-31% of head length
H	*C 8(1)Dermopterotics overlap over half of sphenotics
GSIHPD	*C11(0)Supraoccipital and frontals not separated
D	*D 8(1)Prootics with accessory anterior foramen(a)
SIH	*D11(1)Exoccipital condyles present
S HPD	*D17(1)Prootics reach margin of postorbital foramen
GS PD	*D19 Head length more than 22% standard length
GS H D	*E 2(1)Premaxillae bear ascending process
D	*E10(1)Dorsal and ventral maxilla articular heads connected posteriorly
GSIHPD	E14(0)Palatines toothless
GS HPD	*F 3(1)Dentaries have elevated corohoid processes
H D	*F18(1)Quadrates have distinct shafts
GS HPD	*F27(0)Quadrates articulate with lower jaws in front of the orbits
GS HPD	*G 1(1)Preopercula have dorsal and ventral arms
I	*G 5(1)Posterior borders of preopercula are incised or serrated
GSIHPD	*H 2(0)Glossohyal toothless
G IH D	*H12(1)Epihyals triangular
GSIHPD	*I 4(0)Basibranchials lack toothplates or teeth
H	*I 6(1)Basibranchial #1 deep
D	*I 7(1)Basibranchials with lateral flanges
	*I13(1)Hypobranchial heads bent posteriorly
G I PD	*I24(1)Fifth ceratobranchials expanded laterally
G H	*J22(1)Scapula posterior borders notched to receive actinosts

Table CI.3 continued
G HP *J25(0)Actinosts not elongate
SIHPD *J30(1)Third actinosts attached to coracoids
G *K 5(0)Pelvic plates lack anteromedial flanges
G D *K12(1)Pelvics are thoracic
G P *K13(1)Pelvic fins articulate with ventral projections from the pelvic plates
*K15(1)Pelvic plates bear overlapping medial processes
GS PD K19 Anterior processes make up less than 80% of pelvic plates lengths
G *L 3(1)Soft dorsal with anterior spines
G *L 9(1)Anal spinous
GSIHPD *L15(1)Proximal anal pterygiophores bear flanges
GSI D L21 2 or more dorsal spines
GSIHP *M 9(1)Precaudal neural arches are pierced by lateral foramina
GSIHPD* M15(0)Epineurals absent
GSI PD M27Fewer than 50 vertebrae
GSI PD M30 Fewer than 25 pleural ribs
GSIHPD *N12(0)Preural centrum #2 does not bear an autogenous neural spine
GSIHP N14(0)Lower hypurals are not separated from one another

Percopsis (**Paracanthopterygii**)

H A12(1)Median ethmoid medial plate reduced
S P A23 Snout length more than 40% of head length
GSIH B12(0)Basisphenoid absent
GSIHP B18(0)Sclerotic rings absent
E15(1)Palatines larger than ectopterygoids
I *F22(1)Symplectics bear posterodorsal laminae
I *F23(1)Symplectics bear posteroventral laminae
S HP *H 4(1)Ventral hypohyals overlap ceratohyals
*H11(1)Ceratohyals with toothplates
*H13(1)Epihyals with toothplates
*I 5(1)Ventral toothplate behind last basibranchial
PD I35(0)Third pharyngobranchials lack anterior cylindrical processes
GS P *J17(1)Coracoid fans incised
P *K18 Snout to pelvic base 45% standard length
GS PD K19 Anterior processes make up less than 70% of pelvic plates lengths
GSI PD L 6(0)First dorsal element not supported by a pterygiophore complex
G I D *L13(0)Proximal dorsal pterygiophores not cylindrical
M29 2 epipleural Ribs
GSIHP N18Caudal fin length less than 20% of standard length

Acanthopterygii

S *B 4(1)Frontals reach near posterior end of skull
HPD F19(1)Symplectics bear central laminae
GS HP *H 5(0)Ceratohyals not expanded at anterior end
G HPD *H17(1)Urohyal with ventrolateral flanges
GSIHPD *I14(0)Hypobranchials lack toothplates
I PD *J 5(0)Posttemporals lack anteroventral processes
GSI PD *K10(0)Pelvic actinosts absent
[illegible]D *K14(1)Pelvic plates bear anteromedial spurs
GSI PD K17 Fewer than 8 pelvic rays
D *L 1(1)Anterior spinous dorsal
GSIHPD *L12(1)Proximal and medial pterygiophores fused
G D L21 6 or more dorsal spines
GSI D *L23First dorsal spine less than 19% of standard length
GSIH D L27 Anal base more than 10% of standard length
GSI PD M28 Fewer than 50% of vertebrae are precaudal
SIHPD N 5(0)Uroneural not autogenous
SI PD *N 6(1)Uroneural, if distinct, supports principal caudal rays

Table CI.3 continued

Atherinomorpha

P	A 1 1(0)Median ethmoid lacks lateral faces
SIH	B 9(0)Suborbital rings incomplete
GS H	C 3(1)Supraoccipital with anterior wedge-like process
SI	C 4(0)Parietals absent
D	C12 Supraoccipital more than 36% of head length
S HPD	D 2(1)Parasphenoid expanded between ethmoids
	D10(1)Exoccipitals with second ventral foramina
SI PD	D14(0)Intercalaries absent
G H D	D18 Parasphenoid 59-70% of head length
GSIH	*E 3(0)Premaxillae lack articular processes
H	*E 9(1)Maxillary hooks present
G H D	*E26Palatines 11-26% of head length
I D	F 9(0)Articulars lack elevated coronoid processes
G IHPD	*G 3(0)Opercula lack distinct condylar struts
	G14(1)Subopercula ventral laminae expanded
G IH D	G18(0)Opercula lack distinct anteromarginal struts
GSIHPD	H 3(1)Dorsal hyophals overlap ceratohyals
	*H 7(1)Ceratohyals attached to epihyals by dorsal struts originating on epihyals
GS HPD	*I2 1(0)Fourth ceratobranchials without toothplates
	I3 1(1)Interarcual cartilages present
GS H	J2 1(0)Scapular foramina ovoid
	*J23(0)Scapulae do not bear rays
G I P	*J39Pectoral base - pelvic base 8-20% of standard length
G	*K 8(1)Pelvic plates bear ascending processes
SI	*K 9(0)Pelvic plates lack posteromedial processes
D	L 4(0)No supraneurals before dorsal
GS D	*L20 7-11 dorsal rays
HP	*L22Snout - first dorsal element 45-76% of standard length
I	*L26Snout - first anal element 45-60% of standard length
H	L27 Anal base 18-42% of standard length
	*M 5(1)Neural spines of the first four vertebra are distally expanded
S H	M2740-43 vertebrae
GS HP	M34First vertebra / middle vertebra .9-1.2
SIH	*M35Last vertebra / middle vertebra .85
GSIHPD	N 3(0)Second uroneural absent
GSIHP	N 8(0)Parhypural not autogenous
GSIHPD	N13(0)Upper hypurals are not separate from one another

Percomorpha

	*C 5(1)Epiotic posterior processes present
H D	*E 4(1)Premaxillae bear postmaxillary processes
D	*G 6(1)Preopercula are armed
I	G12(1)Opercula are armed
	*H 1(0)Glossohyal not cylindrical
SIHP	*I26(0)Second epibranchials lack uncinate processes
G D	J39 Pectoral base - pelvic base less than 7% of standard length
G PD	K 7(1)Pelvic plates are joined by medial suture
GSI PD	L 6(0) First dorsal element supported by a single pterygiophore
S H	*L20 12 or more dorsal rays
G	L21 11 or more dorsal spines
	L22 Snout to first dorsal element less than 43%
	*L25 3-4 Anal spines
G D	M30 8-11 pleural ribs

<u>Holocentrus</u> (Beryciformes)

H	A12(1)Median ethmoid medial plate reduced
PD	A19(1)Vomer head connects lateral ethmoids
	*A24 Median ethmoid more than 30% of head length

Table CI.3 continued
*B20 Frontal more than 62% of head length
SI C 4(0)Parietals absent
SI *D 9(0)Exoccipitals lack lateral foramina
GSI PD D12(0)Basioccipital not bowed ventrally
G I D17(0)Prootics do not reach margin of postorbital foramen
*D18 Parasphenoid more than 80% of head length
GS P E 7(1)Maxillae with palatine articular facets
IH D E22(1)Ectopterygoids with long anterior processes
G P F 8(0)Articulars lack subdentary processes
S *F24(0)Hyomandibular cranial condyles are not separate
I *G 8(1)Interopercula expanded anteriorly
IHPD G16(0)Subopercula posterior limbs do not reach the posterior margins of the opercula
G IHPD H19(1)Urohyal blade posteriorly incised
*I15(1)Hypobranchials with teeth
HPD I37(0)Fourth pharyngobranchials absent
S *J 1(0)Posttemporals lack cylindrical median struts
I P J 3(1)Posttemporals resemble lateral scutes or scales
PD *J 4(0)Posttemporals lack anterodorsal processes
*J 8(1)Second supracleithra present
D K16(1)Pelvic plates are pierced by lateral foramina
S L18(0)Soft dorsal not supported anteriorly by precaudal vertebrae
*M 6(1)Precaudal vertebra bear autogenous neural arches
S H M19(1)Posterior transverse processes are present
G I P *M21(1)Haemal arches are pierced by lateral foramina
*M31 Body depth more than 35% of standard length

(Perciformes + Scorpaeniformes)

SIH D B16(0)E[illegible]ck distinct medial postorbital processes
SIHP B18(0)Sc[illegible]ngs absent
SI *D 6(1)Prootics with separate ventral foramina for VIII nerve
G IH D *J10(0)Cleithra lack posteromedial extensions to coracoids
GS H *J38Pectoral fin length 10-17% of standard length
D J39 Distance between pectoral and pelvic fin bases less than 3% of standard length
G D *K11(1)Pelvic and pectoral girdles touch each other

Scorpaeniformes

GSI PD *A 2(1)Lateral ethmoids with broad lateral faces
I PD *A 3(1)Lateral ethmoids extend posteriorly onto orbit roofs
P *A 5(1)Median ethmoid with ventral transverse flange
S H A 7(1)Lateral ethmoid medial projections fused
P *A15(1)Median ethmoid touches lateral ethmoids
D *A23 Snout less than 25% of head length
D A25 Vomer less than 27% of head length
G IHPD *B 4(0)Frontals do not reach near posterior end of skull
PD *B10(1)Suborbital stays present
GSIH B17(0)Dermosphenotics lack infraorbital canals
GSI P *B19 Orbit length less than 25% of head elngth
S P *B20 Frontal length less than 40% of head length
GSI PD*C10(0)Extrascapulars absent
C12 Supraoccipital 10-12% of head length
S HPD D 2(1)Parasphenoid expanded between ethmoids
SI PD D14(0)Intercalaries absent
G D D18 Parasphenoid 62-68% of head length
E15(1)Palatines larger than ectopterygoids
I PD *G17(0)Posterior limbs of subopercula do not closely follow opercular margins
GSIHPD H 3(1)Dorsal hyophals overlap ceratohyals
I D *I12(1)Hypobranchials with anterior processes

Table CI.3 continued

PD	I35(0)Third pharyngobranchials without anterior cylindrical processes
	J12(1)Cleithra shafts with ventral expansion into symphyseal plate
P	*J19(0)Scapular foramina incomplete
G IHPD	*J27(0)Actinosts not constricted centrally
D	*J38 Pectoral fin length more than 25% of standard length
I D	*K18 Snout - pelvic base 26-38% of standard length
SI P	K19Anterior processes make up 80-92% of pelvic plate lengths
SIHPD	L 3(0)Soft dorsal without anterior spines
D	L 4(0)No supraneurals before dorsal.
S HPD	M29 0-5 epipleural ribs
GSIHPD	N 3(0)Second uroneural absent
G H	*N 6(0)Uroneural, if distinct,does not support principal caudal rays
GSIHP	N 8(0)Parhypural not autogenous
GSIHPD	N13(0)Upper hypurals not separate from one another
S HPD	N20 Hypural complex / caudal vertebra length less than 2

Scorpaenoidei

	*A10(1)Vomer with dorsal projections over parasphenoid
P	A11(0)Median ethmoid lacks lateral faces
SHPD	*B 3(0)Frontals lack lateral postorbital processes
I PD	*G 7(0)Interopercula do not extend full length of preopercula
	*K20 Pelvic plate length more than 15% of standard length

Cottoidei

GSI	B12(0)Basisphenoid absent
I PD	B13(0)Posterior myodome absent
GSIHP	*D 8(0)Prootics lack accessory anterior foramina
G I	D17(0)Prootics do not reach the margin of the postorbital foramen
GSIHPD	*I32(0)First pharyngobranchials absent
HPD	I37(0)Fourth pharyngobranchials absent
D	*J 9(0)Cleithra without distinct heads
G I P	K17 2-3 pelvic rays
S P	* K20 Pelvic plate length less than 10% of standard length
SIHPD	L 9(0)Anal not spinous
G D	L21 6-8 dorsal spines
	*M 2(0)First vertebra does not bear a complete neural arch
G IHPD	*N 7(0)Parhypural not separate from hypurals

Cottus

H	*A 2(0) Lateral ethmoids with narrow lateral edges
H	A12(1)Median ethmoid medial plate reduced
I	*B 2(0)Frontals lack mental cross-canals
SIH	B 9(0)Suborbital rings incomplete
G H	C 3(1)Supraoccipital with anterior wedge-like process
G IHP	*D 5(0)Trigeminofacialis anterior foramina incomplete
S	*D 7(0)Prootics and exoccipitals do not meet
S	*D15(0)Prootics do not contact basioccipital
	*E 5(1)Maxillae with forked dorsal articular heads
GSIHPD	E14(0)Palatines toothless
G	*E17(1)Palatine heads bear lateral projections
G	*E20(1)Ectopterygoids lie along dorsal borders of quadrates
IH D	E22(1)Ectopterygoids with long anterior processes
G IHP	*E23(0)Separate endopterygoids [illegible]
SI	F12(0)Angulars are not cylindrical
HPD	F19(1)Symplectics bear central laminae
GS HPD	G 5(0)Posterior borders of preopercula are not incised or serrated
GS HPD	G12(0)Opercula are not armed.
SI PD	*I 6(0)Basibranchial #1 not deep

Table Cl.3 continued
GSIHP *I 7(0)Basibranchials lack lateral flanges
G D *I11(0)Hypobranchials not cylindrical
GSIHPD I29(0)Epibranchials lack toothplates
I P J 3(1)Posttemporals resemble lateral scutes or scales
I P *J20(1)Scapulae reduced to the size of actinosts
G IHP *J32(0)First postcleithra absent
*L14(0)Proximal dorsal pterygioph[illegible]flanges
*L15(0)Proximal anal pterygiophores [illegible]ges
GSI PD *N 4(0)First uroneural not separate f[illegible]hypurals

Asterotheca

I PD *A 6(1)Lateral ethmoid medial pr[illegible]ns fused
H *A 8(1)Ventromedial projections [illegible] posterior processes
P *A 9(1)Ventromedial projections extend posteriorly into orbit
G I *B20Frontal more than 50% of [illegible] length
*C 1(0)Supraoccipital without l[illegible] dorsal plate
D C 2(0)Supraoccipital crest absent
C12 Supraoccipital less than 11% of head length
GS H D D13(1)Length of basioccipital greater than its width
SI P *E 4(0)Premaxillae lack postmaxillary processes
IHP F15(0)Quadrates lack fanlike bodies
IH F17(1)Quadrates extend anterodorsally
P *G19(1)Preopercula bend medially to form the floors of the branchial chambers
G IHPD H19(1)Urohyal blade posteriorly incised
GSIHPD *I19(0)Third ceratobranchials without toothplates
IHP I25(0)First epibranchials without uncinate processes
I P *I33(0)Second pharyngobranchials absent
I P *J24(1)Scapulae and first actinosts fused
H J35(1)Fourth actinosts fused to coracoids
G PD K 7(1)Pelvic plates are joined by medial suture
D K16(1)Pelvic plates are pierced by lateral foramina
S P K19 Anterior processes make up more than 90% of pelvic plate lengths
G I *L16(0)Central pterygiophores flattened dorsoventrally
G I D *L17(1)Distal and medial pterygiophores fused
S L18(0)Soft dorsal not supported anteriorly by precaudal vertebrae
GS L19(0)Anal not supported anteriorly by precaudal vertebrae
I L20 6 dorsal rays
SIHPD *M14(0)Epipleural ribs are absent
SIHPD M29No epipleural ribs
GSIHP N10(0)Epural #3 absent
GSIHP *N11(1)Preural centrum #2 bears a full neural spine
GSIHP N18 Caudal fin length less than 15% of standard length

Perciformes

GSIHP A23 Snout more than 34% of head length
P B14(1)Dermosphenotics bear lateral canals
G C12 Supraoccipital 28-37% of head length
G P D18 Parasphenoid 70-76% of head length
E25(1)Supramaxillae present
G P F 8(0)Articulars lack subdentary processes
I D F 9(0)Articulars lack elevated coronoid processes
SI J13(1)Cleithra with posterolateral laminae over scapular foramina
G IH J16(1)Coracoids with posterior extensions past actinosts
I D *J25(1)Actinosts elongate
GSIHP *L 1(0)Noseparate anterior spinous dorsal
GS L19(0)Anal not supported anteriorly by precaudal vertebrae
SIHP L21 0-5 or 14-16 dorsal spines
GSI PD M28 Fewer than 50% of vertebrae are precaudal
M29 12-45 epipleural ribs

Table Cl.3 continued

G P	M34 First vertebra / middle vertebra .96-1.14

Ammodytes

I PD	A 3(1)Lateral ethmoids extend posteriorly onto orbit roof
GSIHPD	A 16(0)Vomer head toothless
GS H	*A25 Vomer more than 34% of head length
GSIH	B 9(0)Suborbital rings incomplete
	*B 15(0)Dermosphenotics not attached to sphenotics
D	C 2(0)Supraoccipital crest absent
H	*D 19 Head length less than 20% of standard length
GSIHPD	E 14(0)Palatines toothless
	E 15(1)Palatines larger than ectopterygoids
I	I*E 19(0)Ectopterygoids do not lie along anterior borders of the quadrates
G	E20(1)Ectopterygoids lie along dorsal borders of quadrates
P	*F 1(0)Dentaries toothless
G D	*F 2(1)Dentaries with anterolateral foramina
G P	*F 4(1)Dentaries touch angulars
	*F 6(1)Dentaries with anterodorsal struts
GS HP	F 9(1)Articulars bear elevated coronoid processes
G H	*F 10(1)Sesamoid articulars are present
SI	F 12(0)Angulars are not conical
IHP	F 15(0)Quadrates lack fanlike bodies
S	*F 16(1)Quadrate shafts make up over half their lengths
IH	F 17(1)Quadrates extend anterodorsally
GSIHP	*G 6(0)Preopercula are not armed
GSIHPD	*G 10(0)Posterior margins of opercula are not pointed
GS HPD	G 12(0)Opercula are not armed
	G 14(1)Subopercula ventral laminae are expanded
	*G 15(1)Subopercula ventral laminae are lobed
GSIHPD	*I 17(0)Firstceratobranchials lack toothplates
H	*I24(0)Fifth ceratobranchials not expanded laterally
IHP	I25(0)First epibranchials lack uncinate processes
GSIHPD	I29(0)Epibranchials lack toothplates
I	*J 1 1(0)Cleithra lack anterior symphysis
	J 12(1)Cleithra shafts with ventral expansion into symphyseal plate
P	*J 14(0)Coracoid shafts do not reach cleithra
SIH	*K 2(0)Pelvic spines absent
H	K 17 No pelvic rays
H	*K20 Pelvic plates 0% of standard length
SIHPD	L 3(0)Soft dorsal without anterior spines
D	L 4(0)No supraneurals before dorsal
SIHPD	L 9(0)Anal not spinous
H	*L 1 1(1)First anal pterygiophore extends dorsally between ribs
IHPD	L 19(1)Anal supported anteriorly by precaudal vertebrae
S H	L20 More than 17 dorsal rays
S HP	*L21 No dorsal spines
	L22 Snout to first dorsal element less than 30% of standard length
S H	*L24 More than 13 anal rays
	L26 Snout to anal base less than 30% of standard length
S H	M19(1)Posterior transverse processes are present
S H	M27 More than 40 vertebrae
H	*M28 More than 53% of vertebrae are precaudal
	M29 More than 40 epipleural ribs
	*M30 More than 35 pleural ribs
S	*M31Body depth 10% of standard length
PD	*M35 Last caudal vertebra length / middle vertebra length > 1
SIHPD	N 5(0)Uroneural not autogenous
GSIHP	N 8(0)Parhypural not autogenous
GSIHP	N 10(0)Epural #3 absent
GSIHP	N 14(0)Lower hypurals are not separate from one another

Table CI.3 continued

G IH N18 Caudal fin length less than 10% of standard length
P N20 Hypural complex / caudal vertebra 1.2

Table C1.4 : Consequences of placing study groups with different framework groups I: numbers of synapomorphies directly supporting (S) and consistent with (C) different placements.

Sister Group	Gasterosteiformes		Syngnathiformes		*Indostomus*		*Hypoptychus*		*Pegasus*		*Dactylopterus*	
	S	C	S	C	S	C	S	C	S	C	S	C
Saurida	3	3	4	4	7	7	7	7	11	11	3	3
Percopsis + Acanthopterygii	30	30	23	23	19	19	25	25	23	23	27	27
Percopsis	7	37	8	31	6	26	5	30	9	32	4	30
Acanthopterygii	10	40	11	42	10	36	7	37	12	41	15	44
Atherinomorpha	17	61	17	59	15	51	20	57	13	54	14	58
Percomorpha	5	45	3	45	3	39	3	40	3	44	6	50
Holocentrus	6	50	8	53	10	49	6	46	10	54	8	58
Perciformes + Scorpaeniformes	3	47	4	49	4	43	4	44	1	45	4	53
Scorpaeniformes	12	60	16	65	17	60	13	57	23	68	23	76
Scorpaenoidei	0	56	1	61	1	59	1	55	3	68	2	76
Cottoidei	7	63	5	65	8	66	5	59	8	73	7	81
Cottus	13	71	11	66	13	78	14	68	13	81	9	85
Asterotheca	11	67	11	72	18	83	13	68	17	86	10	87
Perciformes	9	56	6	53	8	53	4	48	8	53	3	54
Ammodytes	17	69	24	74	23	75	33	79	24	73	15	65

Table C1.5 : Consequences of placing study groups with different framework groups II: numbers of evolutionary steps within study group trees rooted at a given position (W) and along the internodes connecting study groups to different positions on the framework cladogram (L)

Sister Group	Gasterosteiformes		Syngnathiformes		*Indostomus*	*Hypoptychus*	*Pegasus*	*Dactylopterus*
	W	L	W	L	L	L	L	L
Saurida	76-83	105	156	112	129	95	138	119
Percopsis + Acanthopterygii	76-83	78	"	100	114	84	129	104
Percopsis	74-83	85	"	120	135	93	146	116
Acanthopterygii	74-83	90	"	119	120	93	139	105
Atherinomorpha	80-83	99	"	103	159	107	149	121
Percomorpha	80-83	96	"	108	134	94	132	100
Holocentrus	78-79	101	"	115	138	98	133	102
Perciformes + Scorpaeniformes	78-79	85	"	118	139	104	140	102
Scorpaeniformes	81-83	88	"	111	135	93	132	89
Scorpaenoidei	70-83	91	"	137	156	109	132	97
Cottoidei	70-83	94	"	124	138	108	138	89
Cottus	70-83	70	"	100	113	85	97	71
Asterotheca	70-83	84	"	111	117	91	114	81
Perciformes	81-83	92	"	106	139	93	138	101
Ammodytes	81-83	66	"	63	96	55	100	72

Table C1.6 : Consequences of placing study groups with different framework groups III: Primary weighting. numbers of synapomorphies directly supporting (S) and consistent with (C) different placements after the removal of all which characterize more than one framework group

	Gasterosteiformes		Syngnathiformes		*Indostomus*		*Hypoptychus*		*Pegasus*		*Dactylopterus*	
Sister Group	S	C	S	C	S	C	S	C	S	C	S	C
Saurida	0	0	2	2	2	2	1	1	4	4	0	0
Percopsis + Acanthopterygii	22	22	17	17	13	13	22	22	17	17	21	21
Percopsis	2	24	2	19	3	16	1	23	3	20	1	21
Acanthopterygii	6	27	7	24	6	19	4	26	8	25	9	29
Atherinomorpha	7	34	5	29	6	25	7	33	4	29	3	32
Percomorpha	0	27	2	26	1	20	3	29	1	26	2	31
Holocentrus	1	28	3	29	3	23	0	29	2	28	1	32
Perciformes + Scorpaeniformes	3	30	2	28	2	22	2	31	0	26	2	33
Scorpaeniformes	6	36	4	32	9	31	3	34	12	38	11	44
Scorpaenoidei	0	36	1	32	1	31	1	35	2	39	2	45
Cottoidei	3	39	3	34	3	33	3	37	4	41	3	46
Cottus	8	47	5	39	8	41	5	42	7	48	3	49
Asterotheca	5	44	4	38	10	43	4	41	9	50	4	50
Perciformes	1	31	1	29	2	24	1	32	1	27	1	34
Ammodytes	6	37	8	38	6	30	12	44	7	34	4	38

Table CI.7 : Secondary Weighting: Framework group apomorphies not appearing in any other framework groups examined,
with the study groups in which they occur and the character numbers, states, and descriptions.

