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ABSTRACT

The ichthyodectiform fishes are a nominal order of Mesozoic teleosts that have been assigned to three of the four extant teleostean cohorts in one or another recent work, and whose monophyly and composition have not previously been established. From a detailed anatomical survey, it is concluded that the Ichthyodectiformes is monophyletic, and is characterized by an endoskeletal ethmo-palatine bone (a new term) in the floor of the nasal capsule, and by uroneurals that cover the lateral faces of the preural centra. Ichthyodectiform subgroups are the Allothrissopoidei (new name, *Allothrissops*, Upper Jurassic, only) and Ichthyodectoidei, the latter containing the Ichthyodectidae (nine nominal genera, Upper Jurassic–Upper Cretaceous) and Saurodontidae (two genera, Cretaceous). The Crossognathidae (two genera, Cretaceous) share the ichthyodectiform uroneural character, but show no other ichthyodectiform features, and have certain synapomorphies with higher teleosts. They are placed as Teleostei *incertae sedis.*

A new scheme of teleostean interrelationships is proposed, in which the Euteleostei and Clupeomorpha are sister-groups, these two combined (Clupeocephala, new usage) are the sister-group of the Elopomorpha, and those two combined (Elopocephala, new usage) are the sister-group of the Osteoglossomorpha. Ichthyodectiforms cannot be assigned to any of these teleostean subgroups. This outline of teleostean relationships is extended by specifying a sequence of derived character states shared by extant Teleostei and the Jurassic forms *Tharsis dubius*, *Leptolepis coryphaenoides*, *Proleptolepis* spp., *Pholidolepis dorsetensis*, and *Pholidophorus bechei.* From these character states a corresponding phyletic sequence is inferred such that each named taxon is the sister-group of all those preceding it. Within this scheme, the ichthyodectiforms are the sister-group of *Tharsis* and extant teleosts. Ichthyodectiform relationships therefore lie between members of the Leptolepididae, as that group is currently defined, making it polyphyletic. Various other Mesozoic teleosts are reviewed, and their relationships specified in this scheme as precisely as the available information permits. One "leptolepid," *Leptolepides*, is the sister-group of extant clupeocephalans. Another, "*Leptolepis*" *bahiaensis*, is a clupeocephalan *incertae sedis.* "*Leptolepis*" *macrophthalmus* and "*L.*" *talbragarensis* are Teleostei *incertae sedis*, with relationships in the region of *Tharsis* and the ichthyodectiforms. The nominal genus *Anaethalion* contains one Lower Cretaceous elopomorph, "*A.*" *vidali*, and an unnamed Jurassic elopomorph, whereas the remaining species are Elopocephala *incertae sedis.* The Jurassic "leptolepid" *Ascalabos* and the Upper Jurassic and Lower Cretaceous form genus *Pachythrissops* are Teleostei *incertae sedis*, in the same way as "*Leptolepis*" *macrophthalmus.*

With these and other relationships proposed in a cladogram (fig. 54), possible methods of classifying such extended sister-group systems, including series of fossils in which each is the sister of a group containing extant taxa of high rank, are discussed. To avoid naming taxa of high rank for single paleospecies, and to avoid frequent changes in the names and ranks of extant taxa, a new convention for dealing with fossils is proposed. We recommend that those fossil taxa whose relationships can be inferred be incorporated in the hierarchy of extant taxa simply by listing them in sequence, within the extant taxon of lowest rank to which they belong. A particular list of sequenced fossils is established according to the convention that each listed fossil group is the plesiomorph sister-group of everything beneath it in the taxon. These listed fossil taxa may have names indicative of any rank, whatever rank may have existed by previous convention, but sequenced fossil taxa are always distinguished by the prefix *plesion* (new term). Within a monophyletic group of extinct species, however, usual sister-group ranking procedures are followed. The use of plesions is a convention or compromise which makes it unnecessary to rank extinct taxa formally in the same hierarchy as extant taxa. Many of the fossils we have investigated are too poorly known for their relationships to be specified unambiguously. These fossil taxa are *incertae sedis*, at a specified level in the hierarchy. We recommend that the term *incertae sedis* be restricted to fossils, and discuss the implications of that recommendation.

INTRODUCTION

The work reported here was begun as an investigation into the phylogenetic relationships of the ichthyodectiforms, Mesozoic fishes that have been aligned in recent times with three of the four extant teleostean cohorts. One of these alignments involves the osteoglossomorphs in a scheme in which they arose independently of other teleosteans (e.g., Greenwood, Rosen, Weitzman and Myers, 1966, fig. 1; Taverne, 1974c, fig. 40; 1975c, fig. 17). Since Mesozoic fishes such as the pholidophorids and leptolepids were also included in these schemes, it is clear that the problem of ichthyodectiform relationships potentially concerns all fishes that have been called teleosteans as well as some holosteans. So much has transpired in the time since we began this work (1970) in paleontological and neontological investigations of teleostean and holostean relationships, and in the theoretical approaches to systematic investigations in general, and so many investigators have contributed solutions to these problems, that the scope of the questions about ichthyodectiform affinities has come to involve the phylogenetic interrelationships of all actinopterygian fishes included by Patterson (1973) in the Halecostomi. The objectives of our study, initiated in 1970 by the arrival in the American Museum of Natural History of unusually complete and easily prepared material of the Lower Cretaceous ichthyodectid *Cladocyclus*, may be stated as follows:

1. To review the evidence for interrelationships among the major groups of extant teleosteans and selected early fossil teleosteans.

2. To examine evidence of the monophyletic or nonmonophyletic nature of the Ichthyodectiformes and to place these fishes within an overall scheme of halecostome phylogeny.

An explanation of the term "selected," as stated in our first objective may be helpful to readers unfamiliar with fossils. In anatomical work with fossils the biggest problem is the difficulty of obtaining information. In fossil "groups" like the pholidophorids and leptolepids, and in "genera" like *Pholidophorus* and *Leptolepis*, the majority of nominal species are little more than names: they are based on poorly preserved or incomplete fossils whose stratigraphic position and few visible characters do not disagree with some concept of the genus or higher taxon. In a few species (or specimens) in these groups detailed anatomical information is available, but clearly it is not justifiable to infer that the features observed are characteristic of all nominal members of the group. "Selected" here only means species in which detailed information is available. Very few fossil species are represented by sufficiently well-preserved or well-prepared specimens to yield a full account of the skeleton: within a "genus" or "family" it may happen that in one species, for example, the braincase will be accessible but the postcranial skeleton little-known, whereas in another species the caudal skeleton will be well-known but the braincase completely unknown. Given these conditions, it is necessary to deal with different species according to the part of the skeleton under discussion. Another consequence of the unequal availability of information is that in a cladogram or cladistic classification of fossil forms, certain species or higher taxa may, on present knowledge, turn out to be "interchangeable." This may occur, for example, if information from the skull of one paleospecies suggests a certain placement and information from the caudal skeleton of another suggested the same placement, but the information was insufficient to carry the analysis further. Another possibility is that one relatively well-known species and one poorly known species may, based on available information, occupy the same position in a cladogram. Such coincidence or interchangeability of two fossil taxa in a cladogram is not, of course, evidence that they are each other's closest relatives, but is purely a result of lack of information. In such cases, we choose to classify the more completely known taxon, and to leave the other *incertae sedis*. This point is discussed in greater detail below.

In attempting to evaluate the monophyly and composition of the ichthyodectiforms, by means of shared specializations (synapomorphies), we had to investigate the late Jurassic *Allothrissops* and a variety of Jurassic and early Cretaceous

teleosts, including several species of *Leptolepis* and other genera that had previously been placed in or near the Ichthyodectidae and Leptolepididae. In the course of this work, it became clear to us, and meanwhile to others also, that the genus *Leptolepis* is polyphyletic, that the criteria currently used to assign primitive Mesozoic teleosts to groups, living or extinct, are mostly unsatisfactory, and that the relationships of the ichthyodectiforms, as we now see them, can only be expressed after a revision of the classification of early fossil teleosts. Such a revision only becomes possible within an acceptable theory of relationships of extant teleosts, and we have had to appraise the different interpretations of that problem now current, and also the question of whether fossils can be classified in the same hierarchy as extant organisms, a procedure regarded as invalid by some recent writers. The work has therefore become far more complicated and difficult to present than our original plan.

Our procedure is first to present a review of the structure and composition of the ichthyodectiforms as we now understand them, and then to consider the practical and theoretical background against which ichthyodectiforms may be fitted in an overall phylogeny and classification of the main groups of teleostean fishes. This background involves discussions of a framework of higher actinopterygian classification and of the interrelationships of fossil and Recent teleosteans. We have discussed character transformation series shown by selected pholidophorids and leptolepids, relatively well-known teleosts that lack the synapomorphies necessary to include them in any extant teleostean subgroup. From this we arrive at an outline phylogeny of primitive Mesozoic teleosts within which the relationships of other Mesozoic forms, including ichthyodectiforms, can be considered. Having arrived at a cladogram expressing our inferences on the relationships of all these fishes, we conclude with a discussion of how fossils are to be classified and an outline classification incorporating a novel method of combining fossil and Recent organisms in the same taxonomic system.

Reassignment of various fossil species of *Leptolepis* and *Anaethalion*, as recommended here, will entail nomenclatural changes. Nybelin (1974) has recently reviewed leptolepid taxonomy and has reached conclusions similar to ours so far as the nomenclature of particular species of *Leptolepis* is concerned. For an account of the nomenclature of these species see Nybelin (1974). In *Anaethalion* the problem of nomenclature is complicated by the fact that the characters which appear crucial to us are not yet accessible in the type-species of the genus. We therefore refer to reassigned species as, for example, "*Anaethalion*" *vidali.*

The Recent and fossil material studied is from the collections of the American Museum of Natural History (registration numbers with prefix AMNH† indicate fossils in the Department of Vertebrate Paleontology; AMNH indicates Recent specimens in the Department of Ichthyology) and British Museum (Natural History) (prefix BMNH). Fossils were prepared by the transfer technique (Toombs and Rixon, 1959), and some of the photographic illustrations are positive prints from radiographs of such preparations. The line illustrations are based on camera lucida drawings. For the loan of specimens and other assistance we are indebted to Dr. Bobb Schaeffer, and for technical help to Ms. Alison Longbottom, Mr. Walter Sorensen, and Mr. Chester Tarka. We also thank Drs. Gareth Nelson, Peter Forey and Malcolm C. McKenna for information and comments.

ABBREVIATIONS USED IN FIGURES

ACP, angular component of joint surface with quadrate
ALS, rhombic scales of axial lobe of caudal fin
ANG, angular bone
ANG-ART, fused angular and articular
ANG-RAR, angulo-retroarticular, characteristic of elopomorphs
AO, antorbital bone
AOS, antorbital ossicle found in some *Cladocyclus* specimens
APL, anterior pitline groove
ART, articular bone
ART-RAR, articulo-retroarticular, endoskeletal bone topographically equivalent to these two bones in higher teleosts
BPP, basipterygoid process on parasphenoid
BR 6-9, branched caudal fin rays of upper lobe, numbered from top downward
BSC, basal sclerotic bone
CHO, notochord
CL, cleithrum
COR, coracoid
CRM, corono-meckelian bone
CSC, caudal scute

DCR, distal caudal radial ossifications
DEN, dentary bone
DIC, intercalary hemicentrum in diplospondylous part of vertebral column
DSP, dermosphenotic
ECO, ethmoid (rostral) commissural sensory canal
EP 1-5, epurals
EPI, epioccipital bone
ETPA, ethmo-palatine bone, found in ichthyodectiforms
EXO, exoccipital bone
FAQ, facet for quadrate on lower jaw
FR, frontal bone
FRF, fringing fulcra
H 1-13, hypurals
HCH, hemichordacentrum
IC, intercalar bone
IO 1-5, infraorbital bones, numbered from front to back
LE, lateral ethmoid bone
MCF, Meckelian fossa in dentary
MEM, median membrane developed from anterodorsal surface of first uroneurals
MEP, paired membrane developed from anterodorsal surface of first uroneural
MES, mesethmoid, a compound ossification formed by fusion of the dermal rostrodermethmoid and endoskeletal supraethmoid
MPL, middle pitline groove
NA, nasal bone
NEC, nerve cord
NOT, "leptolepid notch" in oral margin of dentary
NPIT, nasal pit or capsule
NPU1-2, neural arch or spine of numbered preural centrum
NPU1+NU1, compound caudal neural arch characteristic of elopomorphs
NU1, neural arch of first ural centrum
NU1A, NU1P, anterior and posterior neural arches of first ural centrum
PA, parietal bone
PAL, palatine bone
PCL, postcleithrum
PH, parhypural bone
POPR, preopercular process of hyomandibular
PPH, processes on heads of upper hypurals
PRH, posteroventral process on first hypural, characteristic of ichthyodectoids
PRP, postarticular process of angular bone
PSP, parasphenoid
PTF, post-temporal fossa
PTO, pterotic bone (fused auto- and dermopterotics)
PTT, post-temporal (suprascapular) bone
PU1-6, preural centra
RAR, retroarticular bone
RODE, rostrodermethmoid bone
SAG, surangular bone
SBO, suborbital bone
SCA, scapula
SCL, supracleithrum
SCO, opening through which mandibular sensory canal entered angular bone
SMA, SMP, anterior and posterior supramaxillary bones
SOC, supraoccipital bone
SPO, autosphenotic bone
STM, medial supratemporal (extrascapular) bone
STT, supratemporal (extrascapular) bone
SUE, supraethmoid bone
SUO, supraorbital bone
U1, U2, ural centra
U1A, U1P, anterior and posterior parts of first ural centrum
U1+H2, fused first ural centrum and second hypural, characteristic of clupeomorphs
UD 1-3, urodermals
UN 1-8, uroneural bones
VCPH, vascular canal in head of parhypural
VO, vomer (vomero-ventral ethmoid)
I, foramen of olfactory nerve
→, outermost (unbranched) principal caudal fin ray

STRUCTURE AND COMPOSITION OF THE ICHTHYODECTIFORMES

A review of the structure of those fossils that have been previously assigned to the ichthyodectiforms or should, in our opinion, be so assigned, follows. The primary purpose of this survey is to decide whether the ichthyodectiforms are a monophyletic group, what monophyletic subgroups it contains, and what each such subgroup comprises. In making such decisions we are concerned only with a few derived characters, but in order to form a theory on ichthyodectiform relationships to other teleostean subgroups it is necessary to consider a range of other characters, some primitive relative to conditions in extant teleosts.

Among recent workers on the ichthyodectiforms (principally Nybelin, 1964; Bardack, 1965; Cavender, 1966; Patterson, 1967a; Bardack and Sprinkle, 1969; Nelson, 1973a; Taverne, 1973c; 1974b; 1974d; 1975c), only Nelson approached the fossils from the viewpoint of phylogenetic systematics (searching for shared derived characters as evidence of relationship): all the others regarded the group more or less typologically. Nelson examined the lower jaw of four genera but otherwise relied on the literature. We have prepared and examined as many supposed ichthyodectiforms as were available, in as much detail as possible. Since our observations and interpretations of some structures differ from those in papers cited above, and since it is necessary to specify in what forms each structure was observed, this section is an extended review rather than a list of characters.

CANDIDATES FOR INCLUSION

Bardack (1965) considered the Ichthyodectidae (fossil Chirocentridae in his usage) to contain 13 or 14 genera:

Ichthyodectes Cope, Lower Cretaceous (Albian)–Upper Cretaceous (Campanian), North America and Europe
Xiphactinus Leidy, Lower Cretaceous (Aptian according to Taverne and Ross, 1973)–Upper Cretaceous (Campanian), North America, Europe, Australia
Gillicus Hay, Lower Cretaceous (Albian)–Upper Cretaceous (Campanian), North America, Europe
Cladocyclus Agassiz, Lower Cretaceous, Neocomian–Aptian, Brazil
Eubiodectes Hay, Upper Cretaceous, Cenomanian, Lebanon
Proportheus Jaekel, Lower Cretaceous, Neocomian, West Africa
Prymnetes Cope, ?Upper Cretaceous, Mexico
Chirocentrites Heckel, Lower Cretaceous, Albo-Aptian, Europe
Thrissops Agassiz, Upper Jurassic (Kimmeridgian)–Upper Cretaceous (Cenomanian), Europe, North Africa
Allothrissops Nybelin, Upper Jurassic, Kimmeridgian, Europe
Pachythrissops Woodward, Upper Jurassic (Kimmeridgian)–Lower Cretaceous (Barremian), Europe
Mesoclupea Ping and Yen, Upper Jurassic, ?Purbeckian, China
Spathodactylus Pictet, Lower Cretaceous, Neocomian, Switzerland
Platinx Agassiz, Palaeocene–Middle Eocene, Turkmenia (Danil'chenko, 1968) and Monte Bolca, Italy

Bardack gave detailed accounts of the structure of *Ichthyodectes*, *Xiphactinus*, and *Gillicus*. Two of the remaining genera, *Prymnetes* and *Spathodactylus*, are each represented by a single specimen: both are poorly known, we have seen neither specimen, and we have nothing to add to Bardack's comments. Subsequent work indicates that *Pachythrissops* is not related to the ichthyodectiforms (Nybelin, 1971; Forey, 1973a, 1973b; p. 149 below), and that *Platinx* may be an osteoglossomorph (Forey, 1977), as may be *Opsithrissops*, from the Palaeocene of Turkmenia, added to the "Chirocentridae" by Danil'chenko (1968; and see Bonde, 1975, p. 298).

Bardack and Sprinkle (1969) showed that the Saurodontidae, containing *Saurodon* Hays (Upper Cretaceous, Cenomanian–Campanian; North America and Europe) and *Saurocephalus* Harlan (Upper Cretaceous, Turonian–Maastrichtian; North America and Europe), are related to the Ichthyodectidae, and united the two families in an order Ichthyodectiformes. Bardack and Sprinkle included in the Ichthyodectidae only those genera assigned to Bardack (1965) to his "*Xiphactinus* group" of Chirocentridae: *Ichthyodectes*, *Xiphactinus*, *Gillicus*, *Cladocyclus*, *Chirocentrites*, *Prymnetes*, and *Spathodactylus*. Bardack and Sprinkle did not mention *Thrissops*, *Eubiodectes*, and *Proportheus*, assigned by Bardack (1965) to the "*Chirocentrus* group," or *Allothrissops*, designated by Bardack as the stem-genus of his Chirocentridae. Nelson (1973a), in his recent analysis of ichthyodectiforms, also mentioned only the genera of Bardack's "*Xiphactinus* group," and concluded that of those only *Ichthyodectes*, *Xiphactinus*, and *Gillicus* are established members of the Ichthyodectidae.

In addition to the genera mentioned above, a few Middle Jurassic specimens have been assigned to the Ichthyodectidae. These include "*Leptolepis costalis* Egerton" (a *nomen nudum*), represented by a single specimen (BMNH P.937/P.3676) in counterpart, lacking the median

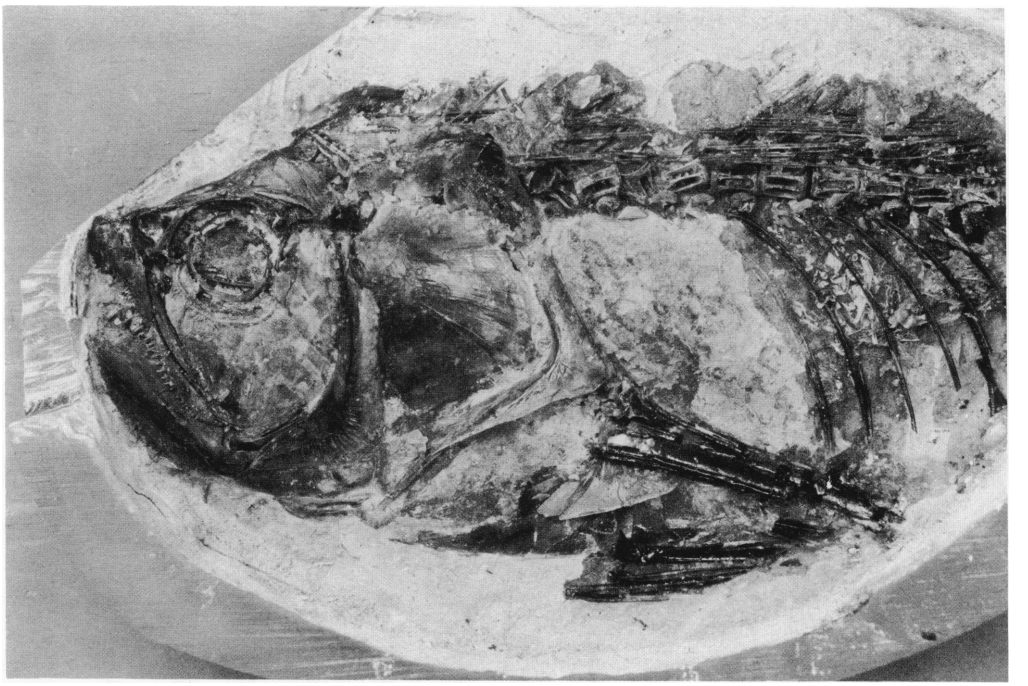
fins, from the Oxford Clay (Callovian) of Wiltshire. This specimen was referred by Woodward (1895, p. 528) to the genus *Thrissops*, and was regarded by Bardack (1965) as the earliest representative of that genus. The specimen is *Allothrissops*-like, but is very defective and shows nothing that can be regarded as positive evidence of ichthyodectiform relationships. Nybelin (1964; 1974) suggested that two other species might be related to *Allothrissops*, *Leptolepis macrophthalmus* Egerton, from the Oxford Clay of Wiltshire, and a preopercular from the Stonesfield Slate (Bathonian) of Oxfordshire, named "*Allothrissops*" *disjectus* (Woodward) by Nybelin (1974). These forms were associated with *Allothrissops* because of similarities in the shape of the preopercular and the numerous branches of the sensory canal in the ventral limb of the bone (see fig. 45B and discussion in Nybelin, 1974, pp. 116, 172). But as Nybelin (1964, p. 41) said, the preopercular of *Pholidophorus bechei* Agassiz is suggestive of the *Allothrissops* type for the same reasons, and since the hypothesis that *P. bechei* is a close relative of *Allothrissops* can easily be refuted (for example, by the typically teleostean braincase and caudal skeleton of *Allothrissops*, in contrast to the much more primitive conditions in *P. bechei*), the hypothesis of close relationship between *Allothrissops* and "*A.*" *disjectus* or *L. macrophthalmus* is suspect (see also p. 143 on *L. macrophthalmus*).

Genera established as members of the Ichthyodectiformes by Nelson (1973a) are **Ichthyodectes*, **Xiphactinus*, **Gillicus*, *Saurodon* and *Saurocephalus*. Candidates for inclusion are **Cladocyclus*, **Eubiodectes*, *Proportheus*, *Chirocentrites*, *Thrissops*, **Allothrissops* and *Mesoclupea*. We have examined material of all these genera except *Mesoclupea*, and acid-prepared specimens were available of genera marked with an asterisk. *Mesoclupea showchangensis* Ping and Yen, the only species of that genus, is not assignable to the Ichthyodectiformes (or any other teleostean subgroup) on the information so far available (Chang, 1963). Evidence presented below indicates that the remaining genera form a monophyletic group. We also considered for inclusion in this group *Crossognathus* Pictet, containing the single species *C. sabaudianus* Pictet from the Lower Cretaceous (Neocomian) of Switzerland and Germany, and another apparently related genus, *Apsopelix* Cope. We conclude that they constitute a group, the Crossognathidae, with relationships elsewhere among the Teleostei (see pp. 131-135).

COMMENTS ON GENUS- AND SPECIES-LEVEL TAXONOMY OF ICHTHYODECTIFORMS

Among the genera here assigned to the Ichthyodectiformes, only three, *Allothrissops* (three species), *Saurodon* (two nominal species, distinguished only on stratigraphic and geographic grounds), and *Saurocephalus* (two nominal species, distinguished only on geographic grounds) can be regarded as sharply distinct morphologically from the *Ichthyodectes*-like genera, which include: *Ichthyodectes* (two nominal species, comment as for *Saurocephalus*), *Xiphactinus* (four nominal species, three distinguished only on geographic grounds), *Gillicus* (two nominal species, comment as for *Saurodon*), *Cladocyclus* (five nominal species), *Eubiodectes* (monotypic), *Proportheus* (monotypic), *Chirocentrites* (monotypic) and *Thrissops* (10 nominal species, five poorly known). We suspect that *Eubiodectes* is not distinct from *Ichthyodectes*, nor are some Cretaceous species of *Thrissops*, whereas other *Thrissops* species may be *Gillicus*. *Chirocentrites* may not be distinct from *Xiphactinus*, and *Proportheus* may be a synonym of *Cladocyclus* (since Brazil and West Africa were contiguous in Wealden times). On the other hand, the three specimens of *Cladocyclus*[1] restored here (figs. 1-3) differ considerably in the premaxilla, the circumorbitals, preopercular, and other features: these variations are not of the kind normally met

[1]The Santana Formation of Brazil, from which our specimens of *Cladocyclus* come, is reported to contain two species of the genus, *C. gardneri* Agassiz, the type-species, and *C. ferus* Santos (1950). Santos distinguished *C. ferus* from the type-species principally on the grounds that it has scales which are smaller, lack pits on the exposed portion, and have fewer basal radii; that the circumorbitals are weakly ornamented; and that the first pectoral ray is twice as large as the second. He also noted that in *C. gardneri* the premaxillary teeth are about twice as large as those on the maxilla, whereas in *C. ferus* they are only slightly larger than the maxillary teeth; and that in *C. ferus* the posterodorsal margin of the opercular and the posterior margins of the subopercular and preopercular are fringed. We have been unable



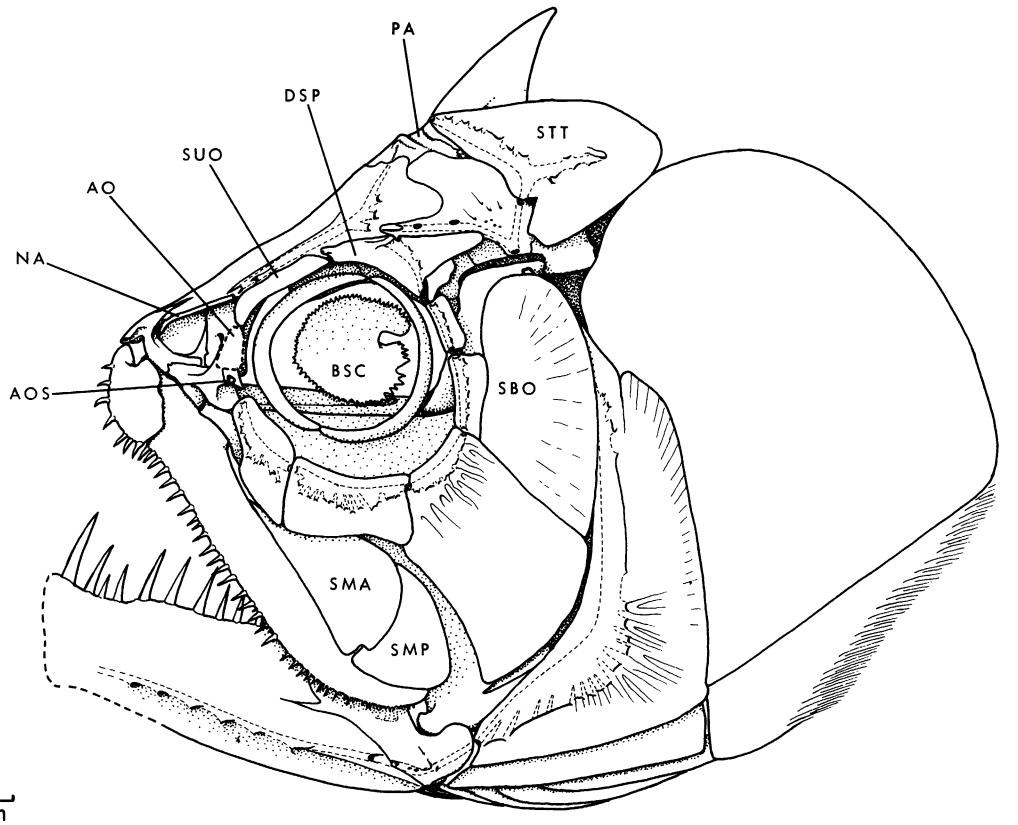


FIG. 1. *Cladocyclus* sp., Lower Cretaceous, Santana Formation, Serra do Araripe, Ceara, Brazil. Above, AMNH† 2982A, a transfer preparation. Below, skull of same specimen; outline of antorbital (lost during preparation) is indicated by a broken line.

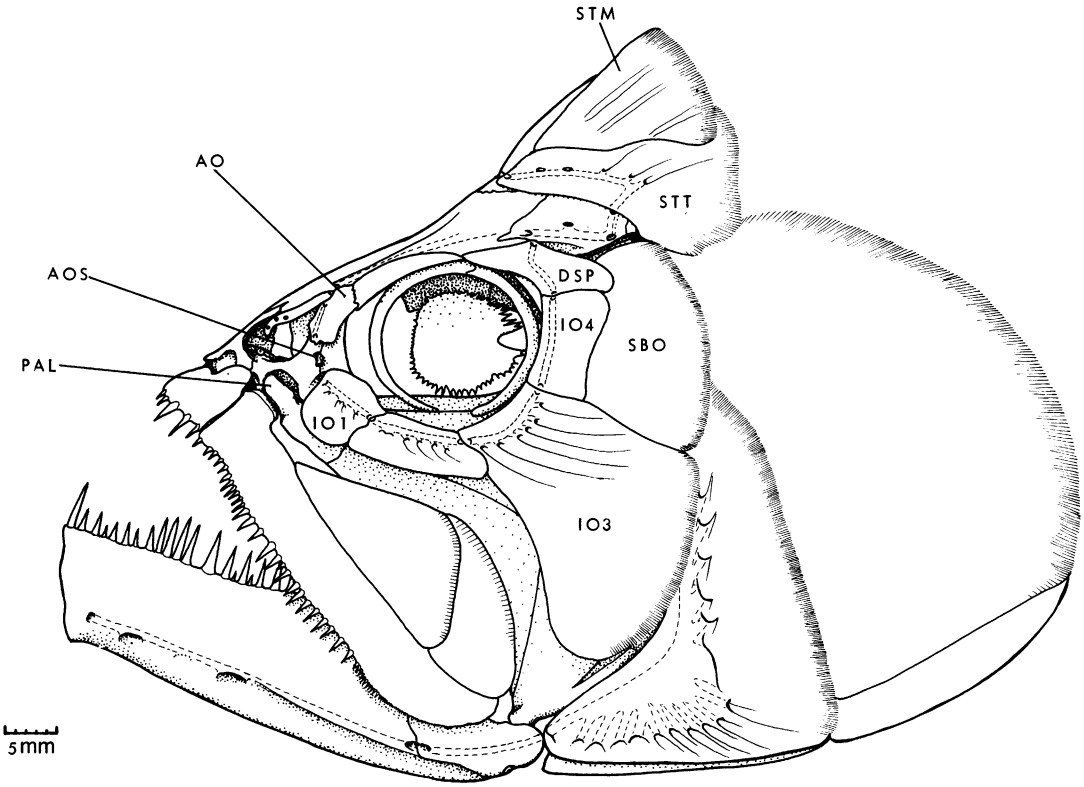


FIG. 2. *Cladocyclus* sp., restoration of skull drawn mainly from AMNH† 9981, fourth infraorbital (IO 4) and antorbital ossicle (AOS) from BMNH P.56471 (AMNH† 9981 has two narrow posterior infraorbitals, not one). Horizon and locality as figure 1.

within a species or genus, but we are unable to form an opinion on whether they represent individual, sexual, specific, or generic differences because of the inadequacy of our sample, and because of the absence of comparable information for other ichthyodectiform "genera." It is clear that current generic and specific taxa in the ichthyodectiforms are highly questionable, but since in almost all these taxa the material is too unsatisfactory for a more realistic approach we will continue to use existing names.

satisfactorily to reconcile these character suites with conditions in our specimens: the specimens shown in figures 2 and 3 agree with *C. ferus* and *C. gardneri* respectively in most features, but that shown in figure 1 shows a mixture of characters. The syntypes of *C. gardneri*, BMNH 28901 and 28901a, are both very poor specimens. They have punctate scales, but our observations suggest that development of punctae on the scales is correlated with the size of the individual, whereas "fringing" of the dermal bones (and scales) occurs variably. We have observed similar "fringing" of dermal bones in other ichthyodectiforms. Since we are unable to identify our specimens of *Cladocyclus* with the two supposed species, we refer to them all as *Cladocyclus* sp.