Saurida (Aulopiformes)

IHP	*M10(0)Preneurapophyses absent

(Percopsis + Acanthopterygii)

S H	*A 3(0)Lateral ethmoids do not extend posteriorly onto orbit roof
GSIHP	*A23 Snout length more than 25% of head length
H	*C 8(1)Dermopterotics overlap over half of sphenotics
GSIHPD	*C11(0)Supraoccipital and frontals not separated
D	*D 8(1)Prootics with accessory anterior foramen(a)
SIH	D11(1)Exoccipital condyles present
S HPD	*D17(1)Prootics reach margin of postorbital foramen
GS PD	*D19 Head length more than 22% standard length
GS H D	D*E 2(1)Premaxillae bear ascending process
D	*E10(1)Dorsal and ventral maxilla articular heads connected posteriorly
GS HPD	*F 3(1)Dentaries have elevated coronoid processes
H D	*F18(1)Quadrates have distinct shafts
GS HPD	*F27(0)Quadrates articulate with lower jaws in front of the orbits
GS HPD	*G 1(1)Preopercula have dorsal and ventral arms
I	*G 5(1)Posterior borders of preopercula are incised or serrated
GSIHPD	*H 2(0)Glossohyal toothless
G IH D	*H12(1)Epihyals triangular
GSIHPD	*I 4(0)Basibranchials lack toothplates or teeth
H	*I 6(1)Basibranchial #1 deep
D	*I 7(1)Basibranchials with lateral flanges
G I PD	*I24(1)Fifth ceratobranchials expanded laterally
G H	*J22(1)Scapula posterior borders notched to receive actinosts
G HP	*J25(0)Actinosts not elongate
SIHPD	*J30(1)Third actinosts attached to coracoids
G	*K 5(0)Pelvic plates lack anteromedial flanges
G D	*K12(1)Pelvics are thoracic
G P	*K13(1)Pelvic fins articulate with ventral projections from the pelvic plates
	*K15(1)Pelvic plates bear overlapping medial processes
G	*L 3(1)Soft dorsal with anterior spines
G	*L 9(1)Anal spinous
GSIHPD	*L15(1)Proximal anal pterygiophores bear flanges
GSIHP	*M 9(1)Precaudal neural arches are pierced by lateral foramina
GSIHPD	*M15(0)Epineurals absent
GSIHPD	*N12(0)Preural centrum #2 does not bear an autogenous neural spine

Percopsis (Paracanthopterygii)

	E15(1)Palatines larger than ectopterygoids
S HP	*H 4(1)Ventral hypohyals overlap ceratohyals
P	*K18 Snout to pelvic base 45% standard length

Acanthopterygii

S	*B 4(1)Frontals reach near posterior end of skull
GS HP	*H 5(0)Ceratohyals not expanded at anterior end
G HPD	*H17(1)Urohyal with ventrolateral flanges
GSIHPD	*I14(0)Hypobranchials lack toothplates

Table CI.7 continued

I PD *J 5(0)Posttemporals lack anteroventral processes
GSI PD *K 10(0)Pelvic actinosts absent
PD *K 14(1)Pelvic plates bear anteromedial spurs
D *L 1(1)Anterior spinous dorsal
GSIHPD *L 12(1)Proximal and medial pterygiophores fused
GSI D *L23First dorsal spine less than 19% of standard length
SI PD *N 6(1)Uroneural, if distinct, supports principal caudal rays

Atherinomorpha

GSIH *E 3(0)Premaxillae lack articular processes
H *E 9(1)Maxillary hooks present
G IHPD *G 3(0)Opercula lack distinct condylar struts
G *K 8(1)Pelvic plates bear ascending processes

Percomorpha

H D *E 4(1)Premaxillae bear postmaxillary processes
D *G 6(1)Preopercula are armed

Holocentrus (Beryciformes)

PD *J 4(0)Posttemporals lack anterodorsal processes

(Perciformes + Scorpaeniformes)

G D *K 11(1)Pelvic and pectoral girdles touch each other

Scorpaeniformes

GSI PD *A 2(1)Lateral ethmoids with broad lateral faces
P *A 5(1)Median ethmoid with ventral transverse flange
PD *B 10(1)Suborbitals reach proepercula
I D *I 12(1)Hypobranchials with anterior processes
P *J 19(0)Scapular foramina incomplete
D *J38 Pectoral fin length more than 25% of standard length

Scorpaenoidei

No distinguishing synapomorphies

Cottoidei

No distinguishing synapomorphies

Cottus

G IHP *D 5(0)Trigeminofacialis anterior foramina incomplete
G *E 17(1)Palatine heads bear lateral projections
G IHP *E23(0)Separate endopterygoids absent
G D *I 1 1(0)Hypobranchials not cylindrical

Table Cl.7 continued
GSI PD *N 4(0)First uroneural not separate from the hypurals

Asterotheca

P *A 9(1)Ventromedial projections extend posteriorly into orbit
I P *I33(0)Second pharyngobranchials absent
G I D *L17(1)Distal and medial pterygiophores fused

Perciformes

No distinguishing synapomorphies

Ammodytes

I *E19(0)Ectopterygoids do not lie along anterior borders of the quadrates
P *F 1(0)Dentaries toothless
G P *F 4(1)Dentaries touch angulars
S *F16(1)Quadrate shafts make up over half their lengths
I *J11(0)Cleithra lack anterior symphysis
H *K20 Pelvic plates 0% of standard length
S *M31Body depth 10% of standard length

Table CI.8 : Tertiary Weighting: Apomorphies appearing in other framework taxa not examined
With the character number and state, the taxon from which it is reported, and the reference

Apomorphies distinguishing (*Percopsis* + Acanthopterygii)

E 2 (1)	Characoidei	Roberts, 1974
F27 (0)	Characoidei	Roberts, 1974
G 1 (1)	Sternoptychidae	Weitzman, 1974
H12 (1)	Sternoptychidae	Weitzman, 1974
K12 (1)	Pantodon	Nelson, 1971
N12 (0)	Sternoptychidae	Weitzman, 1974
	and Characoidei	Roberts, 1974

Apomorphies distinguishing Atherinomorpha

G 3 (0)	Sternoptychidae	Weitzman, 1974

Apomorphies distinguishing Percomorpha

G 6 (1)	Sternoptychidae	Weitzman, 1974

Apomorphies distinguishing Scorpaeniformes

A 2 (1)	Doradidae	Eigenmann, 1925
B10 (1)	Anabantidae	Liem, 1963

Apomorphies distinguishing *Ammodytes*

K20 0	many other groups	Nelson, 1971

Table C1.9 : Consequences of placing study groups with different framework groups IV: Tertiary weighting numbers of synapomorphies directly supporting (S) and consistent with (C) different placements which are apparently not found in any other fishes

	Gasterosteiformes		Syngnathiformes		*Indostomus*		*Hypoptychus*		*Pegasus*		*Dactylopterus*	
Sister Group	S	C	S	C	S	C	S	C	S	C	S	C
Saurida	0	0	0	0	1	1	1	1	1	1	0	0
Percopsis + Acanthopterygii	16	16	13	13	10	10	17	17	14	14	14	14
Percopsis	0	16	1	14	0	11	1	18	2	15	0	15
Acanthopterygii	6	22	6	23	5	16	4	21	8	22	9	23
Atherinomorpha	3	25	1	30	1	17	3	24	0	22	0	23
Percomorpha	0	22	0	29	0	16	1	22	0	22	1	24
Holocentrus	0	22	0	29	0	16	0	22	1	23	1	25
Perciformes + Scorpaeniformes	1	23	0	29	0	16	0	22	0	22	1	25
Scorpaeniformes	0	23	0	29	1	17	0	22	2	24	2	27
Scorpaenoidei	0	23	0	29	0	17	0	22	0	24	0	27
Cottoidei	0	23	0	29	0	17	0	22	0	24	0	27
Cottus	5	28	1	30	3	22	2	24	3	27	2	29
Asterotheca	1	24	0	29	2	23	0	22	2	26	1	38
Perciformes	0	23	0	69	0	23	0	22	0	22	0	25
Ammodytes	1	24	2	31	2	25	0	22	1	23	0	25

Table Cl.10: Consequences of placing study groups with one another I:

numbers of synapomorphies directly supporting (S) and consistent with (C) different placements

	Secondary Study Group											
	Gasterosteiformes		Syngnathiformes		*Indostomus*		*Hypoptychus*		*Pegasus*		*Dactylopterus*	
Primary Study Group	S	C	S	C	S	C	S	C	S	C	S	C
When study groups are placed within Cottoidei												
Gasterosteiformes			36	98	37	104	39	95	33	103	29	111
Syngnathiformes	36	105			46	110	39	93	43	114	31	109
Indostomus	37	106	46	105			44	98	62	129	46	125
Hypoptychus	39	109	39	100	44	108			37	105	34	114
Pegasus	33	102	43	103	62	126	37	90			53	130
Dactylopterus	29	99	31	90	46	110	34	85	53	118		
When study groups are placed with *Ammodytes*												
Gasterosteiformes			26	91	37	104	40	118	36	99	30	96
Syngnathiformes	26	98			33	100	30	107	37	99	25	92
Indostomus	37	108	33	96			35	112	57	119	44	110
Hypoptychus	40	111	30	93	35	100			39	99	37	101
Pegasus	37	107	37	100	57	123	39	114			56	121
Dactylopterus	30	101	25	89	44	110	37	112	56	117		

Table C1.11: Consequences of placing study groups with one another II: numbers of evolutionary steps separating a secondary study group from the internode connecting the primary study group to the framework cladogram

	Secondary Study Group					
Primary Study Group	Gasterosteiformes	Syngnathiformes	Indostomus	Hypoptychus	Pegasus	Dactylopterus
When study groups are placd within Cottoidei						
Gasterosteiformes		45	68	31	59	51
Syngnathiformes	35		58	41	63	63
Indostomus	44	41		44	56	58
Hypoptychus	37	56	77		69	69
Pegasus	39	48	56	43		39
Dactylopterus	43	70	79	56	63	
When study groups are placed with Ammodytes						
Gasterosteiformes		53	68	38	53	49
Syngnathiformes	29		57	47	45	50
Indostomus	32	29		47	39	43
Hypoptychus	27	57	70		60	52
Pegasus	37	58	60	55		41
Dactylopterus	42	76	71	61	55	

Table C1.12: Consequences of placing study groups with one another IV: Primary weighting numbers of synapomorphies directly supporting different placements after the removal of all which characterize more than one framework group

	Secondary Study Group					
Primary Study Group	Gasterosteiformes	Syngnathiformes	*Indostomus*	*Hypoptychus*	*Pegasus*	*Dactylopterus*
When study groups are placed within Cottoidei						
Gasterosteiformes		16	15	17	15	15
Syngnathiformes			17	17	17	14
Indostomus				16	27	23
Hypoptychus					13	19
Pegasus						29
When study groups are placed with *Ammodytes*						
Gasterosteiformes		12	17	21	21	16
Syngnathiformes			14	10	17	9
Indostomus				16	30	23
Hypoptychus					18	18
Pegasus						29

Table Cl.13: Consequences of placing study groups with one another V: Tertiary weighting. numbers of synapomorphies directly supporting different placements and apparently not found in any other fishes

Primary Study Group	Gasterosteiformes	Syngnathiformes	*Indostomus*	*Hypoptychus*	*Pegasus*	*Dactylopterus*
When study groups are placed within Cottoidei						
Gasterosteiformes		3	4	5	2	1
Syngnathiformes			3	1	2	1
Indostomus				4	5	2
Hypoptychus					2	1
Pegasus						5
When study groups are placed with *Ammodytes*						
Gasterosteiformes		3	4	5	2	1
Syngnathiformes			3	1	2	1
Indostomus				4	5	2
Hypoptychus					2	1
Pegasus						6

(Columns: Secondary Study Group)

Table C1.14 : Consequences of placing study groups with different framework groups V: numbers of synapomorphies consistent with different placements and present in both the study group and the framework group with which it is being placed

Framework Sister Group	Gasterosteiformes	Syngnathiformes	*Indostomus*	*Hypoptychus*	*Pegasus*	*Dactylopterus*
Saurida	3	5	7	7	10	3
Percopsis + Acanthopterygii	32	22	20	28	25	29
Percopsis	40	30	26	33	31	32
Acanthopterygii	41	41	36	40	42	47
Atherinomorpha	61	55	50	60	55	59
Percomorpha	43	41	32	38	38	46
Holocentrus	51	51	44	48	53	62
Perciformes + Scorpaeniformes	43	41	37	40	38	52
Scorpaeniformes	54	52	50	48	56	68
Scorpaenoidei	49	46	41	49	61	70
Cottoidei	58	50	51	47	56	67
Cottus	68	60	66	69	80	73
Asterotheca	69	67	77	66	82	89
Perciformes	55	45	45	44	44	52
Ammodytes	56	58	62	78	56	48

Table Cl.15: Consequences of placing study groups with one another VI: numbers of synapomorphies consistent with different placements and present in both study groups being placed together

Primary Study Group	Secondary Study Group Gasterosteiformes	Syngnathiformes	*Indostomus*	*Hypoptychus*	*Pegasus*	*Dactylopterus*
When study groups are placed within Cottoidei						
Gasterosteiformes		92	97	86	96	92
Syngnathiformes	90		98	81	94	86
Indostomus	92	98		86	117	107
Hypoptychus	95	96	98		90	93
Pegasus	91	98	122	81		117
Dactylopterus	86	78	101	73	107	
When study groups are placed with *Ammodytes*						
Gasterosteiformes		83	95	111	93	84
Syngnathiformes	89		90	96	92	78
Indostomus	102	89		101	113	100
Hypoptychus	104	87	91		93	90
Pegasus	102	95	116	106		111
Dactylopterus	98	81	103	105	113	

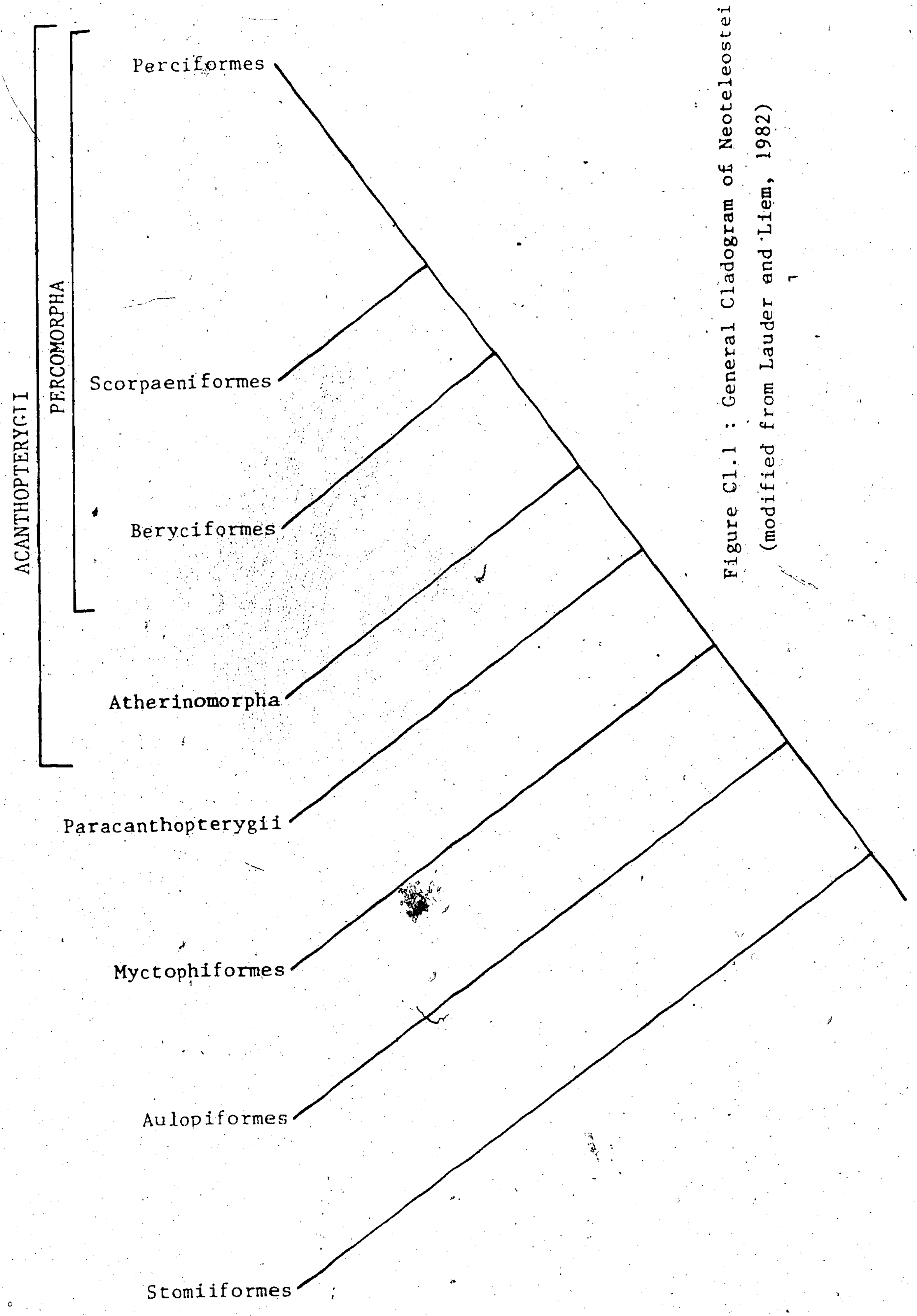


Figure C1.1 : General Cladogram of Neoteleostei (modified from Lauder and Liem, 1982)

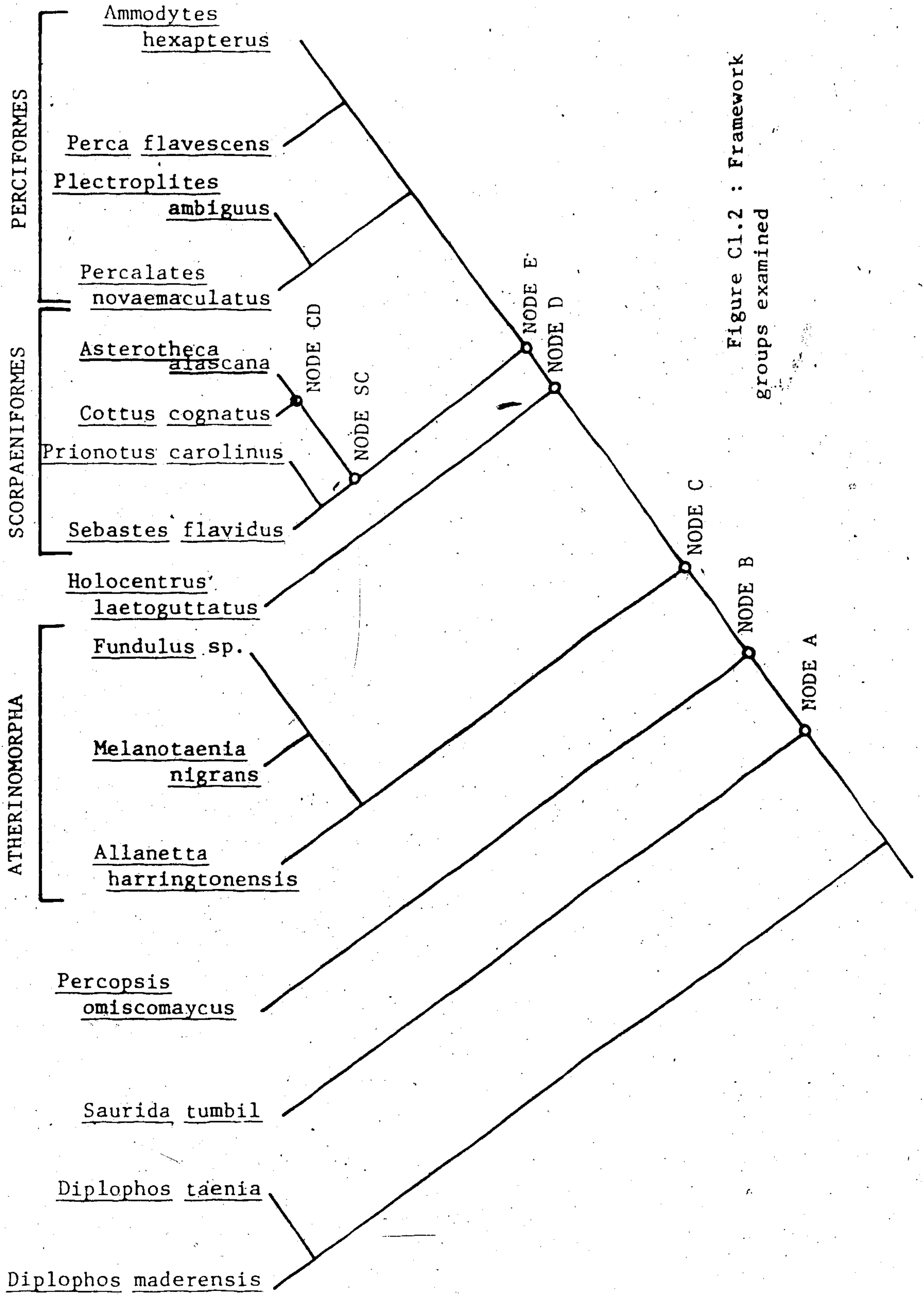


Figure C1.2 : Framework groups examined

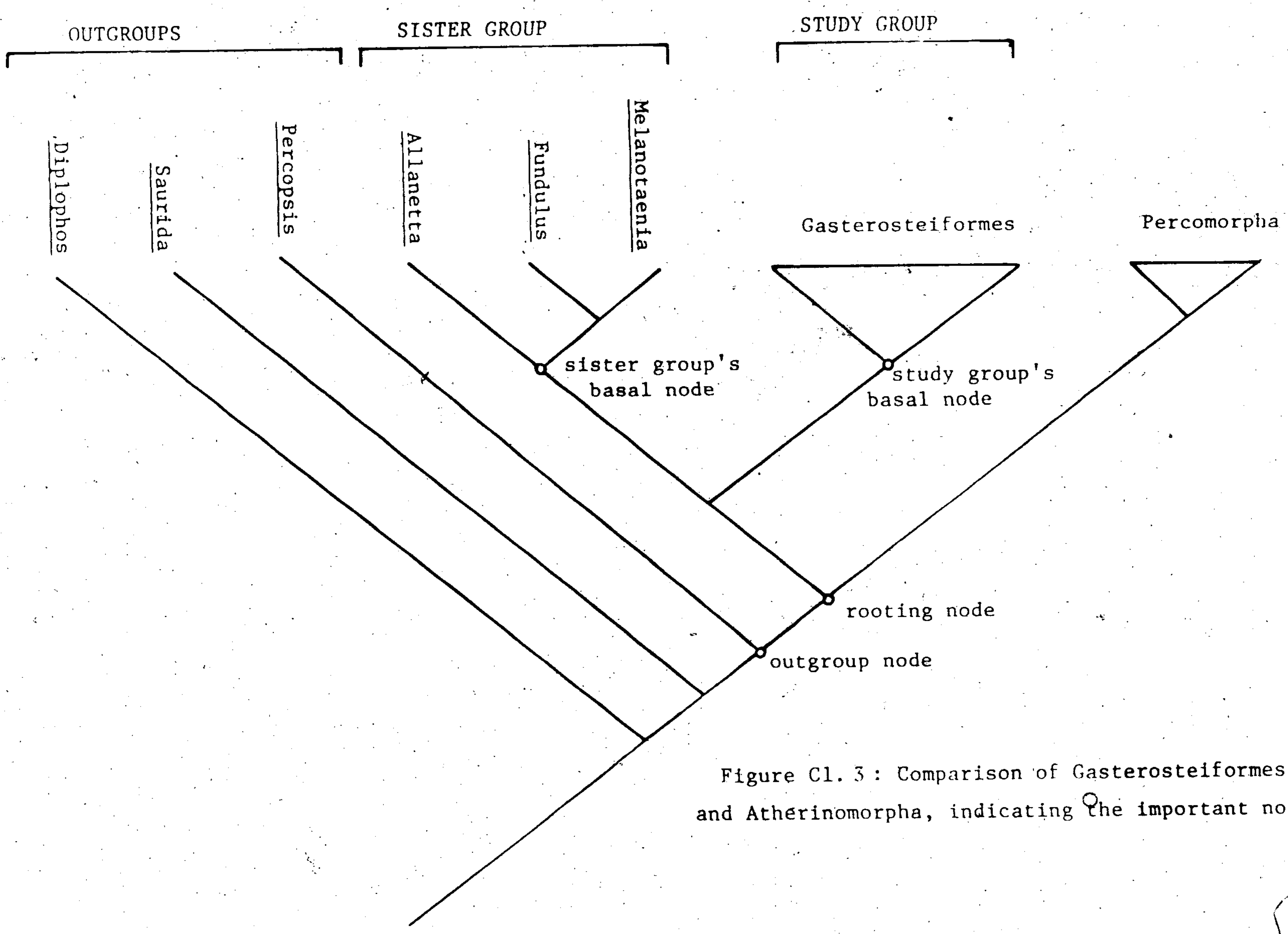


Figure Cl. 3 : Comparison of Gasterosteiformes and Atherinomorpha, indicating the important nodes.

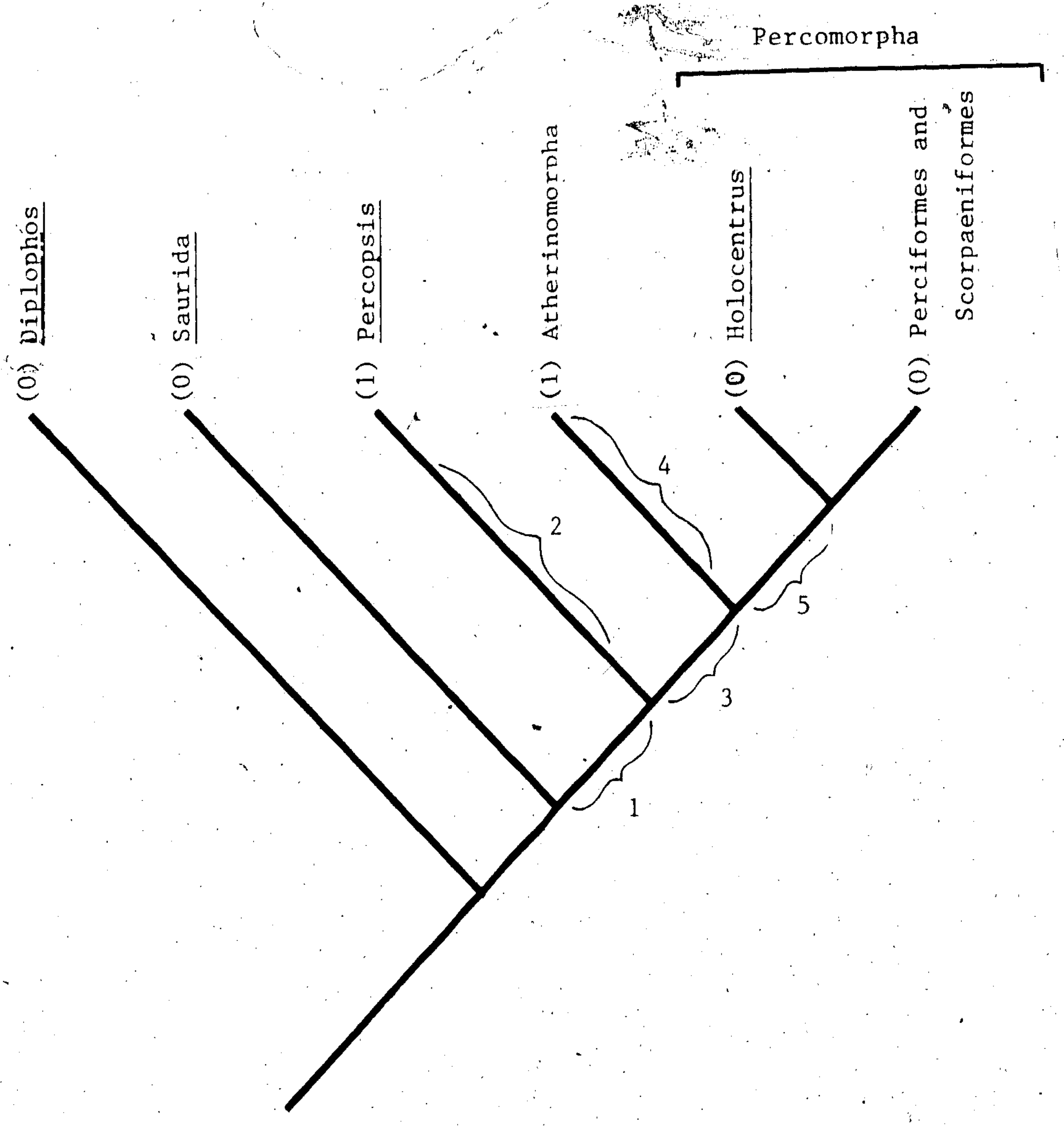


Figure C1.4 : The consistent synapomorphy criterion.