REVIEW OF ICHTHYODECTIFORM STRUCTURE

1. Skull Roof.

Supraoccipital and parietals. In *Thrissops*, *Ichthyodectes*, *Xiphactinus*, *Gillicus*, *Cladocyclus* (figs. 1-4), *Eubiodectes*, and *Saurodon* there is a high, triangular supraoccipital crest, thickened anteriorly, and the supraoccipital extends well forward on the skull roof. The parietals (not well known in *Thrissops* or *Eubiodectes*) are not separated by the supraoccipitals as they are in most

teleosts with a large supraoccipital crest, but are displaced forward to a position above the rear of the orbit. In *Saurodon* the parietals are paired (Bardack and Sprinkle, 1969), as they are said to be in *Thrissops formosus* (Saint-Seine, 1949, p. 288), but in the other genera they are fused into a median bone. The latter arrangement seems to be unique amongst teleosts, but the form of the ichthyodectid parietals is approached in *Hiodon* (Ridewood, 1904, fig. 19; Greenwood, 1973, pl. 1).

In *Allothrissops* (fig. 5) the supraoccipital is small and confined to the posterodorsal angle of the braincase, whereas the parietals (BMNH P.921, *A. regleyi*) are united throughout their length in a median suture, as in leptolepids and other primitive teleosts.

Dermopterotic. In all ichthyodectiforms where this bone is known (including *Allothrissops*, fig. 5) it has an anterodorsal portion that extends forward over the sphenotic, carrying the temporal sensory canal forward and marking off an elongate, triangular dilatator fossa. Because of the forward displacement of the parietal, the dermopterotic has a long contact with the epioccipital. *Hiodon* resembles ichthyodectiforms in all these features.

Supratemporal. The supratemporal (extrascapular) is known only in *Cladocyclus* (figs. 1, 2) and, with less confidence, in *Allothrissops* (fig. 5). The bone is very flimsy, and this is presumably why it has not yet been found in other ichthyodectiforms. In *Cladocyclus* the bone is large, approximately triangular, and extends anteromedially over the supratemporal fossa to meet its fellow in the midline at the base of the anterior margin of the supraoccipital crest. Once again, the bone resembles that of *Hiodon* in form. In *Cladocyclus* the bone contains the usual triradiate sensory canal, and there are four to seven branches from the supratemporal commissure and four or five from the longitudinal canal. Posterodorsal to the supratemporal and lateral to the supraoccipital crest, there is another triangular bone (STM, fig. 2) bearing three or four

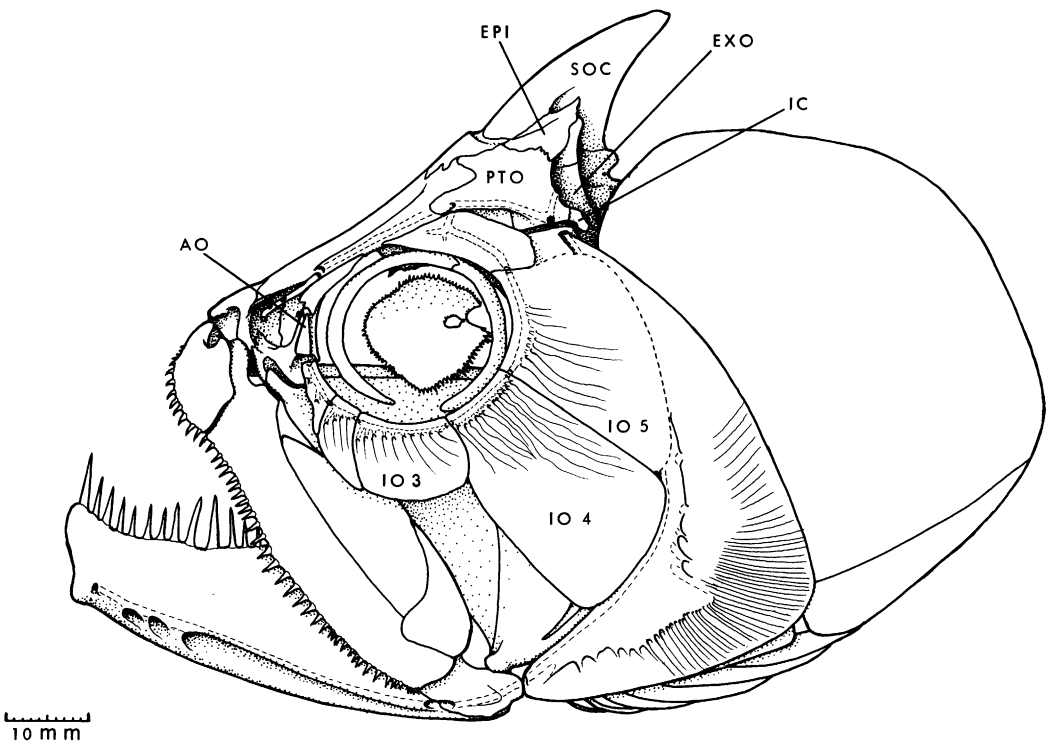


FIG. 3. *Cladocyclus* sp. Skull of AMNH† 9980. Horizon and locality as figure 1.

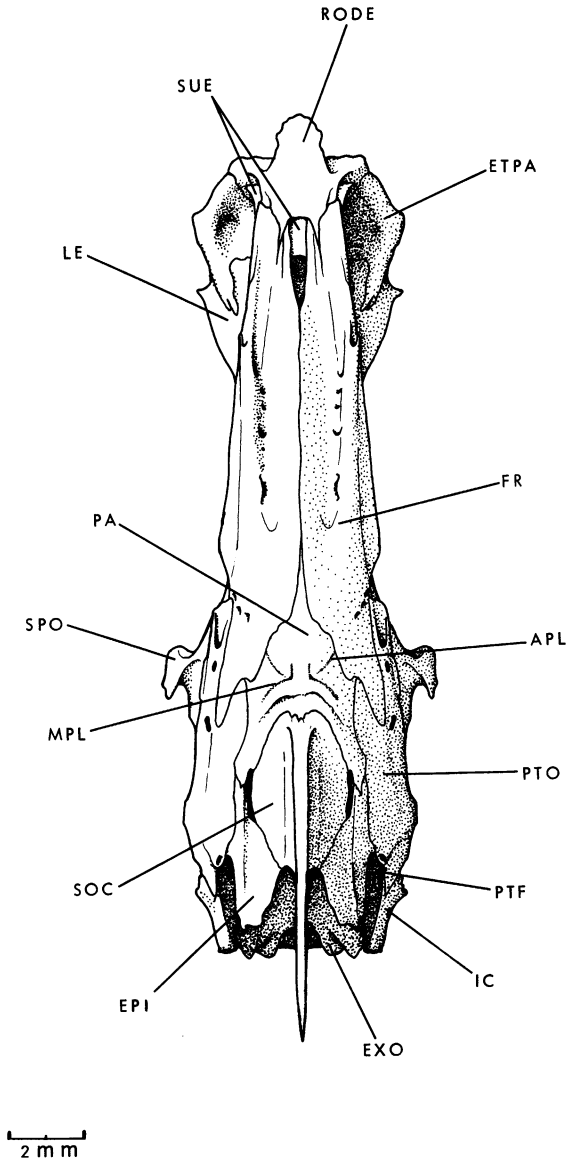


FIG. 4. *Cladocyclus* sp. Braincase of AMNH† 2982A (same specimen as fig. 1) in dorsal view.

grooves that carried the terminal part of the branches from the supratemporal commissure. This bone does not have the structure of a scale and is presumed to be a medial supratemporal.

In *Allothrissops* the supratemporal is imperfectly preserved in all specimens, but it certainly occupied the same position as in other primitive teleosts, transversely placed across the posterior margin of the skull roof and not displaced forward as in *Cladocyclus*. In BMNH P.915a, *A. mesogaster*, the supratemporal appears to be slender, whereas in BMNH 37043, a larger speci-

men, probably of the same species, it is broader, and there are indications of a small bone posteromedial to it, homologous with the medial supratemporal of *Cladocyclus.*

Sensory canals. Bardack (1965) believed that the sensory canals of the skull roof in *Ichthyodectes*, *Xiphactinus*, and *Gillicus* lay free in the skin, having lost contact with the bones. Bardack and Sprinkle (1969) appear to hold the same opinion about *Saurodon.* In fact, the supraorbital and temporal canals were enclosed in the frontal and dermopterotic in ichthyodectiforms (figs. 1-5), as is usual in primitive teleosts. In the dermopterotic the temporal canal takes the normal V-shaped course, with the exit of the preopercular canal at the junction of the two limbs of the V. The supraorbital canal in the frontal opens through a group of pores close to the terminal opening of the temporal canal in the dermopterotic, and there may have been an anastomosis between the two canals in the skin. In *Cladocyclus* and *Allothrissops* there is a parietal branch of the supraorbital canal, leading back to the posterior margin of the frontal and opening into the anterior pitline groove. In some specimens of *Allothrissops* the canal is bone-enclosed in the most anterior part of the parietal. In *Allothrissops*, *Cladocyclus* (fig. 4), and *Thrissops* (Saint-Seine, 1949, fig. 116) there are clearly marked anterior and middle pit-line grooves on the parietal, but the middle pit-line groove does not extend on to the dermopterotic.

The nasal, known in *Allothrissops* (fig. 5), *Cladocyclus* (figs. 1-3), *Thrissops* (Saint-Seine, 1949, fig. 116), *Eubiodectes* (BMNH 39238), *Ichthyodectes*, *Xiphactinus*, and *Gillicus* (Bardack, 1965) is a slender, tubular bone, resembling the nasal of leptolepids. Bardack found that the nasal was separated into two bones in all three genera that he investigated, but this is not so in any of the material we have seen.

2. Neurocranium.

Bardack (1965) gave good accounts of the neurocrania of *Ichthyodectes*, *Xiphactinus*, and

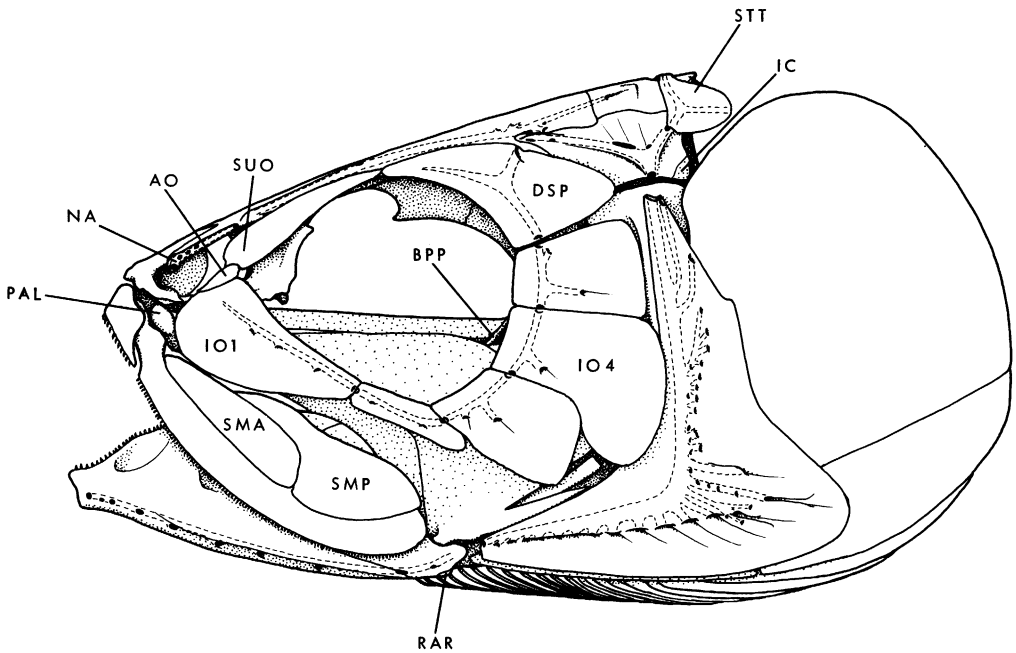


FIG. 5. *Allothrissops mesogaster* (Agassiz). Restoration of skull based on specimens from Kimmeridgian of Kelheim, Bavaria (cf. Patterson, 1967a, fig. 2). ×3 approx.

Gillicus, and Bardack and Sprinkle (1969) described the neurocranium of *Saurodon*. We have acid-prepared neurocrania of *Cladocyclus* (AMNH† 9980, 9981; BMNH P.56471) which agree well with Bardack's findings, and less perfect acid-prepared specimens of *Allothrissops* (BMNH P.4689, *A. regleyi*; BMNH 37043, *A. mesogaster*). Only a few points require comment.

Intercalar. Except in *Allothrissops*, the intercalar is a massive, complex bone, forming a strut across the subtemporal fossa anteriorly (as in pholidophorids, leptolepids, elopoids, and osteoglossids; Patterson, 1975, p. 396), the posterior part of the hyomandibular facet dorsally (as in *Hiodon* and notopterids; Greenwood, 1973, p. 314), and enclosing a passage for the jugular vein medially, as in megalopids (Greenwood, 1970; Forey, 1973a: in fossil megalopids this passage is not developed, whereas in osteoglossines and notopterids there is a similar passage [Greenwood, 1973, fig. 3A], but there it seems to correspond to the opening between the strut across the subtemporal fossa and the lateral wall of the braincase, and is produced by ventral migration of the anterior end of the bridge). Although the intercalar of these ichthyodectiforms is more extensive than in any other teleosts except megalopids, it seems, like the extensive intercalar of megalopids, to be only a hypertrophied version of the typical primitive teleostean intercalar, as in *Elops* and Upper Jurassic leptolepids. A disarticulated braincase of *Cladocyclus* shows that the intercalar is entirely ossified in membrane, and lacks the endochondral component that is still present in pholidophorids and *Proleptolepis* (Patterson, 1975).

In *Allothrissops* the intercalar is smaller and simpler. It does not contribute to the hyomandibular facet or enclose the jugular vein, and resembles the intercalar of *Elops* and Upper Jurassic leptolepids.

Post-temporal fossa. In all ichthyodectiforms there is a deep, roofed post-temporal fossa. In *Allothrissops* the fossa is roofed by the parietal and dermopterotic, as in leptolepids, and the subepiotic fossa is hardly developed. In the Cretaceous ichthyodectiforms the post-temporal fossa is partially roofed by contact between the epioccipital and pterotic, and there is a deep, narrow subepiotic fossa, so that the epioccipital has the same transversely compressed form, between the post-temporal and subepiotic fossae, as in elopiforms, in many clupeoids, osteoglossids, *Chanos*, and in some characins (Patterson, 1975, p. 393). In *Cladocyclus*, the only ichthyodectiform genus in which the full extent of the post-temporal fossa is known, it ends over the sphenotic and does not extend forward on to the pterosphenoid as it does in elopoids and in some pholidophorids.

Pterotic. In all ichthyodectiforms the autopterotic and dermopterotic are fused, as in leptolepids and more advanced teleosts, not separate as they are in pholidophorids.

Glossopharyngeal foramen. In ichthyodectiforms the glossopharyngeal foramen lies in the exoccipital, as in Upper Jurassic leptolepids and more advanced teleosts, not in the prootic as it does in primitive leptolepids and in pholidophorids.

Parasphenoid. There is a large, dermal basipterygoid process in all ichthyodectiforms, as in leptolepids and osteoglossids. The parasphenoid is toothless in the Cretaceous ichthyodectiforms, but in *Allothrissops* there is a broad patch of small teeth at the level of the basipterygoid process. The parasphenoid extends back almost to the level of the occipital condyle in ichthyodectiforms, ending in a pair of processes between which the myodome opens posteriorly, as in primitive teleosts and all but the most primitive leptolepids. In *Allothrissops* (BMNH 37043), there is a deep, cuplike housing for the aortic ligament on the underside of the basioccipital, behind the posterior opening of the myodome, as in leptolepids (Patterson, 1975, figs. 47, 89, 92). This housing for the aortic ligament seems also to be represented in *Cladocyclus*, by a depression in the same position.

Sclerotic. In all ichthyodectiforms the sclerotic is ossified in two sections, fore and aft of the eyeball, as in leptolepids and more advanced teleosts. In the medial wall of the eyeball there is a basal sclerotic bone (described by Bardack, 1965, pp. 44, 56, fig. 16, as a "posterior osseous cup") in *Ichthyodectes*, *Xiphactinus*, *Gillicus* (AMNH† 2326, 8191, 8599), *Cladocyclus* (figs. 1-3), *Eubiodectes* (BMNH 39238), *Proportheus* (AMNH† 8394) and *Thrissops* (BMNH P.917). In all these genera the basal sclerotic is strongly toothed or serrated marginally. There is no basal sclerotic in *Allothris-*

sops, nor has one been found in *Saurodon*. The presence of a basal sclerotic bone is probably a primitive feature, a relic of an original complete bony cup around the eyeball, but where it is recorded in other actinopterygians (pholidophorids, *Caturus*, *Lepidotes*: Patterson, 1975) it is a thin perichondral ossification, with smooth margins passing into cartilage in life, and the serrated margins of the ichthyodectid basal sclerotic are a unique specialization.

Endoskeleton of ethmoid region. In *Ichthyodectes*, *Xiphactinus*, *Gillicus* (Bardack, 1965), *Cladocyclus* (fig. 6A, B), *Eubiodectes* (BMNH 39238) and *Saurodon* (Bardack and Sprinkle, 1969) the ethmoid region is similarly constructed: there are two paired and two median endoskeletal ossifications, the median ventral ethmoid (fused with the vomer) and supraethmoid, the paired lateral ethmoids ["dermal parethmoids" of Bardack (1965) and Bardack

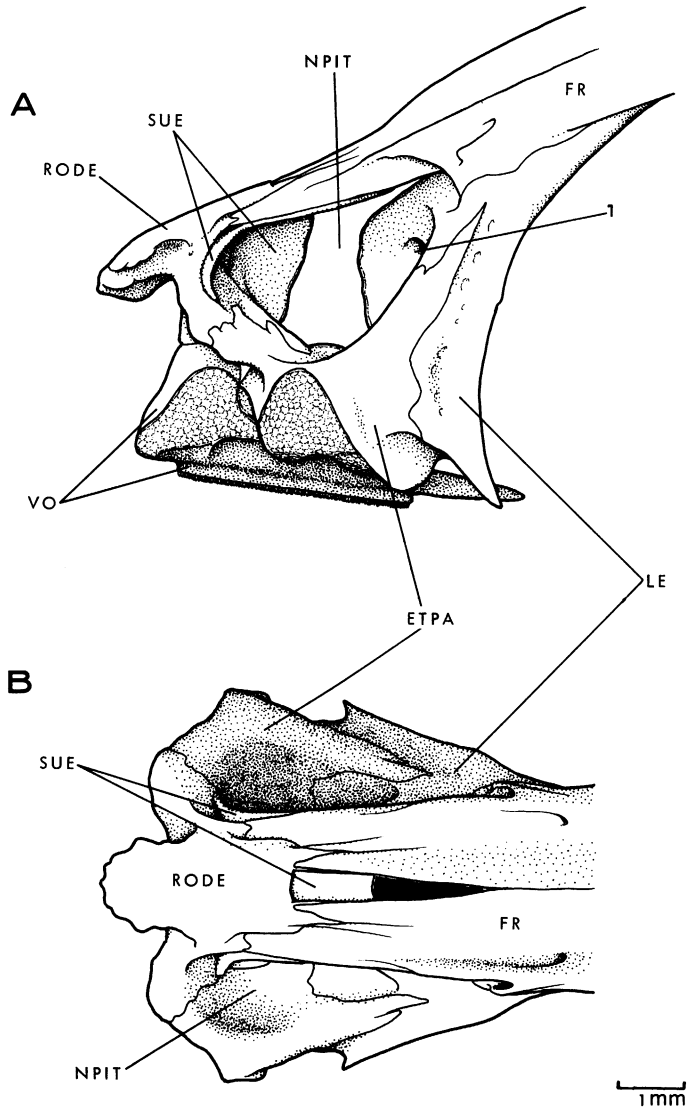


FIG. 6. *Cladocyclus* sp. Restorations of ethmoid region of braincase in lateral view (A, based on AMNH† 2982 and 9981) and dorsal view (B, from AMNH† 2982). Horizon and locality as figure 1.

and Sprinkle (1969)] and paired bones ossifying in the floor of the nasal capsule and forming the articular surface for the palatine malleolus. The latter bone is referred to here as the *ethmo-palatine* (ETPA, figs. 4, 6, 7A). The lateral ethmoid and ethmo-palatine bones have membrane bone outgrowths, those of the ethmo-palatine suturing with the rostro-dermethmoid anteriorly and overlying the anterior face of the lateral ethmoid posteriorly, those of the lateral ethmoid forming a projecting flange, which bounds the orbit anteriorly (fig. 6A).

In *Allothrissops* there is also a separate ethmo-palatine ossification (fig. 7A). It is small, lacks membrane bone outgrowths, and lies beneath the junction of the rostro-dermethmoid and a long, anteriorly directed membrane bone outgrowth from the lateral ethmoid. In all the available specimens of *Allothrissops* the ethmo-palatine bone was separated from the other endoskeletal ethmoid bones by cartilage.

Other teleosts with a paired endoskeletal ossification, which might be homologous with the ichthyodectiform ethmo-palatine, are the esocoids ("pre-ethmoids," not proethmoids or medial rostrals; Allis, 1909, p. 19; Jollie, 1975, p. 68), cyprinoids ("pre-ethmoids," "septo-maxillae"), and the mormyrids and notopterids ("latero-basal ethmoid," Taverne, 1974b, 1975b), but in these groups the bones in question differ in morphology and topography from the ichthyodectiform condition, which we regard as a unique specialization.

Dermal skeleton of ethmoid region. The dermal skeleton of the snout is best known in *Cladocyclus* (fig. 6), where the ethmoid region is roofed by a median bone, the rostrodermethmoid (see below), which projects anteriorly in a rostrum, sutures with the frontals posteriorly, and has a pair of posteroventral wings that extend down in the anterior wall of the nasal capsule, suturing with the ethmo-palatine. In small individuals (AMNH† 2982) this dermal bone is everywhere separate from the underlying supraethmoid, and the two may separate during fossilization. In larger individuals the two bones fuse in the rostrum, and may fuse in the anterior wall of the nasal capsule, where a membrane bone prong or process from the supraethmoid lies superficial (posterior) to the dermal bone. In *Ichthyodectes*, *Xiphactinus*, *Gillicus*, *Eubiodectes*, and *Saurodon* the snout is roofed by a similar bone. In *Xiphactinus* Bardack (1965, p. 41) reported a small, separate bone in the anterior wall of the nasal capsule in some specimens: this may be the posteroventral wing of the rostrodermethmoid, or a membrane bone outgrowth of the supraethmoid like that which overlies the dermal bone in this region in *Cladocyclus*. In *Allothrissops* (fig. 7A) the rostrodermethmoid is similar in form, but sutures with the lateral ethmoid posteroventrally, not the ethmo-palatine. The rostrodermethmoid is fused with the supraethmoid in the rostrum in all available specimens of *Allothrissops*.

Apart from the absence of a bone-enclosed ethmoid commissure or pitline, the bone just described is the same as the rostro-dermethmoid in leptolepids (Patterson, 1975, figs. 127-130), megalopids (Patterson, 1970b, fig. 35) and *Anaethalion* (Nybelin, 1967, pl. 8, figs. 1, 2), whereas *Gaudryella* (Patterson, 1970b, fig. 2) lacks the ethmoid commissure. In one specimen of *Cladocyclus* (AMNH† 9981) and in some examples of the large Kansas ichthyodectiforms the upper surface of the rostrodermethmoid appears to show sutures separating an ovoid, median portion from paired, posterolateral portions, recalling the median rostral and paired lateral dermethmoids of *Proleptolepis* (Patterson, 1975, fig. 123), but in no ichthyodectiform are these sutures sufficiently clear to rule out post-mortem effects. In *Allothrissops* there is no indication of a separate rostral in any specimen. There is no sign of an ethmoid commissure or pitline in any ichthyodectiform: the "sensory canal pores" which Bardack and Sprinkle (1969, p. 309) described on the surface of the rostrodermethmoid in *Saurodon* were misinterpreted.

The vomer of ichthyodectiforms is fused with the ventral ethmoid, as in most teleosts and leptolepids in which this part of the endoskeleton is ossified (Patterson, 1975, p. 514). The vomer bears a median, elongate patch of small teeth in *Allothrissops* and *Cladocyclus*, and this probably occurs in other ichthyodectiforms (cf. Bardack, 1965, pp. 41, 55).

3. Circumorbital Bones.

The complete circumorbital series has not previously been described or illustrated in any ich-

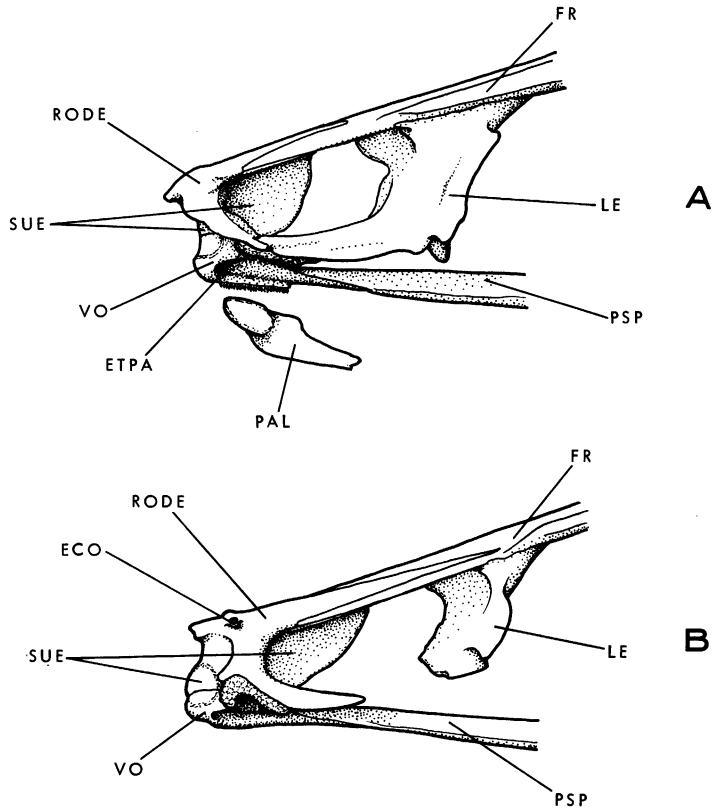


FIG. 7. A, *Allothrissops mesogaster* (Agassiz), ethmoid region of braincase and left palatine (displaced ventrally) in lateral view, restored from AMNH† 8397 and BMNH 37043 and P.915*a*. B, *Tharsis dubius* (Blainville), ethmoid region of braincase for comparison with A, after Patterson (1975, fig. 130). Both ×10 approx.

thyodectiform, except *Allothrissops* (Patterson, 1967a, fig. 2). The series is illustrated here in *Allothrissops* (fig. 5) and in three specimens of *Cladocyclus* (figs. 1-3). The circumorbitals presumably formed a complete ring around the orbit in all ichthyodectiforms, as they do in *Allothrissops* and *Cladocyclus*, the thick supraorbital and the square or triangular antorbital (anterior supraorbital of Bardack, 1965, and Bardack and Sprinkle, 1969) being preserved quite frequently, but the flimsy infraorbitals and dermosphenotic being lost or damaged. In *Cladocyclus* there is much variation in the infraorbitals in the three specimens illustrated. The large posteroventral infraorbital, extending back to the preopercular, is assumed to be homologous in the three. In AMNH† 9980 (fig. 3) there are three bones between this and the antorbital, not two as in leptolepids (Nybelin, 1974) and primitive extant teleosts (Nelson, 1969b), whereas in AMNH† 9981 and 2982 (figs. 1, 2) there are two large bones in front of the posteroventral infraorbital and a minute ossicle, perforated by the sensory canal, between the foremost and the antorbital. Behind and above the large posteroventral infraorbital there are two infraorbitals and a dermosphenotic in AMNH† 9981 and 2982, one infraorbital and a dermosphenotic in BMNH P.56471 and (probably) AMNH† 9980. In *Allothrissops* the pattern of infraorbitals resembles that in *Leptolepis* and primitive extant teleosts, except that the third bone behind the lachrymal, not the second, is the largest. With the available information, it is impossible to reach a decision on homologies between the individual infraorbitals of *Allothrissops* and the various patterns found

in *Cladocyclus*, or to decide on the pattern primitive for ichthyodectiforms. The small ossicle beneath the antorbital in AMNH† 9981 and 2982 may be a much-reduced lachrymal, or a "rostral ossicle," derived in phylogeny from the antorbital, as in elopiforms (Nybelin, 1967a; Forey, 1973a, b). If the largest infraorbital of *Allothrissops* is homologous with the largest infraorbital of *Cladocyclus*, the condition with a single bone above the latter (fig. 2) would be primitive, but if the posteroventral infraorbital of *Allothrissops* is homologous with the bone in the same position in *Cladocyclus*, the condition with two bones above the latter (fig. 1) would be primitive.

In three specimens of *Cladocyclus*, AMNH† 9981, 2982 and BMNH P.56471 (figs. 1, 2), the posterior infraorbital or infraorbitals are slender, and behind them there is a large suborbital (also illustrated by Santos, 1950, pl. 2, fig. 2; pl. 3, fig. 1), extending back across the upper part of the preopercular: this bone is similar in size and position to the suborbital of *Leptolepis coryphaenoides* (Wenz, 1968b, figs. 91, 93, 96; Nybelin, 1974, fig. 4). In AMNH† 9980 (fig. 3) there is no sign of a suborbital, although this region is not well preserved (cf. Santos, 1950, pls. 1, 2). We have seen no other Cretaceous ichthyodectiform in which the preservation is sufficiently good to show whether a suborbital was present, but in BMNH P.54597, an undetermined specimen of *Thrissops* from the Kimmeridge Clay (Upper Jurassic) of Dorset, there is definitely a suborbital, similar in size and shape to that of AMNH† 2982 (fig. 1), and preceded by two infraorbitals, as in that specimen. In *Allothrissops* there is no sign of a suborbital in any specimen that we have examined, and we believe that the bone was absent: exceptional preservation, better than in any available specimen, would be necessary to confirm the absence of the bone.

In the infraorbitals of *Cladocyclus* the sensory canal branches richly, whereas in *Allothrissops* there are very few branches and the canal ends blindly in the lachrymal, without passing into the antorbital as it does in *Cladocyclus*. The lack of a suborbital, the lack of a sensory canal in the antorbital, and the sparse branches of the infraorbital sensory canal appear to be specializations of *Allothrissops*, enabling one to recognize the genus as a monophyletic group within the ichthyodectiforms.

4. Palate.

In all ichthyodectiforms except *Allothrissops* the palatine is highly specialized, with the articular head of the bone modified into a disc that fits between the palatine condyle of the maxilla and the ethmo-palatine bone. The body of the palatine incorporates the dermopalatine, and is short and toothless in ichthyodectids (we have observed a small patch of palatine teeth in AMNH† 1614, *Saurodon leanus*). In *Allothrissops* (fig. 7A) a disclike palatine malleolus is not developed, the articular surfaces for the maxilla and ethmo-palatine lying at an acute angle to each other, but the body of the bone incorporates the dermopalatine and is short, slender and toothless, as in ichthyodectids. The ecto- and endopterygoids are toothed in *Allothrissops*, *Cladocyclus*, *Ichthyodectes*, and *Xiphactinus* (Bardack, 1965, pp. 47, 58). In *Saurodon* the palate is toothless according to Bardack and Sprinkle (1969, p. 320), but AMNH† 1614, *Saurodon leanus*, appears to have ectopterygoid teeth.

5. Dermal Upper Jaw.

In all ichthyodectiforms there is a short premaxilla and a long maxilla, both bearing a single row of teeth, and two supramaxillae (only one supramaxilla is known in saurodontids as yet). Variations in the size and number of teeth have been used extensively as specific and generic characters, but Bardack (1965) showed variations in number to be of little value. One may distinguish forms with minute teeth (*Allothrissops*, *Gillicus*, some *Thrissops* spp.), forms with larger, uniform teeth (*Ichthyodectes*, *Cladocyclus*, *Thrissops sensu stricto*, *Eubiodectes*, *Spathodactylus*, *Saurodon*, *Saurocephalus*), and forms with some teeth much enlarged (*Xiphactinus*, *Chirocentrites* and possibly *Proportheus*, in which the first premaxillary tooth is enlarged according to Bardack, 1965).

In *Allothrissops* the premaxilla and maxilla are very similar to those of *Tharsis dubius* (fig. 34), the only differences being the single row of maxillary teeth in *Allothrissops*, the longer

(rostrocaudally) premaxillary ascending process, and the slightly more posterior position of the palatine condyle on the maxilla.

In saurodontids the teeth of the upper (and lower) jaw have characteristic foramina or notches beneath them on the medial face of the bone. Bardack and Sprinkle (1969) interpreted these as the entry points of replacement teeth.

6. Lower Jaw.

Nelson (1973b) has proposed a theory of the ossification pattern of the lower jaw in fishes, and (1973a) has described the lower jaw of *Ichthyodectes*, *Xiphactinus*, *Gillicus*, and *Saurodon*. In these genera he finds that there are separate articular, retroarticular, and angular bones (a primitive teleostean pattern), that the opening for the mandibular sensory canal is on the medial face of the long postarticular process of the angular, which shields the articular facet in lateral aspect, and that the articular facet for the quadrate lies on the angular and articular bones. A medial sensory canal opening is found in *Elops* and *Megalops* alone amongst Recent actinopterygians, and is interpreted by Nelson as a derived feature indicating relationship between ichthyodectiforms and elopomorphs. The condition of the articular facet in the genera examined by Nelson is unique, for in other fishes an angular component of the facet is possibly present only in teleosts with the angular and retroarticular fused (elopomorphs) or with the angular and articular fused (clupeomorphs, euteleosteans).

Figure 8B, C shows the lower jaw of *Cladocyclus*. Here the sensory canal opening is medial and the angular is not fused with a cartilage bone, as in the ichthyodectiforms studied by Nelson, but the articular facet involves three bones, the articular, retroarticular, and angular: this is evidently a primitive condition relative to the exclusion of the retroarticular from the facet in *Ichthyodectes*, *Xiphactinus*, *Gillicus*, and *Saurodon* (cf. osteoglossines amongst osteoglossoids, Nelson, 1973a, p. 7). In *Allothrissops* (fig. 8A) the angular is not fused with a cartilage bone and the sensory canal opening is medial, as in other ichthyodectiforms, but here there is no angular component of the articular facet, which is formed by the articular and retroarticular, the primitive configuration according to Nelson. In the ossification pattern, articular facet, form of the postarticular process and position of the sensory canal opening, *Allothrissops* agrees with Upper Jurassic leptolepids such as *Tharsis dubius* and an unnamed Callovian species (fig. 32). A medial sensory canal opening, found in *Elops*, *Megalops*, *Anaethalion*, ichthyodectiforms and plethodids by Nelson (1973a), also occurs in *Tharsis dubius*, the unnamed Callovian leptolepid, *L. coryphaenoides*, and *Leptolepides sprattiformis* (fig. 32). Since there is good evidence (see p. 127) that these leptolepids, in particular *L. coryphaenoides*, are not members of a monophyletic group containing only those forms with a medial sensory canal opening (i.e., evidence that elopomorphs are more closely related to other extant teleosts than to leptolepids), we reject Nelson's hypothesis that the medial opening is an elopomorph specialization, and regard it as a synapomorphy of post-*Proleptolepis* teleosts that has been lost in most modern forms.

In ichthyodectiforms the mandibular dentition invariably comprises a single row of teeth, minute in *Allothrissops* and some *Thrissops* spp., larger in others. *Allothrissops* (fig. 9A) has a high coronoid process of leptolepid type, placed in the anterior half of the jaw, and with a concave anterior margin, behind the tooth row. The tooth row is more extensive than in known leptolepids. Some indication of the concavity behind the tooth row persists in *Cladocyclus* (fig. 8C), but in this and other ichthyodectiforms the long tooth row on the dentary is almost horizontal, and the coronoid process is in the posterior third of the jaw. In *Cladocyclus* (and probably in other ichthyodectiforms: Bardack, 1965, figs. 10, 20; Bardack and Sprinkle, 1969, fig. 6) the Meckelian fossa on the inner face of the jaw is minute and placed far forward, as in leptolepids (Patterson, 1970b, p. 266).

In *Saurodon* and *Saurocephalus* there is a median, toothless predentary bone in front of the dentary (Bardack and Sprinkle, 1969). This is the most obvious specialization of the saurodontids.

7. Hyoid Arch and Branchiostegals.

The hyomandibular of ichthyodectiforms is

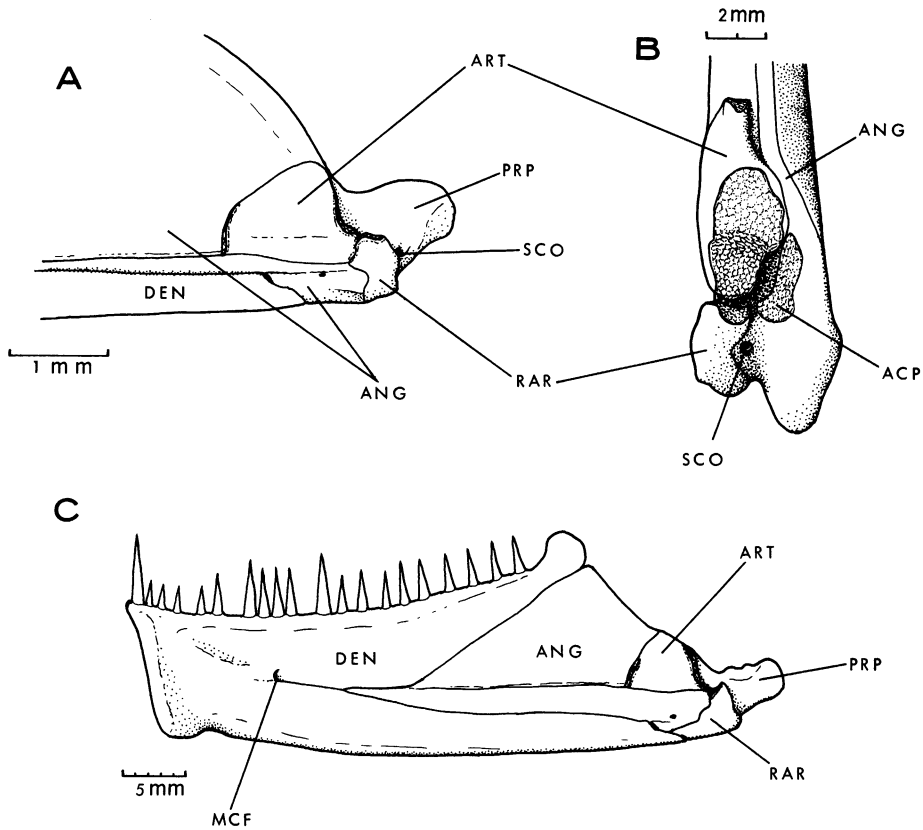


FIG. 8. A, *Allothrissops mesogaster* (Agassiz), posterior part of right lower jaw, medial view, from BMNH P.3680*b*. B, C. *Cladocyclus* sp., AMNH† 9981; B, posterior part of right lower jaw, posterodorsal view; C, right lower jaw, medial view.

not remarkable except that in *Allothrissops* a preopercular process is present (fig. 9B) similar to those illustrated by Nybelin (1974) in *Leptolepis coryphaenoides*, *L. normandica*, *Proleptolepis*, and *Tharsis dubius*. The ceratohyal of *Ichthyodectes* (Bardack, 1965, p. 59) and *Cladocyclus* contains a narrow, elongate fenestra. In *Allothrissops* (fig. 9B) this fenestra is very large, and the bone resembles that of leptolepids and other very primitive teleosts. There are two hypohyals in all ichthyodectiforms where the region is visible.

Bardack (1965, p. 59) and Saint-Seine (1949, p. 270) recorded more than 20 branchiostegals in *Ichthyodectes* and *Thrissops formosus* respectively, whereas *Chirocentrites* is said to have about 20 (Woodward, 1901, p. 90). Nothing else has been published on ichthyodectiform branchiostegals. *Eubiodectes* has at least 23 branchiostegals, perhaps as many as 26 (BMNH 39238), all but the last six or seven slender and threadlike. In *Cladocyclus* we have not found firm evidence of more than six branchiostegals (figs. 1, 3), the last three spathiform, the first two threadlike, all inserting on the posterior part of the hyoid bar, but in AMNH† 2982 there are traces of what may be a few excessively reduced rays (short and hairlike) anteriorly. In *Allothrissops*, BMNH P.3680b shows 18 branchiostegals, eleven on the distal ceratohyal, one on the suture between the two parts of the bone and seven on the proximal ceratohyal. The first 10 are threadlike, the last three spathiform. This condition may be compared with the 22 branchiostegals of

Tharsis dubius (BMNH P.56539), where there are 12 on the distal ceratohyal, one on the suture and nine on the proximal ceratohyal.

8. Gill-arch Skeleton.

Most of the gill-arch skeleton is visible in the acid-prepared *Cladocyclus* specimens, especially AMNH† 9980, and in BMNH 37043, *Allothrissops mesogaster.* The gill-arches are of primitive teleostean type, resembling those of *Elops*, with a minute ossified first infrapharyngobranchial, a long, rodlike first suprapharyngobranchial (both seen in *Allothrissops*), a large dorsal process on the fourth epibranchial like that in *Elops* (Nelson, 1967, fig. 1A), seen in *Cladocyclus*, and all the arches set with dermal plates bearing minute teeth. The tooth-plates are enlarged over the basibranchials and posterior pharyngobranchials, but are nowhere fused with the endoskeletal bone. There are long, toothed gill-rakers (also mentioned by Bardack, 1965, in *Ichthyodectes*, *Xiphactinus* and *Gillicus*), up to 15 mm. long in a *Cladocyclus* of head length 100 mm., 8 mm. long in an *Allothrissops* of head length 40 mm.

9. Opercular Bones.

The preopercular of ichthyodectiforms is broad, with a long dorsal limb extending up to the head of the hyomandibular (there is no suprapreopercular) and a shorter ventral limb lying at about 90 degrees to the dorsal limb. In *Allothrissops* and *Thrissops* the posteroventral angle of the preopercular is thrown out into a projection which carries the longest tubules of the sensory canal. Nybelin (1964, p. 40) compared this with the preopercular of "*Leptolepis*" *macrophthalmus* and *Pholidophorus bechei* (*Pholidolepis* has a similar preopercular: Nybelin, 1966, fig. 16). In our opinion, this resemblance is symplesiomorphic, not indicative of relationship (*Denticeps* and some osteoglossomorphs have a similar preopercular: Greenwood, 1968, p. 261). In pholidophorids and leptolepids (figs. 34, 45B) the bone-enclosed portion of the sensory canal tubules extends almost to the ventral margin of

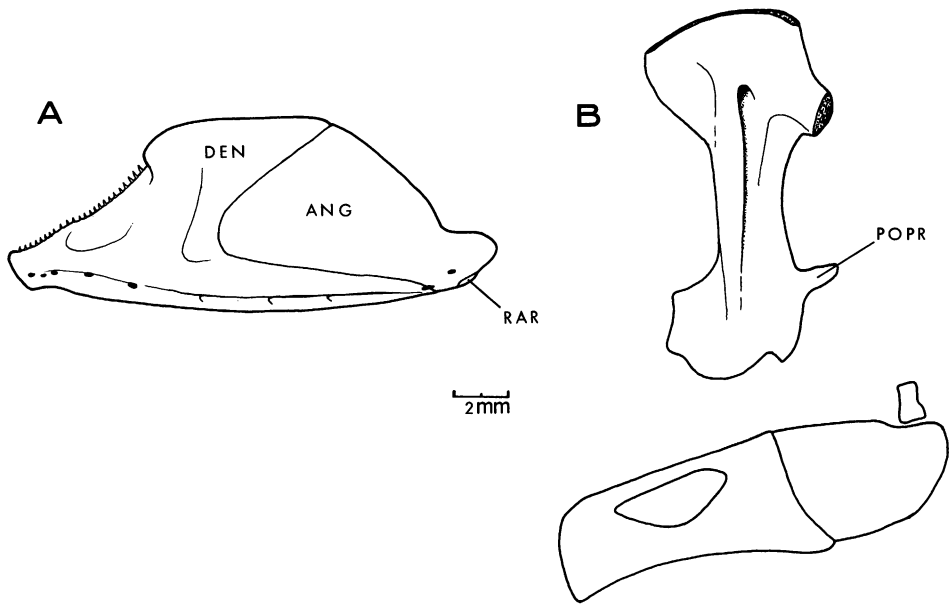


FIG. 9. A, *Allothrissops mesogaster* (Agassiz), restoration of left lower jaw in lateral view, from BMNH 37043, P.915, and P.3680*b*. B, *Allothrissops regleyi* (Thiollière) left hyomandibular, lateral view, and outline of right ceratohyal and interhyal, medial view, from BMNH P.4689, Kimmeridgian, Cerin, Ain, France.

the preopercular: in ichthyodectiforms the tubules are shorter, opening into grooves. In *Allothrissops* (fig. 5), *Cladocyclus* (fig. 1), *Ichthyodectes* and *Xiphactinus* (Bardack, 1965, figs. 9, 16) there is a characteristic notch in the upper part of the posterior edge of the preopercular. The preopercular sensory canal is bone-enclosed in all ichthyodectiforms, and gives off many tubules, those in the lower limb of the bone arranged regularly. In *Cladocyclus* (figs. 1-3) there is much variation in the form and number of the tubules, suggesting that little weight can be given to the arrangement of the tubules in ichthyodectiforms.

The opercular, subopercular, and interopercular (figs. 1-3, 5) show nothing worthy of comment.

10. Pectoral Girdle and Fin.

Bardack (1965) has described the pectoral girdle of *Ichthyodectes*, *Xiphactinus*, and *Gillicus*; that of *Allothrissops* is shown in figure 10. In all ichthyodectiforms the ventral part of the coracoid is very large and meets its fellow in the midline ventrally. The pectoral fin inserts low on the flank, the glenoid surface is inclined at about 45 degrees and a large mesocoracoid is present. In *Cladocyclus* and *Allothrissops* there appear to be three postcleithra, the uppermost with a thickened dorsal end that articulated with the supracleithrum. Bardack (1965, fig. 12) only shows this uppermost postcleithrum; Taverne (1974d, p. 51) is mistaken in supposing that a single postcleithrum relates ichthyodectiforms and osteoglossomorphs. The proximal pectoral radials are probably five in number, the propterygium being fused into the base of the dorsal hemitrich of the first fin-ray (cf. Jessen, 1972). In *Cladocyclus* the distal end of the third free radial is forked. There is a series of ossified distal radials in *Allothrissops* and *Cladocyclus*.

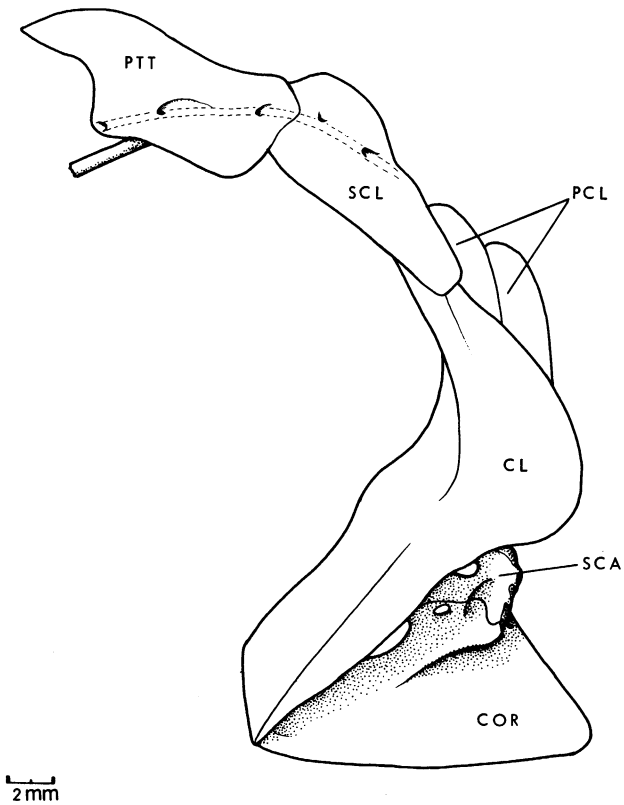


FIG. 10. *Allothrissops mesogaster* (Agassiz), restoration of left pectoral girdle, lateral view, from BMNH 37043.

The pectoral fin contains 16 rays in *Allothrissops mesogaster* (BMNH P.3680b). There is no "splint" at the base of the upper hemitrich of the first pectoral ray in *Allothrissops* or *Cladocyclus*, so that this ray probably has the same compound origin as in nonelopoid teleosts (Jessen, 1972, p. 22). The enlarged first pectoral ray, characteristic of ichthyodectiforms, is probably always segmented distally, despite statements to the contrary.

11. Pelvic Girdle and Fin.

In *Allothrissops* the pelvic girdle is small, slender, and unremarkable, and the pelvic fin contains nine rays and a small pelvic splint. Bardack (1965, p. 50) described the pelvic girdle of *Xiphactinus*, which also has nine pelvic rays.

12. Vertebral Column.

The number of vertebrae recorded in ichthyodectiforms ranges from 40 (19+21) in *Cladocyclus woodwardi* Santos (1949: a very poorly known species that cannot be regarded as an established member of the group) to about 100 in *Saurodon* (Bardack and Sprinkle, 1969). *Allothrissops* (fig. 11) and Jurassic species of *Thrissops* (fig. 12) have 56 (30+26) to 63 (34+29), and this range includes published counts for *Spathodactylus*, *Chirocentrites*, and *Proportheus*. *Eubiodectes* has about 65 vertebrae (37+28), and amongst the larger ichthyodectids *Ichthyodectes* has 68-72, *Gillicus* about 70 and *Xiphactinus* 85-89 (Bardack, 1965). All the neural and hemal arches are autogenous in *Ichthyodectes*, *Gillicus*, *Xiphactinus* (Bardack, 1965) and *Cladocyclus*. In *Allothrissops* the neural arches are all autogenous, but in the caudal region all except the last few hemal arches are fused with the centra. There are long epineural bones on the abdominal vertebrae of all ichthyodectiforms, and at least in *Allothrissops* and *Cladocyclus* they are all developed as outgrowths of the neural arches. In *Cladocyclus* there are four or five pairs of free

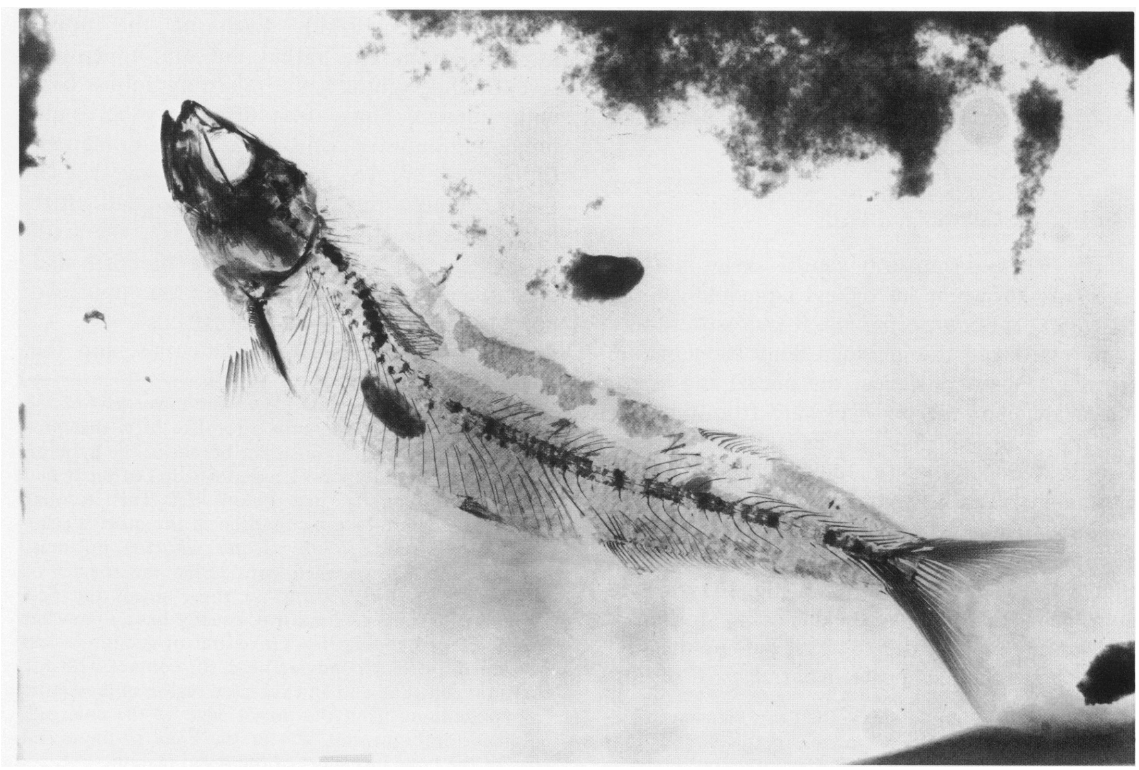


FIG. 11. *Allothrissops mesogaster* (Agassiz), positive print from radiograph of BMNH P.915*a*, a transfer preparation, Kelheim, Bavaria. ×1.5 approx.

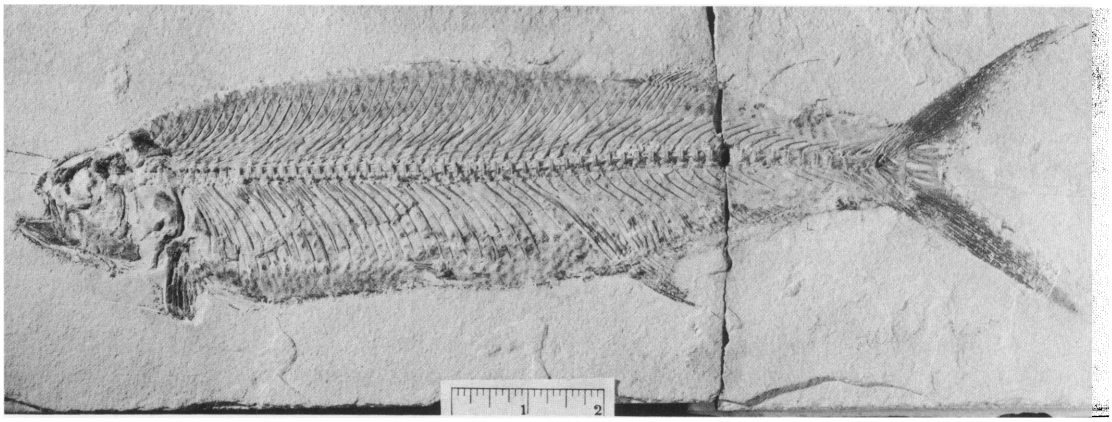


FIG. 12. *Thrissops formosus* Agassiz, BMNH P.3684, Kimmeridgian, Kelheim, Bavaria (scale in inches).

epineurals articulating with the braincase. The epineurals of *Cladocyclus* are extremely long, extending over at least 10 vertebrae in the anterior part of the column, and forming a bundle of parallel rods lateral to the neural arches (fig. 1A). The ribs of ichthyodectiforms are long, reaching the ventral margin of the abdominal cavity, and articulate with the posterior face of the parapophyses proximally. There are no epipleural intermusculars.

13. Caudal Skeleton and Fin.

The ichthyodectiform caudal skeleton (figs. 13-20) is known more or less completely in all genera except *Saurocephalus*. It is dorsoventrally compressed and the included bony elements are crowded together. Hence, the neural and hemal spines are bent sharply backward from the base and they are long. As many as five neural spines and six hemal spines (including the parhypural) may be involved in support of dorsal and ventral procurrent caudal fin rays. There are two ventral hypurals articulating with the first ural centrum (figs. 14, 15). The first hypural (fig. 16) is seated in a deep or shallow socket or in a shallow excavation on the anteroventral half of the first ural centrum.[1] The posteroventral part of this centrum has a smaller notch to receive the base (also condylar in some cases, fig. 15) of the uniformly slender second hypural. The second ural centrum (U2) is associated with six upper hypurals of gradually decreasing length and breadth (figs. 17-19). Each of the upper hypurals, even the rather delicate uppermost seventh and eighth, has a relatively robust base with a lateral flange that often may be found projecting outward beneath the upper uroneurals (PPH, figs. 17, 18; Nybelin, 1963, fig. 12, Ur 9-13). Only the third, fourth, and fifth hypurals articulate directly with U2, the sixth to eighth lying in parallel above the fifth and articulating basally only with the upturned notochordal portion of the caudal axis.

There are six or seven uroneurals, and the

[1] Cavender (1966) first described this element in ichthyodectids: "The anterior portion of this bone is rodlike with a condylar end. Posteriorly the bone is expanded into a spatulate plate. The lower part of the hypural is differentiated into a rod-like form that projects beyond the vertical posterior border of the hypural. This lower part of hypural 1 resembles that of the hemal spine [= parhypural] just below it." This account excellently describes the condition in the most specialized ichthyodectids (*Ichthyodectes*, *Gillicus*), but must be amended slightly when considering the species of *Thrissops* and *Allothrissops*. In those forms the first hypural element is less massive, usually has a somewhat less developed rodlike posteroventral projection, a less developed anterior condylar head for contact with the first ural centrum, and an excavated region of crescentic form extending from the dorsal edge of the enlarged, columnar anteroventral part of the bone to the dorsal edge of the bone just short of the distal margin.

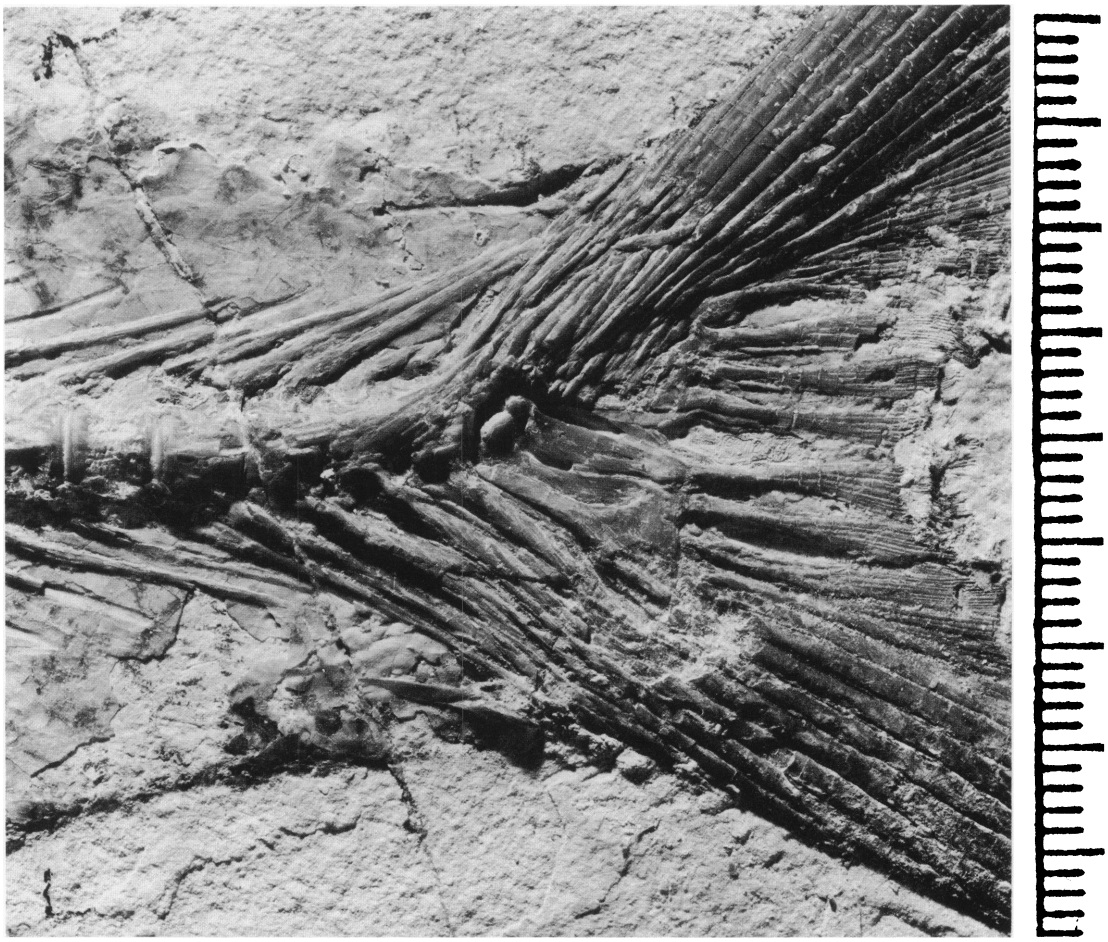


FIG. 13. *Thrissops formosus* Agassiz, caudal skeleton of BMNH P.3684 (same specimen as fig. 12; scale in mm.).

number may vary from side to side of a single specimen (fig. 17A, B). The anteriorly elongated tips of the first few uroneurals cover most of the lateral surfaces of the ural and first two or three preural centra. The first four or five uroneurals are greatly elongate and are subequal in length and rather thick as compared with the more posterior sixth and seventh. Although the enlarged anterior five uroneurals are of nearly the same length, their posterodorsal tips are staggered in position as in leptolepids. The tips of the first four uroneurals (fig. 18) often are flared and somewhat indented and the tip of the fifth tapers to a sharp or narrowly blunt end, or only the first three are flared and the next two tapered, or the tip of each of the enlarged uroneurals is rounded and spatulate rather than indented, or, as in one specimen of *Thrissops* (BMNH P.4663), the first uroneural is deeply bifurcate and the remaining elements are simply rounded. In an occasional individual of *Thrissops* the anteriormost uroneural extends forward well on to PU4 (fig. 14, and Patterson, 1968).

The epurals of ichthyodectiforms are at present known to vary in number from three (in *Thrissops* and *Allothrissops*) to one (in *Clado-*

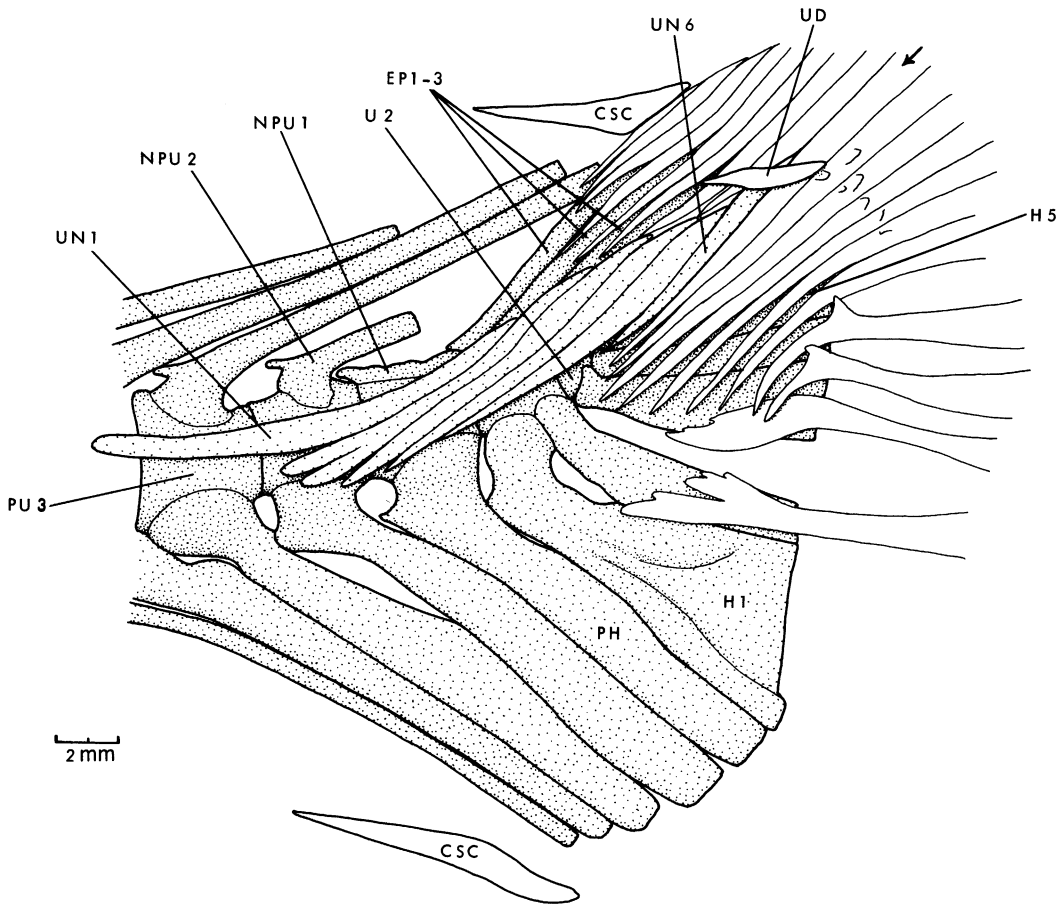


FIG. 14. *Thrissops formosus* Agassiz, caudal skeleton and bases of upper caudal fin rays of BMNH P.3684 (same specimen as figs. 12, 13), slightly restored.