If a study group has state (1), this will be a synapomorphy directly supporting its placement attached to internode 1. The synapomorphy will be consistent with the study group's placement attached to internodes 1-5. It will not be consistent with the study group's placement within Percomorpha.

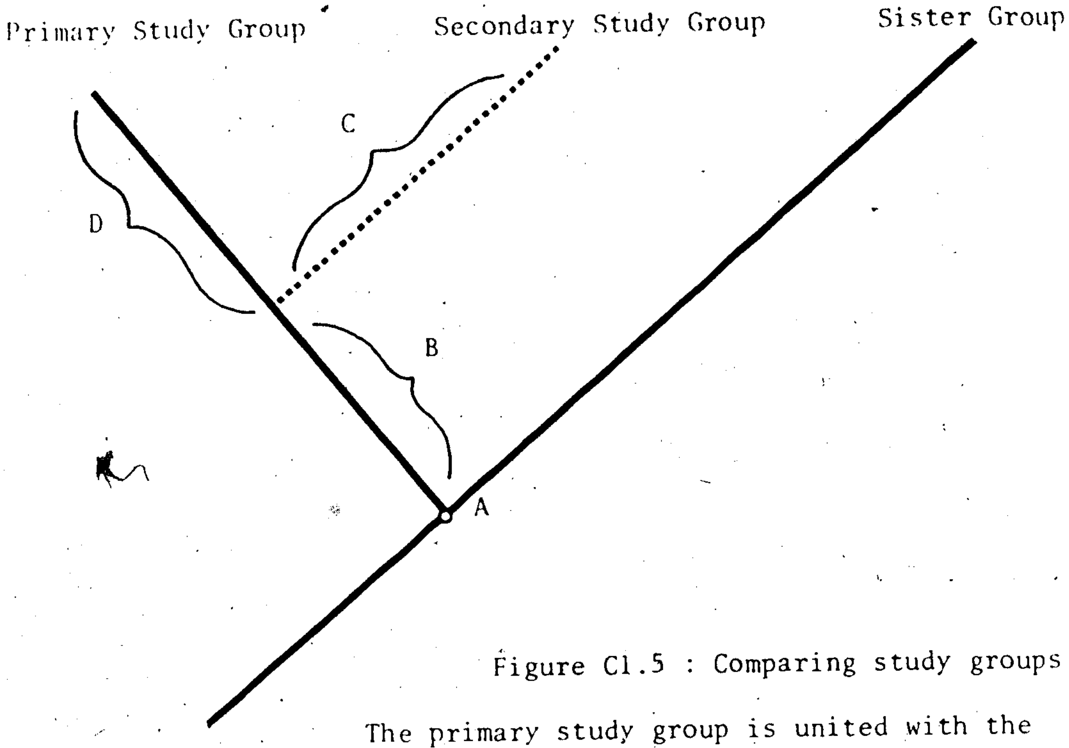


Figure C1.5 : Comparing study groups

The primary study group is united with the sister group via ancestor A. The consequences of forming a group containing the primary and secondary study groups on the cladogram are:

Number of synapomorphies (S) = steps on internode B

Rooting internode length = steps on internode C

The rooting internode length of the reciprocal comparison gives the number of steps on internode D

Figure C1.6 : Within-Gasterosteiformes Wagner trees

A. Rooted at NODE A, least advanced introduced first

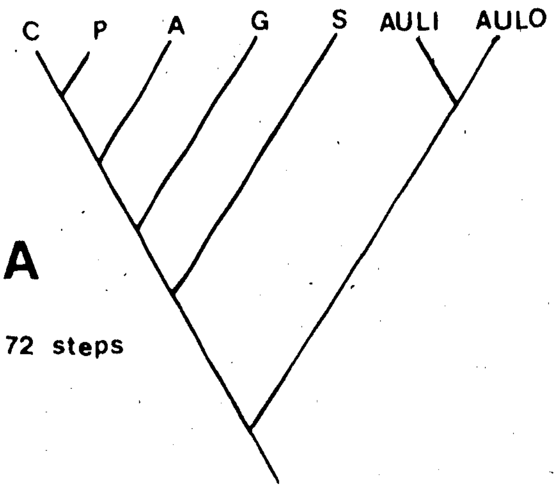
B. Rooted at NODE A, most advanced introduced first

C. Rooted at NODE B, least advanced introduced first,
rooted at NODE C, most advanced introduced first,
and Wagner analysis of complete data set (PHYSYS)

D. Rooted at NODE B, most advanced introduced first

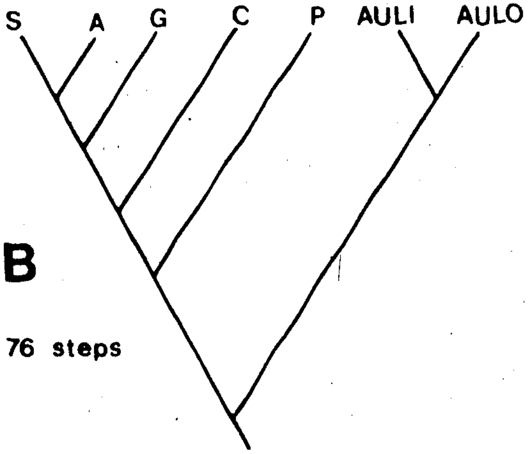
E. Rooted at NODE C, least advanced introduced first

F. Rooted at NODE D, least advanced introduced first



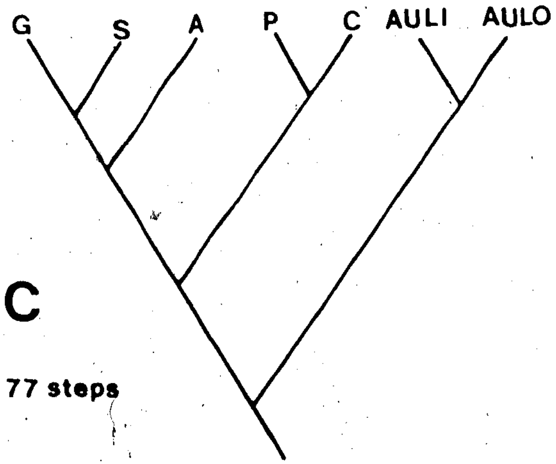
A

72 steps



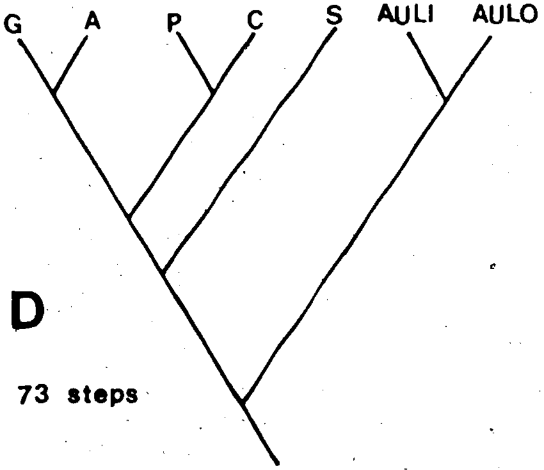
B

76 steps



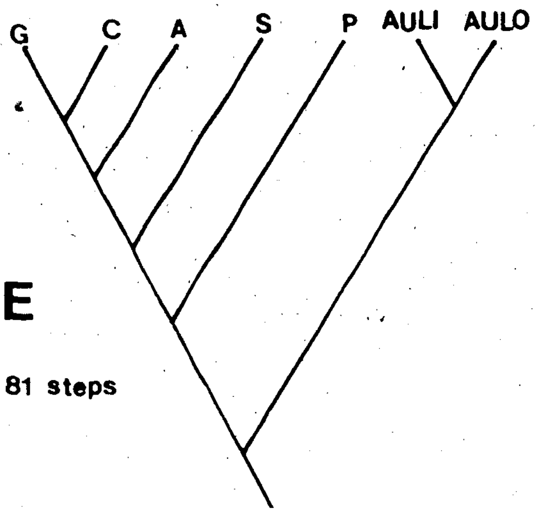
C

77 steps



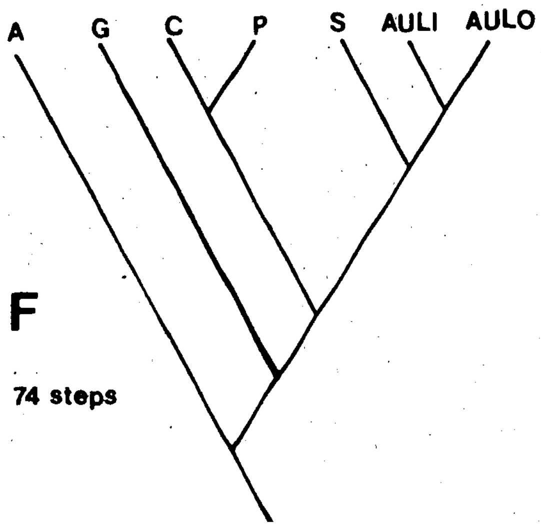
D

73 steps



E

81 steps



F

74 steps

Figure C1.7 : More within Gasterosteiformes Wagner trees

G. Rooted at NODE D, most advanced introduced first

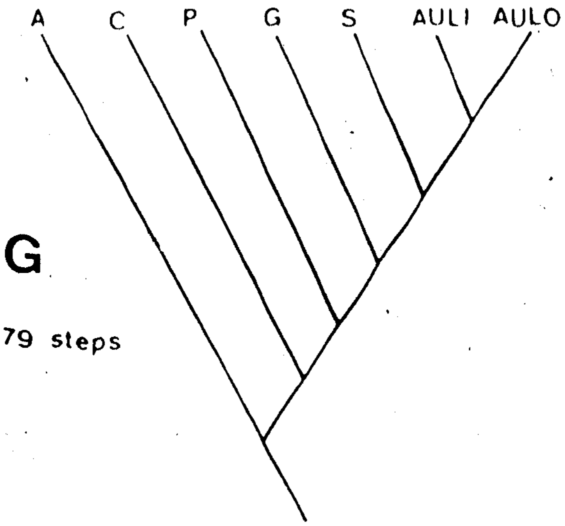
H. Rooted at NODE E, least advanced introduced first

I. Rooted at NODE E, most advanced introduced first and generated at all rootings, except NODE D, whenever *Culaea* and *Spinachia* are introduced together.

J. Rooted at NODE SC, least advanced introduced first

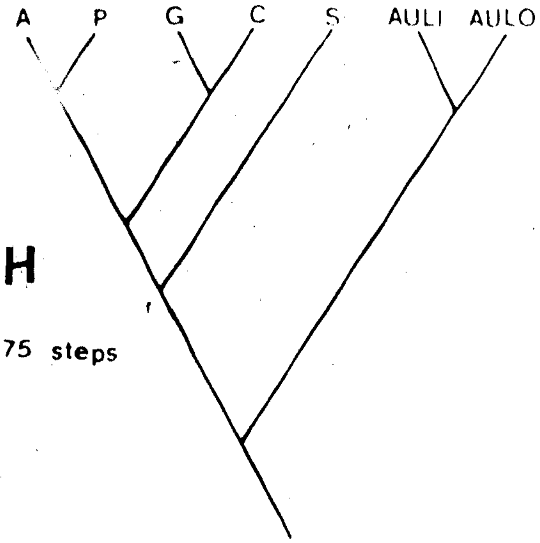
K. Rooted at NODE SC, most advanced introduced first

L. Generated by Wagner analysis of complete data set



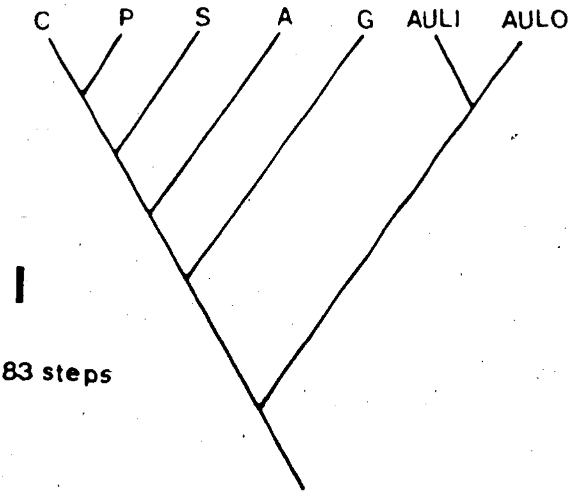
G

79 steps



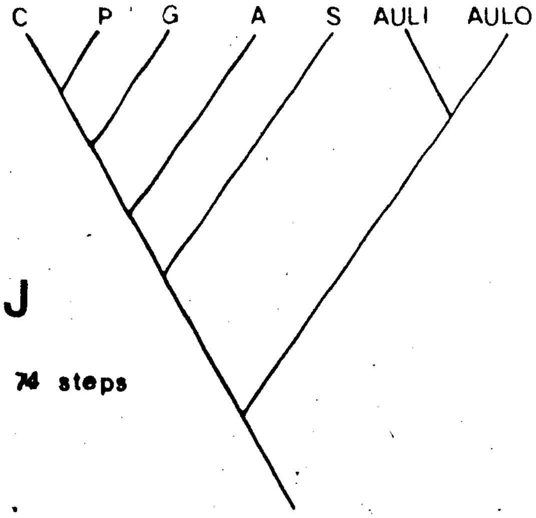
H

75 steps



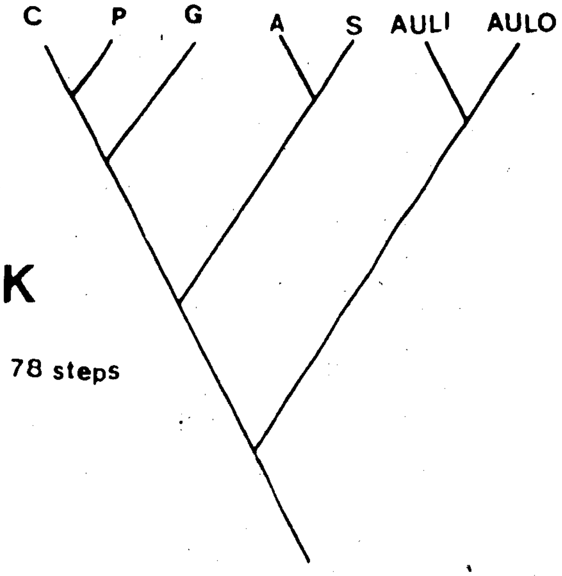
I

83 steps



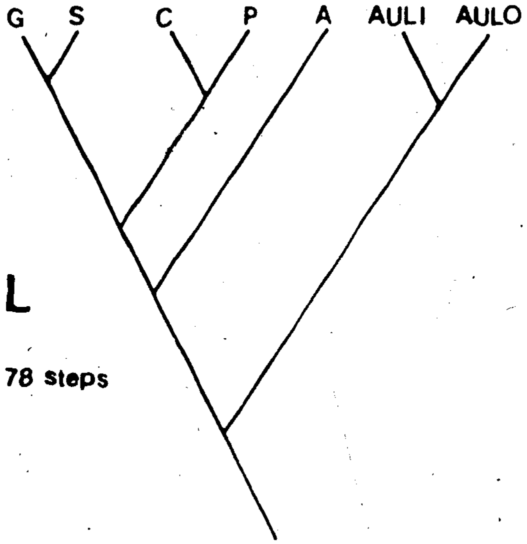
J

74 steps



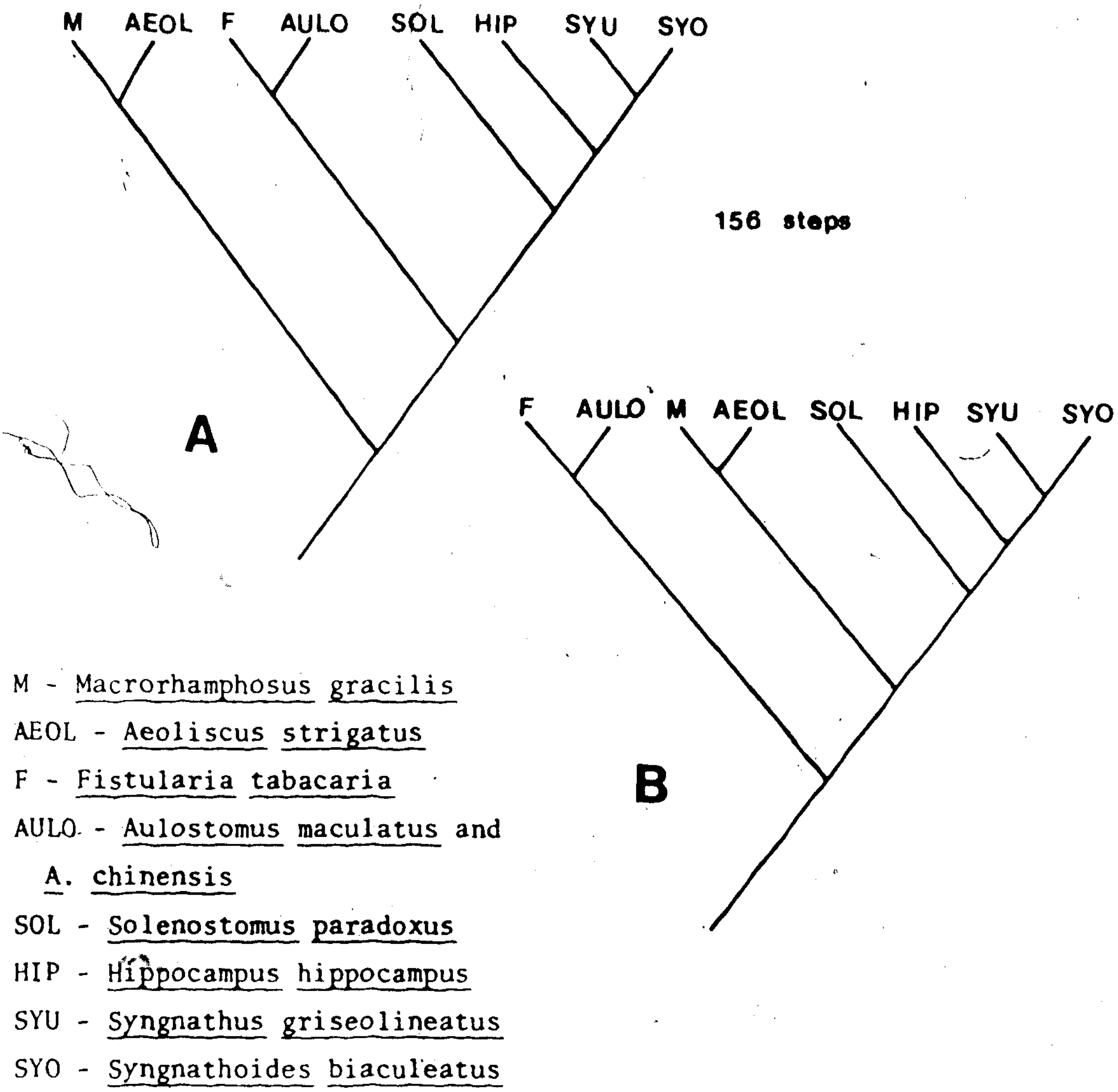
K

78 steps



L

78 steps



M - *Macrorhamphosus gracilis*
AEOL - *Aeoliscus strigatus*
F - *Fistularia tabacaria*
AULO - *Aulostomus maculatus* and *A. chinensis*
SOL - *Solenostomus paradoxus*
HIP - *Hippocampus hippocampus*
SYU - *Syngnathus griseolineatus*
SYO - *Syngnathoides biaculeatus*

Figure C1. 8 : Within-Syngnathiformes Wagner trees

A. Rooted at NODE A, least advanced ETU introduced first,
Rooted at NODE C, both orders of introduction,
Rooted at NODE D, most advanced ETU introduced first,
and Rooted at NODE E, most advanced ETU introduced first

B. Rooted at NODE A, most advanced ETU introduced first,
Rooted at NODE B, both orders of introduction,
Rooted at NODE D, least advanced ETU introduced first,
Rooted at NODE E, least advanced ETU introduced first,
Rooted at NODE SC, both orders of introduction,
and Wagner analyses of complete data set (PHYSYS)