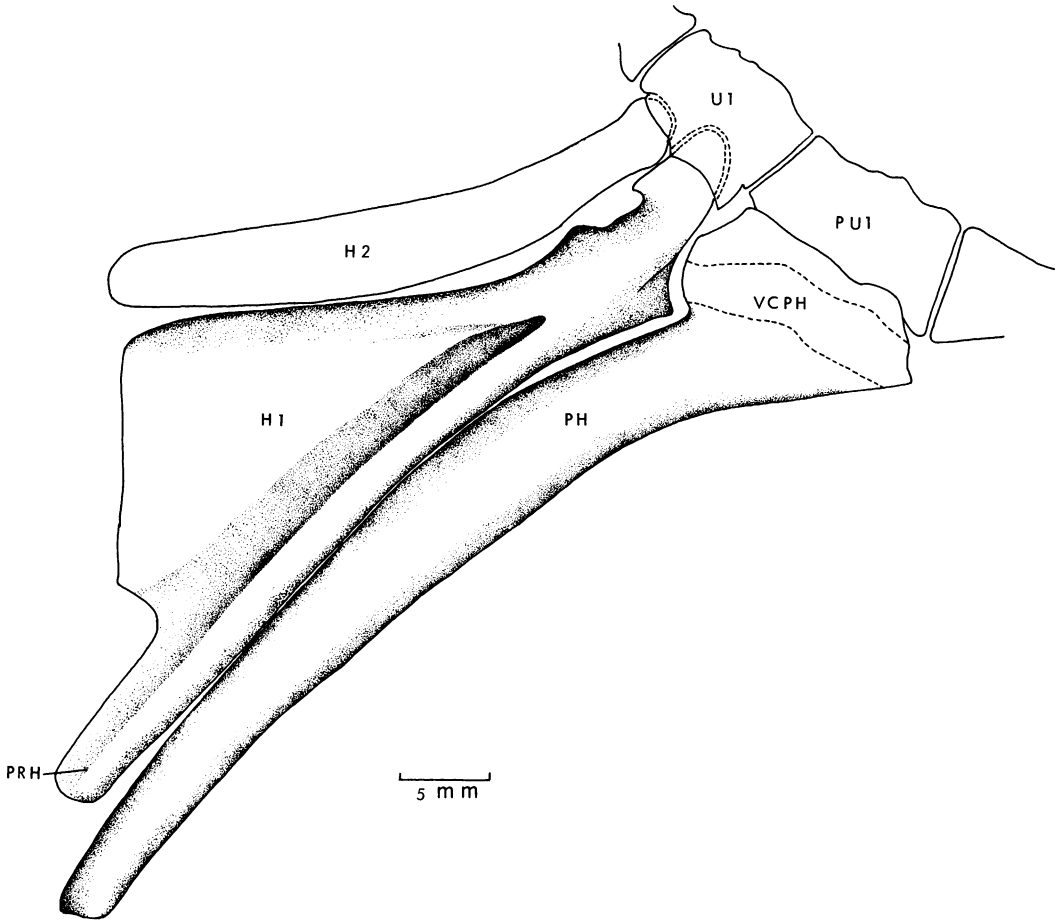


FIG. 15. Part of an undetermined ichthyodectiform caudal skeleton, BMNH P.1482, Chalk (Upper Cretaceous), Sussex, slightly restored.

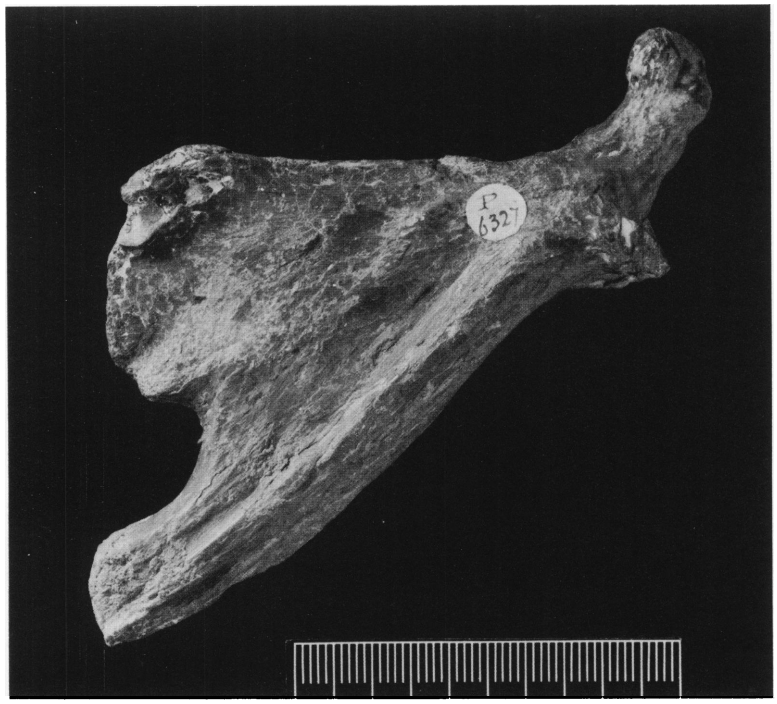


FIG. 16. First hypural of an undetermined ichthyodectiform, BMNH P.6327, Niobrara Formation (Upper Cretaceous), Kansas (scale in mm.).

cyclus, fig. 19, and in the *Ichthyodectes* type of fish according to Cavender [1966]). In *Cladocyclus* the single epural is long and robust, extending from just above a rudimentary neural arch and spine on PU1 obliquely upward to the dorsal limit of the caudal skeleton. In *Allothrissops* the three epurals are short, slender, and of equal length, and they are confined to a dorsal position in front of the uroneurals. In *Thrissops* an intermediate condition exists in which the first epural is long and robust as in *Cladocyclus*, the second is about half as long as the first, and the third is a short element not longer than the small upper hypurals.

The neural arches and spines are variable in the ichthyodectiform caudal skeleton. In *Allothrissops* there may be a rudimentary neural arch on U1 (figs. 17, 18A; Taverne, 1975c, fig. 14), or this structure may be absent (fig. 18C; Taverne, 1975c, fig. 15). Other ichthyodectiforms seem to lack a neural arch on U1. On PU1 there is a neural arch that ranges from rudimentary (fig. 14) to a half-length spine (Taverne, 1975c, fig. 15). There may be two neural arches on this centrum (figs. 18B, 19). On PU2 the neural arch and spine may be short (fig. 14; Taverne, 1975c, fig. 14), full length (figs. 17, 18A, 20; Cavender, 1966, fig. 1; Taverne, 1975c, fig. 15), or double (figs. 18B, C, 19). When double, both neural spines on PU2 may be full length (fig. 19), or one may be full length and the other short (fig. 18B, C).

Nybelin (1971, p. 13), in his detailed account of the caudal skeleton of *Elops*, proposed that the number of neural arches in the caudal region is constant, the arches developing in an exact one-to-one ratio with the centra except over U1, which is hypothesized to bear two arches since it carries two hypurals and is therefore compound in origin. Where two arches are found on PU1 or PU2, the more posterior one is held to be the arch of the succeeding centrum that has been "pushed over" from its own centrum by enlargement of the most posterior arch, the second on U1. This theory is taken further by Nybelin

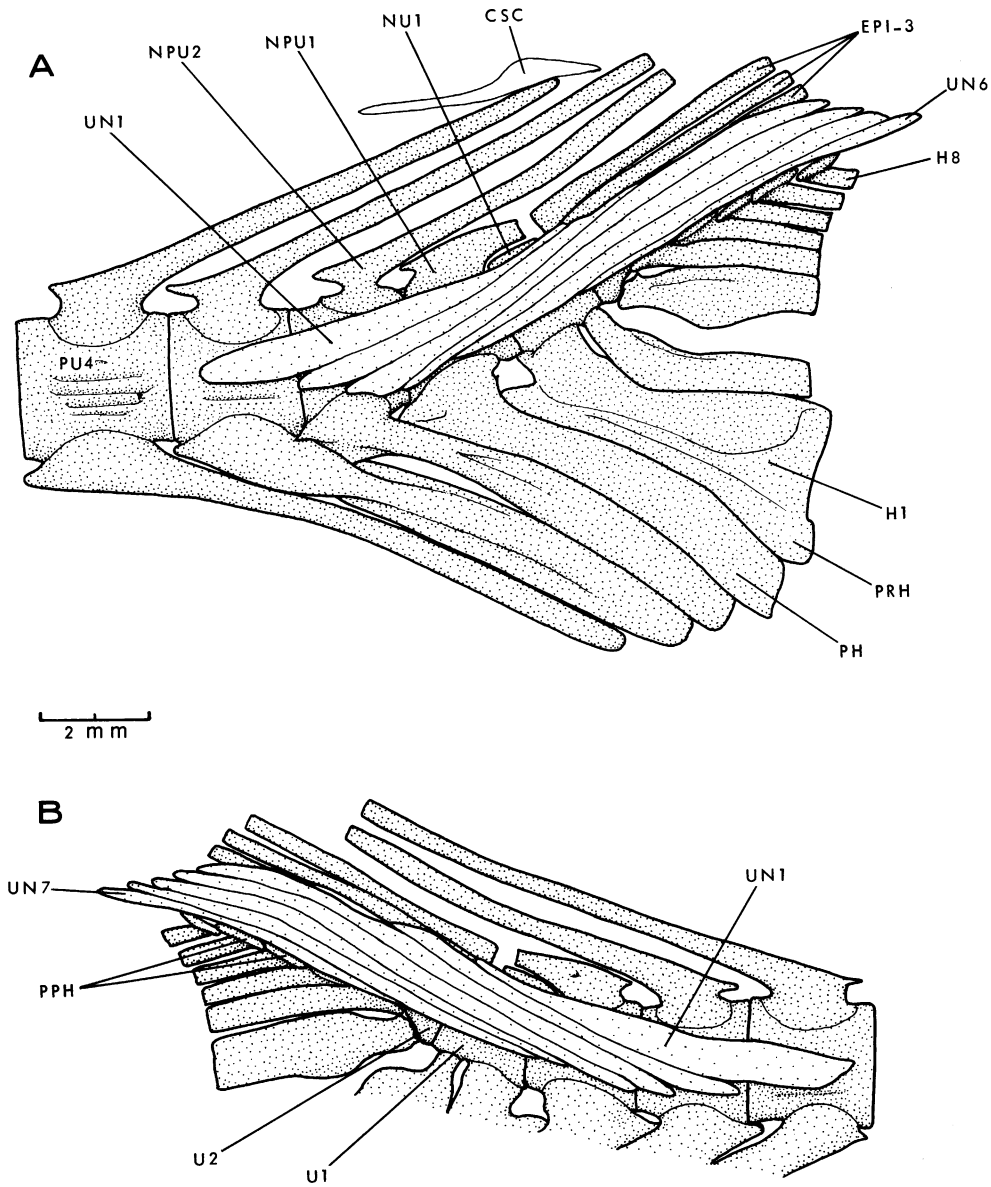


FIG. 17. *Allothrissops mesogaster* (Agassiz), caudal skeleton of BMNH P.3680, Kimmeridgian, Kelheim, Bavaria. A, left side of specimen, showing six uroneurals; B, right side, with seven uroneurals.

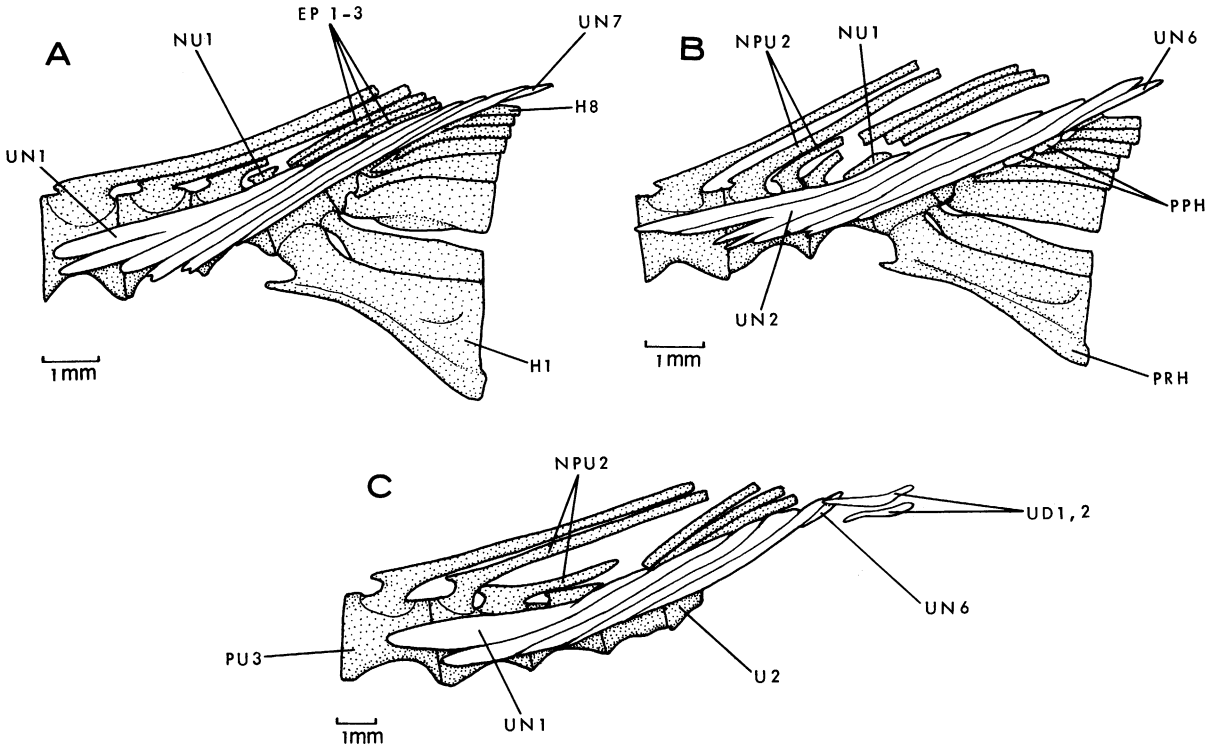


FIG. 18. *Allothrissops mesogaster* (Agassiz), caudal skeleton of A, BMNH P.7663, with seven uroneurals, the first forked anteriorly; B, BMNH P.3680*b*, with six uroneurals, the second forked anteriorly, and a double neural arch on PU2; C, BMNH P.917*a*, with double neural arch on PU2, six uroneurals and two urodermals.

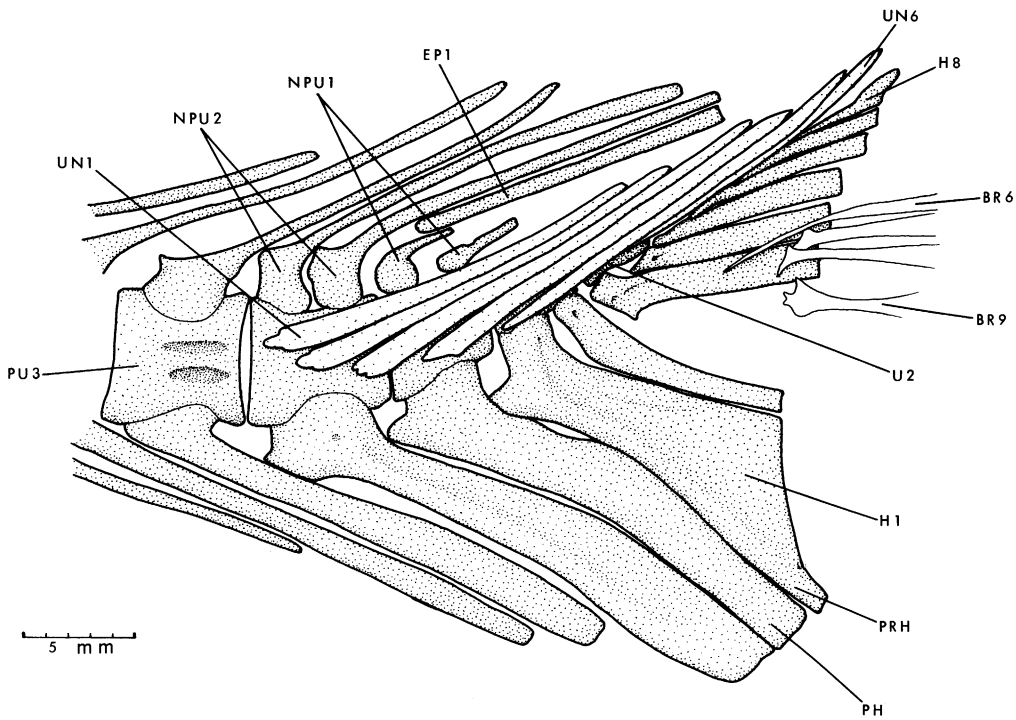


FIG. 19. *Cladocyclus* sp., restoration of caudal skeleton of AMNH† 9982A. Horizon and locality as figure 1.

(1973b, p. 253), Forey (1973b, p. 363) and Taverne (1975c, p. 345), who respectively interpret the caudal neural arches of *Albula*, salmonids and hiodontoids along these lines, drawing conclusions about relationships or ancestry from their interpretations. No evidence has been presented for this supposed ontogenetic shifting of neural arches or their rudiments, and in view of the frequency of variations or "abnormalities" in the neural arches over PU2, PU1, and U1 in lower teleosts, we think that Nybelin's theory is better dropped.

Urodermal number in ichthyodectiforms varies from two (in some examples of *Allothrissops*, fig. 18C) to one (in other specimens of *Allothrissops* and in some *Thrissops*, fig. 14) or none (in other ichthyodectids so far as known). In specimens of *Thrissops* and *Allothrissops* in which urodermals are present and undamaged, these elements in most cases are oblanceolate anteriorly and taper posteriorly to a bluntly pointed cylindrical process.

The number of principal caudal fin rays of ichthyodectiforms is that characteristic of all plesiomorph groups of modern teleosteans except osteoglossomorphs, that is, one simple and nine branched in the upper lobe and eight branched and one simple in the lower lobe.

Although the ichthyodectiform caudal skeleton exhibits many different and discrete patterns, with variation in the methods of articulation of the lower hypurals, number of hypurals, epurals, and urodermals and degree of hypurostegy (that is, the extent to which caudal fin ray bases overlap hypurals, fig. 20), the one invariable and diagnostic feature of the caudal skeleton of all ich-

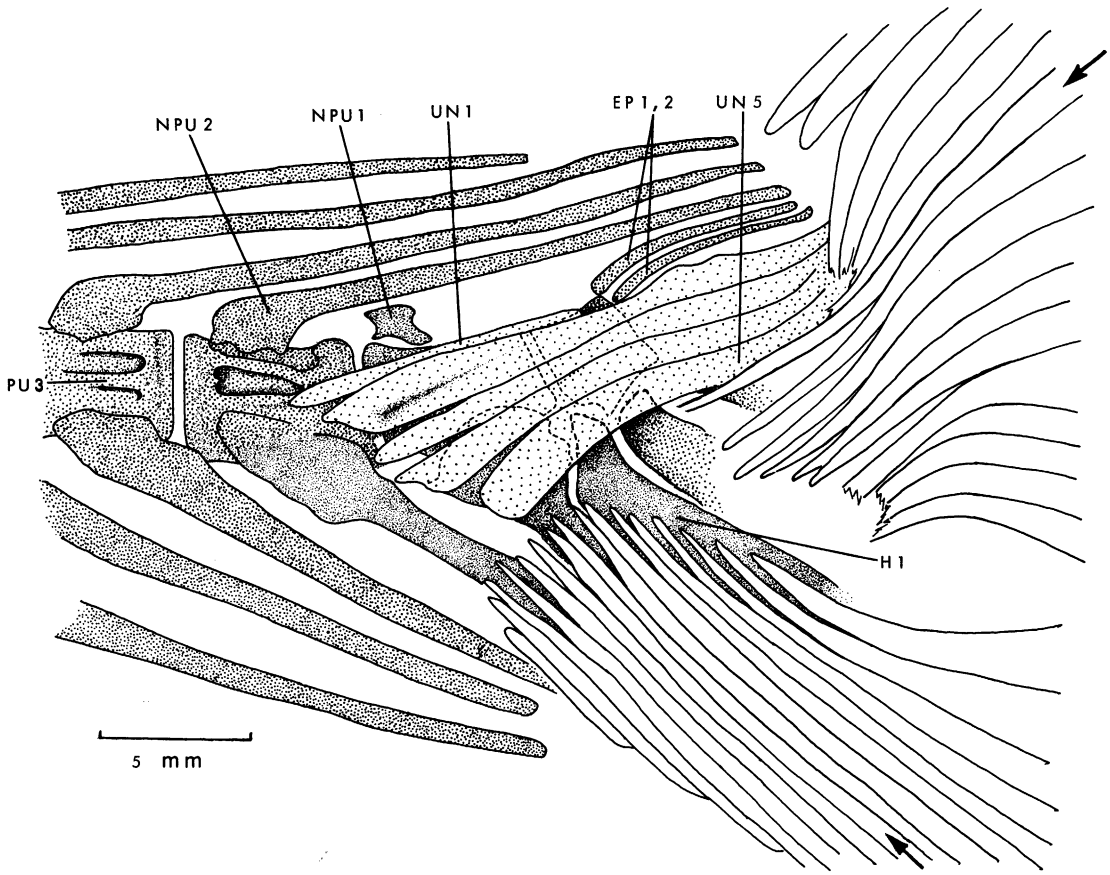


FIG. 20. *Eubiodectes libanicus* (Pictet and Humbert), restoration of caudal skeleton of AMNH† 3799, Upper Cretaceous, Hakel, Lebanon.

thyodectiforms is the manner in which the flared anterior tips of the foremost uroneurals cover and obscure most of the lateral surfaces of the ural and first few preural vertebral centra. Only one other group of fishes known to us (the crossognathids, assignable to a different section of the Teleostei on the basis of other shared derived features), has this enlargement and lateral position of the foremost uroneurals (fig. 21 and pp. 131-135).

14. Dorsal and Anal Fins.

In all ichthyodectiforms where these fins are known (they are unknown in saurodontids) the dorsal is short (10-18 rays) and remote, opposed to the middle part of the elongate, falcate anal fin (24-37 rays) (figs. 11, 12). In *Xiphactinus* Bardack (1965) described a short anal fin, with only 12-14 rays, but it is likely that the fin is incomplete in the three specimens where it is preserved.

15. Squamation.

Ichthyodectiforms have large, ovoid scales, with none to many radii in the anterior field, and in the Cretaceous forms usually with pits on the outer face of the central part of the scale and tubercles on the inner face. In the lateral line scales the sensory canal gives off bone-enclosed branching tubules in *Cladocyclus*, *Ichthyodectes*,

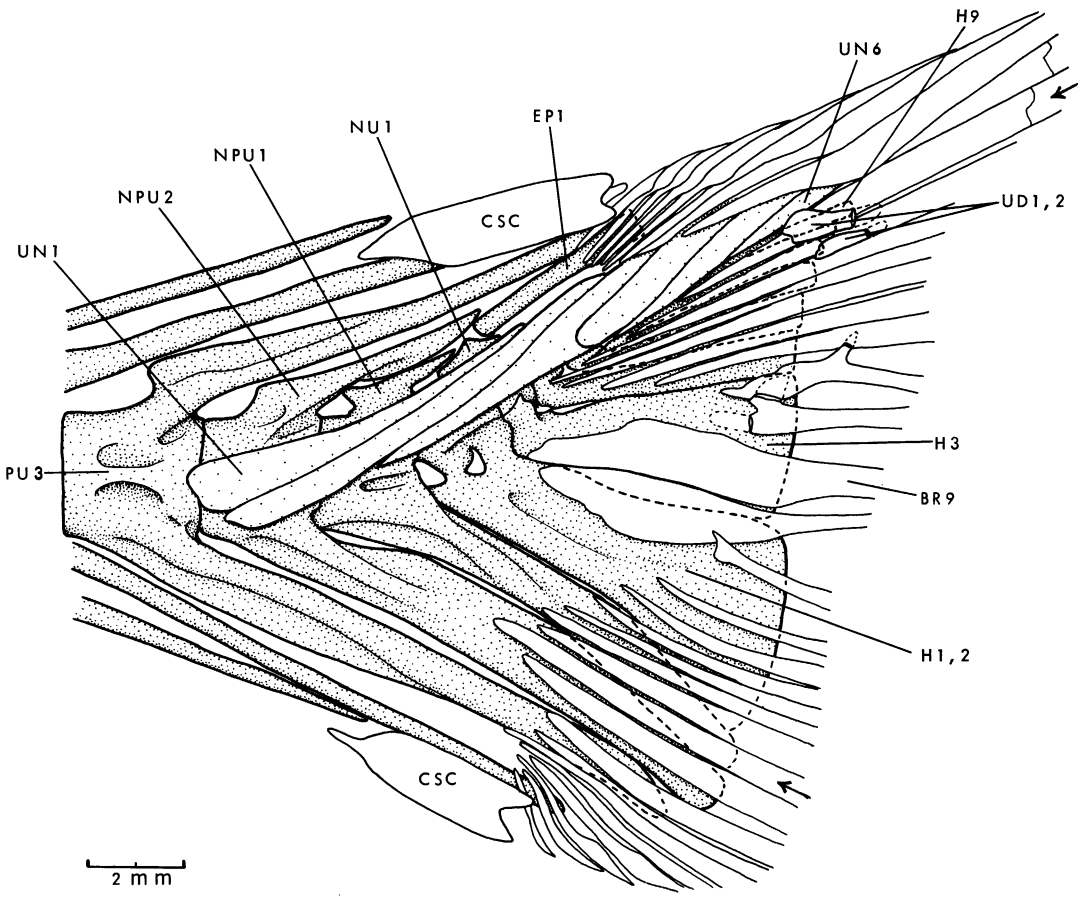


FIG. 21. *Crossognathus sabaudianus* Pictet, caudal skeleton as preserved in BMNH P.8641, with concealed portions of endoskeleton (broken lines) and anterior end of UN4 added from BMNH P.8639. Lower Cretaceous (Neocomian), Hildesheim, Hanover, Germany.

Xiphactinus (Cockerell, 1919), and *Eubiodectes*, as in megalopids (Hollister, 1939). In *Allothrissops* the lateral line is simple (Schultze, 1966, fig. 17). In *Allothrissops* the scales are acellular except for a zone around the lateral line (Schultze, 1966, p. 297). In *Cladocyclus* the scales are densely cellular around the lateral line, but are otherwise acellular, as they are in the other ichthyodectiforms investigated.

16. Soft Anatomy, Feeding, etc.

The predatory feeding habits of most ichthyodectiforms, indicated by the large teeth, are confirmed by the preservation of relatively large fishes in the body cavity of specimens of *Xiphactinus* (a *Gillicus* of standard length 161 cm. in a *Xiphactinus* of standard length 418 cm.: Bardack, 1965, p. 40), *Thrissops* (10 leptolepids, up to 30 mm. long, in a *T. formosus* of standard length 320 mm.: Nybelin, 1958) and *Cladocyclus* (AMNH† 2983, standard length estimated *ca.* 60 cm., contains a *Rhacolepis* of standard length about 14 cm.; AMNH† 2982 contains many disarticulated *?Tharrhias*). Prey was usually swallowed head first, but the *Rhacolepis* in AMNH† 2983 was taken tail first. On the basis of the position of prey and coprolites in *Thrissops*, Nybelin (1958) made a restoration of the gut of *Thrissops*, using *Chirocentrus* as a model. In *Allothrissops*, swallowed prey has never been observed, although gut contents are frequently preserved in the form of an amorphous, phosphatic mass or ribbon: together with the minute teeth of *Allothrissops*, this suggests that the fish was microphagous, not predatory like other ichthyodectiforms.

In several ichthyodectiform genera (*Thrissops*, *Eubiodectes*, *Proportheus*) specimens occur in which the body is folded through 180 degrees in the anterior abdominal region, so that the trunk lies at about 90 degrees to the head, with the opposite side exposed, whereas in *Cladocyclus* the majority of specimens are isolated heads together with the first 4-10 vertebrae. These observations suggest that ichthyodectiforms were highly compressed fishes, with a floppy, easily broken body, like (say) *Aphanopus*. We have seen no dissociated heads or folded bodies in *Allothrissops*, and this was probably a more muscular, round-bodied fish.

The majority of ichthyodectiforms are found in marine sediments, but *Proportheus* and *Cladocyclus* occur in beds of brackish or freshwater character. Parasitic copepods, belonging to a group that is today exclusively marine, have been found in the gill chamber of specimens of *Cladocyclus* which are associated with ostracods belonging to a group that is today exclusively freshwater, suggesting that the fishes were euryhaline (Cressey and Patterson, 1973).

CONCLUSION: CHARACTERIZATION AND CLASSIFICATION OF ICHTHYODECTIFORMES

From this review, we conclude that the ichthyodectiforms are a monophyletic group comprising several monophyletic subgroups as set out in the classification and characterization below. The generic names listed in the Ichthyodectidae should not be regarded as established taxa (see pp. 90-92).

Order Ichthyodectiformes (Bardack and Sprinkle, 1969): Mesozoic teleostean fishes with a (paired) ethmo-palatine ossification in the floor of the nasal capsule, articulating with the palatine; six or seven uroneurals, the first three or four extending anteroventrally to cover the entire lateral surface of the first, second, or third preural centra; teeth in a single series in the jaws; coracoid enlarged ventrally, meeting its fellow in a midventral coracoid symphysis; anal fin long, falcate, opposed by a short, remote dorsal fin.

- Suborder Allothrissopoidei, new: Ichthyodectiform fishes with no suborbital bone; infraorbital canal with few canaliculi, ending blindly in lachrymal without reaching antorbital; hemal arches fused with centra in most of caudal region.
  - Family Allothrissopidae, new: Coextensive with suborder.
    - Genus *Allothrissops* Nybelin
- Suborder Ichthyodectoidei (Romer, 1966): Ichthyodectiform fishes with a high, triangular supraoccipital crest, parietals displaced forward; intercalar enlarged, forming part of the hyomandibular facet and enclosing a canal for the jugular vein; ethmo-palatine bone with membranous outgrowths separating and suturing with the rostrodermethmoid

and lateral ethmoid; palatine head modified into a disclike malleolus; angular contributing to articular facet for quadrate; first hypural set into ural centrum by a ball-and-socket joint.

Family Ichthyodectidae Crook (1892): Ichthyodectoid fishes with the parietals fused into a median bone (?Jurassic *Thrissops*); a basal sclerotic bone with serrated margins present. Genera *Ichthyodectes* Cope, *Xiphactinus* Leidy, *Gillicus* Hay, *Cladocyclus* Agassiz, *Eubiodectes* Hay, *Proportheus* Jaekel, *Chirocentrites* Heckel, *Thrissops* Agassiz, *Spathodactylus* Pictet

Family Saurodontidae Cope (1871): Ichthyodectoid fishes with a median, toothless predentary bone; a notch or foramen at the base of the internal surface of each tooth in the maxilla, premaxilla, and dentary. Genera *Saurodon* Hays, *Saurocephalus* Harlan

FRAMEWORK OF NEOPTERYGIAN INTERRELATIONSHIPS

The fishes with which we are principally concerned are teleosts from the Jurassic and Cretaceous. The phylogenetic relationships of such fossils can only be discussed within a framework dictated by the interrelationships of the major groups of living teleosts and their extant sister-group. In order to exemplify methods of interpreting and classifying such fossils, we will consider them within the classification of higher actinopterygians, the Neopterygii of Regan (1923), Nelson (1969a) and Patterson (1973). Evidence bearing on the phylogenetic classification of the major neopterygian subgroups is summarized in articles by Forey, Greenwood, Nelson, Nybelin, and Patterson in *Interrelationships of Fishes* (1973). Subsequent papers by Forey (1973a), Rosen (1974), Taverne (1973a, 1974c, 1975c), and Nybelin (1973b, 1974) dealt with aspects of the problem.

The infraclass Neopterygii contains two divisions, Ginglymodi (Lepisosteidae) and Halecostomi, and the latter has two subdivisions, Halecomorphi (Amiiformes) and Teleostei. Recent teleosts comprise four groups that were first recognized (as superorders) by Greenwood, Rosen, Weitzman and Myers (1966). Three of these groups were named as cohorts by Greenwood, Myers, Rosen and Weitzman (1967). The four groups are the Elopomorpha (=Taeniopaedia), Osteoglossomorpha (=Archaeophylaces), Clupeomorpha, and Euteleostei. The interrelationships of these groups are still controversial, as discussed in detail below, but we regard the groups as established monophyletic units, since all attempts, overt or covert, to destroy their unity (for example, by demonstrating that *Hiodon* is a clupeomorph, that *Elops* is a euteleostean or a clupeomorph, or that *Albula* is a clupeomorph) have failed, while many investigations of aspects of one or more of the groups have emphasized the individuality of each.