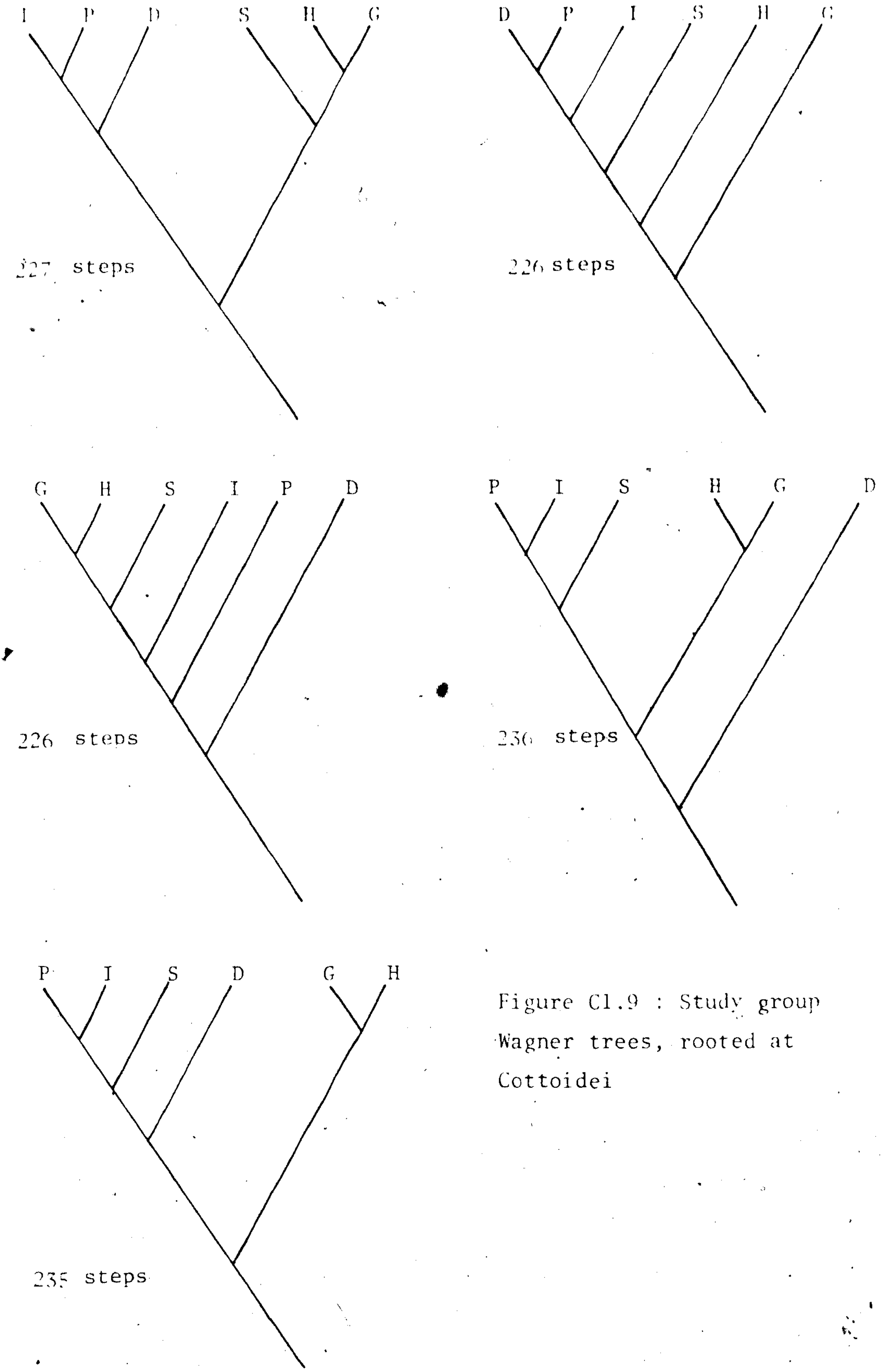


Figure C1.9 : Study group Wagner trees, rooted at Cottoidei

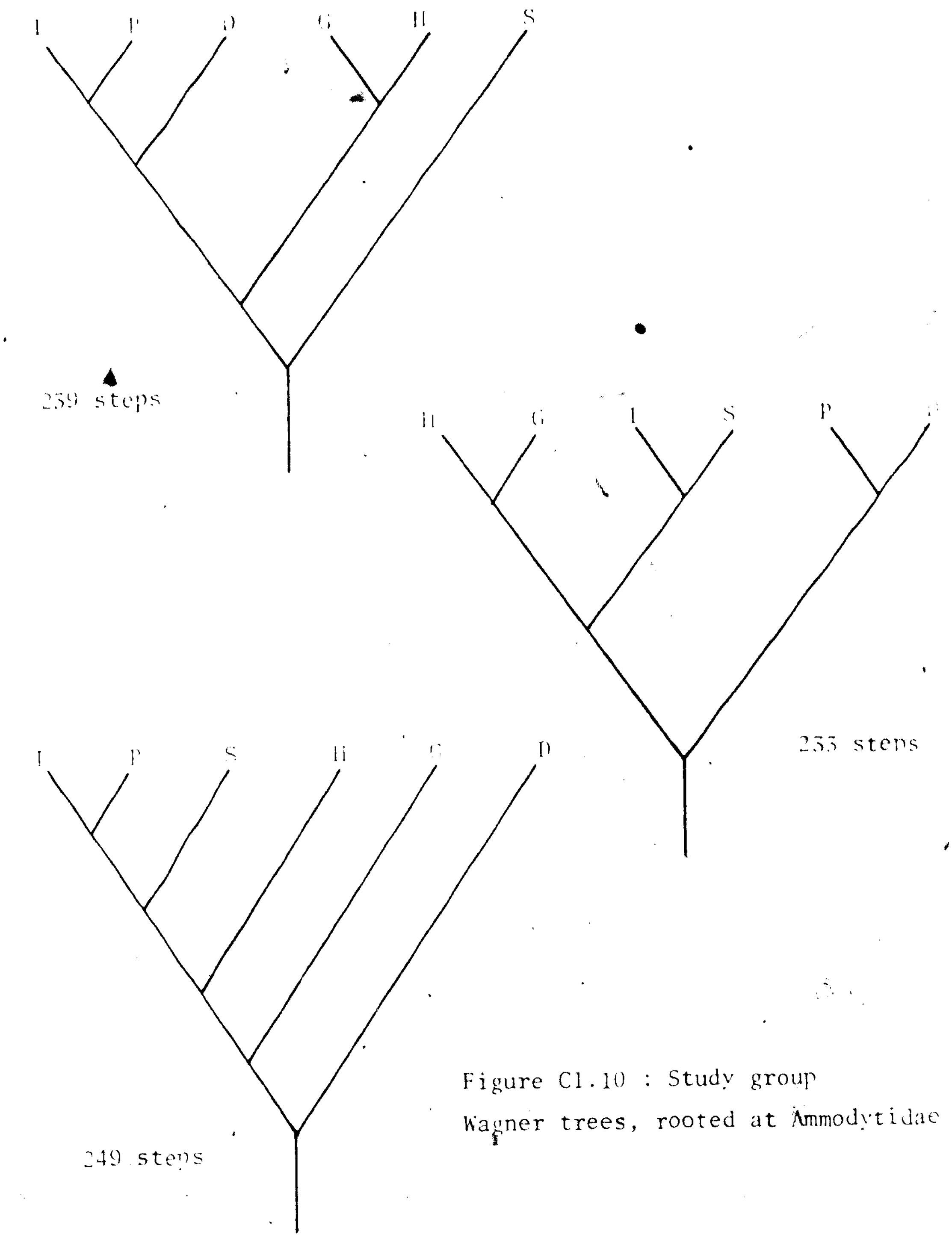


Figure C1.10 : Study group
Wagner trees, rooted at Ammodytidae

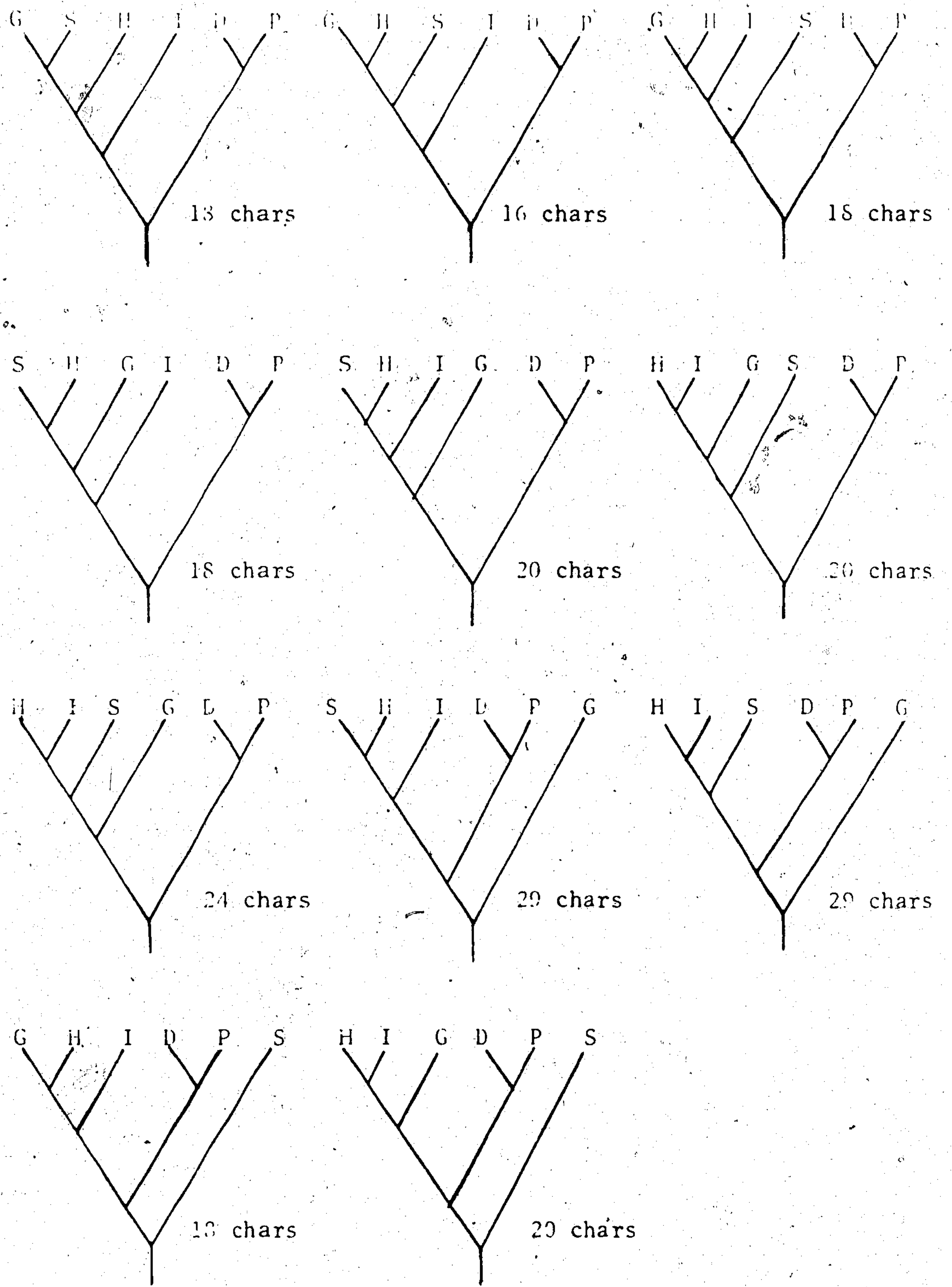


Figure C1.11 : Clique analyses of study groups, rooted at Cottoidei

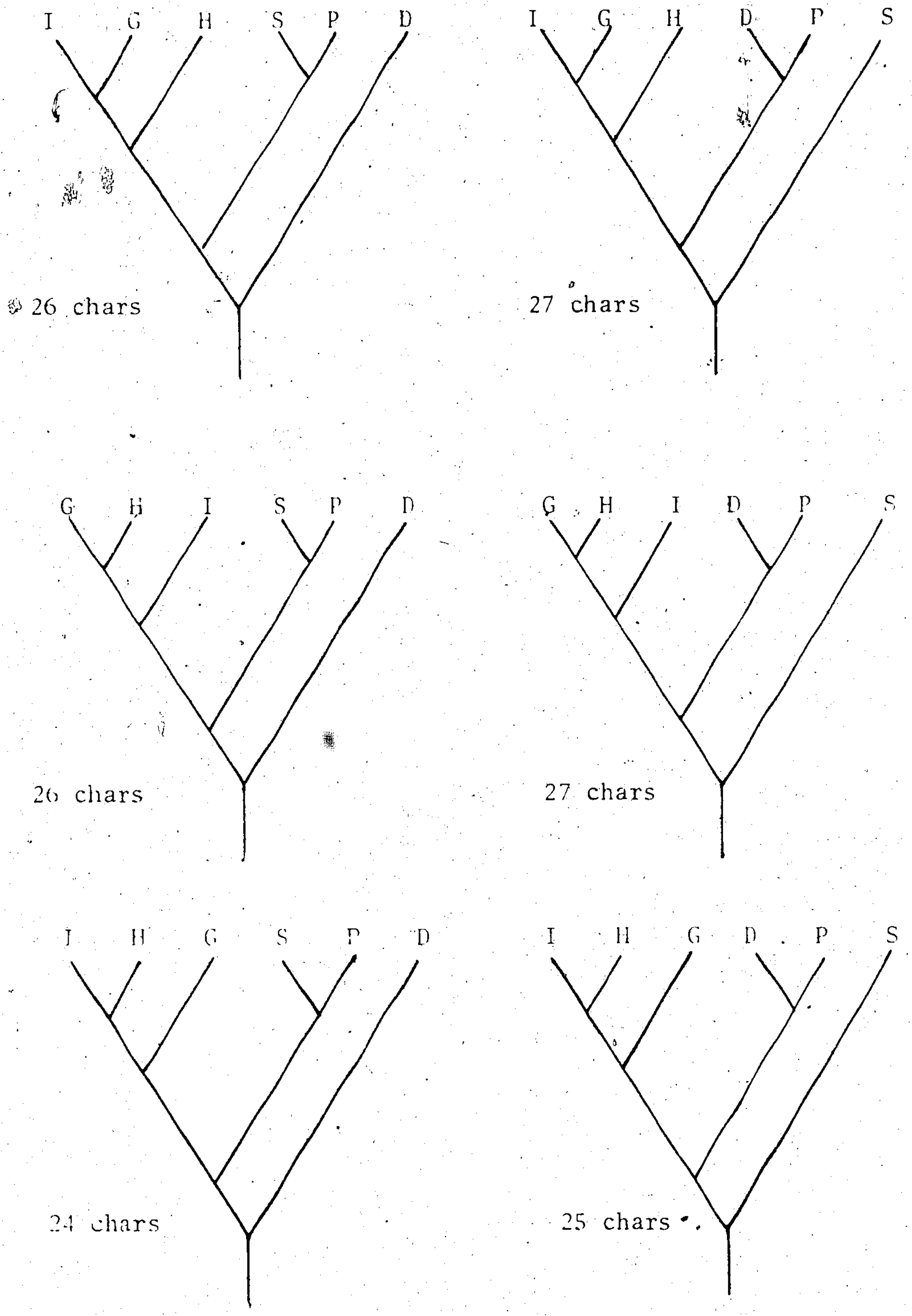


Figure C1.12 : Clique analyses of study groups, rooted at Ammodytidae

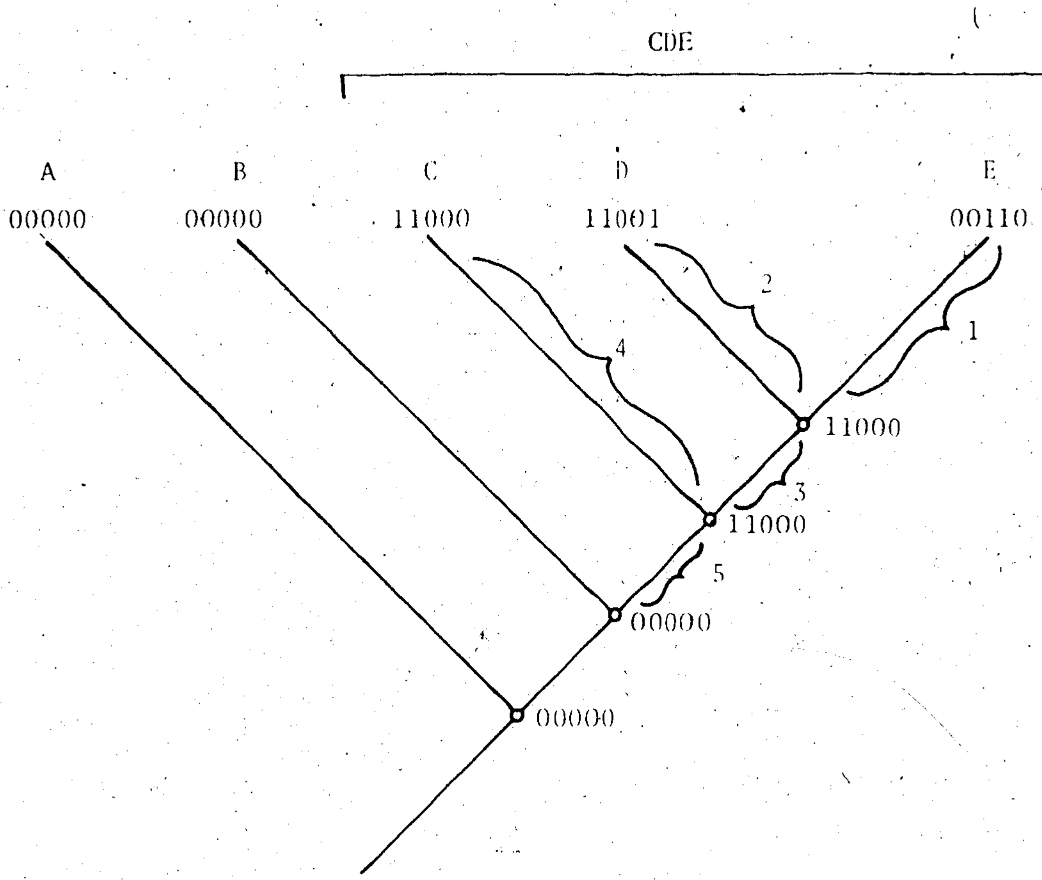
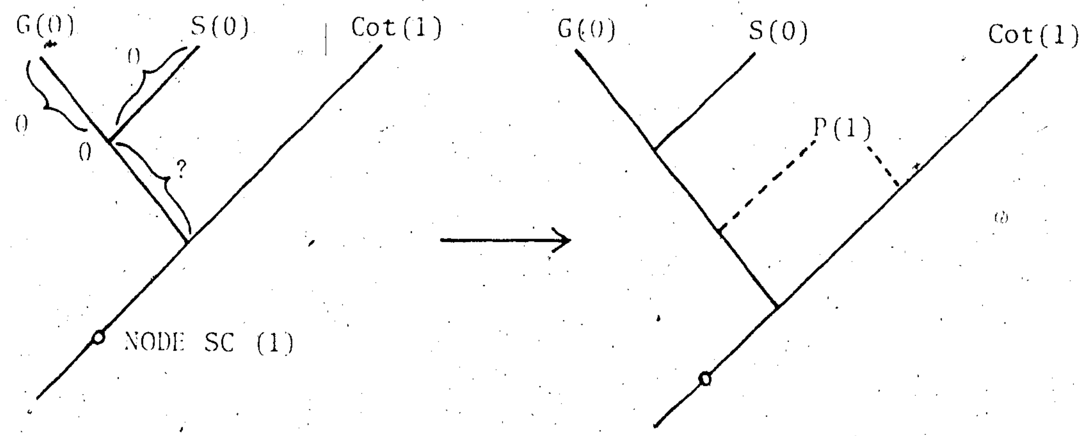


Figure C1.13 : Comparison of synapomorphy and parsimony criteria

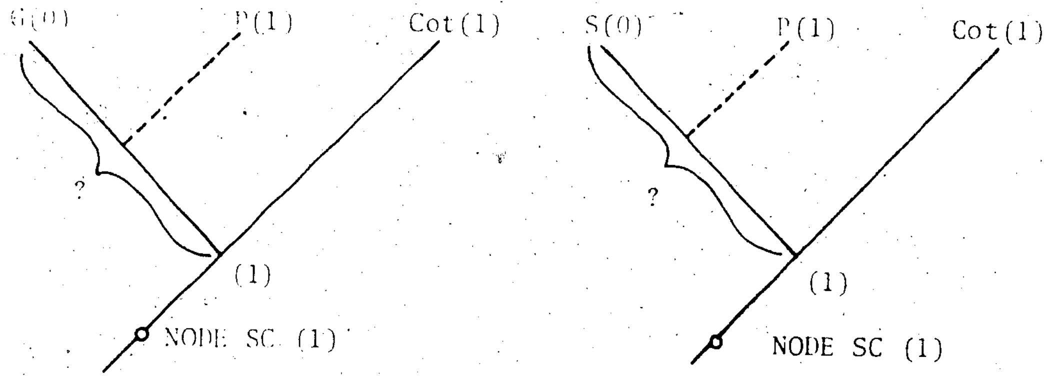
A study group identical to C would be equidistant from internodes 1-5

Total synapomorphy counts (S) would place it with CDE

Consistent synapomorphies would place it with C, D, or E



Wagner method - *Pegasus* (P) is placed by comparison with each previously hypothesized internode ; its placement with either G or S would involve a reversal.



My method - study groups are considered separately ; *Pegasus* may be placed with either without a homoplasy.

Figure C1.14 : Differences between the traditional Wagner method for estimating distances between study groups, and the method used in this thesis

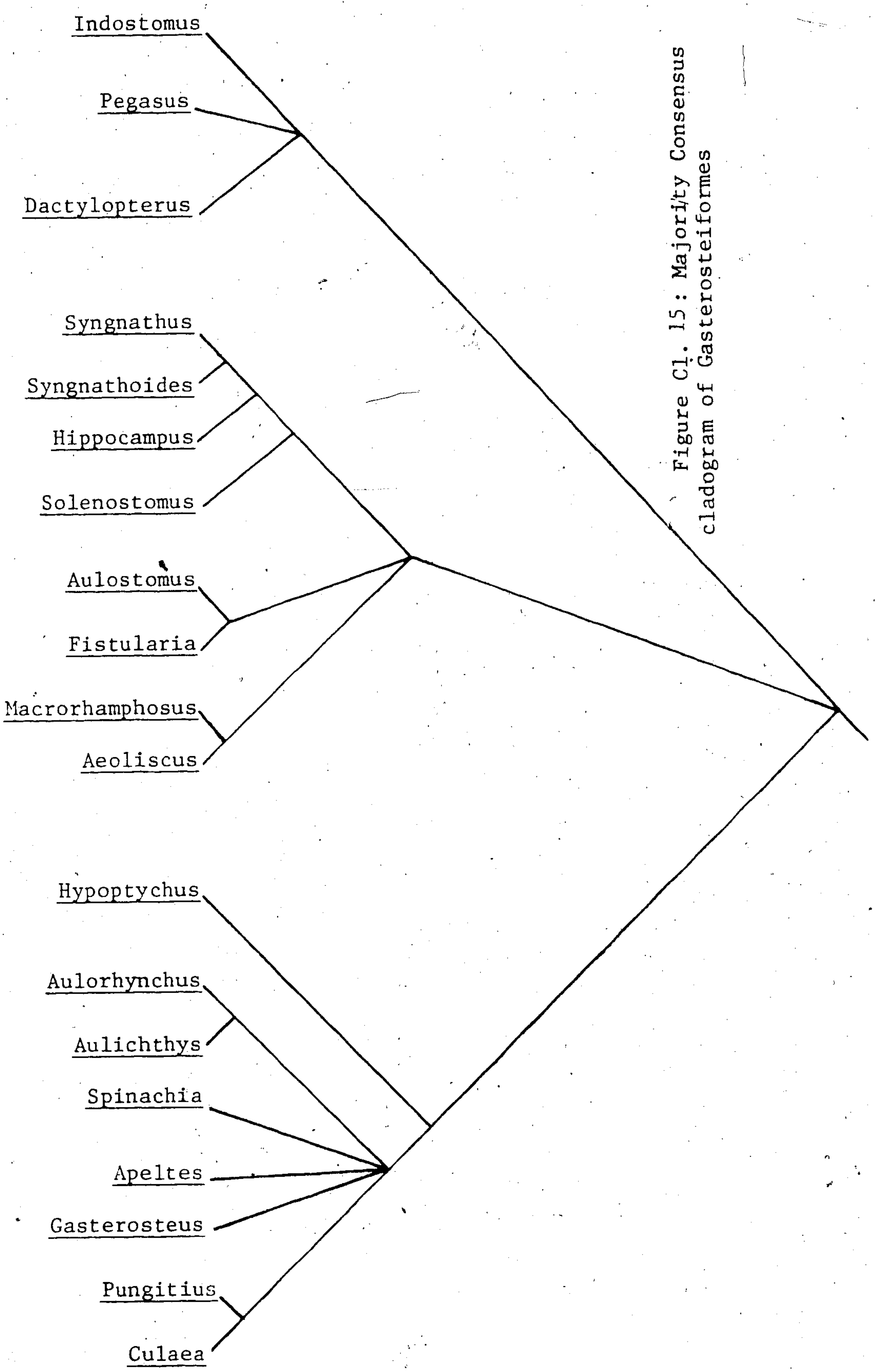


Figure Cl. 15: Majority Consensus cladogram of Gasterosteiformes

D. Evolutionary or Synthetic Systematics

Introduction

Evolutionary and phylogenetic systematics both base phylogeny reconstruction on the analysis of synapomorphy distribution patterns. Classical evolutionary systematic analyses as explained by Mayr (1969), however, recognize two kinds of information which have not yet been integrated into phylogenetic systematics as described in the previous section. These are the information about relationships contained in 'parallel apomorphies' or 'apomorphic tendencies' and the information about the amount of genetic change hypothesized to accompany different kinds of character state changes which is contained in *a priori* weighting.

Apomorphic tendencies are apomorphies which appear in a few members of a group, but not at its basal node. The common ancestor is not hypothesized to have possessed the apomorphy in question, but to have possessed a genome which could readily evolve into the apomorphy.

The inclusion of these apomorphies in phylogenetic systematics is under debate. The arguments in favor of their inclusion draw on the idea that use of such apomorphies is a practical necessity, particularly in higher-level systematics (Cantino, 1982; Saether, 1983). Those against their use point out that diagnosing a group by synapomorphies which are present in only a minority of its members reduces the amount of correct information about group members contained in the classification (Rasmussen, 1983).

A priori weighting according to hypotheses about the relative amounts of genetic change needed to produce different types of apomorphies is one of the basic methods of evolutionary systematics (Mayr, 1969). It can be interpreted either as an attempt to infer genetic similarity from synapomorphy distributions or as an attempt to determine the probability of different apomorphies' independent appearance. While some phylogeneticists have advocated *a priori* weighting on the latter grounds (Hecht and Edwards, 1976; Gosliner and Ghiselin, 1984), it has not yet been incorporated into the school of phylogenetics outlined by Wiley (1981), Eldredge and Cracraft (1980), and the others cited in the previous section. Statements criticising the use of *a priori* weighting appear in the writings of phylogeneticists (see Hennig, 1966:119-120; Gaffney, 1979: 100; Eldredge and Cracraft, 1980:66-67). I therefore view its use as a convention still distinguishing evolutionary phylogeny reconstruction from phylogenetic analysis.

By my definition an evolutionary analysis for the purpose of phylogeny reconstruction is an analysis of synapomorphy distribution in which apomorphic tendencies are considered and all apomorphies are given weights according to the supposed amount of genetic change they represent. Since both of these potential sources of phylogenetic information are being discussed by numerical phylogeneticists, the distinction I draw here between the two schools will probably prove to be ephemeral.

The more obvious differences between evolutionary and phylogenetic systematics lie in the conventions by which a phylogeny, once reconstructed, is expressed in a classification. Evolutionary systematists attempt to express information about both genealogy and similarity in the final classification. To this end they commonly remove a highly derived member of a monophyletic group into its own distinct taxon, leaving its primitive relatives in a separate **paraphyletic** taxon, one which contains some but not all of the descendants of a single ancestral species. They may also use distinctiveness measurements such as the number or hypothesized genetic significance of a taxon's distinguishing character states to determine its taxonomic rank.

Evolutionary systematics, then, is distinguished from phylogenetics by its attempts, through character weighting and a more flexible approach to delineating and ranking taxa (i.e.; recognizing paraphyletic taxa), to include information on unexpressed and primitive genetic similarities in a classification rather than restricting it to a summary of the distributions of apomorphies and/or phylogenetic relationships.

Methods

Evolutionary systematic analyses were performed in the same manner as phylogenetic analyses except for the inclusion of apomorphic tendencies and the application of *a priori* weighting.

Apomorphic Tendencies

Apomorphic tendencies are those apomorphies that appear in some members of a taxon, but not at its basal node. Their recognition introduces an element of vagueness into the analysis, for the apomorphies arising along internodes leading to Cottus, Asterotheca, Cottoidei, and Scorpaenoidei may be viewed as expressions of apomorphic tendencies characterizing Scorpaeniformes. In addition, apomorphies appearing along the internode leading to Ammodytes may be viewed as the expressions of perciform apomorphic tendencies.

Within framework groups, an apomorphy that appears in two places may be viewed either as an expression of an apomorphic tendency or as an example of convergent evolution. The latter is usually invoked when an apomorphy appears in two organisms whose close relatives are not closely related to each other, particularly when the apomorphy in question can be identified as an adaptation to similar habits or environments in the two species possessing it. I have been unable to make such evaluations of the apomorphies used in this study; with few exceptions, I cannot make meaningful statements about their adaptive values. For this reason, I have chosen to regard all multiple occurrences of apomorphies as expressions of apomorphic tendencies.

I identify apomorphic tendencies using the framework cladogram and optimization methods from the preceding section. Apomorphies that appear to have arisen independently several times are regarded as expressions of apomorphic tendencies of the smallest monophyletic framework group containing all of their appearances. This means that all of the apomorphies appearing more than once are reclassified as apomorphic tendencies of larger groups. The data set used for evolutionary systematics, then, corresponds to the apomorphies remaining after secondary phylogenetic weighting plus the hypothesized apomorphic tendencies.

Because apomorphies are regarded as distinguishing only those framework groups which contain all of their appearances, reversals do not appear in the lists of apomorphies. For this reason all of the synapomorphies that unite a study group with a framework group are consistent with the study group's relationship to all members of that framework group.

Apomorphic tendencies of the study groups were identified with reference to the within-study group cladograms presented in Figures Ev. 1-2. The two families of Gasterosteiformes are regarded as sister groups, with Spinachia a probable intermediate between them. Two possibilities are presented for interrelationships of syngnathiform subgroups; in one Centriscoidei is the most primitive group, and in the other Aulostomoidei is the most primitive group (Fig. Ev.2).

Three kinds of apomorphic tendencies were distinguished in these study groups. Type 1 were apomorphies that might have been present in the common ancestor of the group; these are those which appear in most or all of the members of one of the subgroups arising from the basal node (Fig. Ev.1, characters A-C; Fig. Ev.2, characters A-B). Type 2 apomorphic tendencies appear once within the study group (Fig. Ev.1, character D; Fig. Ev.2, characters C-D). Type 3 apomorphic tendencies appear independently in members of more than one subgroup (Fig. Ev.1, character E; Fig. Ev.2, character E). These types of apomorphic tendencies are indicated in the data tables by superscripts (e.g. G^1, S^2).

A priori Weighting

Since I know little about the adaptive values of the characters used, my *a priori* weighting of apomorphies is primarily based on the two criteria of their distributions and whether they represent gain or loss of a character.

First, apomorphies that are present in a a majority of the members of the groups they distinguish are given higher weight than those which are present in only a few members, on the reasoning that since they do not appear to have undergone much reversal in the groups they distinguish they are likely to also persist in other species which have inherited them from the common ancestor.

This means that shared apomorphic tendencies are of less weight than apomorphies found in enough members of a group to be attributed to its ancestral species. Among the apomorphic tendencies found in the study groups type 1 are most highly weighted, since these may be attributed to the ancestral species. Type 3 are given the next highest weight, since their widespread occurrence within the study groups indicates that they are expressions of tendencies shared by all study group members (and, presumably, by the ancestral species). Type 2 apomorphic tendencies are the least reliable, appearing only once within the study group. They are given the least weight, since there is little justification for inferring a tendency of the group from an apomorphy found in only one part of it.

Weighting according to whether the apomorphy represents a loss or a gain of structures is based on the reasoning that since a large number of genetic changes may interfere with a gene's expression, the loss of structures in two species need not indicate that they have undergone the same genetic change. The acquisition or modification of a character, however, is more likely to be associated with a specific change in the genome. Acquisitions are therefore more likely to be homologous to one another than are losses. Apomorphies involving the loss of characters, then, are given less weight than those involving their acquisition.

Results

Comparison between study groups and framework groups

The apomorphies and apomorphic tendencies distinguishing framework groups appear in Table Ev.1, along with the study groups sharing them. The numbers of synapomorphies and shared apomorphic tendencies appear in Table Ev.2. Synapomorphy counts place all study groups within (*Percopsis* + Acanthopterygii), Acanthopterygii, and Scorpaeniformes. Numbers of consistent synapomorphies and shared apomorphic tendencies support relations between the study groups and *Cottus*.

Gasterosteiformes

Gasterosteiformes belong with or within (*Percopsis* + Acanthopterygii) on the basis of synapomorphy counts. Only three of their synapomorphies with (*Percopsis* + Acanthopterygii) and four of the apomorphic tendencies shared by both groups are losses. All four of the apomorphies of (*Percopsis* + Acanthopterygii) which are found in all its members are also found in Gasterosteiformes. These are:

1. Exoccipital condyles are present
2. Quadrates have distinct shafts
3. Pelvic fins are thoracic, articulating with ventral projections from the pelvic plates
4. Precaudal neural arches are pierced by lateral foramina.

The first of these appears in only one member of Gasterosteiformes, but the second appears in both families. The last two apomorphies appear at the basal node of Gasterosteiformes.

Several of the apomorphies and apomorphic tendencies of (Percopsis + Acanthopterygii) appear in members of all its major subgroups - Percopsis, Atherinomorpha, Holocentrus, Scorpaeniformes, and Perciformes. Eleven of these are also found in Gasterosteiformes. These are:

1. Supraoccipital and frontals are not separated
2. Head length is more than 22% of standard length
3. Dentaries have elevated coronoid processes
4. First basibranchials are deeper than succeeding basibranchials
5. Fifth ceratobranchials are expanded laterally
6. Third actinosts are attached to coracoids
7. Soft dorsal has anterior spine(s)
8. Anal has anterior spine(s)
9. Proximal anal pterygiophores have flanges
10. Orbit length is more than 30% of head length
11. Frontal length is more than 40% of head length.

All except three of these are found at the basal node of Gasterosteiformes.

Gasterosteiformes share many fewer apomorphies with Acanthopterygii than with (Percopsis + Acanthopterygii), but share many more apomorphic tendencies with Acanthopterygii. Three of the synapomorphies and eight of the shared apomorphic tendencies are loss characters. None of the remaining synapomorphies and shared apomorphic tendencies are present in all the members of Acanthopterygii examined, and only three are found in all the subgroups of Acanthopterygii. These are:

1. Urohyal has ventrolateral flanges
2. Dentaries have anterolateral foramina
3. Pelvic plates are joined together by a median suture.

The first and last of these are found at the basal node of Gasterosteiformes, and the dentary anterolateral foramina have apparently arisen at least twice within Gasterosteiformes.

Within Acanthopterygii, Gasterosteiformes share four or more apomorphies and apomorphic tendencies with Scorpaeniformes, Scorpaenoidei, and Cottus. All of the similarities with Scorpaeniformes are apomorphic tendencies. They are:

1. Lateral ethmoids bear anterolateral extensions
2. Lateral ethmoid ventromedial projections have posterior processes
3. Central pterygiophores supporting the dorsal spines are flattened and expanded into horizontal plates, the distal pterygiophores fused to their dorsal surfaces
4. Parhypural does not support principal caudal rays.

The last of these is a questionable similarity, since its presence may be due either to modifications of the caudal fin ray - parhypural relationship or to loss of a distinct parhypural. The latter case obtains in Gasterosteiformes.

The fusion of dorsal spine supports is found in several groups of perciforms, but differs from that in Gasterosteiformes and Asterotheca. In Triacanthodidae and Triacanthidae the medial and distal pterygiophores supporting the dorsal spine appear fused (Tyler, 1968), but in both they form a different type of articulation with the spines. In the former, spines articulate with a process which encloses a complete foramen. The dorsal rim of this foramen passes through a hole in the spine, so that the pterygiophore and spine are locked together like two links of a chain. In the latter only the posterior portion of the process remains, again passing through a hole in the spine. Tyler (1970) describes laterally expanded pterygiophores supporting the spines in Acanthuridae. These plates superficially resemble those supporting the spines of Gasterosteiformes, but in Acanthuridae the expanded distal pterygiophores form the posterior portion of each plate. Examination of the transition between pterygiophores supporting the dorsal spines and soft rays of Gasterosteiformes reveals that the cylindrical 'core' of the medial pterygiophore supporting the last spine extends to the posterior edge of the spine-supporting plate, articulating with the distal pterygiophore supporting the first soft ray. This distal pterygiophore lies at the center of the plate supporting the first soft ray (Fig. L3). This indicates that if expanded distal pterygiophores form any portion of the gasterosteiform pterygiophore plates, they would be more likely to form the anterior portions. This may be the case, for gasterosteiform dorsal spines articulate at the midpoint of each plate as opposed to those of Acanthuridae, which articulate at its anterior edge.

Comparison of gasterosteiform dorsal spine supports and those of Asterotheca, the scorpaeniform which best exhibits the fused pterygiophores, further support this hypothesis of the anterior placement of distal pterygiophores, for the anterior dorsal rays of Asterotheca articulate anteriorly with small, laterally expanded plates which may represent distal pterygiophores. The fused dorsal supports in Gasterosteiformes and Asterotheca, then, are distinguished by their expansion anterior to the base of the spine and by the extension of the central pterygiophores to their posterior margins.

Gasterosteiformes share one apomorphy with Scorpaenoidei, the relatively long pelvic plates. The three apomorphic tendencies they share with Scorpaenoidei are all losses.

Gasterosteiformes and Cottus are united by the five synapomorphies:

1. Trigeminofacialis anterior foramina are not completely surrounded by the prootics
2. Palatine heads bear lateral projections
3. Separate endopterygoids are absent
4. Hypobranchials are flattened
5. First uroneural is fused to the dorsal hypurals.

The pterygoid and uroneural - hypural fusions may be viewed as either fusion or loss characters. In the case of the former fusion seems the more likely explanation, since the single anterior pterygoid contains elements filling the positions filled in other fishes by the ecto- and endopterygoids (bordering the anterior and dorsal margins of the quadrates, respectively). The endo- and ectopterygoids appear to be fused in both *Asterotheca* and *Cottus*, although in the former the ectopterygoids may be instead fused to the palatine. In *Cottus* (Fig. E2) the pterygoids are triangular plates, the bases of which are slightly indented in a manner reminescent of the trifurcate pterygoids in Gasterosteiformes (Fig. E4). The posterior portions of the compound pterygoids in *Cottus* do not extend for the full length of the quadrates as in Gasterosteiformes, nor do they touch the symplectic flanges; indeed, the presence in Gasterosteiformes of anterodorsal symplectic flanges extending to the compound pterygoids and separating the quadrates from the metaptergoids appears to be the single major difference between cottoid and gasterosteiform suspensoria.

The anterior trigeminofacialis foramina in Gasterosteidae are bordered posteriorly by the prootics and anteriorly by the overlapping parasphenoid and frontal processes (Fig. B3,A). In Aulorhynchidae the foramina are larger and are laterally bounded by the sphenotics (Fig. B3,B), and in *Cottus* a similar situation exists, with the difference that the frontals and parasphenoid of *Cottus* do not meet, the gaps between them being bridged by the pterosphenoids, which form the anterior margins of the trigeminofacialis foramina (Fig. B2). The pterosphenoids are very similar in shape, size, and position to the medial postorbital processes of the frontals in Gasterosteiformes, and Banister (1967) described separate pterosphenoids in the position of these processes in Aulorhynchidae. Although I did not observe separate pterosphenoids in any Gasterosteiformes, it seems reasonable to hypothesize that the state in Aulorhynchidae evolved from one similar to that in *Cottus*, by fusion of the frontals and pterosphenoids.

The palatine lateral extensions are rudimentary in *Cottus* and Aulorhynchidae, consisting of simple lateral flanges (Figs. E2, E5), but in Gasterosteidae they are developed into backward-pointing hooks which extend ventrolaterally to contact the anterior ends of the lachrymals (Figs. A4, E4).

Gasterosteiformes share very few apomorphies with acanthopterygian groups other than Scorpaeniformes. They resemble Atherinomorpha in:

1. Premaxillae do not bear articular processes
2. Dermopterotics do not bear lateral canals
3. Pelvic plates bear ascending processes.

The first two of these synapomorphies represent losses. The last, although it does not appear in all atherinomorphs, appears to be unique to this series. Ascending processes appear on the pelvic plates of many members of Exocoetidae, including some in which they bend posteriorly to closely resemble the processes in Spinachia and Aulorhynchidae (Figs. K4-5). However, the pelvic plates in exocoetids are relatively delicate and are not ornamented, while those of Gasterosteiformes are usually heavy and appear to be at least partly formed from dermal elements. In Gasterosteus the ascending process is functionally involved in the supportive and protective functions of the lateral scutes (Reimchen, 1983) and is almost indistinguishable from them in structure.

Gasterosteiformes resemble Perciformes in their possession of dentaries touching the angulars and of quadrates whose shafts make up over half their lengths. The second of these has apparently arisen at least twice within Gasterosteiformes, appearing in Pungitius, Culaea, Spinachia, and Aulichthys. It is found within both long-snouted and short-snouted members of the order.

Syngnathiformes

Syngnathiformes, like Gasterosteiformes, show strong affinities with (Percopsis + Acanthopterygii) on the basis of synapomorphies and with Acanthopterygii on the basis of shared apomorphic tendencies. Three of their synapomorphies with (Percopsis + Acanthopterygii) and three of the shared apomorphic tendencies are losses. Of the remaining ones, three are found in all members of (Percopsis + Acanthopterygii). These are:

1. Exoccipital condyles are present

2. Quadrates have distinct shafts
3. Precaudal neural arches are pierced by lateral foramina.

The second of these has apparently arisen independently in Syngnathidae.

Eight synapomorpies and shared apomorphic tendencies with Syngnathiformes are found in all major subgroups of (Percopsis + Acanthopterygii). These are:

1. Supraoccipital and frontals are in contact
2. Head length is more than [illegible]% of standard length
3. Frontal length is more than 40% of head length
4. Dentaries have elevated coronoid processes
5. Fifth ceratobranchials are expanded laterally
6. Third actinosts are attached to coracoids
7. Anal has anterior spine(s)
8. Proximal anal pterygiophores bear flanges.

One of these, the spinous anal, is found only in one member of Syngnathiformes (Macrorhamphosus).

Three of the apomorphies shared by Syngnathiformes and Acanthopterygii are losses, as are seven of their shared apomorphic tendencies. Of the remainder only one is found in all the major subgroups of Acanthopterygii; this is the presence of anterolateral foramina in the dentaries, and it appears to have arisen independently within Syngnathiformes.

Within Acanthopterygii, Syngnathiformes share the most apomorphies and apomorphic tendencies with Scorpaeniformes and Ammodytes. One of the apomorphic tendencies shared with Scorpaeniformes is the loss of epipleural ribs; the other apomorphies and apomorphic tendencies are:

1. Hypobranchials bear anterior processes
2. Lateral ethmoids have anterolateral extensions
3. Medial projections of each lateral ethmoid are fused
4. Lateral ethmoid ventromedial projections bear posterior processes
5. Scapulae are reduced to the size of actinosts

6. Central and distal pterygiophores supporting the dorsal spines are fused.

The anterior processes on the hypobranchials of Macrorhamphosus, the syngnathiform in which they are best developed (Fig. 13), are better-developed than those of the scorpaeniforms examined. Those of the third hypobranchials are flattened and laterally expanded, considerably different from those in Scorpaeniformes from which, however, they might have been derived.

The fusion of the medial projections of each lateral ethmoid into a cube- or funnel-shaped structure opening medially appears to be associated with the development of a strong ethmoid region in which the nasals, ethmoids, and frontals are solidly attached to one another. The lateral ethmoids of fishes with this type of ethmoid region are strongly sutured to the frontals and extend onto the orbit roofs and often into the interorbital septum. They usually have expanded lateral faces, firmly attached to the frontals and nasals. In the framework groups I examined, this type of ethmoid region appears only within Scorpaeniformes. I was unable to determine whether these characters appear in other fishes with highly fused snouts.

The scapulae in Syngnathidae, Solenostomus, and Aulostomoidei are reduced to the size of actinosts, making the pectoral skeletons appear to have five free actinosts (Figs. J6-7). This trend is similar to that seen in Liparis and illustrated from three cottoids by Regan (1913), although the scapulae and actinosts of scorpaeniformes are flat, rounded plates, while those of Syngnathiformes are hourglass-shaped. The presence of scapular reduction in both armored and unarmored members of Syngnathiformes and in the unarmored Liparis indicates that it is not necessarily related to the development of dermal scutes which provide external support for the pectoral skeleton. The reduction is more extreme, however, in the armored Syngnathidae, in which the scapulae lose all contact with the cleithra.

The anterior dorsal spines of Aulostomus are supported by fused proximal, medial, and distal pterygiophores, but these do not resemble those of Gasterosteiformes or Scorpaeniformes. The central pterygiophores are not expanded laterally and the proximal pterygiophores are strongly compressed and expanded antero-posteriorly to resemble wide vertical blades of bone.

Syngnathiformes in addition share four apomorphies with Cottus. These are:

1. Trigeminofacialis anterior foramina are not completely surrounded by the prootics
2. Separate endopterygoids are absent
3. Hypobranchials are flattened
4. Uroneurals are fused to dorsal hypurals.

The trigeminofacialis anterior foramina of Syngnathoides are incomplete as are those of Solegnathus , a genus not examined in detail but notable for also sharing the fusion of pterosphenoid and frontal found in Gasterosteiformes. The ecto- and endopterygoids are fused in both members of Aulostomoidae examined (Fig. E7), the composite pterygoids of both lying along the anterior and dorsal margins of the quadrates. In neither genus do the symplectics interpose between the quadrates and metapterygoids, although symplectic flanges are developed.

Syngnathiformes share two apomorphic tendencies with Perciformes; the interopercula with expanded anterior ends and the shortened haemal laminae. Within Perciformes they share four apomorphies with Ammodytes, one of which is a loss of dentary teeth. The other three are:

1. Quadrate shafts make up over half of the quadrate lengths
2. Cleithra do not meet in an anterior symphysis
3. Body depth is less than 10% of standard length.

The second of these has apparently evolved independently in Fistularia and Syngnathidae. In the latter, it may be a side effect of general reduction in the pectoral skeleton. The third is an effect of elongation, appearing in many fishes.

Indostomus

Indostomus, like all the other study groups, shares more apomorphies with (Percopsis + Acanthopterygii) than with any other framework groups. Only two (quadrates with distinct shafts and precaudal neural arches pierced by lateral foramina) are found in all members of (Percopsis + Acanthopterygii). Five more are found within all major subgroups of (Percopsis + Acanthopterygii). These are:

1. Supraoccipital and frontals are in contact
2. Fifth ceratobranchials are expanded laterally
3. Third actinosts are attached to coracoids
4. Proximal anal pterygiophores bear flanges
5. Frontal length is more than 40% of head length.

None of the synapomorphies of Indostomus and Acanthopterygii are found in all members of Acanthopterygii or in all of its major subgroups. Six of the 21 synapomorphies and shared apomorphic tendencies are losses. Within Acanthopterygii, Indostomus shares the largest number of apomorphic tendencies with Scorpaeniformes and the largest number of apomorphies with Cottus. It is united with Scorpaeniformes by:

1. Hypobranchials bear anterior processes
2. Medial projections of each lateral ethmoid are fused
3. Scapulae are reduced to the size of actinosts
4. Scapulae are fused to first actinosts
5. Central pterygiophores supporting the dorsal spines are flattened and fused to distal pterygiophores.

Indostomus shows most of the characters described above as associated with fusion and strengthening of the ethmoid region. Its pectoral girdle (Fig. J9) is also characterized by fusion. Not only are the scapulae and first actinosts apparently fused but the complexes thus formed are fused dorsally to the cleithra, which are themselves fused posteriorly and ventrally to external scutes which form a hard shield over the entire pectoral girdle. A similar situation obtains in Asterotheca (Fig. J2,B), with the exception of the absence of a lateral scute covering the pectoral girdle, and in Cottus (Fig. J2,A) what may be viewed as an intermediate situation is seen; the scapula bears a reduced first actinost closely applied to its surface. Regan (1913) illustrates pectoral skeletons with only three free actinosts from members of the unarmored scorpaeniform family Synanceidae.

The synapomorphies uniting Indostomus and Cottus are:

1. Trigeminofacialis anterior foramina are not completely surrounded by the prootics
2. Separate endopterygoids are absent
3. Uroneural is fused to the dorsal hypurals.

The trigeminofacialis anterior foramina in Indostomus (Fig. B9) differ from those in Gasterosteiformes and Syngnathiformes and from those of Cottus in the exclusion of the parasphenoid from their margins. The parasphenoid in Indostomus has no lateral processes and as a result the entire anterior margins of the trigeminofacialis foramina are formed by the pterosphenoids. The pterosphenoids are almost square, in contrast to the triangular pterosphenoids of Syngnathiformes and Cottus. Banister (1970) illustrates the foramina with the sphenotics forming their lateral margins but the sphenotics are not distinctly separated from the prootics in my specimens, so I am unable to assess whether Indostomus resembles Cottus in this aspect.

Indostomus is not listed as sharing fusion of the ecto- and endopterygoids with Cottus simply because the single bones which form the pterygoid struts in Indostomus (Fig. E9) contain no components along the dorsal borders of the quadrates, and therefore can be interpreted as ectopterygoids. They may well be composite pterygoids, however, and the possibility must be borne in mind.

Hypoptychus

Hypoptychus shares very few apomorphies or apomorphic tendencies with any framework groups other than (Percopsis + Acanthopterygii) and Acanthopterygii. It shares three of the apomorphies found in all members of (Percopsis + Acanthopterygii), to wit:

1. Exoccipital condyles are present
2. Quadrates have distinct shafts
3. Precaudal neural arches are pierced by lateral foramina.

Six more apomorphies present in all major subgroups of (Percopsis + Acanthopterygii) are present in Hypoptychus. These are:

1. Supraoccipital and frontals are in contact
2. First basibranchial is deeper than succeeding basibranchials
3. Third actinosts are attached to coracoids
4. Proximal anal pterygiophores bear flanges
5. Frontal length is more than 40% of head length.

Only one of the Hypoptychus - Acanthopterygii synapomorphies, the urohyal with ventrolateral flanges, is found in all subgroups of Acanthopterygii. Within Acanthopterygii, Hypoptychus shares apomorphies only with Atherinomorpha, Percomorpha, and Cottus. It shares the absence of premaxillary ascending processes and the development of maxillary hooks with Atherinomorpha, as well as the tendency to develop dentaries whose posterior margins are not deeply concave. These premaxillary and maxillary apomorphies are characteristic of Atherinomorpha.

Hypoptychus shares one apomorphy, the presence of postmaxillary processes on the premaxillae, with Percomorpha. Within Percomorpha it resembles Scorpaeniformes in three apomorphic tendencies, two of which are losses. The third is the presence of posterior processes on the ventromedial projections of the lateral ethmoids.

The two synapomorphies uniting Hypoptychus and Cottus are the incomplete trigeminofacialis anterior foramina and the absence of separate endopterygoids. The anterior trigeminofacialis foramina are not distinct in Hypoptychus; the pterosphenoids and parasphenoid lateral processes are both reduced and do not meet one another, so that if there are anterior foramina their anterior margins are either cartilagous or absent. It is difficult to compare this situation with those of Cottus and the other study groups.

As in Indostomus, a single pterygoid bone is present in each palatopterygoid arch. These are triangular bones, like those of Cottus, but instead of lying along the anterior and dorsal borders of the quadrates they lie flat along their medial surfaces (Fig. E10). This position is most similar to that of the endopterygoids in other fishes, but the bones also extend anteriorly to meet the palatines, a position usually filled by the ectopterygoids.

Pegasus

Pegasus shares two of the apomorphies found in all members of (Percopsis + Acanthopterygii), the pelvic fins articulating with ventral projections from the pelvic plates and the perforate precaudal neural arches. Six more apomorphies are found in Pegasus and in all major subgroups of (Percopsis + Acanthopterygii). They are:

1. Supraoccipital and frontals are in contact
2. Head length is more than 22% of standard length
3. Dentaries have elevated coronoid processes
4. Fifth ceratobranchials are expanded laterally
5. Third actinosts are attached to coracoids
6. Proximal anal pterygiophores bear flanges.

Three apomorphies appear in Pegasus and in all major subgroups of Acanthopterygii - the urohyal with ventrolateral flanges, the pelvic plates with anteromedial spurs, and the pelvic plates joined by medial sutures. Within Acanthopterygii, Pegasus shares the most apomorphic tendencies with Scorpaeniformes. They are:

1. Median ethmoid bears a ventral transverse flange
2. Median projections of each lateral ethmoid are fused.
3. Preopercula bend medially to form the floors of the branchial chambers
4. Scapulae are reduced in size to that of actinosts
5. Scapulae are fused to first actinosts.

The presence of a transverse flange across the median ethmoid and the fused median projections of the lateral ethmoids may be viewed as parts of the tendency towards fusion and strengthening of the ethmoid region.

Pegasus and Asterotheca share almost identical modifications of the preopercula, whose posterior corners bend medially and almost meet at the ventral midline of the head. This modification appears also in Prionotus , Trigla, and Peristedion (Gregory, 1933), making it an apomorphic tendency of Scorpaeniformes. It might be explained as associated with the development of a depressed head. However, in the paracanthopterygian fishes Lophius and Ogcocephalus , which have similarly depressed heads, the preopercula are moved dorsally to lie on the flat dorsal surfaces of the heads.

Pegasus shares three apomorphic tendencies with Scorpaenoidei, but all are losses. It shares three apomorphies with Cottus; these are

1. Trigeminofacialis foramina are incomplete
2. Separate endopterygoids are absent
3. Uroneural is fused to the dorsal hypurals.

The trigeminofacialis anterior foramina are absent, the various nerves usually passing through them perhaps exiting through the ventral trigeminofacialis foramina. The shared lack of separate endopterygoids is of little significance, since all pterygoids are absent in Pegasus.

Two synapomorphies, the extension of the lateral ethmoid ventromedial projections posteriorly to enter the orbits and the absence of the second pharyngobranchials, unite Pegasus and Asterotheca. The latter is a loss character. The former appears to be restricted to these fishes; it does not appear in any of the other species in which the lateral ethmoids have fused medial projections, or in any of the other species with well-developed interorbital septa.

Pegasus resembles Perciformes in two apomorphic tendencies, the dermosphenotics bearing lateral canals and the shortened haemal laminae. It shares two more with Ammodytes, but one is the loss of dentary teeth; the other is the presence of contact between dentaries and angulars.

Dactylopterus

Dactylopterus shares only one of the apomorphies present in all members of (Percopsis + Acanthopterygii), the quadrates with distinct shafts. It shares ten of the apomorphies or apomorphic tendencies appearing in all major subgroups of (Percopsis + Acanthopterygii). These are:

1. Supraoccipital and frontals are in contact
2. Prootics bear accessory anterior foramina
3. Head length is more than 22% of standard length
4. Dentaries have elevated coronoid processes
5. First basibranchials are deeper than succeeding basibranchials
6. Fifth ceratobranchials are expanded laterally
7. Third actinosts are attached to coracoids
8. Proximal anal pterygiophores bear flanges
9. Orbit length is more than 30% of head length
10. Frontal length is more than 40% of head length.

Within (Percopsis + Acanthopterygii), it possesses four of the apomorphies found in all members of Acanthopterygii. These are:

1. Urohyal has ventrolateral flanges
2. Dentaries bear anterolateral foramina
3. Pelvic plates bear anteromedial spurs
4. Pelvic plates are joined by a medial suture.

Within Acanthopterygii, Dactylopterus shares more apomorphies with Scorpaeniformes, Scorpaenoidei, and Cottus than with other groups. It resembles Scorpaeniformes in:

1. Hypobranchials bear anterior processes
2. Pectoral fin length is more than 25% of standard length
3. Median projections of each lateral ethmoid are fused
4. Central dorsal pterygiophores are flattened, distal pterygiophores fused to their dorsal surfaces
5. Epipleural ribs are absent.

The last of these is a loss, and the fusion of the lateral ethmoid medial projections may be part of a general fusion of the ethmoid region. The supports for the dorsal spines (Figure L6) resemble those of Asterotheca and Indostomus, with the exception of the presence of two foramina lying posteriorly to the base of each of the anterior four spines. Similar foramina are present in Gasterosteus.

The synapomorphies uniting Dactylopterus and Scorpaenoidei are interopercula without expanded posterior ends and the absence of prehaemapophyses. The apomorphies shared with Cottus are flattened hypobranchials and fusion of the uroneural and hypurals. Neither of these sets of synapomorphies provides strong evidence for placing Dactylopterus with the group in question.

Summary

All of the study groups belong with or within (Percopsis + Acanthopterygii) on the basis of synapomorphy counts. All also show strong affinity with Acanthopterygii, but this affinity is based in every case on shared apomorphic tendencies. Within Acanthopterygii, all except Pegasus and Dactylopterus share apomorphies and/or apomorphic tendencies with Atherinomorpha but only in Hypoptychus are any of these strong indicators of relationship. All show affinity for Scorpaeniformes and scorpaeniform subgroups based in most cases on characters of the ethmoid region, fused ecto- and endopterygoids, reduction of the trigeminofacialis anterior foramina, reduction of the scapulae with or without their fusion to the first actinosts, and fusion of the central and distal pterygiophores to form flattened supports for the dorsal spines. Hypoptychus alone fails to clearly display any of these apomorphies.

Like the phylogenetic analyses, evolutionary systematics leaves open the possibility that the study groups form a monophyletic lineage near or within Scorpaeniformes. It differs from phylogenetic analyses in providing stronger reasons to remove Hypoptychus from this area to that of Atherinomorpha, and does not indicate Ammodytes as a possible sister group for the study groups.

Relationships among study groups

The apomorphies relevant for comparison between study groups are those which appear only within them, since any which appear in both framework groups and study groups are regarded as apomorphic tendencies of the smallest monophyletic taxon containing both the groups. Apomorphic tendencies, by definition, are likely to appear in parallel and therefore will not yield precise information about the interrelationships of members of the group which they characterize.

Table Ev.3 contains the character states applicable to determining relationships among study groups, with summaries of their distributions. Table Ev. 4 shows the numbers of synapomorphies uniting various study groups. The first number refers to the number of shared apomorphies which appear to be present at the basal nodes of both study groups; the second number, in each pair involving either Gasterosteiformes or Syngnathiformes, refers to the number of shared apomorphies occurring within Gasterosteiformes or Syngnathiformes, but not at the basal node. These would represent apomorphic tendencies.

Study groups share many more apomorphies and apomorphic tendencies with one another than with any framework groups except (Percopsis + Acanthopterygii) and Acanthopterygii. Only one apomorphy is found in all the study groups, however, and this is the loss of dentition on the second ceratobranchials. A set of apomorphies related to snout and body elongation is found in most study groups. These include increases in the relative lengths of the snout and vomer and decreases in the relative lengths of the fins, orbit, and the cranial bones which do not form the snout. These may be common in elongate fishes.

Another set of apomorphies are losses - of the cranial canal system and supracleithra, the teeth on premaxillae and the teeth, toothplates, and bones of the branchial apparatus, the metapterygoids, the anterior branchiostegal rays, postneurapophyses, and portions of the caudal skeleton.

The introduction of apomorphic tendencies increases the perceived similarities between all groups and Gasterosteiformes and Syngnathiformes. All of the study groups share more apomorphies and apomorphic tendencies with Syngnathiformes than with one another.

Gasterosteiformes

Gasterosteiformes resemble Syngnathiformes in four shared apomorphies and 18 apomorphic tendencies, many of which are associated with elongation or skeletal reduction. Those not associoted with these tendencies are:

1. Ectocoracoids are present
2. Fourth actinosts are attached to coracoids by anteroventral processes
3. Frontals bear medial postorbital processes touching the parasphenoid lateral processes
4. Coracoid shafts are incised anteriorly
5. Soft dorsal is preceded by separated dorsal spines
6. Vertebrae bear lateral processes extending to the scutes
7. Urohyal flanges are not incised posteriorly.