Greenwood et al. (1966, p. 350) originally considered that the elopomorphs and clupeomorphs are related, but the characters they cited are either primitive, found in only one of the two groups, or are not exclusive to the two. Greenwood (1968) later suggested that clupeomorphs are the sister-group of the osteoglossomorphs, but as he admitted, the uniting characters are indecisive. Still later, Greenwood (1970a) proposed that the clupeomorphs should be given independent cohort status, and no longer thought them related to osteoglossomorphs, instead mentioning (unnamed) characters relating clupeomorphs and euteleosteans. More recently (1973), Greenwood named the cohort containing the clupeomorphs Clupeocephala, and concluded that the clupeomorphs and osteoglossomorphs are sister-groups because of detailed correspondences in certain aspects of the otophysic connection of *Hiodon* and clupeomorphs, and (*Ibid.*, p. 325) that clupeomorphs and osteoglossomorphs shared a common ancestor with an otophysic connection of the type found in *Hiodon*. His interpretation requires that the osteoglossoids have lost an otophysic connection of that type. Yet the otic region of the braincase in osteoglossoids shows a suite of characters (a very deep subtemporal fossa, a large intercalar that extends

forward to form a bridge across the subtemporal fossa, and a long jugular canal) that are also found together in pholidophorids, leptolepids, and *Elops*. This type of otic region appears, therefore, to be symplesiomorphic for osteoglossoids and *Elops*, rather than derived (apomorphous) as a result of a secondary reduction. It is unparsimonious to assume that the osteoglossoid-*Elops* type of otic region represents a reversal from *Hiodon*-like conditions. We therefore regard Greenwood's demonstration of clupeomorph features in the otophysic connection of *Hiodon* as suggestive of a more restrictive hypothesis: "considering the Hiodontidae as the closest living relatives of the Clupeomorpha" (Greenwood, 1973, p. 325). That hypothesis is refuted to our satisfaction by those specializations of *Hiodon* that indicate that it is an osteoglossomorph (in the circumorbital bones, upper jaw, gill-arch skeleton and musculature, vertebral column, caudal skeleton and fin, and gut).

Taverne (1973a) took up Greenwood's demonstration of resemblances in the otophysic connection of *Hiodon* and clupeomorphs, and also saw clupeomorph features in the otophysic connection of *Gymnarchus* and *Papyrocranus*. Greenwood (1973, p. 332) contested the validity of these comparisons and Taverne (1974c, p. 87) later agreed with the criticism. Taverne cited several other characters which he regarded as evidence of osteoglossomorph/clupeomorph relationships, but some of these features are not exclusive to the two groups, others are drawn from one or another clupeomorph or osteoglossomorph subgroup, and others are without substance. All in all, we regard the characters offered as evidence of sister-group relationships between the osteoglossomorphs and clupeomorphs as unconvincing.

Forey (1973b) proposed a sister-group relationship between the elopomorphs and the euteleosteans on the grounds of similarities, which he interpreted as advanced, in the snout (ossification pattern and ligaments) and caudal skeleton. In the caudal skeleton, Forey based his conclusions partly on the work of Nybelin (1971), who compared the caudal skeletons of *Elops* and coregonine euteleosteans. The characters in question here are the long, stout neural spines on PU3-5 and the short neural spine on PU2, the possibility that the neural arch of PU1 has migrated forward on to PU2 in some specimens of *Elops* and various salmonids, and the possibility that the stegural of euteleosteans is formed by fusion of the first uroneural with a ural neural arch of the type found on U1 in *Elops* (the second ural neural arch in Nybelin's terminology). Most of these similarities seem to be of doubtful status, and in the caudal skeleton both Nybelin's and Forey's analyses depend on the interpretation of selected variations in the neural arches over the ural and last two preural centra as phylogenetic sequences. We have examined this part of the caudal skeleton in a variety of larval and young elopomorphs, clupeomorphs, and euteleosteans (see below) and find that the neural arches over PU1 and U1 provide an easily recognizable derived character state of elopomorphs, but that the stegural of euteleosteans is constructed in a fundamentally different way from that proposed by Nybelin.

Whereas Forey (1973b) maintained that the elopomorphs are a monophyletic group whose sister-group is the Euteleostei, Nybelin sought to show that Elopomorpha are not monophyletic, recommending (1971) that the elopids be transferred to the Salmoniformes (Euteleostei), and later (1973b) proposing a relationship between *Albula* and clupeomorphs. That proposal stems from Nybelin's interpretation of the first uroneural of *Albula* and clupeomorphs (fused with PU1 in extant clupeoids, but autogenous in *Denticeps*, †*Diplomystus* [fig. 37] and †*Ornategulum* [Forey, 1973c]) as the product of fusion of two uroneurals, lying side by side. Nybelin's interpretation of conditions in *Albula* is discussed below (p. 119): it may be correct. But our observations of young and larval clupeoids indicate that the flange on the anterodorsal surface of the first uroneural, which Nybelin (1973b) interpreted as a product of fusion with another uroneural, arises in membrane that does not resemble a uroneural, and if it ossifies it does so long after the first uroneural. Forey (1973c, p. 1315) also described this flange in young *Clupea harengus* and concluded that it is not a uroneural. Nybelin did not comment on those features of *Albula* that are indicative of elopomorph relationships, and of relationships with halosaurs and notacanths within that group (see

McDowell, 1973; Nelson, 1973b; Forey, 1973a), features which in our opinion refute his hypothesis of albulid/clupeomorph relationships.

Taverne (1974c), in his detailed account of the skeleton of *Elops*, also concluded that the elopomorphs and euteleosts are sister-groups. But the characters he cited in support of this are, in our opinion, all either primitive or resemblances between *Elops* and one or another euteleostean which are without significance for this problem.

The results of several investigations of tooth-bearing elements in the gill-arches (Nelson, 1966, 1968, 1969a, 1970; Rosen, 1973, 1974) provide evidence that clupeomorphs and euteleosteans are related. Nelson (1968, 1969a) concluded that the condition of having dermal tooth-bearing bones not fused with endoskeletal gill-arch bones is primitive for teleosts. The conclusion was based upon the observation that in fishes such as *Elops* (Elopomorpha) and *Hiodon* (Osteoglossomorpha) tooth-plates are never ankylosed with the first, second, or third infrapharyngobranchials, with the fifth ceratobranchials, or with the basibranchials. Our work supports these conclusions for all elopoids and albuloids (and see Rosen, 1973, fig. 2, of the dorsal gill-arch skeleton of *Elops*). Nelson's (1966) review of these structures in 18 eel families shows that fusions between tooth-plates and endoskeletal supports occur only between certain elements in some species of ophichthyids and nemichthyids in an unpredictable pattern. The scarcity and mosaic nature of such fusions, and the absence of fusions in such generalized forms as congrids suggests the likelihood that the few instances of bone fusion in eels are secondary phenomena and that elopomorphs are primitively without such fusions. Similarly, in osteoglossomorphs (Nelson, 1968) fusions occur only in two of the three groups of notopterids and in *Pantodon*, and in these fishes only between tooth-plates and the fifth ceratobranchials. In contrast, when tooth-plates are present in the regions of the first to third infrapharyngobranchials and fifth ceratobranchials in clupeomorphs, they are invariably fused with their endoskeletal supports (Nelson, 1970), and the same is apparently true of primitive euteleosteans [Rosen, 1973, figs. 3 (*Bramocharax*, a characoid), 5 (*Salmo*), 58 (*Novumbra*, an esocoid); Rosen, 1974, figs. 11B (*Galaxias*), 12B (*Hypomesus*, an osmeroid)] as well as more derived groups (Rosen, 1973). The only exception among euteleosts known to us is *Ateleopus japonicus* (Rosen, 1973, figs. 113, 114) in which the tooth-plates in the dorsal gill-arch skeleton are divided into many small plates and lie free of the unossified infrapharyngobranchials. There is, thus, a strong presumption that the almost entirely consistent fusion of tooth-plates with the first three pharyngobranchials and the fifth ceratobranchial (the only exception being a probably secondary general breakdown in gill-arch ossification in *Ateleopus*) is a synapomorphy uniting clupeomorphs with euteleosteans.

Nelson's (1973b) investigation of ossification patterns in the lower jaw also produced evidence that clupeomorphs and euteleosteans are related. This evidence and a phylogenetic argument may be summarized as follows:

1) The most plesiomorphous teleost for which there is evidence of the presence of the three endoskeletal bones characterizing the modern teleostean lower jaw (articular, retroarticular, corono-meckelian) is the Mesozoic *Leptolepis coryphaenoides*. It shows a pattern in which all three bones and the angular can fuse in late ontogeny into a single unit without visible sutures, and in which the retroarticular component contributes to the joint surface for the quadrate (fig. 32B, C).

2) More apomorphous groups of Mesozoic teleosts such as ichthyodectids and *Tharsis dubius* show lesser degrees of fusion so that visible sutures between some of the bones remain even in large adults (figs. 8, 32D, E).

3) The fact that osteoglossomorphs show two different conditions of fusion (between the angular and retroarticular, and between the angular and articular) as well as a condition of no fusion allows the inference that the derived condition ancestral for all osteoglossomorphs is the complete loss of the primitive fusion pattern.

4) If we assume that all modern teleosts form a monophyletic group, the observations that osteoglossomorphs show different fusion patterns, or the absence of fusion, that elopomorphs show one pattern

like that of *Hiodon* and the Mormyridae (angular and retroarticular fused), and that clupeomorphs and euteleosteans show another like that of notopterids and osteoglossines (angular and articular fused), allow the additional inference that the loss of the primitive fusion pattern is a derived condition also ancestral for all modern teleosts.

5) Secondary inferences [suggested by (4) above] are that the phylogenetic pattern in which the angular fuses, or fuses first, with the retroarticular is an apomorphy uniting elopomorphs, and that the pattern in which the angular fuses, or fuses first, with the articular is a synapomorphy of clupeomorphs and euteleosteans.

6) Additional evidence that clupeomorphs and euteleosteans are sister-groups is that the retroarrticular is not included in the joint surface for the quadrate [see (1)], that is, has withdrawn ventrally and is greatly reduced or rudimentary, and is situated entirely ventral to the plane of the joint surface (the retroarticular is also excluded from the joint surface in notopterids and osteoglossines but it is not withdrawn to the ventral edge of the fused angular-articular or so reduced in size as it is in clupeomorphs and euteleosteans).

Hence, in both clupeomorphs and euteleosteans the angular is primitively fused with the articular, and the retroarticular is excluded from the joint surface for the quadrate. In elopomorphs the angular is primitively fused with the retroarticular, and where an independent articular is present both this bone and the angulo-retroarticular contribute to the joint surface for the quadrate. In osteoglossomorphs the three bones at the back of the jaw are primitively separate (*Arapaima*, *Heterotis*, †*Phareodus*), and the articular and retroarticular both contribute to the joint surface. Within the osteoglossomorphs, a lower jaw resembling that of elopomorphs occurs in some forms (*Hiodon*, mormyroids), whereas others (osteoglossines, notopterids) have a condition like that in clupeomorphs and euteleosteans. This independent development of both the elopomorph and euteleostean/clupeomorph type of lower jaw in osteoglossomorph subgroups indicates that parallel evolution of these patterns is possible, but it does not in itself falsify the theory that clupeomorphs and euteleosteans inherit their characteristic lower jaw from an ancestor that had already developed the pattern. Nor is that theory refuted by any known fossil clupeomorph or euteleostean. The gill-arch and lower jaw evidence therefore suggests a hypothesis of teleostean interrelationships in which clupeomorphs and euteleosteans are sister-groups, and clupeomorphs/euteleosteans form an unresolved trichotomy with the elopomorphs and the osteoglossomorphs. We have made every effort to find alternative explanations of the lower jaw evidence, without success, but our investigations of the caudal skeleton have produced evidence that resolves the trichotomy into the series of dichotomies shown in figure 22. This new evidence from the caudal skeleton is set out below.

1. In elopomorphs, euteleosteans, and clupeomorphs there are never more than two elongate uroneurals extending forward beyond U2. The first extends to PU1 or farther forward, the second ends on or near U1. In osteoglossomorphs the primitive condition (*Hiodon*, †*Eohiodon*, †*Lycoptera*) is to have three or four straplike uroneurals extending forward beyond U2. This suggests that osteoglossomorphs are the primitive sister-group of elopomorphs, clupeomorphs, and euteleosteans. The only recorded exception to the two large uroneurals of the three groups (apart from a few fossils previously assigned to one or another of these groups on indecisive evidence) is in *Albula*. In some specimens of *Albula vulpes* (larger young, 36-47 mm. standard length) Hollister (1936) found a pair of elongate ossifications that lie dorsolateral to the ural centra beneath (medial to) and completely hidden by the first uroneural. Hollister referred to these bones as "fourth uroneurals." She did not find them in leptocephali or in fully adult specimens, but in a 206 mm. specimen she found an apparent remnant. These bones are not present in our 30 mm. specimen (fig. 23), nor did Monod (1968) find them in the leptocephali or the four adult specimens he examined (in Monod's fig. 105 of *Albula*, however, there is a small bone not mentioned in the text lateral to the posterior tip of U2, and Rosen, 1973, fig. 43, showed a similar bone in *Aulopus filamentosus*). Nybelin (1973b)

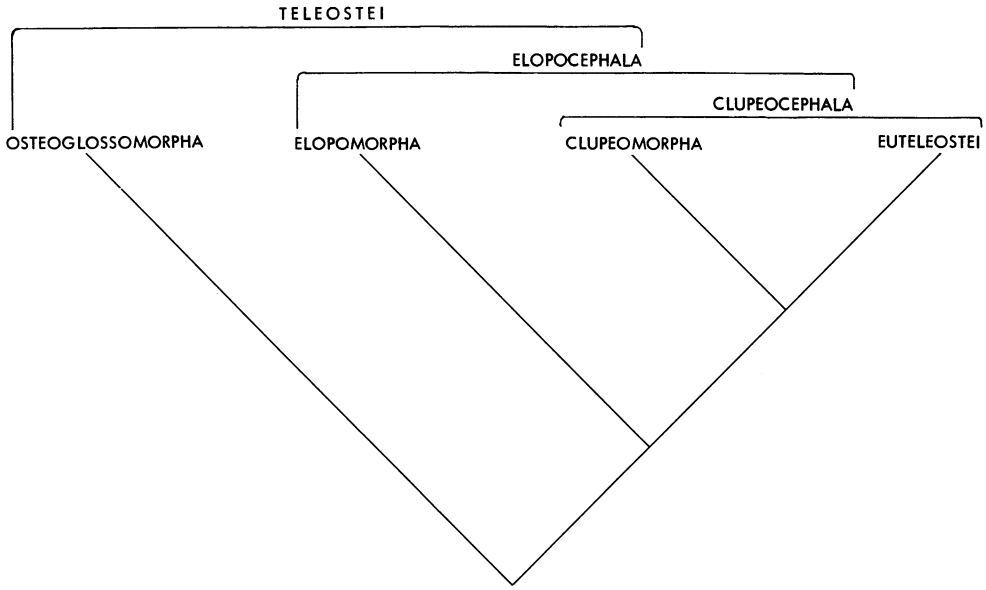


FIG. 22. Cladogram showing hypothesis of teleostean relationships adopted here, based on lower jaw, gill-arch, and caudal skeleton evidence.

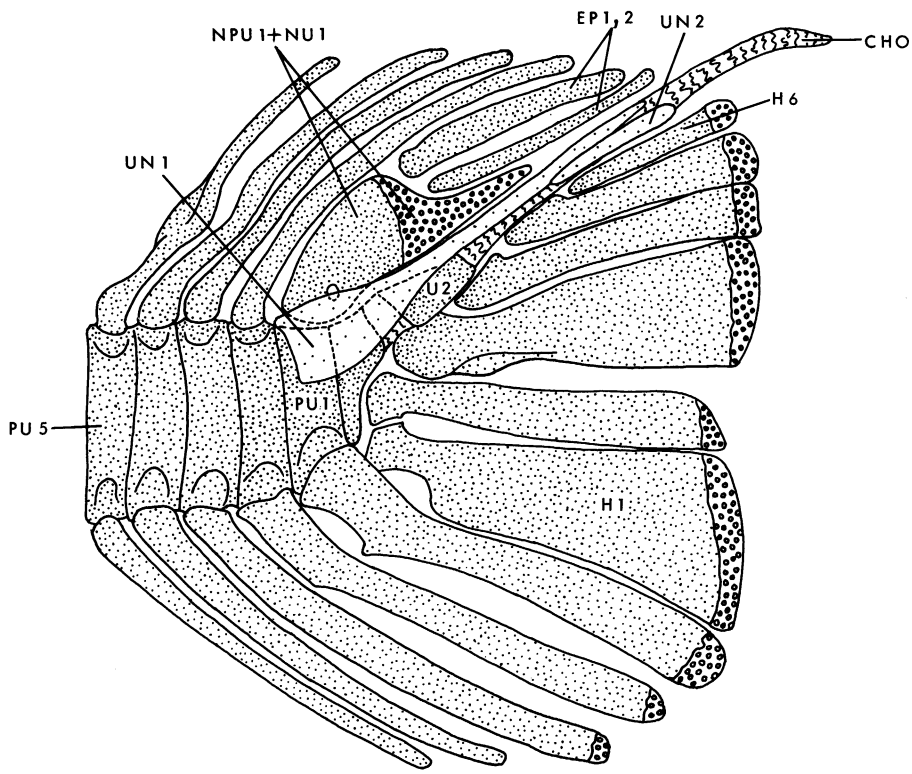


FIG. 23. *Albula vulpes* Linnaeus, caudal skeleton of AMNH 16057, standard length *ca.* 30 mm.

found a bone resembling that illustrated by Hollister on one side of a 210 mm. specimen, but on the other side of that specimen and in 170 and 190 mm. specimens there was only a ridge on the inner face of the first uroneural. Nybelin therefore concluded that the first uroneural of "normal" *Albula* is the product of fusion between two uroneurals, lying side by side. It is possible that there is a similar separate ossification in the Cretaceous albulid *Lebonichthys gracilis* (Forey, 1973a, p. 181, fig. 90), but there is no other known fish in which such a bone occurs, unless it is represented by the structure mentioned in *Aulopus*. Monod's sections through an *Albula* leptocephalus (1968, figs. 34-60) show that these extra bones are not preformed in cartilage, as are the uroneurals. The occasional occurrence of this bone in *Albula*, and perhaps in a Cretaceous albulid, may justify the interpretation (first made by Regan in 1910 and since repeated by many writers) that the first uroneural of elopomorphs, clupeomorphs, and euteleosteans is the result of phylogenetic fusion of uroneurals, but we do not regard the nature of this bone in *Albula* as established, nor do we regard it as invalidating the presence of only two elongate uroneurals as a shared derived character of elopomorphs, clupeomorphs, and euteleosteans—a synapomorphy that, combined with the lower jaw evidence discussed above, suggests the hypothesis of dichotomous relationships shown in figure 22.

Patterson suggested (1968, p. 229) that elopomorphs, clupeomorphs, and euteleosteans are also distinguished from osteoglossomorphs by the differentiation of a series of one to three small posterior uroneurals that lie lateral to the second uroneural. This proposal is invalidated by the discovery of a uroneural of this type in the osteoglossomorph †*Lycoptera* (figs. 24, 25; Taverne, 1975c, fig. 10), and differentiation of the posterior uroneurals now appears to characterize all extant teleost groups, in contrast to some Mesozoic forms.

2. Early in the ontogeny of primitive (i.e., tailed) elopomorphs (elopoids, albuloids) there is a large mass of cartilage above the notochord at the level of the parhypural and first two hypurals (figs. 23, 26, 27; and Monod, 1968, figs. 30, 32, 61). In postlarval and adult forms this cartilage is represented by a complex structure that extends back beneath the epurals and articulates with two centra, PU1 and U1, by means of dorsolateral pits in the centra. This manner of

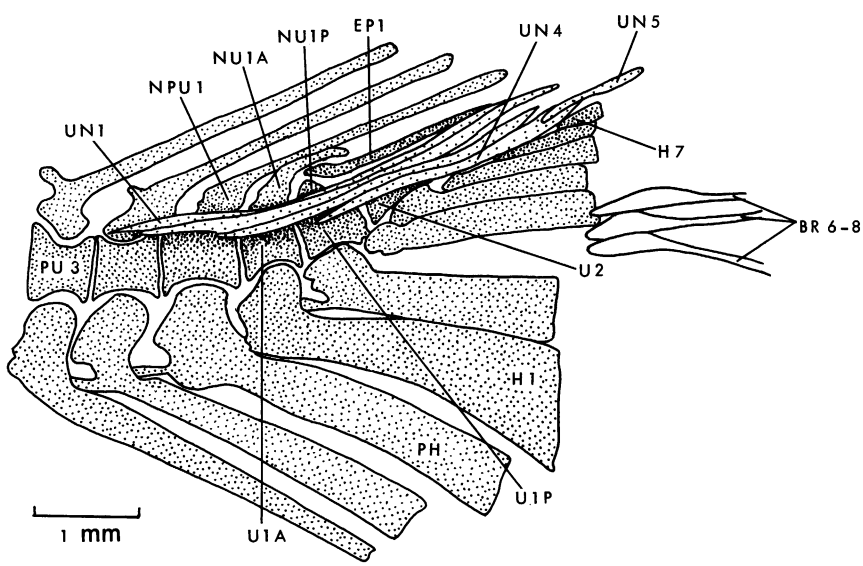


FIG. 24. *Lycoptera middendorfii* Müller, caudal skeleton as preserved in BMNH P.20930, Upper Jurassic, Jehol, Manchukuo, China, showing two first ural centra.

articulation resembles that of the preceding neural arches, and implies that the structure is compound, representing at least two neural arches (fig. 26). In *Elops* and *Megalops* only the anterior part of this structure, over PU1, ossifies at first (fig. 27). The posterior part may ossify later in a variety of ways (e.g., Monod, 1968, figs. 20-29, structure labeled "3"; Nybelin, 1971, figs. 1, 6D, structure labeled N2U1), but a cartilage-filled suture between the two portions seems always to persist. In *Albula* (fig. 23) the structure is apparently specialized because of the shortness of the segments: the last few vertebrae of *Albula* are greatly foreshortened so that the two contacts between the structure and the centra are very close together, and ossification of the structure appears to proceed as a single unit (fig. 23; Hollister, 1936, figs. 21-39; Monod, 1968, figs. 96-103; Nybelin, 1973, figs. 1, 2). In *Pterothrissus* the structure has the same form as in *Albula* (Gosline, 1961, fig. 1A; Monod, 1968, fig. 108; Forey, 1973a, fig. 68).

This structure appears to be a characteristic specialization of tailed elopomorphs: there is nothing resembling it in osteoglossomorphs (where PU1 and, usually, U1 bear full neural spines), clupeomorphs or euteleosteans.

Euteleosteans are characterized by the development of a stegural, a first uroneural that has an anterodorsal outgrowth of membrane bone extending forward beneath the epurals toward NPU1 or NPU2. This structure has been interpreted by many workers (e.g., Nybelin, 1963; Patterson, 1970b; Taverne, 1975e) as compound in origin, resulting from phylogenetic fusion between the first uroneural and the first ural neural arch and, perhaps, the last preural neural arch. This interpretation is not corroborated by the ontogeny of the salmonoid stegural (fig. 28; Cavender, 1970, fig. 6; Monod, 1968,

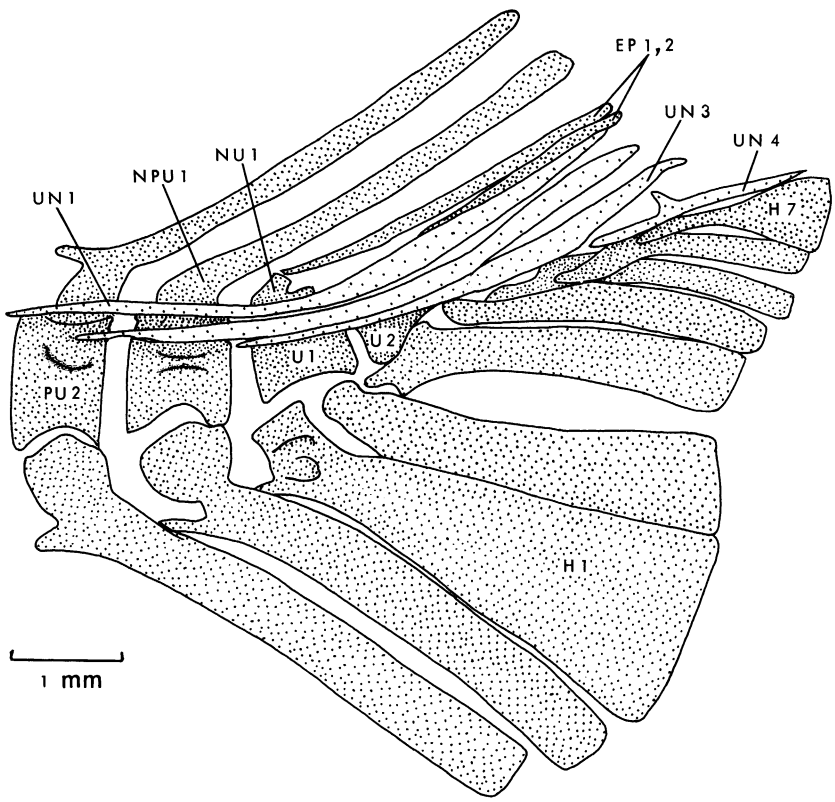


FIG. 25. *Lycoptera wangi* Gaudant, caudal skeleton of the holotype, BMNH P.28847, slightly restored. Upper Jurassic, Cheng Chia Pien, Hengshan, Shensi, China.

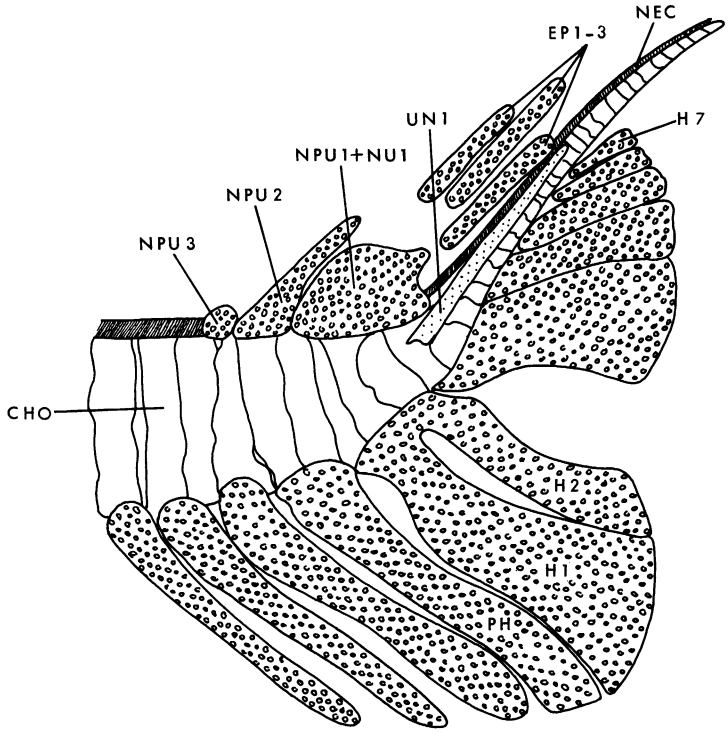


FIG. 26. *Megalops atlantica* Valenciennes, caudal skeleton of a transforming leptocephalus, AMNH 27393, standard length 23 mm.

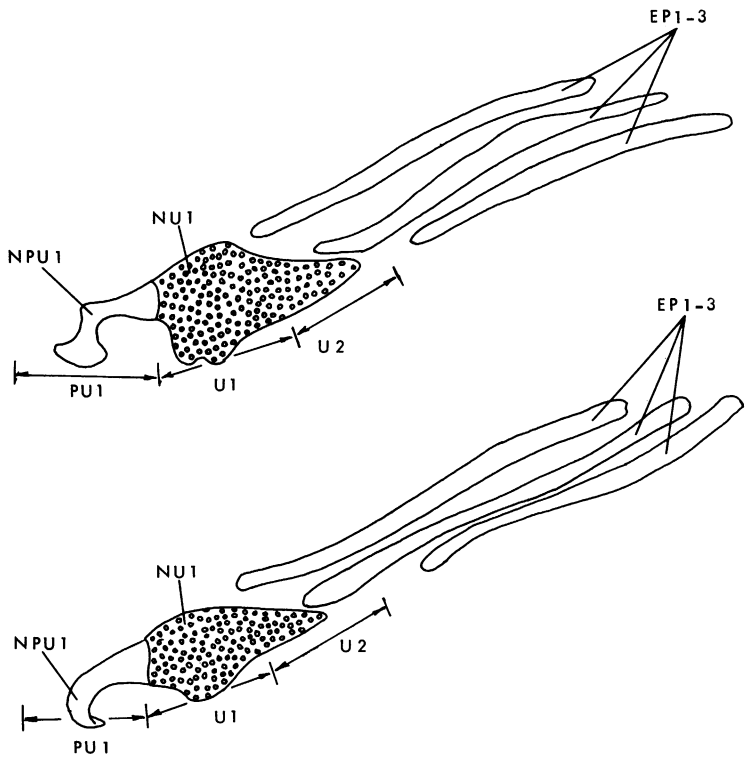


FIG. 27. Caudal neural arches and epurals of juvenile *Elops saurus* Linnaeus, AMNH 27480 (above), and *Megalops atlantica* Valenciennes, AMNH 27478 (below).

figs. 281-392), since the anterodorsal outgrowth is preformed in membrane, not in cartilage as are the neural arches and uroneurals. Monod (1968), Nybelin (1971) and Forey (1973a, 1973b) interpret the anterodorsal outgrowth of the euteleostean stegural and the large neural arch over PU1 and U1 in elopomorphs as homologues, the latter structure having fused with the first uroneural to produce the stegural. Although the two structures are topographically similar, they differ in composition, ontogeny, and mode of growth, and we regard them as divergent specializations.

In clupeoids there is an outgrowth beneath the epurals on the anterodorsal surface of the first uroneural (figs. 29, 30; Monod, 1968, "crête pleurostylaire"; Hollister, 1936, figs. 43-52; Nybelin, 1973b, figs. 3C, D, "Un1"; Forey, 1973c, fig. 9). In most clupeoids there is a neural arch with a laterally compressed, membrane-bone neural spine on PU1, and the crests on the first uroneurals are small and paired. But in some dussumieriines (*Jenkinsia*, fig. 29; Hollister, 1936, fig. 44: *Spratteloides*, Monod, 1968, fig. 261) the neural spine on PU1 is reduced or absent, and the outgrowth from the uroneurals is large, ossifying in a median membrane. These different configurations in clupeoids recall conditions in primitive euteleosteans, the armored herring pattern, with a laminar NPU1 and small uroneural outgrowths, resembling argentinoids, the round-herring condition resembling salmonoids and osmeroids. The similarity of the clupeoid caudal skeleton to that of ostariophysans is noted by Gosline (1961, p. 8) and Roberts (1973, p. 375), amongst others: although these similarities are presently interpreted as the result of parallel evolution, they nevertheless suggest that the clupeomorph and euteleostean caudal skeletons have similar developmental patterns, whereas that of elopomorphs is divergently specialized. Whether these ontogenetic similarities can be regarded as synapomorphies significant for resolving euteleost and clupeomorph relationships is not clear to us. If it is significant, this evidence is consistent with the alignment of these groups shown in figure 22. Interpreted most conservatively, the different types of membrane precursors of stegural formation in primitive euteleosts and in clupeomorphs represent autapomorphies and do not test

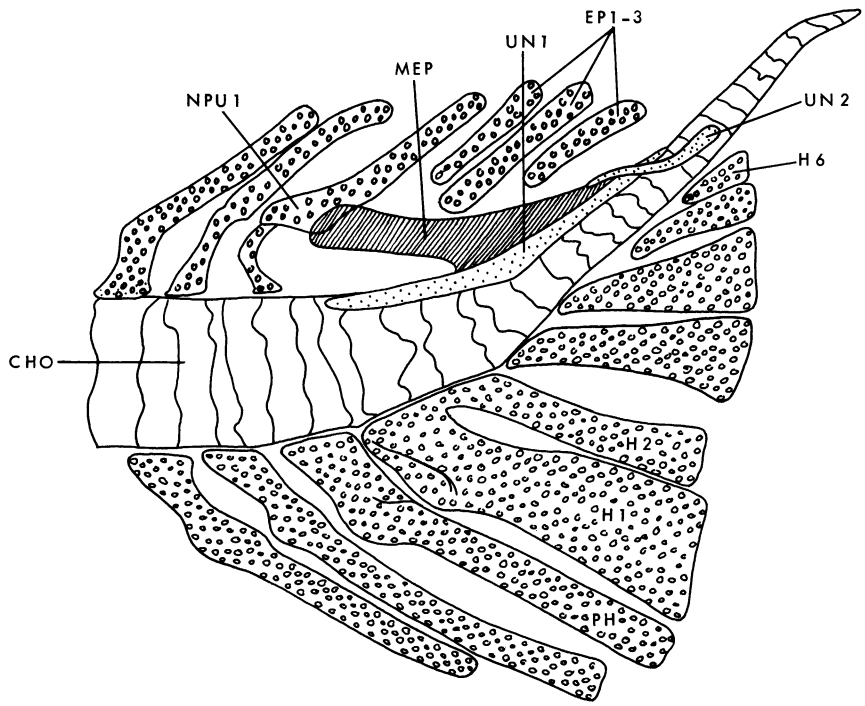


FIG. 28. *Salmo trutta* Linnaeus, caudal skeleton of AMNH 21164, standard length 13.5 mm.