Ectocoracoids, sculptured dermal bones lying laterally to the coracoids (Figs. J3-4), appear only in Fistularia among extant Syngnathiformes. They are distinctive in Fistularia, being large and elongate, extending almost to the pelvic girdles. Apparent ectocoracoids are visible in the fossil syngnathiform Gasterorhamphosus (Sorbini, 1981); these are extremely large, leaf-shaped bones similar to neither those of Gasterosteiformes nor those of Fistularia.

The anteroventral processes of the fourth actinosts of Gasterosteiformes (Figs. J3-4) are relatively small, while in Centroscoidei, the only syngnathiform group possessing them, they may exceed the entire actinost complexes in size (Fig. J8).

The gasterosteiform frontal-parasphenoid connections have been discussed above. They appear in all the members of Gasterosteiformes I examined (Fig. B3) and in three members of the syngnathid lineage of Syngnathiformes (Fig. B8). While the connections are distinctive and similar, they must be viewed as apomorphic tendencies since they are restricted, within Syngnathiformes, to the highly apomorphic Syngnathidae. Separate anterior dorsal spines appear in Mastacembelidae, Notacanthidae, Rachycentridae, and Cheimarrichthyiidae (Nelson, 1976), and those found in Syngnathiformes differ from those in Gasterosteiformes both in size and strength and in the nature of their internal supports.

Among Gasterosteiformes, only Aulorhynchus has well-developed connections between the vertebrae and the lateral scutes (Fig. M4). Triangular lateral processes extend from the vertebrae to overlap similar processes extending medially from the scutes. In Macrorhamphosus and Syngnathidae (Figs. M6-7), the scutes and vertebrae are connected by similar triangular vertebral processes, but there are no medially extending processes from the scutes; in Aeoliscus, the vertebral processes extend the full length of each of the anterior, elongated centra.

Gasterosteiformes share almost the same number of apomorphic character states with Indostomus, Hypoptychus, and Pegasus. All have urohyal flanges which are not incised posteriorly and a decrease in the relative length of the median ethmoid. Gasterosteiformes share characters of snout and body proportions with all three, as well as reduced dentition and the loss of branchial bones. In addition, Gasterosteiformes and Hypoptychus share coracoid shafts incised anteriorly and fourth actinosts connected to the coracoids by anteroventral processes. Hypoptychus resembles one member of Gasterosteiformes, Aulichthys, in the fusion of its fourth actinosts and coracoids and in its sexually dimorphic dentition. In the absence of any other unique synapomorphies, these do not seem to outweigh the shared apomorphies uniting Hypoptychus and Atherinomorpha.

Gasterosteiformes and Indostomus share the development of anteroventral processes on the fourth actinosts, the presence of separate dorsal spines preceding the soft dorsal, and reduction in the number of pleural ribs. The homology of the last is very questionable, since Indostomus has no ribs. The actinost projections of Indostomus resemble those of

Gasterosteiformes in size (Fig. J9) rather than those of Syngnathiformes; the actinosts themselves, however, are very different from those of either group.

Gasterosteiformes and Pegasus share, in addition to characters of elongation and skeletal reduction, actinosts attached to one another by sutures, as opposed to those of Syngnathiformes which are attached by overlapping laminae, and pelvic plates with posterior processes developed so that their anterior processes make up less than 70% of their lengths.

Syngnathiformes

Although Syngnathiformes share many apomorphies and apomorphic tendencies with Gasterosteiformes, as discussed above, they show a higher affinity for Pegasus in Table Ev.4. A closer investigation of the shared apomorphies and shared apomorphic tendencies, however, shows that most of them represent losses or morphometric characters associated with elongation. Some of the remaining synapomorphies, particularly the entire urohyal flanges and shortened anterior processes of the pelvic plates, are found in the majority of the study groups. Syngnathiformes and Pegasus also share:

1. Preopercula are expanded posteriorly
2. Opercula are reduced
3. Posttemporals are co-ossified with the cranium
4. Neural arches are closed for their full lengths
5. Fewer than 23 vertebrae are present
6. The anterior four vertebrae are fused.

All of these apomorphies are also found in Dactylopterus. In most of them the states in Syngnathiformes are quite distinct from those found in Pegasus and Dactylopterus. The preopercula of Syngnathiformes are expanded posteriorly but do not form much of the gill covers, whereas in Pegasus and Dactylopterus they form a large portion of the gill covers, filling the positions filled by the subopercula in Syngnathiformes (compare Figs. A6, B10 with Figs. A12, G2). The anterior vertebra of Pegasus and Dactylopterus are similar in length to succeeding vertebra and are connected by complex sutures between the centra (Figs. M10-11) while those of Syngnathiformes are elongated, with simple connections between centra and confluent lateral and dorsal flanges (Figs. M5-6).

Syngnathiformes share as many apomorphies and apmorphic tendencies with Indostomus as with Gasterosteiformes, many of them in the same loss or elongation characters. In both Syngnathiformes and Indostomus:

1. Pectorals have more than 19 rays (also found in Dactylopterus)
2. Pelvic plates lack medial processes
3. Ossified tendons are present in the axial musculature
4. Neural arches are closed for their full lengths (also found in Pegasus and Dactylopterus)
5. Haemal arches are closed for their full lengths
6. Fewer than 23 vertebrae are present (also found in Pegasus and Dactylopterus).

Ossified tendons or intramuscular bones appear in the axial musculature of Aulostomus and Indostomus. Such bones appear in primitive fishes (e.g. Ostariophysi), although those of Aulostomus and Indostomus seem to be longer and placed in a unusual longitudinal orientation. Still, this character can represent nothing more than an apomorphic tendency, if that.

The haemal canals closed for their full lengths appear in Fistularia and Centriscoidei, so they may have been present in the common ancestor of Syngnathiformes.

Indostomus

Indostomus shares the largest numbers of apomorphies and apomorphic tendencies with Syngnathiformes but, as described above, most of them are also found in other study groups or are loss characters or related to elongation. Indostomus shares equal numbers of apomorphies and apomorphic tendencies with Gasterosteiformes and Pegasus.

The only Indostomus - Gasterosteiformes apomorphies not associated with elongation or skeletal reduction are the presence of fourth actinosts with anteroventral processes and of anterior separated dorsal spines. The actinost processes of Indostomus resemble those of Gasterosteiformes more than they resemble those of other study groups, but the actinosts themselves are quite different in size and shape. The separated dorsal spines, as noted above, occur in several groups outside the study groups.

All of the apomorphies shared by Indostomus and Pegasus involve the elongation of snout and body and the reduction of the skeletal system. While Indostomus shares many scorpaeniform apomorphic tendencies with Pegasus and Dactylopterus, these cannot be used to indicate relationships between them.

Hypoptychus

Hypoptychus shares similar numbers of apomorphies and apomorphic tendencies with Gasterosteiformes and Syngnathiformes, as discussed above. The only distinctive synapomorphies uniting it with Gasterosteiformes are the anteroventral processes on the fourth actinosts, which are also found in Indostomus and Syngnathiformes, and the sexually dimorphic dentition, which appears in only one member of Gasterosteiformes. Most of the [illegible] apomorphies and shared apomorphic tendencies uniting Hypoptychus and Syngnathiformes, like those uniting it with Gasterosteiformes, are related to skeletal reduction and elongation. The fourth actinosts of both bear anteroventral processes but they are very different in morphology. The coracoid shafts are incised anteriorly (Fig. J10), but this character is also found in Gasterosteiformes. None of these apomorphies seems to provide as strong evidence to support a link between Hypoptychus and one of these study groups as is provided supporting a link between Hypoptychus and Atherinomorpha.

Pegasus

Pegasus shares by far the most apomorphies and apomorphic tendencies with Syngnathiformes, but most represent elongation and skeletal reduction. Two of the shared apomorphies remaining after these are removed, the expanded preopercula and the fused anterior vertebrae, are quite different in the two groups, leaving them united by reduced opercula, posttemporals co-ossified with the crania, and neural arches closed for their full lengths; all of these are also found in *Dactylopterus*.

Pegasus shares the same number of apomorphies with Gasterosteiformes and *Dactylopterus*. It is united to Gasterosteiformes by characters of the actinosts, which are sutured together, and the pelvic plates, whose anterior processes make up less than 70% of their lengths.

Several of the shared apomorphies of *Pegasus* and *Dactylopterus* also appear in Syngnathiformes, but with important differences as described above. The preopercula form significant portions of the gill covers in these fishes, the posttemporals are co-ossified with the crania, the pelvic anterior processes are short, the first four vertebra are suturally united, and the neural arches are closed for their full lengths. In addition, each has transversely extending bones arising from the posterior precaudal vertebrae, and the fused nasals of both are excavated ventrally to form a deep cavity which receives the bones of the upper jaws.

Dactylopterus

Dactylopterus shares the most apomorphies and apomorphic tendencies with Syngnathiformes, many of them associated with skeletal reduction and several more found in *Pegasus* as well, as discussed. The synapomorphies most strongly supporting a *Dactylopterus* - Syngnathiformes link are the absence of branchiostegal rays arising from the posterior heads of the ceratohyals and an increased number of pectoral rays (which is also found in *Indostomus*). The ceratohyals of Syngnathidae and Aulostomoidei are almost completely covered laterally by the epihyals (Fig. H5), to which the branchiostegals are attached; this is in strong contrast to the relatively unspecialized hyoid arches of *Dactylopterus* (Fig. H7). The high numbers of pectoral rays are also found in Paracanthopterygii and in salmoniform fishes (Hart, 1973); they are therefore either primitive character states or the apomorphic tendencies of a much larger group. In either case, they are not good indicators of relationship among study groups.

The strongest evidence for a placement of Dactylopterus seems to be that presented above for its relationship with Pegasus.

Summary

Few distinctive apomorphies unite study groups, and most of these are losses or are associated with elongation and are likely to appear in many unrelated fishes with similar elongated bodies and/or snouts. Some unique shared apomorphies link Gasterosteiformes and Syngnathiformes, most of them appearing independently in each group. These are the presence of symplectic dorsal laminae, frontal-parasphenoid connections, lateral extensions from the vertebrae to the lateral scutes, and ectocoracoids. Likewise, Pegasus and Dactylopterus are linked by expanded preopercula, reduced opercula, fused anterior vertebrae, the presence of transverse bones, and development of the fused nasal bones to form a cavity into which the upper jaw retracts. Indostomus shows a few links with (Gasterosteiformes + Syngnathiformes) - separate anterior dorsal spines and actinosts with anterodorsal processes. The (Gasterosteiformes + Syngnathiformes) and (Pegasus + Dactylopterus) lineages share tendencies towards fusion of the anterior vertebrae, neural canals closed for their full lengths, and co-ossification of the crania and posttemporals. There seems to be no strong evidence supporting the placement of Hypoptychus with any of the study groups; it is linked to Aulichthys by two synapomorphies, but the same number place it with Atherinomorpha.

Discussion

All of the study groups share more apomorphies with (Percopsis + Acanthopterygii) than with any other framework groups, as in the phylogenetic results. They are united to Acanthopterygii by apomorphic tendencies, although few of these are among the tendencies regarded as distinguishing Acanthopterygii by previous workers (e.g, Greenwood et al., 1966; Lauder and Liem, 1983). The study groups likewise all share some apomorphies or apomorphic tendencies with Atherinomorpha, but only in the case of Hypoptychus are any of them recognized as characteristic of the series. Hypoptychus shares the maxillary hooks, structures which I did not see in, or find recorded from, any fishes outside Atherinomorpha and which Rosen (1964) recorded from all atherinomorph subgroups which possessed maxillae. It possesses several other atherinomorph characters given high weight by Rosen, including the supraoccipital with a wedge-shaped anterior process, the premaxillae without ascending processes, the supracleithra contained within the borders of the cleithra, the scapulae notched posteriorly to receive the actinosts, and the ceratohyals expanded posteriorly. All of these apomorphies, however, were also observed in non-atherinomorph fishes.

Relatively few apomorphies or apomorphic tendencies distinguish Percomorpha in my study, which agrees in this respect with most others. Study groups share few apomorphies with this group, accordingly; they also possess few apomorphies linking them directly to (Perciformes + Scorpaeniformes). All, however, share several apomorphic character states with Scorpaeniformes and Cottus.

A group containing the scorpaeniformes examined, and all the study groups except Hypoptychus, may be characterized by its members' possession of strengthened and fused ethmoid regions, with lateral ethmoids enlarged to form part of the orbit roof and part of the posterior walls of the snout. Their medial projections are often fused. The nasals are fused or meet anteriorly in a symphysis; posteriorly, they are tightly sutured to the frontals. Most of these fishes have reduced opercula, the preopercula or subopercula forming the ventral parts of the gill covers. Often the preopercula form the ventral gill covers and the subopercula are displaced posteriorly, not following the opercular margins. The scapulae are often reduced in size and their foramina incomplete; often they are fused to the first actinosts. The dorsal spines are supported by fused central and distal pterygiophores, the central pterygiophores expanded laterally into plates under the bases of the spines.

The presence of suborbital stays is traditionally a highly weighted apomorphy, regarded as diagnostic of Scorpaeniformes (Gosline, 1971; Nelson, 1976). Their presence among the study groups, then, is an important link among these groups. However, since the stays are not present in all of the study groups, they would be less universally present in a (Scorpaeniformes + study groups) taxon, and their weight might decrease.

The suborbital stays in Scorpaeniformes are formed by posterior expansion of the third suborbitals to touch the ascending arms of the preopercula (Fig. A3), but they vary in their development from extension into broad flat plates like those in Pegasus, which may also touch the anterior limbs of the preopercula, to extension into narrow struts extending horizontally backward to the preopercula. In Gasterosteiformes the suborbital-preoperculum connection does not usually involve the ascending arm of the preoperculum, except in Spinachia (Fig. B5). In Aulorhynchidae the third suborbitals lie over the anterior preopercula limbs but are not expanded, and both their lack of expansion and contiguity with the preopercula might be explained as due to snout elongation. In Gasterosteidae the third suborbitals resemble the anterior halves of those in Spinachia, extending ventrally to the anterior limb of the preopercula but not posteriorly to their ascending limbs. A classical scorpaeniform suborbital stay, then, is present only in Spinachia among gasterosteiforms.

The suborbital stays in Dactylopterus (Fig. B14,B) resemble those of Scorpaenidae and Cottidae, extending posteriorly to the ascending arm of the preoperculum. They involve, however, the second suborbitals rather than the third. It should also be noted that similar connections between the suborbitals and preopercula have evolved in at least one unrelated group (Anabantidae; Liem, 1963). This casts doubt on the importance of the suborbital stay as a diagnostic character of Scorpaeniformes.

Within Scorpaeniformes, the study groups seem to fit into the cottoid lineage, in which the anterior trigeminofacialis foramena are incomplete or absent, the ecto- and endopterygoids are often fused, and the lateral ethmoids may extend posteriorly into the interorbital septum.

Three separate lineages can be distinguished among the study groups. Syngnathiformes, a large and variable group, shares the largest numbers of apomorphies with all of the other study groups. Most are reduction characters; members of Syngnathiformes have reduced cranial canal systems, branchial arches and dentitions, nasals and parietals, hyoid arches, suborbital series, pectoral and pelvic girdles, vertebral processes, ribs, and caudal skeletons. Several of these trends in reduction, however, seem to have occurred within Syngnathiformes, appearing in its most specialized members. The syngnathid lineage, for example, shows most of the derived reductions while Macrorhamphosus, on the other hand, has fully developed nasals and branchial arches, well-developed if small pectoral girdles, a full complement of anterior and posterior vertebral processes, and a caudal skeleton in which not only two distinct hypural plates but a second ural centrum are distinguishable. This means that many of the reductions which unite Syngnathiformes and other study groups must be viewed as apomorphic tendencies; such apomorphies can hardly be weighted highly.

When parallel losses are discounted, Syngnathiformes still shares the most apomorphies with Gasterosteiformes. Among these are:

1. Frontals and pterosphenoids are fused, forming direct connections between the frontals and parasphenoid
2. Anterodorsal or posterodorsal laminae extend from the symplectics, separating the endopterygoids and hyomandibulae
3. Subopercula are expanded ventrally to form part of the gill covers
4. The anterior series of branchiostegal rays is absent
5. Coracoid shafts are anteriorly bifurcated, laterally supplemented by ectocoracoids
6. Fourth actinosts are larger than the others, connected to the coracoids by anteroventral processes
7. Dorsal fin is preceded by separated spines
8. Lateral scutes are connected to lateral processes of the vertebrae.

Based on these apomorphies, I identify a lineage containing Gasterosteiformes and Syngnathiformes. This study was not designed to investigate relationships between genera within these groups, but when they are placed together within Scorpaeniformes some hypotheses about those relationships can be made.

Within Gasterosteiformes, Aulorhynchidae appears to be the more primitive lineage. Its members lack the highly developed spines and scutes of Gasterosteidae; they also possess complete suborbital rings, four pairs of pharyngobranchials, postmaxillary processes on the premaxillae, well-developed preoperculomandibular canals, and actinosts of equal sizes and, in Aulichthys, urogenital papilla similar to those found in members of Cottoidei (Sasaki, 1977). Aulorhynchidae share two apomorphies with

Syngnathiformes which are not found in Gasterosteidae - the expanded subopercula and the vertebral processes to lateral scutes. The first of these is found in the oldest fossil syngnathiform, *Gasterorhamphosus* (Sorbini, 1981), suggesting that it may have been present in the common ancestor of Gasterosteiformes and Syngnathiformes. The second cannot be observed in *Gasterorhamphosus* but is present in its living relatives *Macrorhamphosus* and *Aeoliscus* and in Syngnathidae.

Within Syngnathiformes the macrorhamphosid-centriscid lineage appears to be the most primitive, including members with complete nasal bones, separate ecto- and endopterygoids, angulars with a conical component, interopercula with expanded posterior ends, two basibranchials, third and fourth epibranchials articulating via uncinate processes, scapulae of normal size relative to the actinosts and enclosing complete scapular foramina, anterior spinous dorsal fins not composed of separated spines, spinous anal fins, scales, autogenous parhypurals, and distinct second ural centra. The fossil *Gasterorhamphosus* has, in addition, three separate epurals and an interorbital septum composed of the orbitosphenoids. Members of this group possess all the heavily-weighted Gasterosteiformes -Syngnathiformes synapomorphies except fusion of the frontals and pterosphenoids. It seems reasonable to hypothesize that both the gasterosteiform and syngnathathiform lineages arose from a common ancestor. The relationships between syngnathiform lineages are, however, still unclear. Macrorhamphosid and centriscid fishes share with aulostomids the highly developed median ethmoids with ventrolateral ridges, distinctive lateral ethmoids with anterior extensions, elongate dermopterotics, flattened hypobranchials, ectocoracoids, elongated and fused anterior vertebrae, and posterior transverse processes on the vertebrae. However, the macrorhamphosid and syngnathid lineages share lateral ethmoids with fused medial projections, reduced interorbital commisures, loss of teeth, posteriorly expanded preopercula, narrow fifth ceratobranchials, and vertebral processes supporting the scutes. Of these two sets of shared apomorphies, the latter seems weakest. It involves many fusion and reduction characters. Its one strong shared apomorphy, the presence of vertebral processess to the scutes, cannot be evaluated in the scuteless aulostomid fishes, and may be represented by the posterior transverse processes on their vertebrae.

Aulostomid and syngnathid lineages are united by their possession of dorsal hypohyals lying along the ceratohyals, reduction in the branchial basket (particularly, the loss of the third basibranchial, the uncinate processes of the third epibranchials, and the anterior processes of the hypobranchials, and the development of elongate, narrow pharyngobranchials), reduction of the scapulae to bones resembling actinosts, and reduction of the haemal laminae to narrow struts of bone. Again, most of these shared apomorphies represent reduction or loss, with the exception of the first.

Gasterosteiformes and Syngnathiformes, although they appear to be fishes of cottoid ancestry, have lost some of the distinguishing characteristics of Scorpaeniformes and, in the case of Syngnathiformes, many of the distinguishing characters of Acanthopterygii and Percomorpha. Including them in Scorpaeniformes, therefore, would adversely affect the definition of this group and imply that members of Gasterosteiformes and Syngnathiformes possessed scorpaeniform characters which they have in fact lost. For these reasons I have assigned these fishes to their own order, **Gasterosteiformes**.

Pegasus and Dactylopterus are the study groups which show the most scorpaeniform characters; in particular they possess suborbital stays, nasals meeting in the dorsal midline, and, in Dactylopterus, armed opercular apparatus. For these reasons, I include them within Scorpaeniformes as a suborder, **Dactylopteroidei**, placed near Cottoidei. Of these fishes, Dactylopterus appears to be less derived than Pegasus. It has retained a short snout, scales, an anterior spinous dorsal, ribs, and separate hypurals. Two of these characters, scales and the anterior spinous dorsal, are present in the fossil pegasid Rhamphosus, suggesting that they are also primitive for Pegasidae.

The (Pegasus + Dactylopterus) lineage and the (Gasterosteiformes + Syngnathiformes) lineage share very few apomorphies other than skeletal reductions. Both groups contain members with fused anterior vertebrae, but those of Pegasus and Dactylopterus are connected via complex sutures between centra while those in Syngnathiformes are elongate, with simple connections between centra and fused lateral and dorsal flanges. The neural canals are closed for their full lengths in Syngnathiformes, Pegasus, and Dactylopterus, as they are in Indostomus, but this may be another manifestation of the common trend towards skeletal reduction and fusion, as may the posttemporals co-ossified with the cranium. Indostomus may be placed with

Syngnathiformes on the basis of its network of intermuscular bones and the presence of anteroventral processes on its fourth actinosts, and as such it might provide a link between the two groups; but, as noted above, the first of these synapomorphies must be regarded as a parallelism at best, and the second is so dissimilar in Indostomus and Syngnathiformes as to be questionable. There is not strong enough evidence either to unite (Gasterosteiformes + Syngnathiformes) with (Pegasus + Dactylopterus) or to unite either with Indostomus. I therefore leave Indostomus in its own order, **Indostomiformes**.

Conclusions

These relationships are summarized in Fig. Ev.3. The three groups Gasterosteiformes, Indostomiformes, and Dactylopteroidei all are hypothesized to have arisen from cottoid ancestors, but there is not enough evidence to decide whether they form a monophyletic group. Within Gasterosteiformes, the macrorhamphosid lineage is most primitive, having given rise to modern macrorhamphosids, aulostomids, and syngnathids on one hand, and to aulorhynchids and gasterosteids on the other. The former groups have diverged greatly from the ancestral condition, retaining few scorpaeniform characters.

Although the members of Dactylopteroidei are specialized, they retain more cottoid characters than do either lineage within Gasterosteiformes. Dactylopterus is the more primitive of the two dactylopteroid lineages.

Indostomus is a lineage with approximately equal ties to Gasterosteiformes and Dactylopteroidei, and for this reason its position must be left uncertain. Hypoptychus does not appear to belong anywhere in this assemblage, but rather to be a derived atherinomorph.

The classification suggested is;

Order Scorpaeniformes (in part)
  Suborder Cottoidei
  Suborder Dactylopteroidei
    Superfamily Dacylopteroidae
    Superfamily Pegasoidae
Order Gasterosteiformes

Suborder Gasterosteoidei

Family Gasterosteidae

Family Aulorhynchidae

Suborder Syngnathoidei

Superfamily Macrorhamphosoidae

Family Macrorhamphosidae

Family Aulostomidae

Superfamily Syngnathoidae

Family Solenostomidae

Family Hippocampidae

Family Syngnathidae

Order Indostomiformes

The monotypic order Hypoptychiformes is removed from Gasterosteiformes and placed provisionally with Atherinomorpha, although its affinities are still unclear.

This classification leaves Scorpaeniformes as a paraphyletic group, from which two separate orders have arisen. Its major advantage is its retention of the characteristics distinguishing Scorpaeniformes, the suborbital [illegible] cranial and opercular spines, rounded pectorals with free anterior rays, and rounded caudal fins (Nelson, 1976). Scorpaeniformes thus remains a well-distinguished group of bony-headed, mainly bottom-dwelling fishes. Dactylopteroidei is one of the several bottom-dwelling lineages within Scorpaeniformes, and as such has retained or evolved in parallel a large number of characters found in other scorpaeniforms. It is distinguished by fusion of the nasals into a median bone with a ventral cavity into which the upper jaw bones fit, enlarged posttemporals and preopercula, sutured anterior vertebrae, and "transverse bones".

The new order Gasterosteiformes is a lineage of open-water or weed-dwelling fishes. These fishes lack the suborbital stays and head spines of Scorpaeniformes, having evolved instead elongate, tubular snouts (partially formed by dorsal flanges from the symplectics), expanded subopercula, reduced branchiostegal series and pelvic plates, strong connections between the fourth actinosts and the coracoids, and lateral processes connecting the vertebrae with the lateral scutes.

The order Indostomiformes shares some characteristics of both the other lineages. It is apparently a benthic fish which feeds on the bottom or in mid-water, and it shows a combination of characters found in benthic cottoids and in Gasterosteiformes.

Table Ev.1 : Apomorphies and apomorphic tendencies of framework groups
with the study groups in which they occur and the character numbers, states, and descriptions. Apomorphic tendencies appearing within Gasterosteiformes and Syngnathiformes are indicated as follows:

G^1 - may appear in the common ancestor of Gasterosteiformes
G^2 - appear once within Gasterosteiformes
G^3 - appear independently more than once within Gasterosteiformes

Saurida (Aulopiformes)

Apomorphies

S^2IHP	M10(0)	Preneurapophyses absent

(Percopsis + Acanthopterygii)

Apomorphies

G^2S H	A 3(0)	Lateral ethmoids do not extend posteriorly onto orbit roof
G S IHP	A23	Snout length more than 25% of head length
G^1S^2 H	C 8(1)	Dermopterotics overlap over half of sphenotics
G S IHPD	C11(0)	Supraoccipital and frontals not separated
D	D 8(1)	Prootics with accessory anterior foramen(a)
G^2S IH	D11(1)	Exoccipital condyles present
S HPD	D17(1)	Prootics reach margin of postorbital foramen
G S PD	D19	Head length more than 22% standard length
D	E10(1)	Dorsal and ventral maxilla articular heads connected posteriorly
G S HPD	F 3(1)	Dentaries have elevated coronoid processes
G^3S^2 H D	F18(1)	Quadrates have distinct shafts
I	G 5(1)	Posterior borders of preopercula are incised or serrated
G S IHPD	H 2(0)	Glossohyal toothless
G S IHPD	I 4(0)	Basibranchials lack toothplates or teeth
G^3 H	I 6(1)	Basibranchial #1 deep
D	I 7(1)	Basibranchials with lateral flanges
G S^1I PD	I24(1)	Fifth ceratobranchials expanded laterally
G S^1 H	J22(1)	Scapula posterior borders notched to receive actinosts
G S^1 HP	J25(0)	Actinosts not elongate
G^2S IHPD	J30(1)	Third actinosts attached to coracoids
G S^3	K 5(0)	Pelvic plates lack anteromedial flanges
G P	K13(1)	Pelvic fins articulate with ventral projections from the pelvic plates
	K15(1)	Pelvic plates bear overlapping medial processes
G	L 3(1)	Soft dorsal with anterior spines
G S^2	L 9(1)	Anal spinous
G S IHPD	L15(1)	Proximal anal pterygiophores bear flanges
G S IHP	M 9(1)	Precaudal neural arches are pierced by lateral foramina
G S IHPD	M15(0)	Epineurals absent

Apomorphic tendencies

G^2 H	A12(1)	Median ethmoid medial plate reduced
G S IHPD	A16(0)	Vomer head toothless
G S I	B12(0)	Basisphenoid absent
G^2 H D	B19	Orbit length over 30% of head length
G S IH D	B20	Frontal length over 40% of head length
S	D 7(0)	Prootics and exoccipitals do not meet

Table Ev.1 continued
E15(1)Palatine larger than ectopterygoid
G^2S^3I F22(1)Symplectics bear posterodorsal laminae
G^2 I F23(1)Symplectics bear posteroventral laminae
I 5(1)Ventral toothplate behind last basibranchial
G^2S^3 PD I35(0)Third pharyngobranchial without anterior cylindrical process
G S P K18 Snout - pelvic base more than 40% of standard length
G I D L13(0) First anal element supported by a single pterygiophore

Percopsis (Paracanthopterygii)

Apomorphies
G^2S HP H 4(1)Ventral hypohyals overlap ceratohyals
G^2 P K18 Snout to pelvic base 45% standard length

Acanthopterygii

Apomorphies
S B 4(1)Frontals reach near posterior end of skull
G S HP H 5(0)Ceratohyals not expanded at anterior end
G HPD H17(1)Urohyal with ventrolateral flanges
G S IHPD I14(0)Hypobranchials lack toothplates
G^3S^3I PD J 5(0)Posttemporals lack anteroventral processes
G S I PD K10(0)Pelvic actinosts absent
PD K14(1)Pelvic plates bear anteromedial spurs
S^2 D L 1(1)Anterior spinous dorsal
G S IHPD L12(1)Proximal and medial pterygiophores fused
G S I D L23First dorsal spine less than 19% of standard length
S I PD N 6(1)Uroneural, if distinct, supports principal caudal rays

Apomorphic tendencies
G^2S H A 7(1)Lateral ethmoid ventromedial projections with anterior processes
P A15(1)Median ethmoid touches lateral ethmoids
PD A19(1)Vomer head connects lateral ethmoids
G^1 IH B 9(0)Suborbital rings incomplete
B15(0)Dermosphenotics separate from sphenotics
G S^1I C 3(1)Supraoccipital with anterior wedge-like process
G S I PD C10(0)Extrascapulars absent
S I D 6(1)Prootics with separate ventral foramina for VIII nerve
G S I PD D12(0) Basioccipital ventral surface flat
S I PD D14(0)Intercalaries absent
PD E 6(1)Ventral articular heads of maxillae long
G^3S^2 D F 2(1)Dentaries with anterolateral foramena
G H F10(1)Sesamoid articulars are present
S^2 HPD F12(0)Angulars are noncylindrical
S^2I PD G 7(0)Interopercula are shorter than preopercula
I15(1)Hypobranchials with teeth
S^2IHP I25(0)First epibranchials without uncinate processes
G S IHPD I29(0)Epibranchials without toothplates
G S IHPD I32(0)First pharyngobranchials absent
G S^2IH D J10(0)Cleithra without posteromedial extensions to the coracoids
G S^1IH J16(1)Coracoids with posterior extensions past actinosts
G^3S^3 P J19(0)Scapular foramina incomplete
G S^3 H J21(0)Scapular foramena circular
G^1S^1 J29(1)Fourth actinosts enlarged
G PD K 7(1)Pelvic plates are joined by medial sutures
G^2 D K16(1)Pelvic plates are pierced by lateral foramena

Table Ev.1 continued
S^2 K17 5 pelvic rays
G^1S L18(0)The anterior end of the soft dorsal lies over caudal vertebrae
G S^2[illegible] M21(1)Haemal arches are pierced by lateral foramina
G[illegible] N 7(0)Parhypural fused to hypurals
G[illegible] N 8(0)Parhypural not autogenous
G[illegible] D N13(0)Upper hypurals are fused to one another

Atherinomorpha

Apomorphies
G S IH E 3(0)Premaxillae lack articular processes
H E 9(1)Maxillary hooks present
G K 8(1)Pelvic plates bear ascending processes

Apomorphic tendencies
G^1S^3 C 7(0)Dermopterotics do not bear lateral canals
E16(1)Palatines fused to ectopterygoids
S^1IHPD F 5(0)Posterior borders of dentaries slightly cleft
K 4(0)Pelvic plates lack anteromedial processes

Percomorpha

Apomorphies
G^1 H D E 4(1)Premaxillae bear postmaxillary processes

Apomorphic tendencies
G S^2 P F 8(0)Articulars lack subdentary processes
S^1 P I37(0)Fourth pharyngobranchials absent
G^1S^3I P J 3(1)Posttemporals resemble lateral scutes

Holocentrus (Beryciformes)

Apomorphies
G^1S^2 PD J 4(0)Posttemporals lack anterodorsal processes

(Perciformes + Scorpaeniformes)

Apomorphies
G D K11(1)Pelvic and pectoral girdles touch each other

Apomorphic tendencies
G^1S IHP B18(0)Sclerotic rings absent
D C 2(0)Supraoccipital crest absent

Scorpaeniformes

Apomorphies
P A 5(1)Median ethmoid with ventral transverse flange

Table Ev.1 continued

S^3I D I12(1)Hypobranchials with anterior processes
D J38 Pectoral fin length more than 25% of standard length

Apomorphic tendencies

G^1S A 4(1)Lateral ethmoids with anterolateral extensions
S^3I PD A 6(1)Medial projections of each lateral ethmoid fused
G^3S^3 H A 8(1)Lateral ethmoid ventromedial projections with posterior processes
P G19(1)Preopercula bend medially to form the floors of the branchial chambers
S I P J20(1)Scapulae reduced to the size of actinosts
I P J24(1)Scapulae and first actinosts fused
G S^2I L16(0)Central dorsal pterygiophores flattened dorsoventrally
S IHPD M30 Epipleural ribs are absent
G H N 9(0)Parhypural does not support principal caudal raYS

Scorpaenoidei

Apomorphies

G^1 K20 Pelvic plate length more than 15% of standard length

Apomorphic tendencies

G^2S^2 P F25(0)Hyomandibulae lack medial foramina on shafts
S^2 D G 9(0)Posterior ends of interopercula are not expanded
G^2S^3I PD M22(0)Prehaemapophyses are absent
G S^2I P M23(0)Posthaemapophyses are absent

Cottoidei

No distinguishing synapomorphies

<u>Cottus</u>

Apomorphies

G S^3IHP D 5(0)Trigeminofacialis anterior foramina incomplete
G E17(1)Palatine heads bear lateral projections
G IHP E23(0)Separate endopterygoids absent
G S^3 D I11(0)Hypobranchials not cylindrical
G S I PD N 4(0)First uroneural not separate from the hypurals

<u>Asterotheca</u>

Apomorphies

P A 9(1)Ventromedial projections extend posteriorly into orbit
I P I33(0)Second pharyngobranchials absent
G I D L17(1)Distal and medial pterygiophores fused

Perciformes

Table Ev.1 continued

No distinguishing apomorphies

Apomorphic tendencies

	P	B14(1)Dermosphenotics bear lateral canals
S^1I		G 8(1)Anterior ends of interopercula are expanded
S	P.	M24(0)Haemal laminae short

Ammodytes

Apomorphies

I		E19(0)Ectopterygoids do not lie along anterior borders of the quadrates
S^1	P	F 1(0)Dentaries toothless
G	P	F 4(1)Dentaries touch angulars
G^3S		F16(1)Quadrate shafts make up over half their lengths
S^3I		J11(0)Cleithra lack anterior symphysis
S		M31Body depth 10% of standard length

Table Ev.2 : Consequences of placing study groups with different framework groups VI: numbers of synapomorphies (S) and shared apomorphic tendencies (A) supporting different placements and the sum of both consistent with (C) each placement

	Gasterosteiformes			Syngnathiformes			*Indostomus*			*Hypoptychus*			*Pegasus*			*Dactylopterus*		
Sister Group	**S**	**A**	**C**	**S**	**A**	**C**	**S**	**A**	**C**	**S**	**A**	**C**	**S**	**A**	**C**	**S**	**A**	**C**
Saurida	0	na	0	1	na	1	1	na	1	1	na	1	1	na	1	0	na	0
Percopsis + Acanthopterygii	22	10	32	20	7	27	11	6	17	17	4	21	14	3	17	14	5	19
Percopsis	2	na	34	1	na	28	0	na	17	1	na	22	2	na	19	0	na	19
Acanthopterygii	7	21	62	8	23	59	6	15	38	4	14	39	8	17	42	9	15	43
Atherinomorpha	2	1	65	1	3	63	1	2	41	2	1	42	0	2	44	0	1	44
Percomorpha	1	2	65	0	3	62	0	1	39	1	0	40	0	3	45	1	0	44
Holocentrus	1	na	66	1	na	63	0	na	39	0	na	40	1	0	46	1	0	45
Perciformes + Scorpaeniformes	1	1	67	0	1	63	0	1	40	0	1	41	0	1	46	1	1	46
Scorpaeniformes	0	4	71	1	6	70	1	5	46	0	3	44	1	5	52	2	2	50
Scorpaenoidei	0	4	75	0	4	74	0	2	48	0	0	44	0	3	56	0	2	52
Cottoidei	0	0	71	0	0	70	0	0	48	0	0	44	0	0	56	0	0	52
Cottus	5	na	76	4	na	74	3	na	51	2	na	46	3	na	59	2	na	54
Asterotheca	1	na	72	0	na	70	2	na	50	0	na	44	2	na	58	1	na	53
Perciformes	0	0	67	2	0	65	1	0	41	0	0	41	2	0	48	0	0	46
Ammodytes	2	na	69	5	na	70	2	na	43	0	na	41	2	na	50	0	na	46

Table Ev.3 : Apomorphies appearing only within study groups
with the study groups in which they appear, character number, state, and description.

S^2	A1(0) nasals absent
S	A13(1) Median ethmoid with ventral ossification
S	A14(1) Median ethmoid with ventrolateral ridges
I	A18(1) Vomer head fused to median ethmoid
S^2	A21(0) Vomer shaft does not meet parasphenoid
S	A22(1) Vomer shaft exposed dorsally
G S IHP	A23 Snout length over 25% of head length
G^2 HP D	A24 Median ethmoid length less than 17% of head length
S^3	A24 Median ethmoid length more than 39% of head length
G^2	A25 Vomer length less than 9% of head length
G S^1 H	A25 Vomer length more than 25% of head length
S^2	B1(0) Frontals lack supraorbital canals
G S^2	B5(1) Frontals touch parasphenoid ventrolaterally
S I	B6(0) Lachrymals lack infraorbital canals
S^3	B8(1) Lachrymals subdivided anteriorly
G	B11 (0) Pterosphenoids are absent
G^2S P^1	B19 Orbit length less than 21% of head length
P	B20 Frontal length less than 36% of head length
S^2	C6(1) Epiotics articulate with ossified ligaments
S^2	C12 Supraoccipital length less than 10% of head length
S^2IH	D3(0) Parasphenoid without distinct lateral processes
S	D16(0) Exoccipitals do not separate pterotics and basioccipital
S^2I P	D18 Parasphenoid length less than 48% of head length
S^2	D19 Neurocranium length less than 16% of standard length
S^3	D19 Neurocranium length more than 33% of standard length
S P	E1(0) Premaxillae not toothed
S^2I P	E11(0) Palatine heads not cylindrical
S^1	E13(1) Palatine shafts lie over lateral surfaces of pterygoids
I	E18(1) Palatines fused to median ethmoid
S^1 P	E24(0) Separate metapterygoids absent
G^2S	E26 Palatine length less than 11% of head length
G S	F20(1) Symplectics bear anterodorsal laminae
G^2 H	F26(0) Hyomandibulae lack anterior laminae
S^2I	G2(0) Preopercula lack preoperculomandibular canals
S P D	G4(1) Posterior borders of preopercula are expanded
S^2 P D	G11(0) Opercula do not form most of the gill covers
G S H	H9(0) Ceratohyal shafts lack branchiostegals
S D	H10(0) Ceratohyal posterior heads lack branchiostegals
S	H14(0) Interhyals not cylindrical
G^1S^1 HP D	H18 (1) Urohyal flanges entire
S	I1(0) Basibranchial #1 absent
S^1	I2(0) Basibranchial #2 absent
S^2 P	I9(0) Second hypobranchials absent
S^2 P	I10(0) Third hypobranchials absent
G S IHP D	I18(0) Second ceratobranchials without toothplates
S H	I23(0) Fifth ceratobranchials without teeth
S^1I P	I27(0) Third epibranchials lack uncinate processes
S^3	I30(1) First epibranchials with teeth
S^3	I34 (0) Second pharyngobranchials toothless
S^3	I36 (0) Third pharyngobranchials toothless
S^3 P D	J6(1) Posttemporals co-ossified with cranium
S D	J7(0) Supracleithra absent
G S^2 H	J15(1) Coracoid shafts incised anteriorly
G S^1	J18(1) Ectocoracoids present
S	J26(1) Actinosts with lateral distal flanges
G S^1IH	[illegible] Fourth actinosts with anteroventral spikes
G^1 P	[illegible] ctinosts attached to one another via sutures

Table Ev.3 continued

H		J36 Fewer than 10 pectoral rays
S^2I	D	J36 More than 19 pectoral rays
S^2		J37 Snout - pectoral base less than 17% of standard length
S^1		J37 Snout - pectoral base more than 42% of standard length
G^2S I		J38 Longest pectoral ray less than 10% of standard length
S^3I		K6(0) Pelvic plates lack medial processes
S		K18 Snout - pelvic base more than 56% of standard length
G^4S^2	P^1D	K19 Anterior process of pelvic plate less than 70% of plate length
S H		K20 Pelvic plate length less than 5% of standard length
G^2		K20 Pelvic plate length more than 18% of standard length
G S^2I		L2(1) Separated dorsal spines
G		L5(1) Supraneurals behind dorsal
S		L7(1) Posterior dorsal pterygiophores fused
G^1		L21 More than 16 dorsal spines
S		L22 Snout - first dorsal element more than 67% of standard length
G^3S^2I		L23 First dorsal spine length less than 5% of standard length
S^2IHP		L24 Fewer than 8 anal rays
S		L26 Snout - anal base more than 70% of standard length
S^3		L27 Anal base length less than 9% of standard length
S^1	P D	M3(1) First four vertebra are fused
G S^2IHP		M11(0) Postneurapophyses absent
S^2I		M12(1) Ossified tendons are present in the axial musculature
S^3I	P D	M13(1) Neural arches are closed for their full lengths
S^2	D	M17(0) Anterior transverse processes absent
	P D	M18 (1) Transverse bones are present
S^1I		M25(1) Haemal canal closed over its full length
G^2S		M26(1) Vertebrae bear lateral processes to scutes or scales
S^2I	P^1D	M27 Fewer than 23 vertebrae
S^2		M28 Less than 29% of vertebrae are precaudal
G^2S I	P	M30 Fewer than 7 pleural ribs
S^2		M31 Body depth less than 9% of standard length
	P D	M32 Body width less than 22% of standard length
S	P D	M33 Length of first four vertebrae more than 11% of standard length
S^1		M34 Average length of first six vertebrae more than 1.2 times average length of central vertebrae
I		M34 Average length of first six vertebrae less than 0.7 times average length of central vertebrae
G^2	D	M35 Average length of last six vertebrae more than 1.1 times average length of central vertebrae
S^3		M35 Average length of last six vertebrae less than 0.67 times average length of central vertebrae
S^2		N1(0) Caudal absent
S	P D	N16 Fewer than 6 dorsal principal caudal rays
S^1	P	N17 Fewer than 5 ventral principal caudal rays
G^3S^3IH		N18 Longest caudal ray less than 10% of standard length
S	P	N19 Depth of caudal peduncle less than 4% of standard length
S^1	P^1	N20 Length of hypural complex ;ess than 1.7% of standard length
G^2S^2	P	N21 Length of hypural complex less than 1.2 times average length of central vertebrae

Table Ev.4: Consequences of placing study groups with one another, VII: numbers of synapomorphies (S) and apomorphic tendencies (A) supporting each placement

	Gasterosteiformes		Syngnathiformes		*Indostomus*		*Hypoptychus*		*Pegasus*		*Dactylopterus*	
	S	A	S	A	S	A	S	A	S	A	S	A
Gasterosteiformes			4	18	5	4	7	4	4	6	2	3
Syngnathiformes					5	17	4	8	6	21	5	12
Indostomus							6	na	9	0	5	na
Hypoptychus									5	0	3	na
Pegasus											10	0

	AULI	AULO	S	G	C	P	A
A	0	0	1	1	1	1	1
B	1	1	0	0	0	0	0
C	1	1	1	0	0	0	0
D	1	0	0	0	0	0	0
E	1	0	0	1	1	0	0

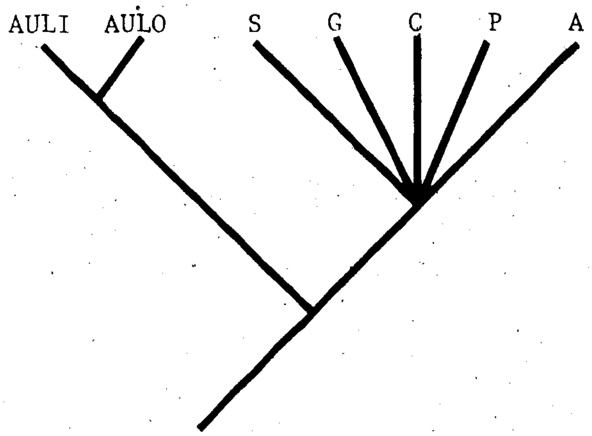
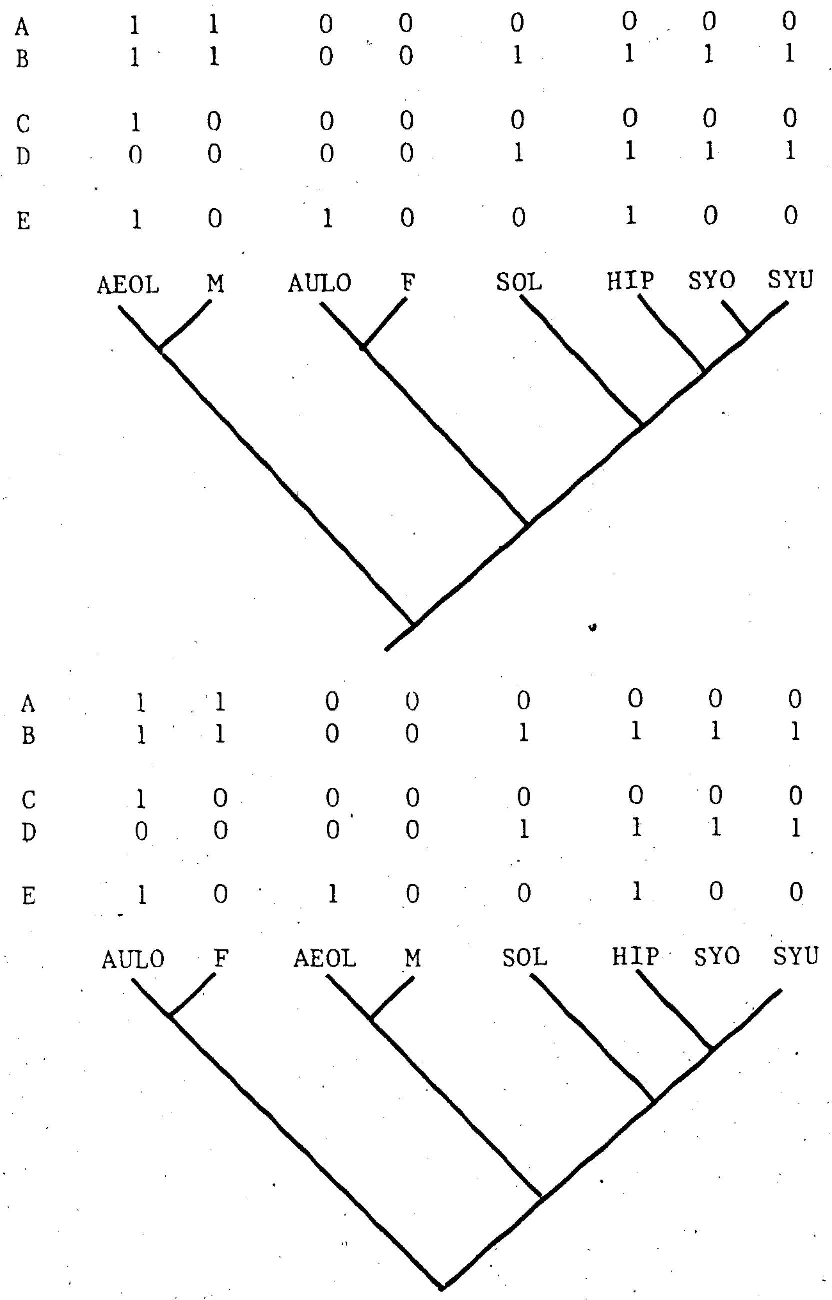


Figure Ev.1 : Apomorphic tendencies of Gasterosteiformes

Characters A–C – Type 1 apomorphic tendencies, may appear in the common ancestor of Gasterosteiformes

Character D – Type 2 apomorphic tendency, appearing independently once within Gasterosteiformes

Character E – Type 3 apomorphic tendency, appearing independently two or more times within Gasterosteiformes



	AEOL	M	AULO	F	SOL	HIP	SYO	SYU
A	1	1	0	0	0	0	0	0
B	1	1	0	0	1	1	1	1
C	1	0	0	0	0	0	0	0
D	0	0	0	0	1	1	1	1
E	1	0	1	0	0	1	0	0

	AULO	F	AEOL	M	SOL	HIP	SYO	SYU
A	1	1	0	0	0	0	0	0
B	1	1	0	0	1	1	1	1
C	1	0	0	0	0	0	0	0
D	0	0	0	0	1	1	1	1
E	1	0	1	0	0	1	0	0

Figure Ev.2 : Apomorphic tendencies of Syngnathiformes

Characters A and B - Type 1 apomorphic tendencies, may appear in the common ancestor of Syngnathiformes

Characters C and D - Type 2 apomorphic tendencies, appearing independently once within Syngnathiformes

Character E - Type 3 apomorphic tendency, appearing independently two or more times within Syngnathiformes

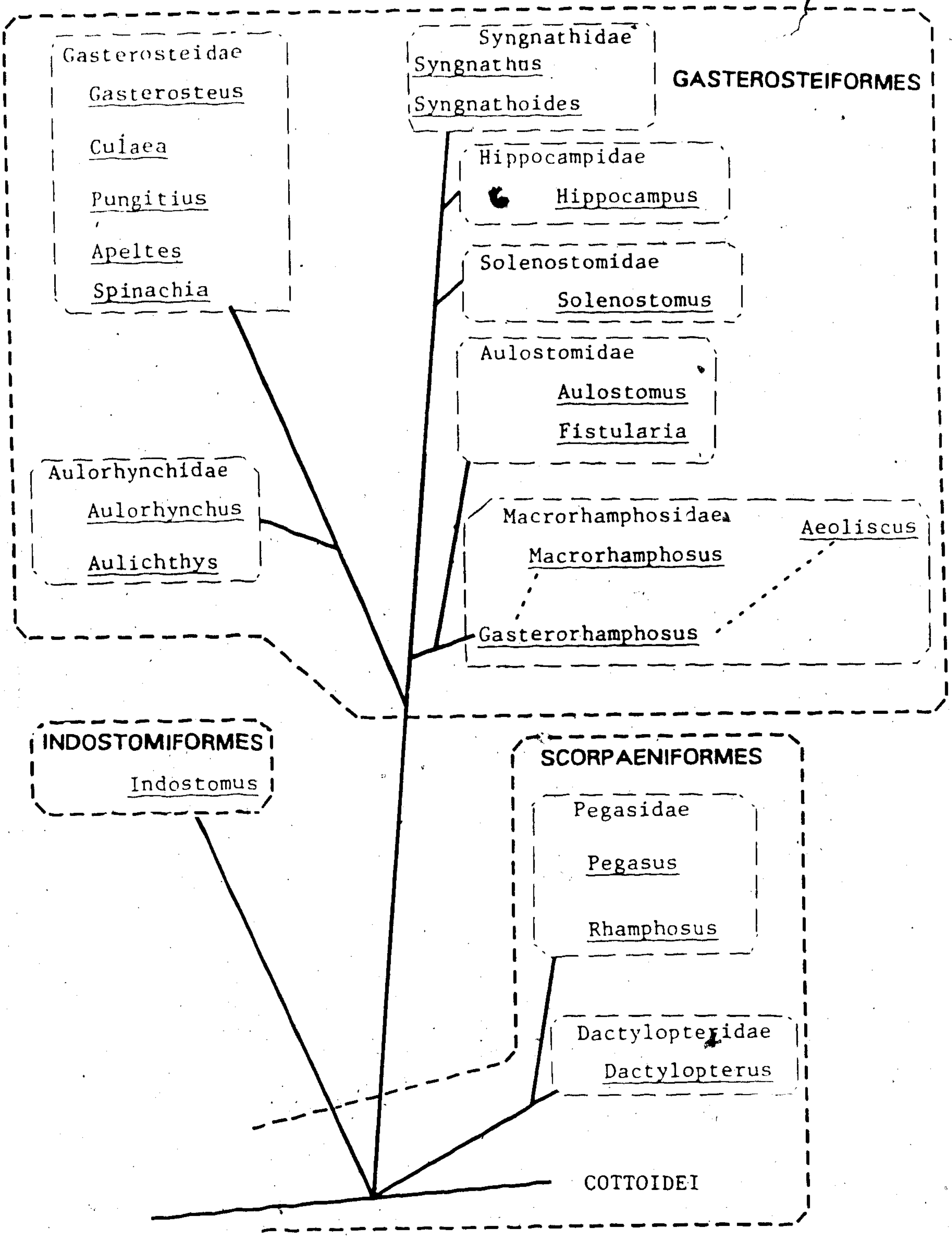


Figure Ev.3: Evolutionary tree of the study groups

V. Discussion

All three schools of systematics recognize particular relationships both among study groups and between study groups and framework taxa. All recognize affinities between Dactylopterus and Pegasus and between Dactylopterus and Scorpaeniformes, particularly Asterotheca. All also find Gasterosteiformes-Scorpaeniformes relationships and find that Syngnathiformes and Indostomus are more closely related to other study groups than to any framework taxa.