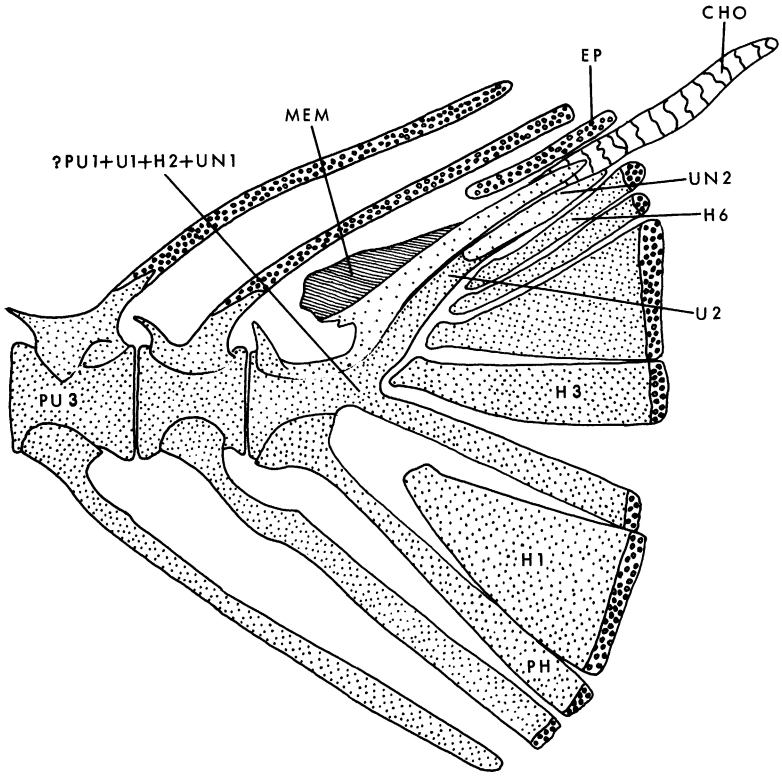


FIG. 29. *Jenkinsia lamprotaenia* (Gosse), caudal skeleton of AMNH 25960, standard length *ca.* 15 mm.

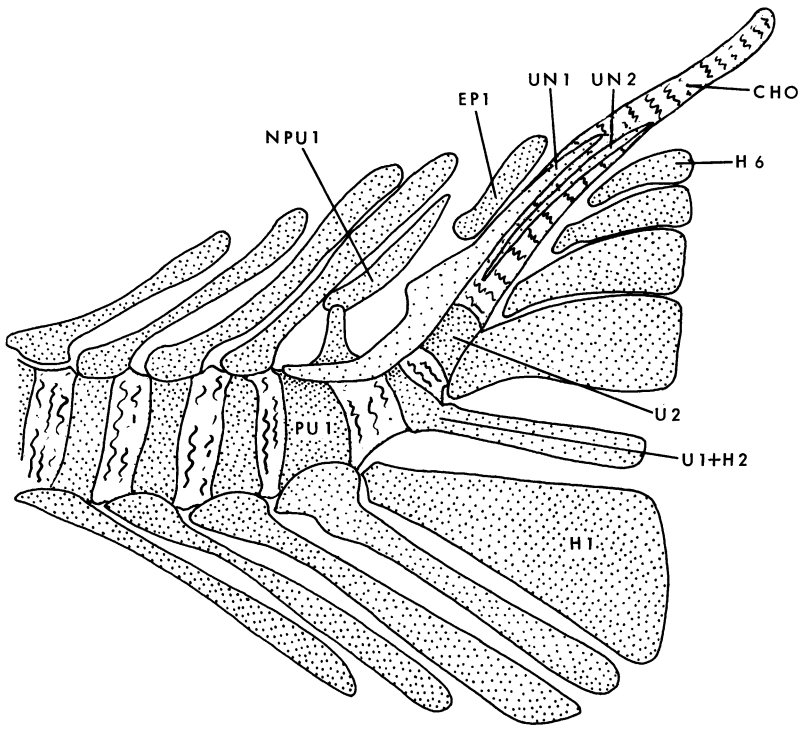


FIG. 30. *Alosa* sp., caudal skeleton of AMNH 26488, standard length 14 mm.

hypotheses of their sister-group relationship. At most, the stegural evidence and other aspects of caudal anatomy are in no known way inconsistent with clupeomorph-euteleost relationship but refute an alignment of osteoglossomorphs and clupeomorphs because the latter share derived features of uroneural structure with elopomorphs and euteleosts.

In summary, we adopt the hypothesis of teleostean interrelationships shown in figure 22. This grouping is not one that has been used explicitly before, and to write it as a classification requires either the use of new names, or the use of existing names for unfamiliar groupings. We believe it essential not to alter the meaning of the names of the four main extant teleostean groups (osteoglossomorphs, elopomorphs, clupeomorphs, euteleosteans), and therefore propose the following classification and characterization based on shared derived characters:

Infraclass Neopterygii: actinopterygians in which the fin rays are equal in number to their supports in the dorsal and anal fins; premaxilla with an internal process lining the anterior part of the nasal pit; articular bone with coronoid process; symplectic developed as an outgrowth of hyomandibular cartilage; upper pharyngeal dentition consolidated; clavicle lost or reduced to one or more small plates overlying postbranchial lamina of cleithrum.

Division Ginglymodi: neopterygians with opisthocoelous, holospondylous centra; teeth with plicidentine; a chain of toothed infraorbital bones[1]

Division Halecostomi: neopterygians with median neural spines; a mobile maxilla; a supramaxilla; an interopercular; quadratojugal either lost or fused with quadrate.

Subdivision Halecomorphi: halecostomes in which the symplectic forms an auxiliary articulation with the lower jaw[1]

Subdivision Teleostei: halecostomes in which the ural neural arches are elongated as uroneurals; unpaired basibranchial toothplates; a mobile premaxilla[1]

Supercohort Osteoglossomorpha: teleosteans in which the caudal fin contains 18 principal rays; a full neural spine on PU1; a large posteroventral infraorbital bone representing the third and fourth infraorbitals of other teleosts; gut coiled so that the intestine passes to the left of the stomach.

Supercohort Elopocephala (Taverne, 1973a, name used for elopomorphs and euteleosteans); teleosteans in which primitively only two uroneurals extend forward beyond U2; epipleural intermuscular bones well developed.

Cohort Elopomorpha: elopocephalans in which there is a leptocephalus larva; angular and retroarticular bones fused; rostral and prenasal ossicles present; a compound neural arch formed in cartilage over PU1 and U1.

Cohort Clupeocephala (Greenwood, 1973, name used for clupeomorphs only): elopocephalans in which the angular and articular bones are fused, and the retroarticular is excluded from the articular surface for the quadrate; toothplates primitively fused with first three pharyngobranchials and fifth ceratobranchial; neural arch over U1 reduced or absent, anteriorly directed membranous outgrowths develop from the anterodorsal margin of the first uroneural; six hypurals.[2]

Subcohort Clupeomorpha: clupeocephalans in which the second hypural is fused with U1 at all stages of development and the first hypural is free proximally; supratemporal commissural sensory canal primitively passing through parietals[2] and supraoccipital; otophysic connection involving a diverticulum of the swimbladder that penetrates the exoccipital and extends into the prootic within the lateral wall of the braincase.

Subcohort Euteleostei: clupeocephalans in which there is primitively an adipose fin; breeding tubercles and contact organs often present; a stegural present or a tendency to develop outgrowths of laminar bone from neural arches and spines in the caudal skeleton (see Greenwood and Rosen, 1971; Rosen, 1974). This definition of euteleosteans is far from satisfactory: esocoids, because of their posterior dorsal fin position, can have no adipose, and they and argentinoids lack breeding tubercles. See also discussion of dorsal gill arches in Rosen (1973).

[1] This restricted definition applies when the comparisons with extant forms also include the known fossils.

[2] We have examined the material of *Ornategulum sardinioides* (Pictet) described by Forey (1973c), and find that there are six hypurals and that the supratemporal commissure penetrates the parietal, as in other primitive clupeomorphs.

INTERRELATIONSHIPS OF FOSSIL AND RECENT TELEOSTEANS

"PHOLIDOPHORIDS," "LEPTOLEPIDIDS," AND EXTANT TELEOSTEANS

In the preceding section we adopted a cladistic scheme of extant teleosteans. The ichthyodectiform fishes, whose relationships we wish to establish, have been assigned to several positions in that scheme by one or another recent author. We shall here make no prior assumption except that their relationships will be found somewhere within a system that includes all the fossil and extant fishes that have traditionally been considered teleosteans. And in this section we extend the cladistic framework to include some of these fossil forms.

The group that has customarily been considered to stand at the base, or as the plesiomorph sister-group, of teleostean fishes is the Pholidophoridae. For reasons mentioned by Patterson (1973, p. 264, 1975, p. 281), the Pholidophoridae cannot yet be considered to be a monophyletic group, but rather are a grade or paraphyletic group, including paleospecies that have been grouped phenetically. Among the fishes of this grade, however, we can select for comparison forms that are relatively well known, such as *Pholidophorus bechei* and *Pholidolepis dorsetensis.*

To keep the initial phylogenetic hypotheses simple and precise we have chosen to restrict the following primary analysis to a few relatively well-known forms. We have therefore selected for comparison three well-known representatives of the main fossil group that stands between pholidophorids and extant teleosts, the traditional grade or phenetic group Leptolepididae. This group has recently been reviewed by Nybelin (1974), who has added new forms to the family and excluded other species from it. Nybelin considered the group, as limited by him, to be "natural" or monophyletic. Taverne (1975c, 1975d, 1975e), who has also discussed the group, treated it in the same way. Our analysis of three of the better-known representatives, *Proleptolepis* spp.,[1] *Leptolepis coryphaenoides*[1] and *Tharsis dubius*, indicates that it is not monophyletic.

In the following analysis a hierarchy of shared derived features is given for the series *Pholidophorus bechei*, *Pholidolepis dorsetensis*, *Prolep-*

[1] Previously undescribed specimens of a Sinemurian "leptolepid" from the Lower Lias of Lyme Regis were the object of a study by Nybelin (1974) that led to the creation of the genus *Proleptolepis* to contain three new paleospecies, *furcata*, *elongata*, and *megalops.* The three forms recognized by Nybelin are represented by very uneven material, *furcata* by a head and anterior part of the axial skeleton, *elongata* by a poorly preserved head but reasonably well-preserved body and fins, including the caudal skeleton, and *megalops* mainly by the skull and shoulder girdle and a few anterior centra and ribs. Our information on the braincase and lower jaw of this genus is derived from acid-prepared fragments which are not determinable to species in Nybelin's scheme (cf. Nybelin, 1974, p. 109). It is evident, therefore, that the genus *Proleptolepis* is best treated as a form-genus whose definition incorporates features of the head of some specimens and the trunk and caudal skeleton of others. Indeed, Nybelin's definition is just that, and is noteworthy by including only characters that are primitive with respect to comparable characters in all non-"pholidophorid" teleosts: "Leptolepids with elongate body. Premaxillary small, almost triangular. Suborbital rather broad, 'accessory suborbital' present. Preoperculum with a notch in its posterior margin. Vertebral centra slightly constricted bony cylinders. Caudal skeleton with four epurals, about eleven hypurals and about six (?) uroneurals, the two anterior ones reaching anteriorly to the first ural centrum. Fringing fulcra numerous, on the dorsal as well as on the ventral margin of the caudal fin." (Nybelin, 1974, p. 80).

Leptolepis coryphaenoides presents a similar problem. Nybelin (1962, 1974) has divided the material previously placed under this name between two species, *L. coryphaenoides* (Bronn) and *L. normandica* Nybelin. According to Nybelin, these species are distinguished only by features of the skull, principally the branches of the sensory canals, so that specimens can only be allotted to one or other form if the head is more or less complete and well preserved. Our information about the braincase and lower jaw comes from bone-bed and stomach content material (Patterson, 1975, p. 283), not determinable to species within Nybelin's scheme. We therefore interpret the name *L. coryphaenoides* in the same sense as Wenz (1968b) and Patterson (1975, p. 311), a wider usage than Nybelin's.

tolepis spp., *Leptolepis coryphaenoides*, *Tharsis dubius*, osteoglossomorphs, elopomorphs, clupeomorphs, and euteleosteans. The reasons for selecting certain paleospecies for comparison with extant teleostean groups are given in the Introduction and below in the discussion of the classification of fossils. Ichthyodectiforms and other groups such as *Anaethalion* are discussed in relation to this analysis in the following section.

As preface, it should be noted that this type of analysis is a method in which derived features are progressively added to the system as new species or groups are incorporated. Hence, the first set of features (A, 1-3) are the synapomorphies of a group comprising *Pholidolepis dorsetensis* and all higher teleosts, features that separate them all from *Pholidophorus bechei.* The final group of fishes, the euteleosteans, is distinguished by a set of autapomorphies (H, 46-48), that is, derived characters unique to themselves, or, looked at another way, synapomorphous features that unite only euteleosteans. But euteleosteans also share all the derived features that distinguish *P. dorsetensis* (A, 1-3), *Proleptolepis* (B, 4-12), and so on. The hierarchic sequence of taxa is therefore based on sets of character transformation series each of which specifies an increasingly derived condition or state of a particular character such that each transformation series is the most parsimonious one that can be devised, i.e., involves the fewest assumptions or explanations concerning evolutionary change. Parsimony, it should be emphasized, is an attribute of the analytical method, not necessarily of the evolutionary process. The following cladistic analysis represents our best estimate of the phylogenetic sequence of the five fossil species and four extant groups of teleosts based on an analysis of 48 character sequences which we conclude to be most parsimoniously interpreted as synapomorphies (on *Pholidophorus bechei* see also Nybelin, 1966, Patterson, 1968, 1975; on *Pholidolepis*, Nybelin, 1966, Patterson, 1968; *Proleptolepis*, Nybelin, 1974, Patterson, 1975 [as "Sinemurian *Leptolepis*"]; *Leptolepis coryphaenoides*, Wenz, 1968b, Nybelin, 1974, Patterson, 1975; *Tharsis dubius*, Nybelin, 1974, Patterson, 1975, Taverne, 1975c):

A. *Pholidolepis dorsetensis* differs from *Pholidophorus bechei* and resembles "leptolepidids" and extant teleosteans in having:

1. Lost the enamel layer from all but a few skull bones (Nybelin, 1966, p. 387).
2. Cycloid scales, rather than interlocking rhombic scales (Nybelin, 1966).
3. Principal fin rays of upper lobe of caudal fin reduced to one simple and nine branched rays (fig. 31).

B(i). *Proleptolepis* spp. have the derived features of *Pholidolepis dorsetensis*, differ from *Pholidophorus bechei*, and resemble *Leptolepis coryphaenoides* in having:

4. Partial closure of the fissura otico-occipitalis (Patterson, 1975, p. 417).
5. Post-temporal fossa and fossa bridgei confluent rather than separated by a transverse bony wall (Patterson, 1975, p. 384).
6. Separate openings in the prootic for the jugular vein on the one hand and for the orbital artery and the hyomandibular branch of the facial nerve on the other, rather than a common opening for all (Patterson, 1975, p. 387, fig. 86).
7. A vertically keeled rostrum with paired facets for maxillary attachment (Patterson, 1975, fig. 123).
8. Loss of separate prearticular bone from lower jaw (fig. 32).

B(ii). *Proleptolepis* spp. also differ from *Pholidolepis dorsetensis* and resemble *Leptolepis coryphaenoides* in having:

9. No enamel layer on skull bones (Nybelin, 1974).
10. Thin-walled, holospondylous unsculptured autocentra that weakly constrict notochord, as opposed to hemichordacentra, diplospondylous in the mid-caudal region (Patterson, 1968, figs. 3, 4; Nybelin, 1974, fig. 19 and pl. 17).[1]
11. A single centrum (U_1) supporting the first two hypurals (Nybelin, 1974, fig. 19).[1]

[1] In the Upper Jurassic hiodontoid *Lycoptera* young fishes have centra (presumably chordacentra) that are diplospondylous throughout the column, and the first ural centrum remains double in occasional full-grown individuals (fig. 24; Greenwood, 1970b). We do not regard this ontogenetic or individual variation as invalidating features 10 and 11.

12. Hypurals nine in number, rather than 11 or 12.[1]

C. *Leptolepis coryphaenoides* has the derived features of *Pholidolepis dorsetensis* and *Proleptolepis* but differs from them and resembles extant teleosteans in having:

13. Complete closure of the fissura otico-occipitalis (Patterson, 1975, fig. 90).
14. Separate openings in the prootic for the jugular vein, orbital artery, and the hyomandibular branch of the facial nerve (Patterson, 1975, fig. 86).
15. Foramen for the oculomotor nerve enclosed in prootic, rather than on the basisphenoid-prootic suture (Patterson, 1975, fig. 89).
16. Spiracular canal greatly reduced, not fully penetrating bone of postorbital process, the canal for otic nerve not stopping at spiracular canal, but continuing on through postorbital process (Patterson, 1975, fig. 88).
17. Rostral bone fused with lateral dermethmoids, rather than as an independent ossification (Patterson, 1975, figs. 123, 127).
18. Posterior myodome with a ventral compartment and posterior opening, rather than without either (Patterson, 1975, p. 542).
19. Loss of a separate surangular and appearance of independent retroarticular in the adult lower jaw (fig. 32).
20. Postarticular process of lower jaw well developed with the posterior opening of the sensory canal medial to it (fig. 32, Nelson, 1973a).
21. In caudal skeleton, three epurals, rather than four or more (fig. 33).
22. Uroneurals inclined toward horizontal and elongate, the longest ones anterior and extending forward to PU2 or PU3 (figs. 31, 33).
23. Principal rays of lower caudal lobe reduced to eight branched and one simple ray, rather than nine or more branched rays (Patterson, 1968, p. 215).
24. Fringing fulcra lost from ventral margin of lower caudal fin lobe, rather than present on both lobes (Nybelin, 1974, cf. pls. 11 and 17).

D. *Tharsis dubius* has all the derived features of *L. coryphaenoides* but resembles extant teleosts in having:

25. Sutures between cartilage bones in braincase retained throughout life, rather than being lost ontogenetically (Patterson, 1975, fig. 92).
26. Foramen for glossopharyngeal nerve (IX) in exoccipital, rather than in prootic (Patterson, 1975, cf. figs. 90 and 92).
27. No ossified aortic canal (Patterson, 1975, p. 319).[2]
28. No canals for occipital arteries in basioccipital bone (Patterson, 1975, p. 316).
29. No spiracular canal (Patterson, 1975, p. 386).
30. First infrapharyngobranchial articulating directly with parasphenoid, rather than with prootic (Patterson, 1975, p. 525).
31. Middle pitline groove never crossing dermopterotic (fig. 34; Nybelin, 1974, figs. 23, 27).
32. No suborbital bones (fig. 34; Nybelin, 1974, p. 126).
33. Vertebral centra present as sculptured autocentra strongly constricting or obliterating the notochord (cf. figs. 33, 35).
34. Epipleural intermuscular bones developed in the middle part of the trunk, rather than absent.
35. In caudal skeleton, uppermost three uroneurals forming a series that over-

[1] *Pholidolepis* has 11 hypurals (Patterson, 1968, fig. 4). In *Proleptolepis elongata*, Nybelin (1974, p. 100) interpreted the single specimen as having 11, rather than 9, as we interpret it. Should Nybelin be correct, this character state would be transferred to section C, but this transfer would not, in turn, alter our conclusions.

[2] Taverne (1973b) reported a short aortic canal beneath the basioccipital in adult *Xenomystus nigri* (Notopteridae), and believed it to be an archaic feature, exactly homologous with the aortic canal of palaeoniscoids, parasemionotids, *Pholidophorus*, etc. The topography of the otic region is highly modified in notopterids because of the ear/swimbladder connection (Greenwood, 1963; 1973, p. 314), and the aortic canal in *Xenomystus* seems to be foreshadowed in other, less specialized, notopterids such as *Papyrocranus*. We interpret the aortic canal of *Xenomystus* as a neomorph.

laps, and lies at an angle to, longer anterior ones (fig. 35).

E. Osteoglossomorphs have the derived features of *Tharsis dubius*, but more closely resemble other extant teleosts in having:
   36. No specific cuplike structure on ventral surface of basioccipital for the cranial attachment of the aortic ligament (Patterson, 1975, p. 319).
   37. In caudal skeleton, hypurals seven or fewer in number, rarely with a rudimentary eighth, rather than nine or more (figs. 24, 25, 36, 40).
   38. Caudal axis turned sharply upward at level of PU_1, rather than gradually from PU_3 to PU_5 (cf. figs. 33, 35 with 25, 36).
   39. Hypurals and fin ray bases aligned so that no fin ray base of the upper lobe attaches to or overlies more than one hypural, rather than having all fin ray bases save the last crossing obliquely over the entire upper hypural series (cf. figs. 35, 37, and Monod, 1968).

F. Elopomorphs have the derived features of osteoglossomorphs (other than autopomorphic ones not listed here), and resemble clupeomorphs and euteleosteans in having:
   40. Primitively only two uroneurals, rather than three or four, extending forward beyond U2 (cf. figs. 24, 25 with 36, 37).

G. Clupeomorphs have the derived features of all preceding groups, but resemble euteleosteans in having:
   41. The articular bone in the lower jaw co-ossified with the angular, as opposed to having all (fig. 32) or none of the bones fused, or the retroarticular and angular fused (Nelson, 1973b).
   42. The retroarticular excluded from the joint surface for the quadrate (Nelson, 1973a, b).
   43. With an anteriorly directed membranous outgrowth from the anterodorsal margin of the first uroneural (cf. figs. 26-30).
   44. Neural arch over U1, when present, greatly reduced, rudimentary, lying free over U1 or nestled against the posterior face of the neural arch of PU1, or ankylosed with other neural arch and uroneural complexes, or, in most cases, absent. (See, for example, figs. in Greenwood and Rosen, 1971, and Rosen, 1974.)
   45. Tooth-plates, when present, fused with first three pharyngobranchials and fifth ceratobranchial.

H. Euteleosteans primitively have all the derived features of preceding groups (other than autopomorphic ones), plus:
   46. An adipose fin.
   47. Nuptial tubercles (Wiley and Collette, 1970).
   48. Anterior membranous outgrowth of first uroneural (stegural) not joining opposite member in midline.

ICHTHYODECTIFORMS AND OTHER MESOZOIC TELEOSTEANS

Ichthyodectiformes. Referring to the foregoing cladistic analysis, it can be seen that ichthyodectiforms possess all the derived features present in *Pholidolepis dorsetensis* (A.1-3), *Proleptolepis* spp. (B.4-12),[1] *Leptolepis coryphaenoides* (C.13-24), and they also have all but three of the 11 derived features specified for *Tharsis dubius* (D.32, 34, 35). In other words, ichthyodectiforms share eight derived features of the skull and vertebrae with *Tharsis dubius* and more apomorph groups, whereas *T. dubius* shares three others (loss of suborbital, presence of epipleurals, and modified posterior uroneurals) with extant teleosts. In this particular sequence, therefore, ichthyodectiforms are the plesiomorph sistergroup of *Tharsis dubius* and extant teleosts,[2]

[1] Taverne (1975c, p. 348) reported a prearticular (feature B8) in ichthyodectiforms, by a reference to Bardack (1965). Taverne (p. 344) described the prearticular as an ossification in Meckel's cartilage, whereas the accepted usage of the name prearticular, and our usage, is for a dermal bone. We suppose that Taverne mistakenly identified the ichthyodectiform coronomeckelian, described and so named by Bardack, as the prearticular.

[2] This theory of ichthyodectiform relationships is different from those previously proposed. The traditional view, first proposed by Heckel (1849), is that the ichthyodectiforms are related to the clupeomorph *Chirocentrus*, and this has been most recently advocated by Nybelin (1964), Bardack (1965), Danil'chenko (1968) and Applegate (1970), among others. The foundations of this theory were, in our opinion, ignorance of the derived features common to all extant clupeomorphs, and mistaking convergent resemblances

and can be so entered in the cladogram (fig. 54). Assignment of ichthyodectiforms to this position reduces the number of *Tharsis*-teleost synapomorphies in our list from 11 to three, the other eight characters becoming synapomorphies defining the group comprising ichthyodectiforms and all higher teleosts.

The relationships of other Mesozoic teleosts can be specified in relation to our sequence in the same way, but the precision with which this can be done will decrease as more and more are added, since the addition of each form will "use up" one or more of the specified synapomorphies. In other cases, information that might allow a particular form to be placed in the cladogram is not yet available for fossils. Below we discuss the relationships of some of these Mesozoic fishes.

Crossognathidae. Family Crossognathidae (Woodward 1901, p. 348; including Syllaemidae Cragin, Apsopelicidae Romer). Under this name we include two monotypic Cretaceous genera, *Crossognathus* Pictet and *Apsopelix* Cope, which share one of the specializations of ichthyodectiforms, uroneurals that cover the lateral faces of the ural and first two preural centra (fig. 21). The nomenclature of the crossognathids is thoroughly confused. Woodward (1901) named the family Crossognathidae to include two genera, *Crossognathus*, containing a single species from the Lower Cretaceous (Neocomian) of Switzerland and Germany, and *Syllaemus* Cope, with one species from the Upper Cretaceous of North America and one from the Cretaceous (Albian-Turonian) of England. As probable crossognathids Woodward also mentioned "the fragments described under the following names": *Apsopelix sauriformis* Cope, *Pelecorapis varius* Cope, and *P. berycinus* Cope, all from the Upper Cretaceous of Kansas. He also (1901, p. 616) regarded *Leptichthys agilis* Stewart, from the Upper Cretaceous of Kansas, as close to *Syllaemus*, and later (1903, p. 88) treated *Leptichthys* as a synonym of *Syllaemus*. In the same year as Woodward named the Crossognathidae, Cragin (1901, pp. 25, 31) named a family Syllaemidae for *Syllaemus* and a family Pelecorapidae for *Pelecorapis*.

The four nominal "syllaemid" genera, *Syllaemus*, *Pelecorapis*, *Apsopelix*, and *Leptichthys*, were briefly discussed by Dunkle (1958), who believed that *Syllaemus*, *Apsopelix*, *Leptichthys*, and *Pelecorapis berycinus* are very similar, if not identical, but that *Pelecorapis varius*, the type-species of that genus, belongs to a different group ("*Thrissopater*"). Romer (1966, p. 354), presumably following Dunkle, listed *Syllaemus*, *Leptichthys*, and *Pelecorapis* as synonyms of *Apsopelix*, the oldest generic name, and further compounded the confusion by naming the family Apsopelicidae, containing only that genus.

We have examined the type-material, in the American Museum of Natural History, of *Apsopelix sauriformis*, *Pelecorapis varius*, and *P. berycinus*, and the British Museum material of *Crossognathus sabaudianus* and *Syllaemus anglicus*, including type-material of the latter. We agree with Dunkle (1958) that *Pelecorapis varius* is a different type of fish, and we can detect no differences between *Syllaemus anglicus*, *P. bery-*

(in dentition and body form) for evidence of relationship. The second theory, that ichthyodectiforms are members of the Osteoglossomorpha, was first proposed by Greenwood et al. (1966), and is recommended by Patterson (1967a, b, 1968), Bardack (1968), Forey (1973a), Taverne and Ross (1973), and Taverne (1973c; 1974b, 1974c, 1974d; 1975c). The basis for this theory is, in our opinion, regarding symplesiomorphies as evidence of relationship. Nelson's (1973a) theory, that ichthyodectiforms are related to elopomorphs, is due to concentrating on one part of the skeleton alone, the lower jaw; taking one derived feature, the medial position of the sensory canal opening on the angular, as a synapomorphy of taeniopaedians (Elopomorpha *sensu lato*), whereas it is found in a more extensive group; and another derived feature, an angular component of the articulatory facet, as a synapomorphy of all ichthyodectiforms, whereas it is found in a less extensive group. A fourth theory (Bardack and Sprinkle, 1969), that ichthyodectiforms are a group of high rank unrelated to any extant teleostean subgroup, is closer to our own, but is based, in our opinion, on the idea that a taxon merits high rank because its relationships are unknown. A final theory, proposed by Taverne (1975c), is that most ichthyodectiforms are osteoglossomorphs, but that *Allothrissops*, which we include in the ichthyodectiforms, is not related to that group, but to the leptolepids, which in turn are most closely related to euteleosteans. The reasoning behind this proposal seems to be that since *Allothrissops* cannot be ancestral to other ichthyodectiforms, its relationships must lie elsewhere. Taverne's scheme is the result of combining a relentless search for ancestors with a respect for symplesiomorphic resemblances.

cinus, and *Apsopelix sauriformis*, or between these and North American specimens determined as *Syllaemus latifrons* (AMNH† 2436) and *Leptichthys agilis* (AMNH† 8330; BMNH P.9184). We therefore treat *Apsopelix anglicus* (Dixon) as the valid name for material previously named *Syllaemus latifrons* Cope, *S. anglicus* (Dixon), *Apsopelix sauriformis* Cope, *Pelecorapis berycinus* Cope, *Leptichthys agilis* Stewart, *Helmintholepis vermiculatus* Cockerell, *Paleoclupea dakotaensis* Dante, and *Syllaemus albiensis* Wenz. Regarding *Helmintholepis* and *Paleoclupea* see Dunkle (1958). According to Wenz (1965), *S. albiensis*, represented by a single specimen from the Albian of France, is distinguished from *S. anglicus* by reduction of the parietals, so that they are separated by the frontals and largely covered by the supratemporals, but specimens of *S. anglicus* in which the supratemporals are preserved, such as BMNH 47195, show just the same configuration of these bones as Wenz's specimen.

Crossognathus is very imperfectly known. So far as published records tell, it is represented only by Pictet's holotype, in Geneva, and by the seven British Museum (Natural History) specimens listed by Woodward (1901). The caudal skeleton (fig. 21) is well preserved in several of these specimens, and is distinctive. *Apsopelix* is represented by several well-preserved specimens from Europe and North America, and with suitable preparation this material could provide a fairly complete account of the skull. The caudal skeleton is not complete in any specimen of *Apsopelix* that we have seen, but enough of it is visible in AMNH† 8330 and in several British Museum specimens to show that it is almost identical with that of *Crossognathus*, differing only in having the neural and hemal spines more strongly inclined and pressed together, and in the increased hypurostegy, so that the proximal ends of the upper and lower principal rays almost meet.

Apsopelix is a distinctive fish, most readily recognized by the very large scales and pelvic fins, which lie farther back than in any other teleost we know (prepelvic length equals 70 percent of standard length in BMNH P.9184), and are supported by massive, broad pelvic bones with a strong midline symphysis. The caudal part of the vertebral column is very short, containing only 12 to 14 vertebrae out of a total of about 38-40, and the anal fin must have been very short (it is said to be absent by Woodward and Wenz, but fragments are preserved in AMNH† 1602 and 8330). *Crossognathus* has smaller pelvics and an unmodified pelvic girdle, and the prepelvic length is about 60 percent of the standard length. There are about 35 vertebrae, with 15 caudal (excluding the ural centra). There are well-developed epipleural intermusculars in both *Crossognathus* and *Apsopelix*.

Not much is known about the head in *Crossognathus*. In *Apsopelix* there is a suite of resemblances between the braincase (BMNH 47195, 47302) and that of megalopids. The postorbital part of the braincase is deep and short, with a very large myodome and hypertrophied posttemporal fossae which are confluent above the cranial vault and extend forward to the orbitosphenoid. As Forey (1973a, p. 198) said, enlarged posttemporal fossae of this sort are a unique feature of megalopids. In *Apsopelix* the condition is not precisely the same as in Recent megalopids, since in the latter the foremost part of the posttemporal fossa is roofed by the frontal and floored by the orbitosphenoid, whereas in *Apsopelix* it is roofed by the body of the frontal and floored by a posteroventrally directed descending lamina from the frontal. The intercalar of *Apsopelix* resembles that of the Eocene megalopids illustrated by Forey (1973a, figs. 36, 43), and is not modified as it is in living megalopids, but there is a deep pit in the lateral surface of the posterior part of the basioccipital suggesting the possibility of a simple otophysic connection (cf. Greenwood, 1970a).

In the ethmoid region of the braincase there are also resemblances between *Apsopelix* and megalopids. *Apsopelix* has a strongly ossified ventral ethmoid fused with the vomer (also present in *Crossognathus*, BMNH P.7185), and the vomerine tooth patch is partially paired, as in *Elops* and megalopids. There is no ethmopalatine bone [the paired bone in *Apsopelix* that Wenz (1965, p. 14, fig. 3, pl. 2, fig. C) called "préethmoide" is the autopalatine]. There is no bone-enclosed ethmoid commissure. If *Apsopelix* were known by the braincase alone, we should undoubtedly regard it as a megalopid, but the caudal skeleton is of a different, more primitive type, and the lower jaw does not show the characteristic angulo-retroarticular of elopomorphs.

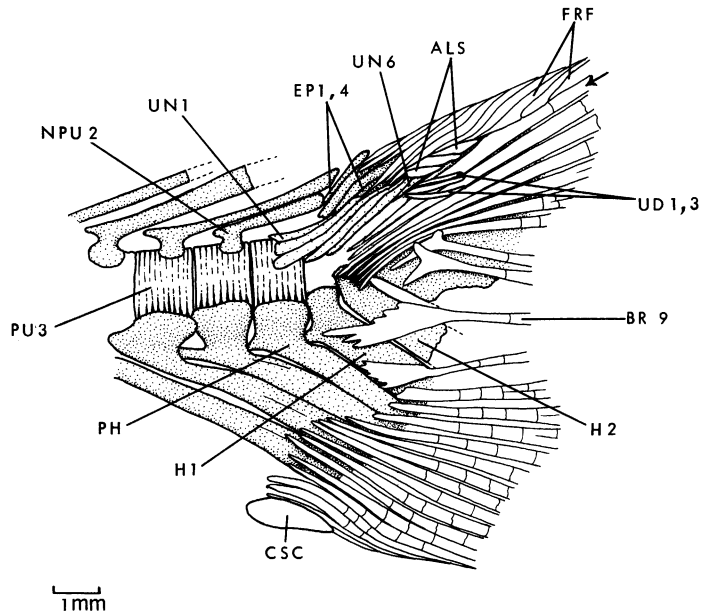


FIG. 31. *Pholidolepis ?dorsetensis* Nybelin, caudal skeleton as preserved in a specimen in a private collection, Lower Lias, Charmouth, Dorset (drawing reversed left to right).

In the single specimen where the lower jaw is accessible (BMNH 47302), the sensory canal opening is in the primitive medial position (cf. fig. 32), the angular and articular are fused, and the retroarticular is free except in the surface of the facet for the quadrate, where all three bones appear to be fused.

Crossognathus and *Apsopelix* have previously been assigned, separately or in association, to such groups as the clupeids or clupeoids, and elopids or elopoids, but no good reason has ever been presented for these assignments. We regard the two genera as a monophyletic unit, characterized by specializations in the vertebral column and caudal skeleton. The caudal skeleton shows one feature that is otherwise unique to the ichthyodectiforms: extension of the uroneurals over the lateral surface of the ural and preural centra. But there are no other indications of relationship with ichthyodectiforms, since there is no ethmopalatine bone or basal sclerotic bone, and there are indications of relationships with more advanced teleosts, such as the presence of well-developed epipleurals and differentiation of the uroneurals into anterior and posterior series. The braincase of *Apsopelix* shows at least one feature that is otherwise unique to megalopids, confluence of the post-temporal fossae above the cranial vault, but the structure of the lower jaw, the nine hypurals, and the primitive arrangement of the uroneurals and the ural neural arches oppose elopomorph relationships.

Referring to the list of characters in the preceding section it can be seen that the crossogna-

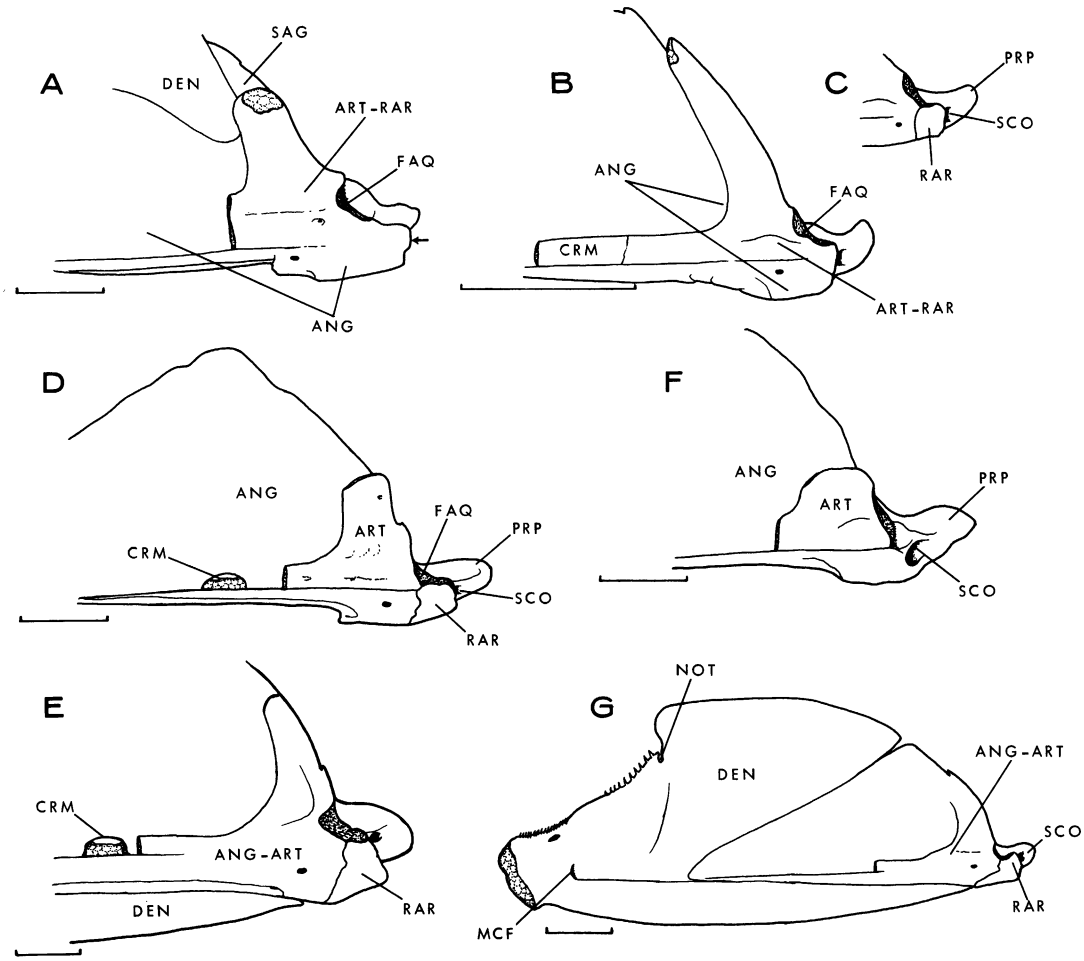


FIG. 32. Lower jaw structure in "leptolepids," right side jaws in medial view, scale beneath each 1 mm. A., *Proleptolepis* sp., isolated posterior part of jaw, BMNH P.58190, from a coprolite, Lower Lias, Charmouth, Dorset. Showing a primitive condition in which a surangular (SAG) is present, the post-articular process is rudimentary, the sensory canal opening (arrowed) is posterior, and there is no separate retroarticular. The endoskeletal bone (ART-RAR) is topographically equivalent to both the articular and retroarticular of higher teleosts, and this bone is fused with the angular. The same condition is found in "pholidophorids" (Patterson, 1973, fig. 7) and other primitive fossil actinopterygians. B, C, *Leptolepis coryphaenoides* (Bronn), isolated bones from the stomach contents of BMNH P.7626, *Pachycormus curtus* Agassiz, Upper Lias, Ilminster, Somerset. B, BMNH P.58191 (reversed), resembles A, *Proleptolepis*, in having a single endoskeletal bone, topographically equivalent to the articular and retroarticular, partially fused with the angular. The coronomeckelian (CRM) is still distinct, but is on the point of fusing with the articular. C. BMNH P.58192 (same scale as B), showing an independent retroarticular and partial fusion of the angular and articular, is interpreted as an earlier ontogenetic stage than B. Other specimens from the same source as B and C show no fusion between the angular and articular, a still earlier ontogenetic stage. D, E, *Tharsis dubius* (Blainville), Kimmeridgian, Solnhofen district, Bavaria. D, BMNH P.58193, from an individual about 7 cm. in standard length, from the stomach contents of BMNH P.12070, *Pholidophorus macrocephalus* Agassiz, with the retroarticular (missing in P.58193) added to scale from BMNH 36028, a larger specimen, about 10 cm. in standard length. E, BMNH P.56539, a specimen about 15 cms. in standard length. In D the angular, articular and retroarticular are independent; in E the angular and articular are fused, a later ontogenetic stage. F, Callovian *Leptolepis* sp. (cf. Patterson, 1975, p. 284), BMNH P.58194 (reversed), isolated bones from the stomach contents of BMNH 32579, *Pholidophorus* sp., Oxford Clay, Dives, Normandy, France. The retroarticular has fallen away and was independent, and the angular and articular are not fused. G, *Leptolepides sprattiformis* (Blainville), Kimmeridgian, Solnhofen district, Bavaria. Outline of jaw (and scale) from AMNH† 8686, standard length 54 mm.; endoskeletal bones from AMNH† 1441, standard length 67 mm. The retroarticular is independent and the angular and articular are fully fused.

thids, so far as they are known, share the derived characters of *Tharsis dubius* and extant teleosts, but none with more apomorph groups. Under these circumstances, the ichthyodectiform and megalopid features in crossognathids are most parsimoniously interpreted as convergent, and we place these fishes as a nominal family, *incertae sedis* in the group containing *Tharsis dubius* and extant teleosts.

Anaethalion. This nominal genus, traditionally included in the Leptolepididae, contains seven or eight species from the Kimmeridgian lithographic stones of Germany and France, and one species from the Lower Cretaceous of Spain.[1] These species have recently been reviewed by Nybelin

[1] The fish-bearing limestone of Montsech, Lerida, Spain, has been previously treated as Kimmeridgian in age, like the classic localities of Germany and France. But recent work (Brenner, Geldmacher and Schroeder, 1974) shows it to be Lower Cretaceous in age, probably Valanginian. Wenz (1968a, p. 117) showed that the two nominal species of *Anaethalion* from Montsech, *A. vidali* Sauvage (1903) and *A. gigas* Sauvage (1903) are synonymous under the former name.

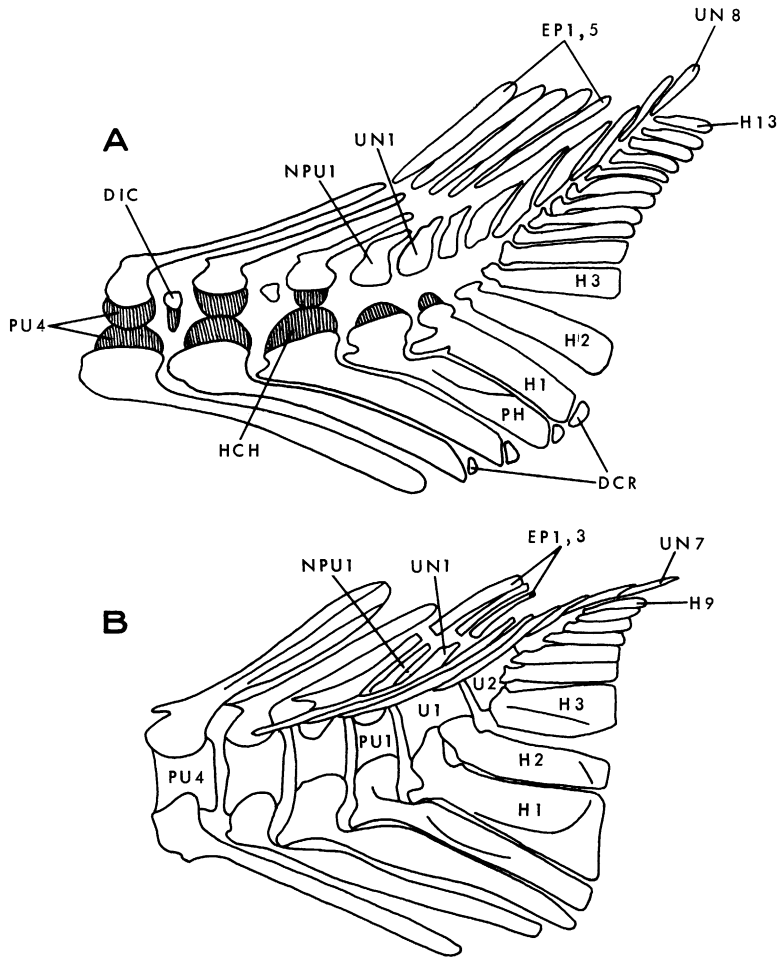


FIG. 33. Caudal skeletons, in diagrammatic form, of A, *Pholidophorus bechei* Agassiz, based on specimens from the Lower Lias, Lyme Regis, Dorset, illustrated by Patterson (1968); and B, *Leptolepis coryphaenoides* (Bronn), based on BMNH 32456, 32467, P.42857 (all from Upper Lias, Curcy, Normandy, France), and P.7622 (from the Upper Lias, Ilminster, Somerset).

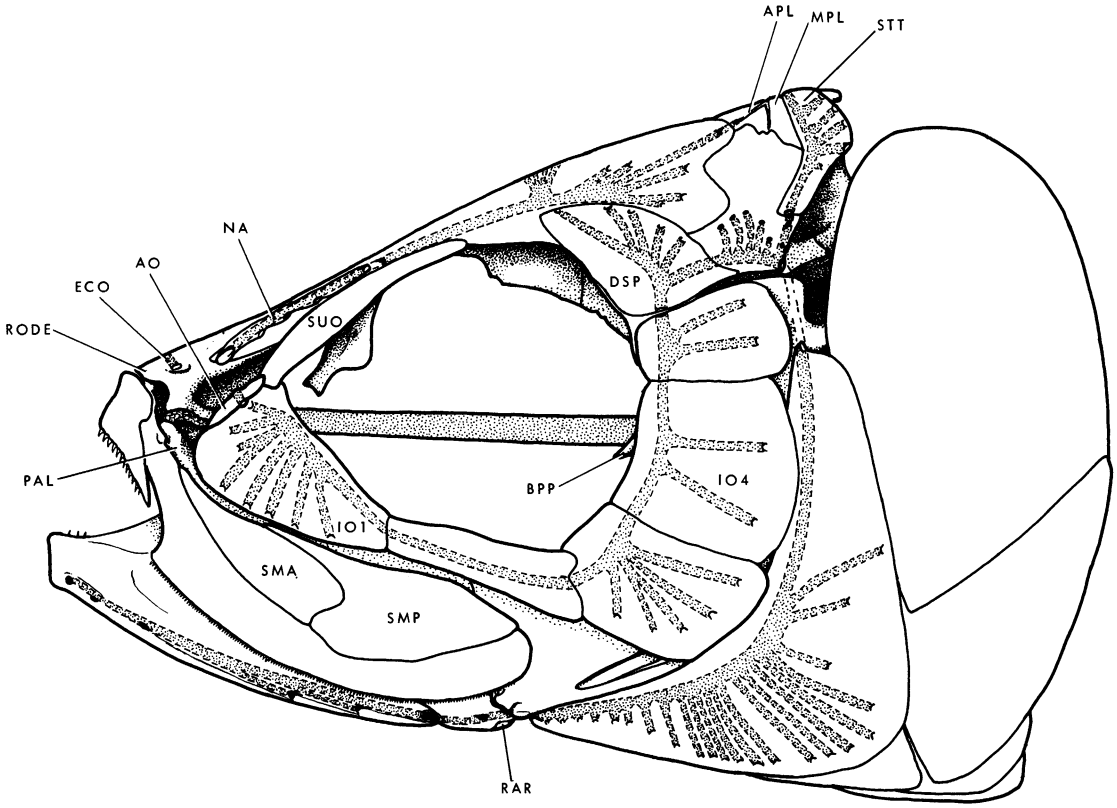


FIG. 34. *Tharsis dubius* (Blainville), restoration of skull based mainly on BMNH P.51759, Kimmeridgian, Solnhofen district, Bavaria. ×3 approx. Modified from Patterson (1967a, fig. 4).

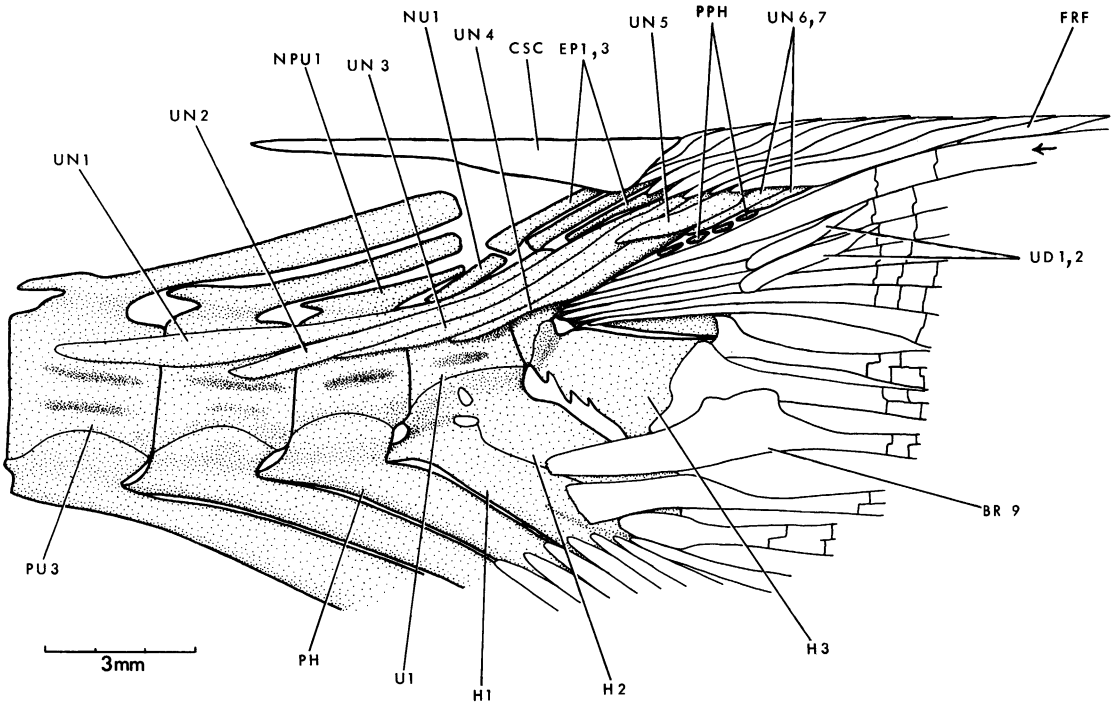


FIG. 35. *Tharsis dubius* (Blainville), caudal skeleton drawn mainly from BMNH P.927, slightly restored. From Patterson (1968, fig. 10).

(1967, 1971), Gaudant (1968a), and Forey (1973a, 1973b). Gaudant named a family Anaethalionidae for these species, and Nybelin (1971) placed the family in the Elopoidei. Forey (1973b) recognized three species-groups, one (*A. vidali*) probably related to the megalopids, one (*A.* cf. *subovatus*, *A.* sp.) probably related to the elopids, and one (*A. knorri*, *A. angustus*, *A. angustissimus*) probably related to euteleosteans.

On caudal skeleton and lower jaw evidence, *Anaethalion vidali* can be identified as an elopomorph, but in our opinion it cannot be assigned to any elopomorph subgroup. In the caudal skeleton (fig. 39; Forey, 1973b, fig. 4) it has the specialized compound neural arch associated with PU1 and U1 that ossifies in anterior and posterior sections and extends back beneath the epurals (cf. figs. 26, 27). In the lower jaw (fig. 40B) the angular and retroarticular bones are fused (cf. Nelson, 1973a, b). Forey (1973a) described the skeleton of *A. vidali*, and it shows nothing inconsistent with elopomorph relationships.

BMNH 37048, from the Kimmeridgian of Solnhofen, was illustrated by Nybelin (1963, fig. 6) as an "*Elops*-ähnlicher Fisch," and later referred to as *Anaethalion* sp. (Nybelin, 1967, pl. 8, figs. 4, 10; 1971, pl. 10, fig. 3, text-fig. 5D). Forey (1973a) suggested that the specimen is an elopid. In the caudal skeleton (fig. 41) the specimen shows the characteristic elopomorph neural arch structure. The preservation is not perfect, but our and Nybelin's interpretations (1971, fig. 5D) are consistent. Lower jaw evidence is lacking, and we know of nothing that allows the specimen to be assigned to any elopomorph subgroup.

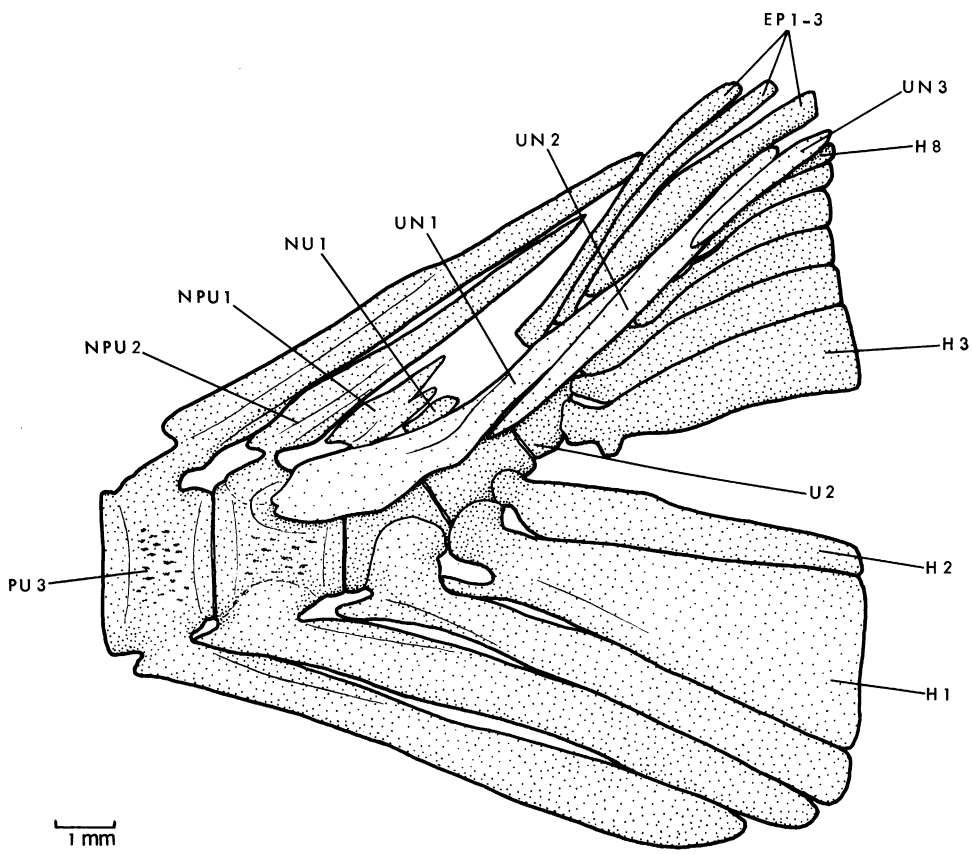


FIG. 36. *Anaethalion* cf. *subovatus* (Münster), caudal skeleton as preserved in BMNH P.3723, Kimmeridgian, Kelheim, Bavaria.

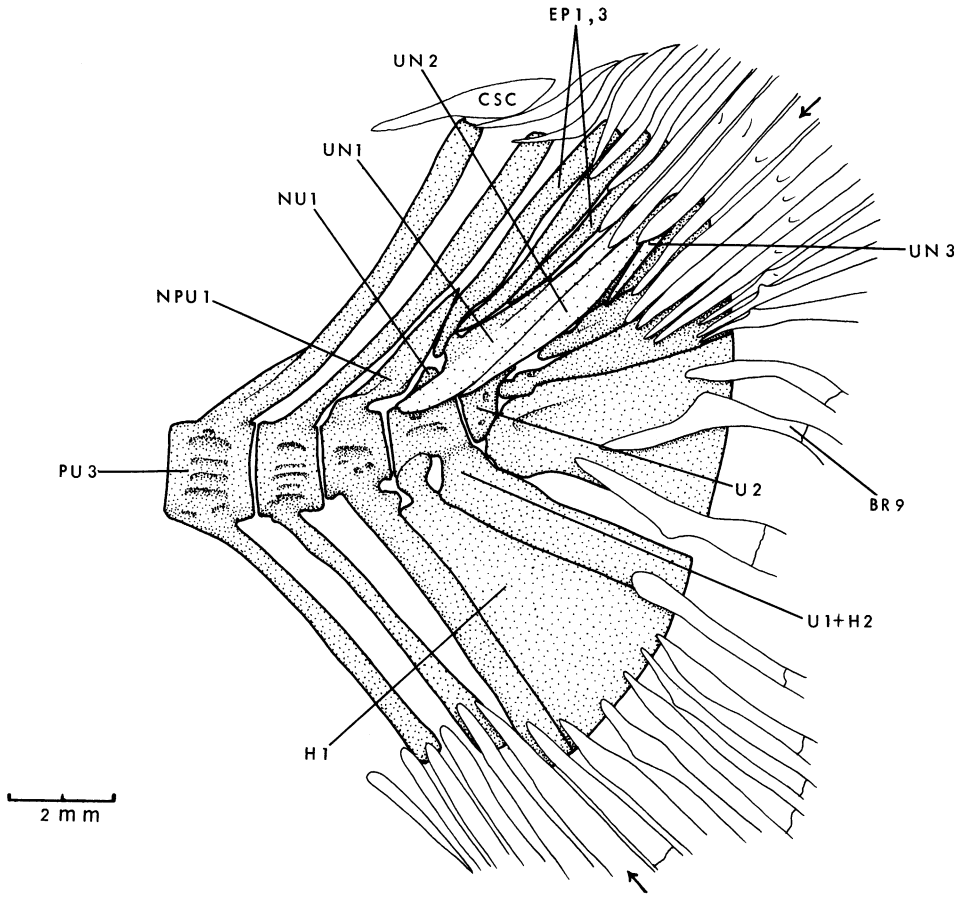


FIG. 37. *Diplomystus longicostatus* Cope, a primitive clupeomorph, caudal skeleton as preserved in BMNH P.7109, Lower Cretaceous (Neocomian), Ilhas Formation, Itacaranha, Bahia, Brazil.

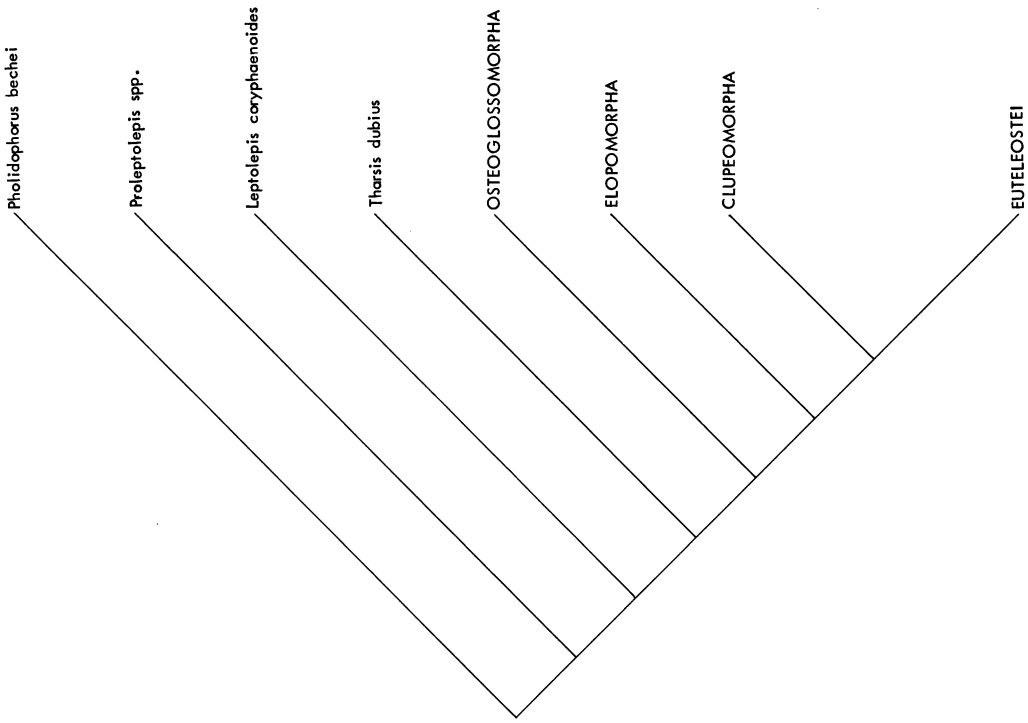


FIG. 38. Cladogram showing a theory of relationships of extant teleosteans and certain "pholidophorids" and "leptolepids."

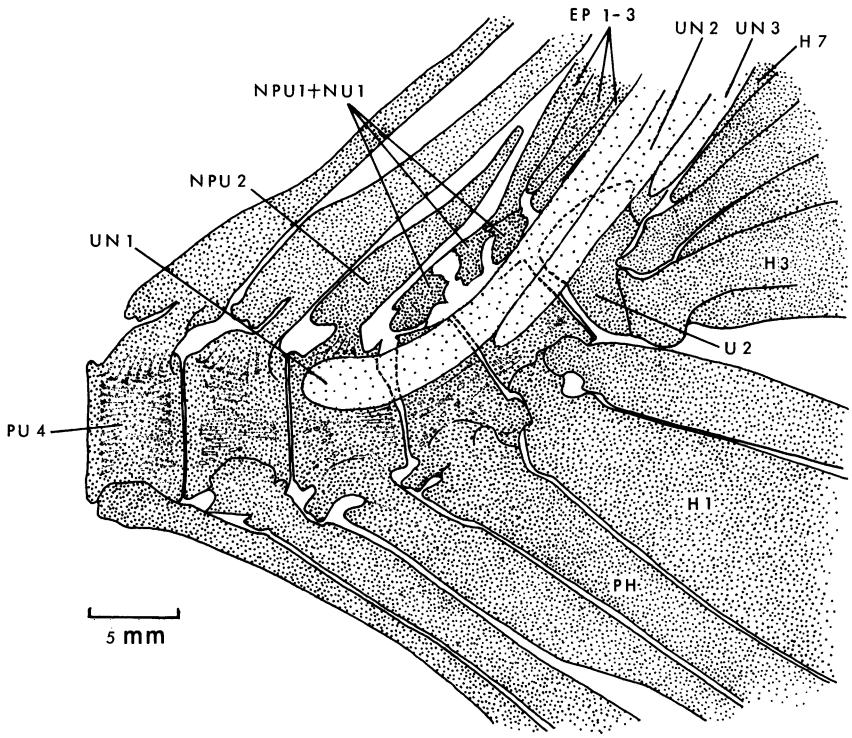


FIG. 39. "*Anaethalion*" *vidali* (Sauvage), caudal skeleton of BMNH P.10380, slightly restored. Lower Cretaceous (Valanginian), Santa María de Meyá, Montsech, Lerida, Spain.

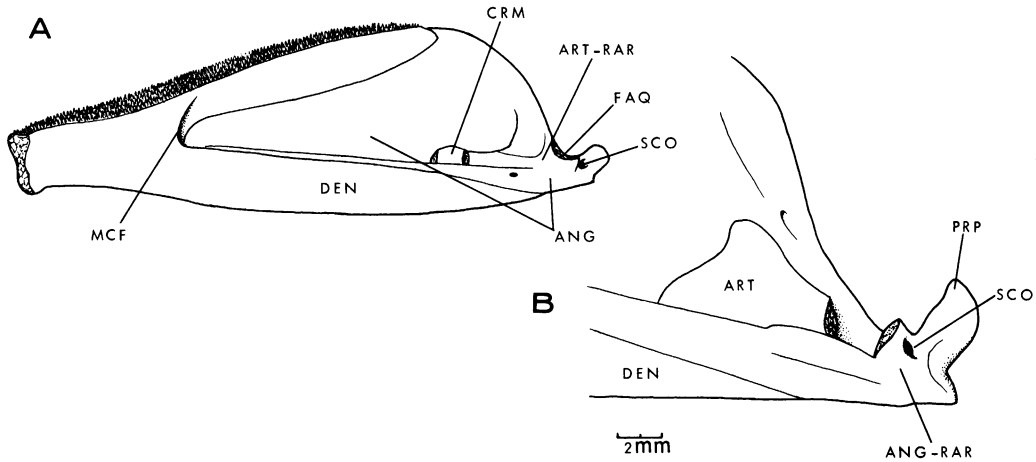


FIG. 40. A, *Anaethalion* cf. *knorri* (Blainville), right lower jaw in medial view, restored from BMNH P.58195, Kimmeridgian, Solnhofen, Bavaria, ×3 approx. Note absence of independent retroarticular, and fusion between angular and endoskeletal bone. B, "*Anaethalion*" *vidali* (Sauvage), posterior part of right lower jaw in medial view, from BMNH P.10927 (reversed), same horizon and locality as figure 39. Note free articular and fused angular and retroarticular.