The three schools yield results disagreeing on five main points. These are:

1. Is Gasterosteiformes more closely related to Hypoptychus than it is to Cottoidei? (Phylogenetics and phenetics - yes; evolutionary systematics - no)
2. Is Gasterosteiformes more closely related to Syngnathiformes than it is to Cottoidei? (Evolutionary systematics and phylogenetics - yes; phenetics - no)
3. Is Gasterosteiformes more closely related to (Pegasus+Dactylopterus) than either is to Cottoidei? (Phylogenetics - yes; evolutionary systematics and phenetics - no)
4. Is Gasterosteiformes more closely related to Syngnathiformes than it is to (Pegasus+Dactylopterus)? (Evolutionary systematics - yes; phylogenetics and phenetics - no)
5. Is (Pegasus+Dactylopterus) more closely related to Indostomus than it is to Cottoidei? (Phylogenetics and phenetics - yes; evolutionary systematics - no)

Comparison between the different schools' answers to these problems is possible only if they can be tested against a criterion which is not dependent on the particular aims and philosophical bases of one of the schools. The criterion which has been most widely recommended for this purpose is 'Information content' (Farris, 1979a) or 'Predictivity' (Gower, 1974). Proponents of all three schools have recommended this as a criterion for evaluating classifications (for examples, see Farris, 1979a; Archie, 1984). Information content is the extent to which the classification, or hierarchical scheme of relationships, expresses the distributions of the character states used to construct it. The ideal classification or relationship scheme expresses all the data in as few statements as possible, thus maximizing both its informativeness and its efficiency.

One measure of information content is Gower's W, used above to compare phenetic methods (see Fig. P1). This method is not applicable to phylogenetic or evolutionary classifications, however, because it measures the extent to which the distributions of all states of a character are reflected in the groups recognized. In Figure Di.1, for example, the '1' state of the character shown is described by the group AB at the three-cluster level, but the '0' state appears in two separate groups; the hierarchy's failure to explicitly predict the distribution of the '0' state appears, in the measurement of Gower's W, at the two- and one-cluster levels, where the majority character states of the groups ABC and ABCD fail to correctly predict the states found in C and D.

Phylogenetic criteria for measuring information content view each hierarchical group as representing a statement about one character state, the apomorphic state. Indices like Farris' (1980) statement count or Archie's (1980; 1984) predictive value, therefore, view the hierarchy in Figure Di.1 as maximally informative, containing both the explicit information "A and B have state (1)" and the implied information, "C and D do not have state (1)". I will call such statements, which imply their complements, "ONLY" statements (e.g. "(ONLY) A and B have state (1)"). Phylogeneticists measure the information content of a hierarchy by the number of ONLY statements required to describe the distributions of all character states. Farris measures this simply by counting the statements; Archie uses a numerical index similar to Gower's W but only considering the number of correct predictions made within the hierarchical group that contains all occurrences of the character state (the minimally inclusive taxon). This approach is identical to that used in the evolutionary systematic analyses, where all apomorphies appearing more than once are regarded as apomorphic tendencies of the smallest monophyletic group that contains all their occurrences.

Are information content indices which measure how well a hierarchy explicitly describes one state of each character applicable to the results of analyses which aim to explicitly describe the distributions of all character states, or vice versa? The goal accepted by proponents of all schools is simply to describe the distributions of all character states in the fewest statements, so unless explicit statements are viewed as intrinsically more valuable than their implied complements there is no reason not to apply phylogenetic information content indices to phenetic results. The results of both schools should be compared for information content by that index which expresses their maximum possible information content.

Farris (1979a, 1980) presents a mathematical argument to show that while the total numbers of shared character states can be recovered from a matrix of apomorphic similarities (i.e. from the set of ONLY statements describing the hierarchy), the converse is not true; this is intuitively obvious in that the use of ONLY statements allows one statement to describe the distributions of two character states. Given this attribute of ONLY statements they must be accepted as the most efficient way of expressing information about the data, and information indices relying on them must be applicable to any systematic method which gives efficient expression of the data as its major goal, which phenetics does.

The question of these indices' applicability to evolutionary systematics is more difficult, since evolutionary systematics attempts not to most efficiently express all the data but to most efficiently express the distributions of the most highly weighted characters and character states. Farris (1979a) has indirectly addressed this question in his discussion of rooting, or of the problem of deciding which state of a character shall be described by an ONLY statement and which left to implication.

Farris' argument deals mainly with presence/absence characters, and is based on the concept that an ONLY statement about the presence of a character contains more information than one about its absence. In his example, the statement "Articulars are present" implies the presence of heads, jaws, bone, etc., and is thus a more informative statement than "articulars are absent". This is essentially an argument about correlation, a highly informative character state being one that is logically correlated with a number of characters not used in the study, but it can also be stated in terms of the directly and indirectly implied information about the distribution of the other character state, as follows.

In an analysis of chordata the statement "(ONLY) gnathostomes have the articular" directly implies the statement "non-gnathostome chordates do not have the articular". It INDIRECTLY implies the statement "All organisms except gnathostomes do not have the articular", and since we hope the immediate hierarchy will be part of an overall hierarchy of all organisms, we are concerned with these indirect implications. The alternative ONLY statement, "(ONLY) non-gnathostome chordates do not have the articular", has an equally accurate direct implication ("gnathostomes have the articular"), but its indirect implication ("all organisms except non-gnathostome chordates have the articular") is obviously false.

The idea of choosing to describe the distributions of character states in a way that maximizes the accuracy of both explicit ONLY statements and of their implied complements is not new. It corresponds to the ideal of character homogeneity within groups and heterogeneity between them held by all three schools (again see Farris, 1979a and Archie, 1980; 1984) and even more directly to the phenetic goal of minimizing exclusion errors; the number of occurrences of a character state outside the cluster which it distinguishes (Gower, 1974). It provides an information-content based rationale not only for character / character state weighting but for the use of comparison with other organisms in determining weights. If a character / character state is present in many other organisms, the information implied by an ONLY statement about its distribution within the immediate classification will be less accurate.

All three schools of systematics share the goal of expressing the most information about characteristics in the fewest statements; therefore the efficiency of all in recognizing the most informative groupings of the species studied can be fairly judged on the numbers of ONLY statements, and modifiers of these, which they require to express the distributions of the most informative character states, these being the ones not found in organisms outside the groups being studied (The most informative character states for the study groups are listed in Table Di. 1). This is equal to the length of the hierarchical tree containing the study species, since a new statement must be made at every character state change.

Since the criteria used to recognize the most informative character states are those used in evolutionary weighting, one would expect evolutionary systematic results to yield the hierarchy which best expresses their distribution. This is true, but by a narrow margin; the evolutionary systematic tree (Fig. Ev:3) requires 247 statements (or steps) to express the distributions of highly informative characters (Table Di. 1), as opposed to 250 statements for phenetics (Figs. P2-5) and 252 for phylogenetics (Fig. Cl. 15). The slightly shorter evolutionary and phenetic trees seem to be due to their recognition of a separate (<u>Pegasus</u>+<u>Dactylopterus</u>) grouping; when phylogenetic results are revised to contain this group, they express the data in only 248 statements. The presence or absence of a (Gasterosteiformes+<u>Hypoptychus</u>) group does not make much difference. Two characters can be explained more parsimoniously with the introduction of this group, and one requires an extra statement. The presence of a (Gasterosteiformes+Syngnathiformes) group also makes little difference, saving one statement, and the amalgamation of all the study groups saves two statements.

No attempt was made to assess information contents with respect to framework group interrelationships. There are several characters, however, which distinguish such groups as (Percopsis + Acanthopterygii), Acanthopterygii, Percomorpha, and (Perciformes + Scorpaeniformes), and which would be explained by the phylogenetic and evolutionary results better than by the phenetic results, which do not recognize these groups.

Comparison of the results by information criteria does not provide strong reason to prefer any one of the three hypotheses of relationship listed above. In the absence of more data, therefore, it is necessary either to accept only the points on which all three schools agree, dividing the study groups into four separate lineages which form a pentachotomy with Cottoidei, or to choose among the competing results on other grounds. I have accepted the results of the evolutionary analysis.

My preference for this analysis is based on the fact that it includes both all the information prescribed above for a theoretically 'most informative' hierarchy and some additional information which is not recognized by any other analyses; this is information on apomorphic tendencies (Cantino, 1982; Saether, 1983). The use of these characters in determining relationships is not justified by information content, for it involves describing groups as possessing, and being distinguished by the possession of, character states which in fact appear independently in a few species of each group (Rasmussen, 1983). They appear to represent a real phenomenon, however, and one which is significant in the diagnoses of higher taxa (Cantino, 1982). In addition, parallelism is prevalent in Gasterosteiformes at the species level (e.g. Bell, 1974). Parallelism is certainly a problem for the systematist, and it both obscures relationships and reduces the information content of the hierarchy (which are really the same thing). If we interprete the character states in organisms as the results of evolutionary change, however, we can view even parallelisms as containing information about relationships, since the likelihood of two closely related (genetically similar) organisms' developing the same apomorphic trait is higher than the likelihood of its appearance in two distantly related and/or genetically dissimilar organisms. The use of apomorphic tendencies is an attempt to extract information about unexpressed portions of the genome from apomorphic character states which would otherwise be discarded as intractable.

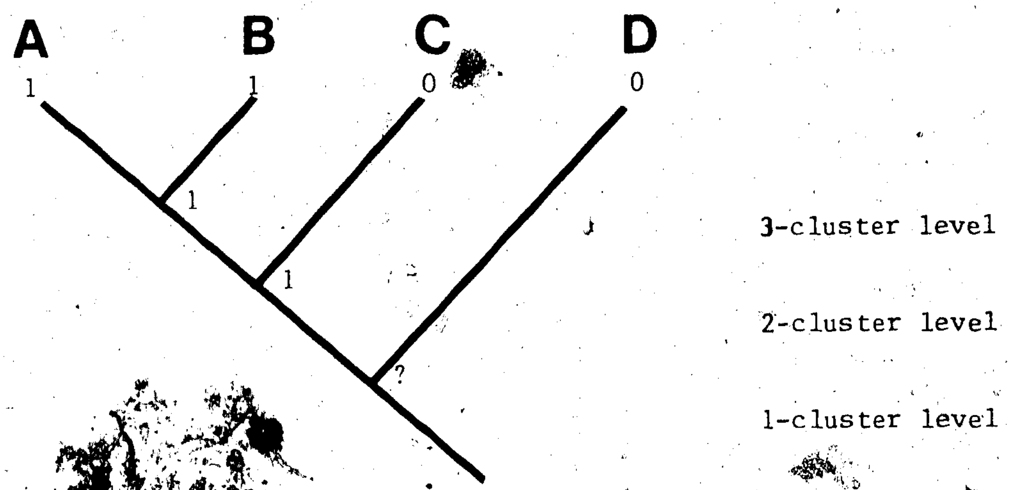
My classification of all multiple occurrences as apomorphic tendencies errs on the side of optimism as much as classifications which regard all multiple occurrences as uninformative homoplasies err on the side of pessimism. It is the same assumption, however, that Archie (1980, 1984) found necessary for the measurement of information content. As such, it is compatible with numerical phylogenetic analyses. Ideally, hard data on the genetic implications of different character state changes should be used to identify possible apomorphic tendencies. In the absence of these data, I feel it is still more useful to identify the possibility of a shared genetic basis for apomorphies occurring several times, particularly when they are apparently unique to and widespread among the groups being compared, than to classify them as uninformative homoplasies simply because their distribution does not correspond to a monophyletic grouping.

Table Di.1 : **Highly informative character states appearing only within study groups** with the study groups in which they appear, character number, state, and description.

S	A13(1) Median ethmoid with ventral ossification
S	A14(1) Median ethmoid with ventrolateral ridges
I	A18(1) Vomer head fused to median ethmoid
S^2	A21(0) Vomer shaft does not meet parasphenoid
S	A22(1) Vomer shaft exposed dorsally
G S IHP	A23 Snout length over 25% of head length
G^2 HP D	A24 Median ethmoid length less than 17% of head length
S^3	A24 Median ethmoid length more than 39% of head length
G^2	A25 Vomer length less than 9% of head length
G S^1 H	A25 Vomer length more than 25% of head length
G S^2	B5(1) Frontals touch parasphenoid ventrolaterally
S^3	B8(1) Lachrymals subdivided anteriorly
G^2S P^1	B19 Orbit length less than 21% of head length
P	B20 Frontal length less than 36% of head length
S^2	C6(1) Epiotics articulate with ossified ligaments
S^2	C12 Supraoccipital length less than 10% of head length
S	D16(0) Exoccipitals do not separate pterotics and basioccipital
S^2I P	D18 Parasphenoid length less than 48% of head length
S^2	D19 Neurocranium length less than 16% of standard length
S^3	D19 Neurocranium length more than 33% of standard length
S^1	E13(1) Palatine shafts lie over lateral surfaces of pterygoids
I	E18(1) Palatines fused to median ethmoid
G^2S	E26 Palatine length less than 11% of head length
G S	F20(1) Symplectics bear anterodorsal laminae
S P D	G4(1) Posterior borders of preopercula are expanded
S^2 P D	G11(0) Opercula do not form most of the gill covers
G S H	H9(0) Ceratohyal shafts lack branchiostegals
S D	H10(0) Ceratohyal posterior heads lack branchiostegals
S	H14(0) Interhyals not cylindrical
$G^1$$S^1$ HP D	H18 (1)Urohyal flanges entire
S^3	I30(1) First epibranchials with teeth
S^3 P D	J6(1) Posttemporals co-ossified with cranium
G S^2 H	J15(1) Coracoid shafts incised anteriorly
G S^1	J18(1) Ectocoracoids present
S	J26(1) Actinosts with lateral distal flanges
G S^1IH	J28(1) Fourth actinosts with anteroventral spikes
G^1 P	J31(1) Actinosts attached to one another via sutures
H	J36 Fewer than 10 pectoral rays
S^2I D	J36 More than 19 pectoral rays
S^2	J37 Snout - pectoral base less than 17% of standard length
S^1	J37 Snout - pectoral base more than 42% of standard length
G^2S I	J38 Longest pectoral ray less than 10% of standard length
S^3I	K6(0) Pelvic plates lack medial processes
S	K18 Snout - pelvic base more than 56% of standard length
G S^2 P^1D	K19 Anterior process of pelvic plate less than 70% of plate length
S H	K20 Pelvic plate length less than 5% of standard length
G^2	K2[illegible]elvic plate length more than 18% of standard length
G S^2I	L2(1) Separated dorsal spines
G	L5(1) Supraneurals behind dorsal
S	L7(1) Posterior dorsal pterygiophores fused
G^1	L21 More than 16 dorsal spines
S	L22 Snout - first dorsal element more than 67% of standard length
$G^3$$S^2$I	L23 First dorsal spine length less than 5% of standard length
S^2I P D	L24 Fewer than 8 anal rays
S	L26 Snout - anal base more than 70% of standard length
S^3	L27 Anal base length less than 9% of standard length
S^1 P D	M3(1) First four vertebra are fused

Table Di.1, continued

S^2I		M12(1) Ossified tendons are present in the axial musculature
S^3I	P D	M13(1) Neural arches are closed for their full lengths
S^1I		M25(1) Haemal canal closed over its full length
G^2S		M26(1) Vertebrae bear lateral processes to scutes or scales
S^2I	P^1D	M27 Fewer than 23 vertebrae
S^2		M28 Less than 29% of vertebrae are precaudal
G^2S I	P	M30 Fewer than 7 pleural ribs
S^2		M31 Body depth less than 9% of standard length
	P D	M32 Body width less than 22% of standard length
S	P D	M33 Length of first four vertebrae more than 11% of standard length
S^1		M34 Average length of first six vertebrae more than 1.2 times average length of central vertebrae
I		M34 Average length of first six vertebrae less than 0.7 times average length of central vertebrae
G^2	D	M35 Average length of last six vertebrae more than 1.1 times average length of central vertebrae
S^3		M35 Average length of last six vertebrae less than 0.67 times average length of central vertebrae
S	P D	N16 Fewer than 6 dorsal principal caudal rays
S^1	P	N17 Fewer than 5 ventral principal caudal rays
G^3S^3IH		N18 Longest caudal ray less than 10% of standard length
S	P	N19 Depth of caudal peduncle less than 4% of standard length
S^1	P^1	N20 Length of hypural complex ;ess than 1.7% of standard length
G^2S^2	P	N21 Length of hypural complex less than 1.2 times average length of central vertebrae



Gowe[illegible]

[illegible]level...........W = 4 out of 4
2-cluster level...........W = 3 out of 4
1-cluster level...........W = 2 out of 4
TOTAL W.........................9 out of 12

Farris' statement number criterion:

"AB has state (1)" completely explains the distribution of state (1) it implies, "C and D have state 0 " (assuming there are only two possible states); this completely explains the distribution of state (0)

One statement explains one character; maximum information content.

Archie's Predictive Value:

Minimally inclusive taxon for state (1) is AB. Its majority character state is (1). Two correct predictions about states within AB are made by the majority state.

Predictive value = 2 correct predictions/ 2 possible predictions

PV = 1 : maximum predictive value

Figure Di.1: Comparing phenetic and phylogenetic criteria of information content

VI. Conclusions

The groups Gasterosteiformes, Syngnathiformes, Indostomus, Hypoptychus, Pegasus, and Dactylopterus may form a single monophyletic polythetic taxon arising from the cottoid lineage of Scorpaeniformes, but no highly informative characters define this group. All members of it, however, share a larger number of synapomorphies with one another than with any framework taxa. Two separate lineages are evident, one giving rise to (Pegasus+Dactylopterus), the other to Syngnathiformes and Gasterosteiformes (Figure Ev. 1). The position of Indostomus is ambiguous; although total numbers of synapomorphies and overall similarities place it with (Pegasus+Dactylopterus), few of the character states uniting them are highly weighted. It does, however, appear to be related to Cottoidei and to the syngnathiform, and dactylopterid lineages. Hypoptychus is likewise placed with Gasterosteiformes by total synapomorphies and overall similarities, but only two of the shared character states are of high weight. Hypoptychus also shares one highly weighted character with Atherinomorpha, so it cannot be firmly placed with either group and must be made *incertae sedis*.

The relationships among the study groups are not obvious or precisely determined, and many of them are based on apomorphic tendencies rather than on distinguishing apomorphies. My use of the evolutionary systematic concepts of apomorphic tendencies and *a priori* weighting do not, however, dictate the use of evolutionary systematic methods of constructing a classification. The evolutionary classification contains paraphyletic groups (e.g. Scorpaeniformes), which potentially reduce the efficiency of the classification; for example, if the paraphyletic taxon Scorpaeniformes is separated from Gasterosteiformes it is then impossible to describe the distribution of a synapomorphy uniting Gasterosteiformes and Cottoidei in fewer than two statements. Since only the presence of synapomorphies uniting Gasterosteiformes and Cottoidei justifies my placing Gasterosteiformes as the descendants of a cottoid ancestor, the rejection of the paraphyletic taxon Scorpaeniformes results in a classification which obscures the data which I view as indicating relationships.

The advantage of the evolutionary classification is the amount of definition associated with its groups; the paraphyletic Scorpaeniformes can be distinguished by possession of suborbital stays (and, by implication, of a particular genetic makeup resulting in their development). It is not clear to me, however, that it is valuable to retain a set of distinguishing apomorphies whose justification is their indication of underlying genetic similarity, when the data indicate that the actual genetic similarity shared by all the scorpaeniform fishes and their derivatives is the presence of a genome which tends to evolve into these apomorphic characters. If apomorphies like the suborbital stay, which appears in several different morphologies within the taxon it distinguishes, are viewed as the expressions of an apomorphic tendency, there is no reason to exclude those members of the scorpaeniform lineage which have lost them from the taxon Scorpaeniformes.

In the interests of most clearly expressing the distributions of both apomorphies and hypothesized apomorphic tendencies, I choose to represent the relationships in Figure Ev. 1 as directly as possible in an indented classification, avoiding the construction of paraphyletic taxa. The three study group lineages are all assigned subordinal status, because there are not enough data to justify placing one of them as the sister group of the other two. Families within the syngnathoid lineage are named by phyletic sequencing (see Wiley, 1981). The proposed classification is:

Order Scorpaeniformes (in part)
    Suborder Cottoidei
    Suborder Gasterostoidei
        Superfamily Gasterosteoidae
            Family Aulorhynchidae
            Family Gasterosteidae
        Superfamily Syngnathoidae
            Family Centriscidae
                Subfamily Macrorhamphosinae
                Subfamily Aulostominae
            Family Solenostomidae
            Family Syngnathidae
    Suborder Dactylopteroidei
        Superfamily Dactylopteroidae
        Superfamily Pegasoidae

Suborder Indostomoidei

The suborder **Gasterostoidei** is distinguished by only a few synapomorphies found in all its members, or even at the basal nodes of its subgroups. These are:

1. Suborbital series are incomplete
2. Basisphenoid is absent
3. Supraoccipital bears anterior wedge-like process
4. Ventral hypohyals overlap ceratohyals
5. Ceratohyal shaft does not support branchiostegal rays
6. Pelvic plates do not bear anteromedial spurs

It is, however, distinguished by the possession within both superfamilies of several parallel synapomorphies, or apomorphic tendencies. These include the following:

7. Symplectic laminae extend between the endo- and metapterygoids
8. Frontals and pterosphenoids are fused
9. Subopercula are expanded
10. Ectocoracoids are present
11. Bodies are elongated
12. Snouts are elongated and tubular
13. Dermal armor is present
14. Coracoid shafts are incised anteriorly
15. Fourth actinosts are connected to the coracoids by anteroventral processes
16. Vertebrae are connected to the lateral scutes by lateral processes.

Superfamily **Gasterosteoidae** is distinguished by the following characters:

1. Nasals bear ventromedial flanges
2. Prootics are excluded from the postorbital foramen
3. Palatine heads bear spurlike lateral projections
4. Ceratohyals and epihyals are connected by a dorsal strut
5. Urohyal bears dorsolateral flanges
6. Pelvic plates lack anteromedial flanges
7. Pelvic plates bear ascending processes
8. Supraneurals are present behind the soft dorsal

9. Pelvic spines are present.

The apomorphies distinguishing the families **Aulorhynchidae** and **Gasterosteidae** are listed in the phylogenetic section, in Table Cl.1.

Superfamily **Syngnathoidae** is distinguished by possession of the following characters:

1. Median ethmoid is ossified ventrally
2. Median ethmoid bears ventrolateral ridges
3. Vomer shaft is exposed dorsally
4. Prootics do not meet exoccipitals or basioccipital
5. Exoccipitals separate pterotics and basioccipital
6. Maxilla shafts are greatly expanded
7. Cranial condyles of each hyomandibula are connected
8. Ceratohyals are not constricted centrally
9. Interhyals are not cylindrical
10. Basibranchials are absent
11. Anterior vertebrae are elongated and fused
12. Soft dorsal is supported by caudal vertebrae only
13. Body is elongate, cased in armor.

The characters distinguishing the individual families of Syngnathoidae have been listed in the phylogenetic section (Table Cl.2).

Dactylopteroidei share with one another the following synapomorphies:

1. Nasals are fused, with ventral concavities into which the upper jaws retract
2. Posterior borders of preopercula are expanded to form most of the gill covers; opercula are reduced
3. Posttemporals are co-ossified with the cranium
4. Transverse bones are present
5. First four vertebrae are connected by complex sutures between the centra.

Dactylopterus is further distinguished by:

1. Supraoccipital crest is absent
2. Hyomandibulae have complex heads, with five articular surfaces
3. Hyomandibulae bear large posterior flanges

4. Ectopterygoids have long anterior processes
5. Posterior heads of ceratohyals do not support branchiostegals
6. Basibranchials have lateral flanges
7. Supracleithra are absent
8. Cleithra do not have distinct "head" and "shaft" regions
9. Postcleithra are present
10. First actinosts are pierced by foramina
11. Pelvic plates bear dorsomedial struts reaching to the cleithrum
12. Pelvic plates are pierced by lateral foramina
13. Supraneurals are absent
14. Anterior transverse processes are absent
15. Vertebrae bear dorsolateral spines on each side of the neural spines.

<u>Pegasus</u> is distinguished by:

1. Body depressed, with bony armor
2. Nasals fused into a rostrum
3. M[illegible]jections of lateral ethmoids extend posteriorly into the orbits
4. Median ethmoid lacks lateral faces
5. Vomer shaft is short, not extending posteriorly past lateral ethmoids
6. Pterygoids are absent
7. Hyomandibulae lack medial foramina
8. Preopercula bend medially to form the floors of the branchial chambers
9. Ceratohyals are attached to epihyals by complex lateral sutures
10. Third basibranchial is absent
11. Second and third hypobranchials are absent
12. Hypobranchials lack anterior processes
13. Cleithra bear posteromedial extensions to coracoids
14. Coracoid shafts do not touch cleithra
15. Scapular foramina are incomplete
16. Actinosts are sutured together, and to scapulae and coracoids
17. Haemal laminae do not extend the full length of each caudal vertebra.

Indostomoidei shares several characters with both Gasterosteidei and Dactylopteroidei. It resembles the former in the following:

1. Separate dorsal spines are present before the soft dorsal
2. Fourth actinosts are connected to coracoids via anteroventral projections
3. Dentaries and articulars do not bear sensory canals
4. Pelvic fins are spineless
5. Pelvic plates lack medial processes and sutures
6. Ossified tendons are present in the axial musculature
7. Haemal canals are closed for their full lengths,

and resembles Dactylopteroidei in:

1. Posterior myodome is absent
2. Dermosphenotics bear infraorbital canals
3. Interopercula are shorter than preopercula
4. Subopercula do not follow the opercular margins
5. Pterygoid arch is reduced; palatines are apparently fused to pterygoids, metapterygoids are absent
6. Scapulae and first actinosts are fused.

Indostomoidei is distinguished from all other study groups by:

1. Median ethmoid, palatines, and vomer are fused
2. Exoccipital lateral foramina are absent
3. Quadrates articulate with lower jaws behind the orbits
4. Preopercula lack preoperculomandibular canals
5. Fourth ceratobranchials are toothed.

The relationships suggested here are of course provisional. Further investigation is needed in several areas, including a more detailed study of relationships among scorpaeniform suborders and investigation of the possible relationships between these orders and the study groups, since many of the apomorphies present in the study groups are apparently expressions of apomorphic tendencies widespread within Scorpaeniformes. It will also be necessary, since these study groups are all highly derived, [illegible] consider [illegible] possibility of their having arisen from derived members of other groups. I did not examine any very derived members of paracanthopterygian lineages, of Atherinomorpha, or of Beryciformes, and the only derived perciform examined was Ammodytes. The further interrelationships of the study groups are not likely to become more obvious unless (a) closer relatives of the individual groups are found in the course of a more thorough investigation of Percomorpha, or (b) new apomorphic characters are discovered, probably in the soft anatomy. The high amount of parallelism known to occur within members of this group, [illegible] and below the species level, and apparent in the ambiguity of their relationships and the numbers of apomorphic tendencies they share, suggests that a clear picture of their phylogeny may be unattainable until methods of interpreting parallelisms have been further developed. This group offers an excellent study set for the investigation of parallelisms, since its members also show parallelisms with members of their sister groups within Scorpaeniformes and, in the case of Centriscoidae, with Triacanthodidae (Perciformes).

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