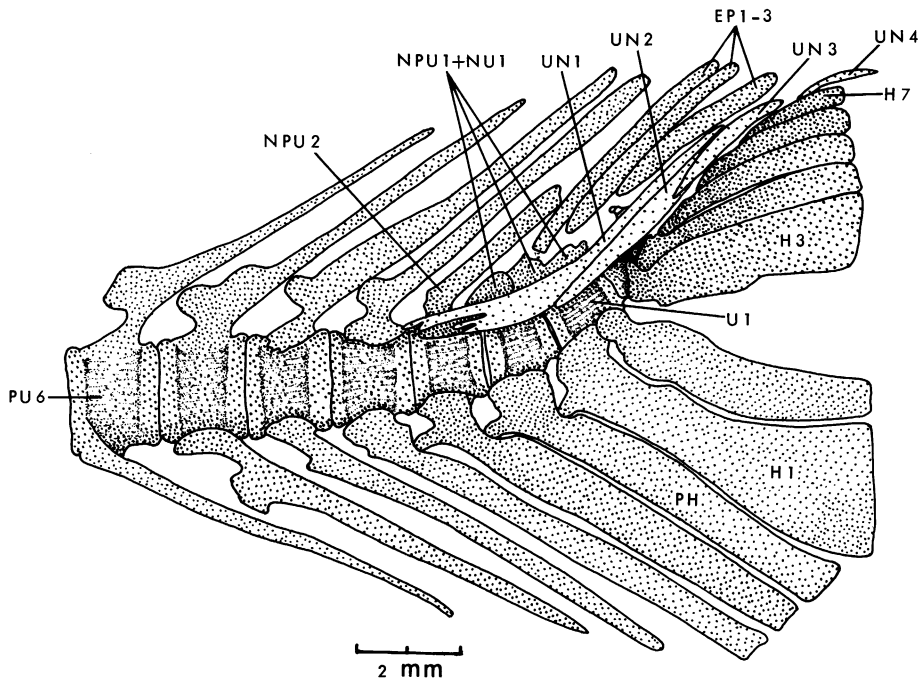


FIG. 41. "*Anaethalion*" sp., caudal skeleton of BMNH 37048, slightly restored. Kimmeridgian, Solnhofen, Bavaria.

Among the other Upper Jurassic species of *Anaethalion*, *A. angustus*, the type-species, is not assignable to the Elopomorpha. In the caudal skeleton (fig. 42; Forey, 1973a, fig. 18B, said to be of the same specimen, shows marked differences) the characteristic elopomorph neural arch structure is not present. Lower jaw evidence is lacking, and we know of nothing to substantiate Forey's opinion that the species is a euteleostean. *A. angustissimus* (fig. 43; Nybelin, 1971, pl. 10,

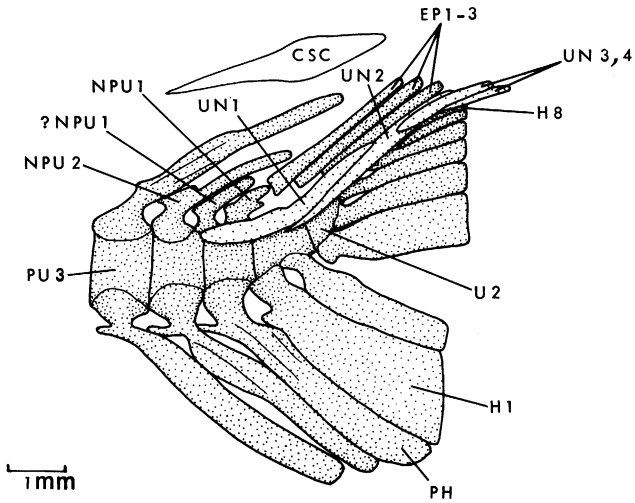


FIG. 42. *Anaethalion angustus* (Münster), caudal skeleton as preserved in BMNH 37927, Kimmeridgian, Solnhofen, Bavaria.

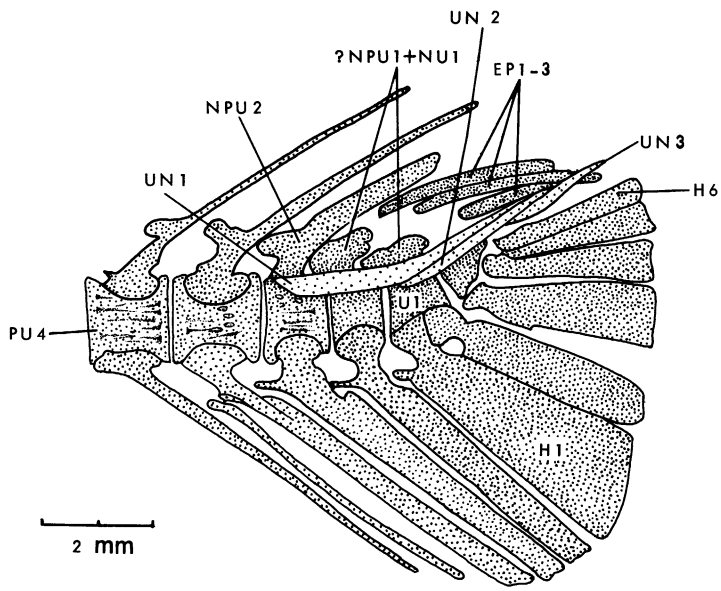


FIG. 43. *Anaethalion angustissimus* (Münster), caudal skeleton of BMNH 37901, reversed and slightly restored. Kimmeridgian, Solnhofen, Bavaria.

fig. 2; Forey, 1973a, fig. 18C) could be an elopomorph on caudal structure, but that evidence is indecisive, and in the lower jaw (Nybelin, 1967, pl. 8, fig. 7) the angular and retroarticular are not fused. *Anaethalion knorri* (fig. 44; Nybelin, 1971, pl. 11; Forey, 1973a, fig. 18D) appears to have the first epural too low for the elopomorph neural arch structure to have been present. The medial face of the lower jaw is visible in BMNH 37042, where it agrees with BMNH P.58195 (fig. 40A), an incomplete acid-prepared specimen (also showing most of the braincase), which shows fusion of the articular and retroarticular with each other and with the angular, a primitive condition that is not suggestive of elopomorph or euteleostean (Forey, 1973b) relationships. *A.* cf. *subovatus* (fig. 36; Forey, 1973a, fig. 18A), assigned to the Elopidae by Forey, does not show the characteristic elopomorph caudal neural arch structure. Lower jaw evidence is lacking.

In summary, all the species of *Anaethalion* that we have examined show, so far as they are known, all the derived features of elopocephalans (nos. 1-40 in the preceding analysis), including the two long uroneurals (no. 40) that characterize elopocephalans. One species, *A. vidali*, can be unequivocally assigned to the Elopomorpha, but not to any elopomorph subgroup, on caudal skeleton and lower jaw evidence (fig. 54, as "*Anaethalion*" *vidali*), and one specimen, BMNH 37042, can be so assigned on caudal evidence. The remaining species, including the type-species of the genus, are Elopocephala *incertae sedis* (fig. 54).

Leptolepis. As restricted by Nybelin (1974), this genus contains *L. coryphaenoides*, *L. normandica*, *L. jaegeri*, *L. saltviciensis*, *L. autissiodorensis*, *L. woodwardi*, and *L. nathorsti.* Among these, we have examined only *L. coryphaenoides*, the type-species (see note p. 127 above). Nybelin transferred several species and specimens, previously included in *Leptolepis*, to

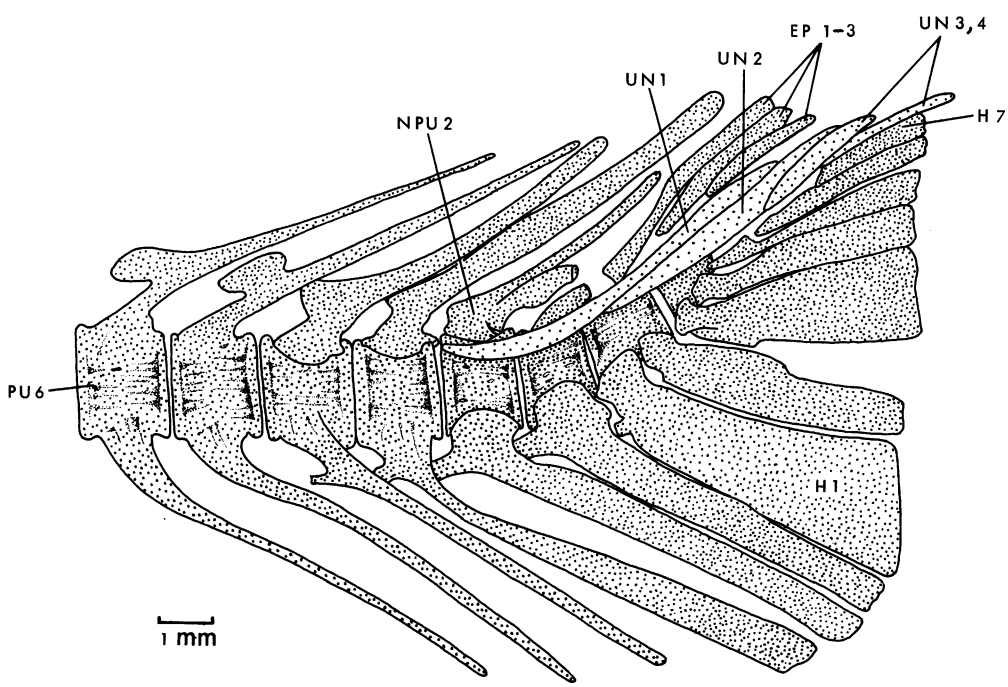


FIG. 44. *Anaethalion knorri* (Blainville), caudal skeleton of BMNH 37839, slightly restored. Kimmeridgian, Solnhofen, Bavaria.

other, mostly monotypic (M) genera: *Seefeldia* (M), *Pholidolepis*, *Proleptolepis* (see note p. 127 above), *Tharsis* (M), *Leptolepides* (M), *Ascalabos* (M). He reviewed two other species, *L. talbragarensis* and *L. macrophthalmus*, both of which we have examined, and concluded that neither belongs in *Leptolepis sensu stricto.*

Taverne (1975a, 1975d, 1975e; 1976; In press) has also redescribed several species previously placed in *Leptolepis* and transferred some to other monotypic genera: *Wenzia, Nybelinoides* and *Pattersonella*, supposed argentinoids, and *Pseudoleptolepis*, a supposed salmoniform. We have not seen material of these species.

There are many other nominal species of *Leptolepis*, some fairly well known, such as *L. koonwarri* (Waldman, 1971) and *L. caheni* (Taverne, 1975d), others poorly known.

In the cladistic analysis in the preceding section we have placed *L. coryphaenoides* in a scheme of relationships. Here we shall discuss the place of *L. macrophthalmus*, *L. talbragarensis*, and *L. bahiaensis* in that scheme.

Leptolepis macrophthalmus Egerton is from the Oxford Clay (Oxfordian, Upper Jurassic) of Wiltshire (Woodward, 1895, p. 508, pl. 18, fig. 3). As Nybelin (1974, p. 172) says, "the material of this species, kept in the British Museum (Natural History), is not very suitable for a detailed analysis." In 1964 Nybelin (p. 40) suggested that *L. macrophthalmus* might be related to *Allothrissops* because of the pattern of the preopercular sensory canal (fig. 45B; see discussion on p. 103) and the number of anal fin rays (12-13, as against 8-10 in leptolepids) and pelvic fin rays (nine, against 11-15 in leptolepids). The first of these fin ray differences has no significance, since Nybelin (1974) found the same number of anal rays in *Tharsis dubius*, and we do not believe that any weight can be given to the correspondence in pelvic ray number between *L. macrophthalmus* and ichthyodectiforms.

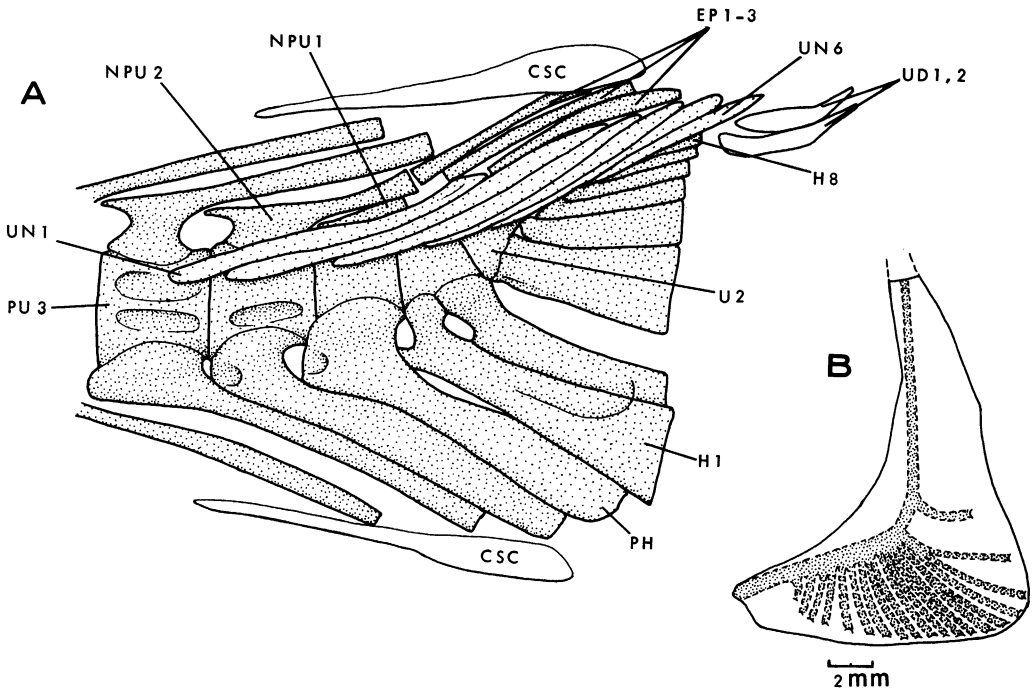


FIG. 45. "*Leptolepis*" *macrophthalmus* Egerton, Oxford Clay (Upper Jurassic), Christian Malford, Wiltshire. A, restoration of caudal skeleton based on BMNH 20090*a*, 20090*h*, and 46344. ×5 approx. B, preopercular as preserved in BMNH P.45012.

In 1974, Nybelin again commented on *L. macrophthalmus* and its possible relations with *Allothrissops*, noting that the shape of the lower jaw and hyomandibular could not be made out in the material of *L. macrophthalmus*. The significance of these structures to Nybelin is that in the leptolepids *Proleptolepis*, *Leptolepis coryphaenoides*, *L. normandica*, *L. woodwardi*, and *Tharsis dubius* there is a notch or excavation in the margin of the dentary, behind the tooth-row and immediately in front of the coronoid process, and on the posteroventral margin of the hyomandibular there is a preopercular process. Nybelin construes these two features as synapomorphies of his Leptolepididae *sensu stricto*. In our opinion, these features do not have that significance. There is a preopercular process on the hyomandibular of *Allothrissops* (fig. 9B), and the same structure seems to be present in *Pholidophorus germanicus* (Patterson, 1973, fig. 7). And as Nybelin (1974, p. 189) noted, the notch in the margin of the dentary is larger and more open in *Proleptolepis* than in *Leptolepis*, and is represented in several pholidophorids by a similar notch. The notch is small in *Tharsis* (Nybelin, 1974, fig. 24), smaller in *Leptolepides* (fig. 32G), and there is a trace of it in the Cretaceous salmoniform *Gaudryella* (Patterson, 1970b, fig. 8). These distributions indicate that each of these features is a synapomorphy of a group more extensive than the Leptolepididae, and their presence or absence in *L. macrophthalmus* would give little information about the relationships of that species.

Our examination of the material of *L. macrophthalmus* has produced little relevant information about the head. The dermopterotic has the same form as in *Allothrissops* (fig. 5), with no pitline groove, the sensory canal sharply angled at the junction with the preopercular canal, and a large, triangular dilatator fossa. There is a raised, posterolaterally directed tube at the posterolateral corner of the parietal, perhaps carrying a sensory canal branch. In the lachrymal, the infraorbital sensory canal has four long branches, like those in *Tharsis dubius* (fig. 34). The rostrodermethmoid resembles those of *Tharsis* or the Callovian *Leptolepis* (Patterson, 1975, figs. 129, 130). There is no evidence regarding the presence or absence of a suborbital or of the characteristic ichthyodectiform ethmo-palatine bone.

The caudal skeleton (fig. 45A) does not show the ichthyodectiform uroneural pattern, in which the anterior uroneurals cover the lateral surfaces of the ural and preural centra. No epipleural intermuscular bones are visible in *L. macrophthalmus*, but the material is too imperfect to be sure that they were absent.

Referring to the analysis in the preceding section we find that *L. macrophthalmus* has, so far as it is known, all the synapomorphies of the group comprising ichthyodectiforms, *Tharsis dubius* and extant teleosteans. Like the ichthyodectiforms, it has all the derived characters specified for *Leptolepis coryphaenoides*, and appears to lack one or two of the characters specified for *Tharsis*, numbers 34 and 35, epipleural intermusculars and differentiation of the uroneurals into anterior and posterior series. At the present level of analysis, therefore, *L. macrophthalmus* might be the sister-group of *Tharsis* and extant teleosteans, of ichthyodectiforms plus that group or of ichthyodectiforms alone, and we cannot place it in the cladogram (fig. 54) except by indicating the area of uncertainty.

Leptolepis talbragarensis Woodward is from the Purlawaugh Formation, of unknown age within the Jurassic, Talbragar, New South Wales, Australia. We have examined latex casts from the British Museum material of the species, which is preserved as natural moulds. The species is well described by Cavender (1970), and is commented on by Nybelin (1974, p. 170), who suggested that it might be related to *Leptolepides sprattiformis*. *Leptolepis talbragarensis* appears to have no suborbital bone and no epipleural intermusculars.

Both Cavender and Nybelin found the caudal skeleton to be informative. Cavender (1970, fig. 1B) illustrated four epurals, whereas in our material (fig. 46) only three are visible. Cavender illustrated seven uroneurals, partially differentiated into an anterior group of four long, straplike bones and a posterior group of three shorter ones. Our illustrated specimens both have six uroneurals, with three in each group, but one British Museum specimen seems to show seven as in Cavender's. Although the uroneurals are partially differentiated into anterior and posterior groups, the posterior uroneurals have the same alignment as the anterior ones, and do not show feature 35, as specified for *Tharsis* and more advanced teleosts in the preceding section.

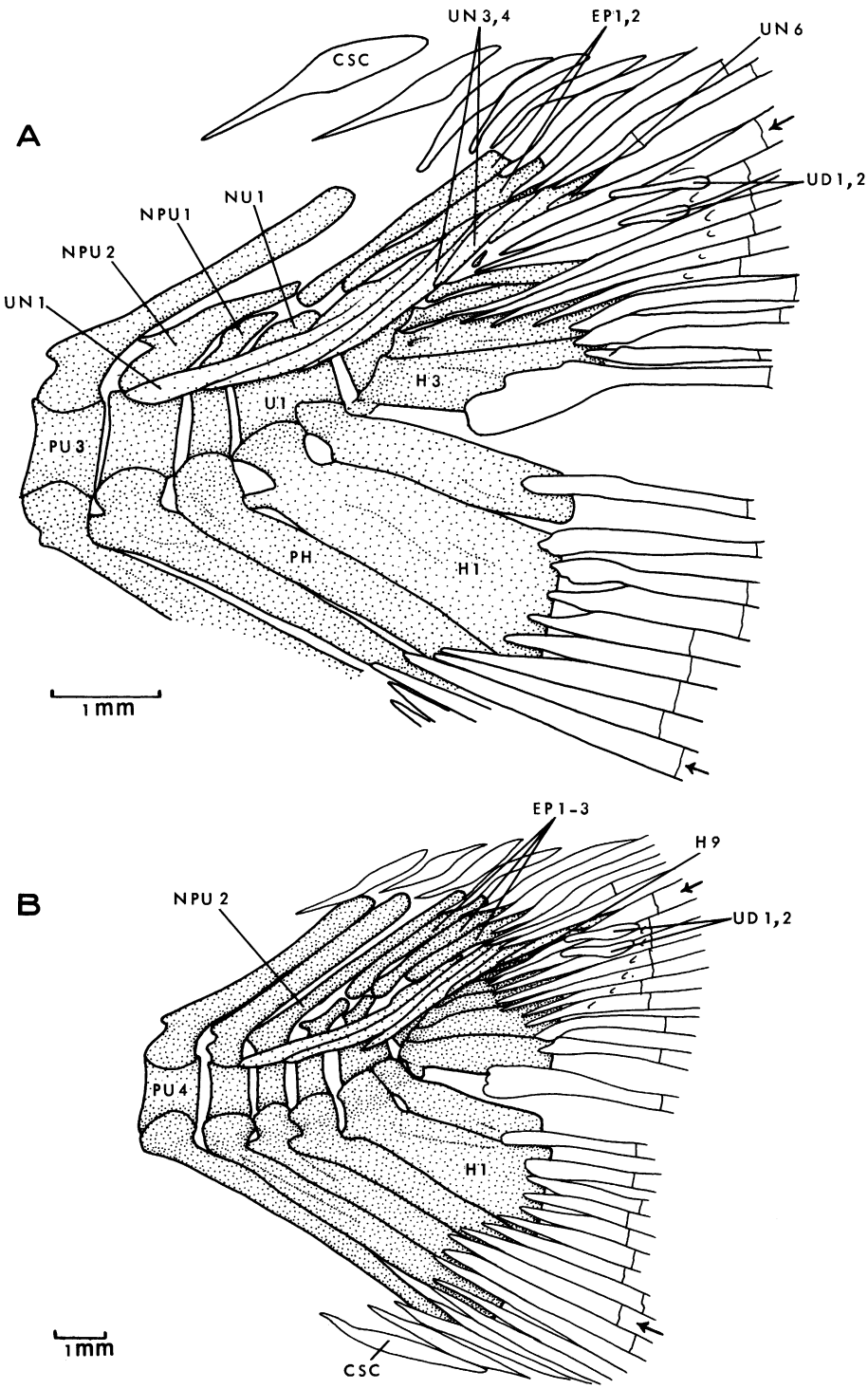


FIG. 46. "*Leptolepis*" *talbragarensis* Woodward, caudal skeleton as preserved in A, BMNH P.37973, with short neural spine on PU2 and only two epurals preserved; and B, BMNH P.12439, with full length neural spine on PU2, nine hypurals and three epurals. Jurassic, Purlawaugh Formation, Talbragar, New South Wales, Australia.

One other feature of interest is the apparent loss of flanges from the bases of branched caudal rays seven and eight (counting from the top down), and the grouping together of the bases of rays six, seven and eight, as in *Lycoptera* and *Hiodon* (cf. figs. 24, 46, with figs. 14, 31, 35, 50, 53). But we do not think this can be safely regarded as evidence of relationship.

Leptolepis talbragarensis has, so far as it is known, all the derived features of *Tharsis dubius* [nos. 1-35 in the preceding section], except that the centra are rather thin-walled (no. 33), there are no epipleurals (no. 34), and the uroneurals are not fully differentiated into two series (no. 35). It has none of the derived features (nos. 36-46) of higher groups. In the present analysis, therefore, *L. talbragarensis* might be the sister-group of *Tharsis dubius* and higher teleosts, of this group and *L. macrophthalmus*, or of any one of these subgroups, and it cannot be placed precisely in the cladogram (fig. 54).

Leptolepis bahiaensis Schaeffer (1947) is from the Lower Cretaceous (Neocomian) Ilhas Formation of Bahia, Brazil. We have examined the type-material, two fishes on a single slab. This species was briefly discussed by Patterson (1970b, p. 289), who noted resemblances between it and *Scombroclupeoides scutata* Woodward, also from the Ilhas Formation of Bahia. Two differences were also mentioned between *L. bahiaensis*, as described by Schaeffer, and the type-material of *S. scutata*: the apparent absence of caudal scutes and epipleural intermusculars in the former. But our examination of *L. bahiaensis* shows that caudal scutes and epipleurals are present, so that the two species are probably synonymous. Patterson (1970b) also noted the similarity between *S. scutata*, *L. bahiaensis*, and *Leptolepis congolensis* Arambourg and Schneegans (1936) from the Neocomian (Cocobeach Series) of Angola, West Africa, which was contiguous with the Bahia region of Brazil in Lower Cretaceous times. We have seen no material of *L. congolensis*, but Taverne (1976) has redescribed it as *Wenzia congolensis* and assigned it to the Argentinoidei. Taverne's restorations of the caudal skeleton (1976, figs. 3, 4) do not resemble our figure of *L. bahiaensis*.

The caudal skeleton of *L. bahiaensis* (fig. 47) shows derived characters relating it to extant teleosts: numbers 37-40, and perhaps 43 and 44 in the series in the preceding section. Character 40 places the species in the Elopocephala, and the well-developed outgrowth on the first uroneural (43) relates it to the Clupeocephala, but no more precise statement is possible on present information, and it can only be placed as Clupeocephala *incertae sedis* (fig. 54). With these relationships the species has clearly nothing to do with *Leptolepis* or leptolepids. The generic name *Scombroclupeoides* is available for it.

Leptolepides. This monotypic genus was created by Nybelin (1974) for *Leptolepis sprattiformis* (Blainville), from the Kimmeridgian of Bavaria and Cerin, France. Nybelin described the species in some detail. He was uncertain whether *Leptolepides* belongs in his Leptolepididae *sensu stricto*, but retained it tentatively in the family because of the possibility of relationship with the poorly known *Leptolepis nathorsti.* Nybelin noted similarities between the caudal skeleton of *L. sprattiformis* and those of coregonids, writing (p. 194) "however, there are some differences which suggest convergence." Taverne (1975d, p. 849) also commented on *L. sprattiformis* and coregonids, writing that the fossil species is "un ancêtre idéal" for the Recent group.

We have examined acid-etched transfer preparations of several specimens of *L. sprattiformis* (figs. 32G, 48-50). Our restoration of the skull (fig. 49) differs from Nybelin's (1974, fig. 29) in a few details: Nybelin shows two supraorbitals where we find only one, and also shows the middle pitline groove extending on to the dermopterotic, a mistake in our opinion. Like Nybelin, we noted the parasphenoid dentition of *L. sprattiformis* (his pl. 25, figs. 1, 2), but we do not attach the same significance to these teeth—that they differentiate the species from all other leptolepids—for parasphenoid teeth are also found in other leptolepids (Patterson, 1975, figs. 141-144).

In the caudal skeleton, Nybelin's restoration (1974, fig. 32) agrees with ours (fig. 50) in most respects, but his third and fourth hypurals seem to be together equivalent to our third, and in one of his photographs (pl. 26, fig. 1) the third hypural is certainly more slender than in our material. Nybelin interpreted the first uroneural as compound, incorporating two uroneurals which he thought were partially distinct in some

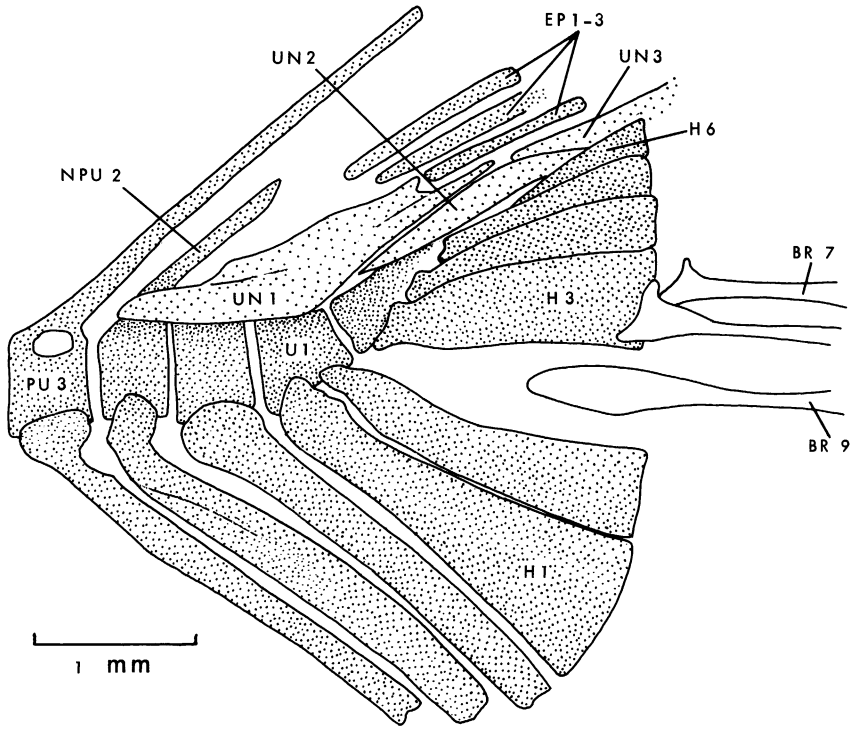


FIG. 47. "*Leptolepis*" *bahiaensis* Schaeffer, caudal skeleton of holotype, AMNH† 10014, slightly restored. Lower Cretaceous (Neocomian), Ilhas Formation, Bacuparytuba, Bahia, Brazil.

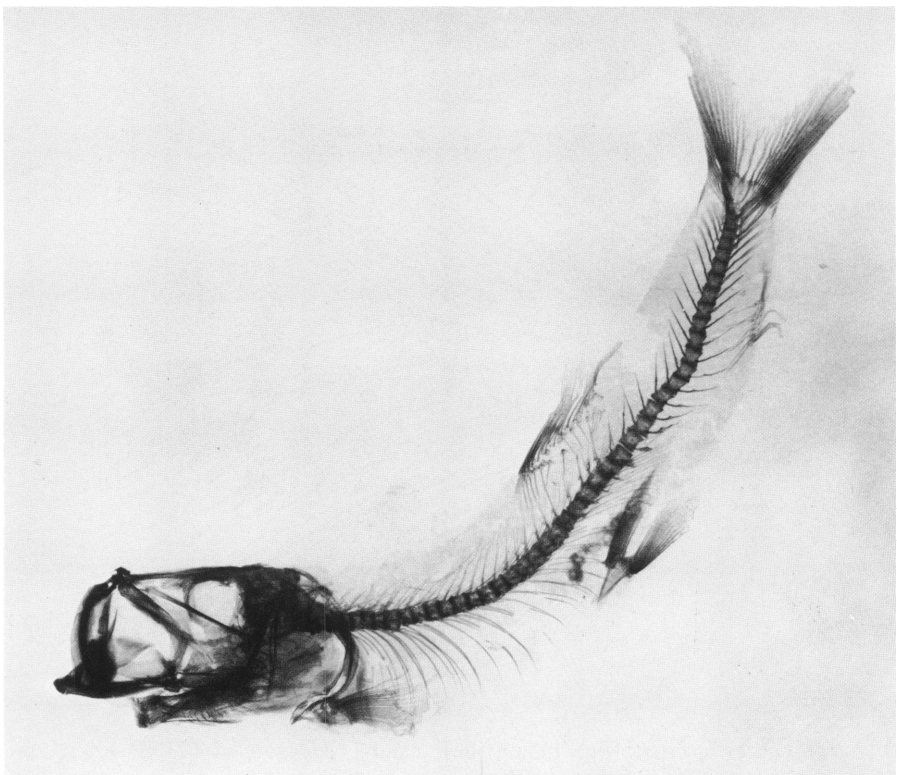


FIG. 48. *Leptolepides sprattiformis* (Blainville), positive print from radiograph of BMNH P.4999, a transfer preparation, Kimmeridgian, Solnhofen, Bavaria. ×2.

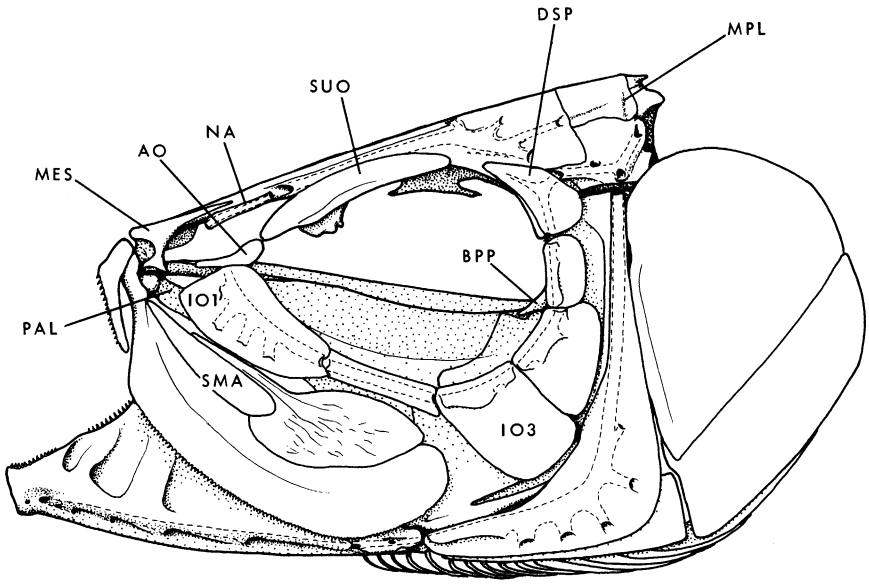


FIG. 49. *Leptolepides sprattiformis* (Blainville), restoration of skull based on BMNH 22521, 37883, P.926, P.932 and P.4999 (all transfer preparations), outline of dermosphenotic is in part speculative. Kimmeridgian, Solnhofen and Kelheim, Bavaria. × 10 approx.

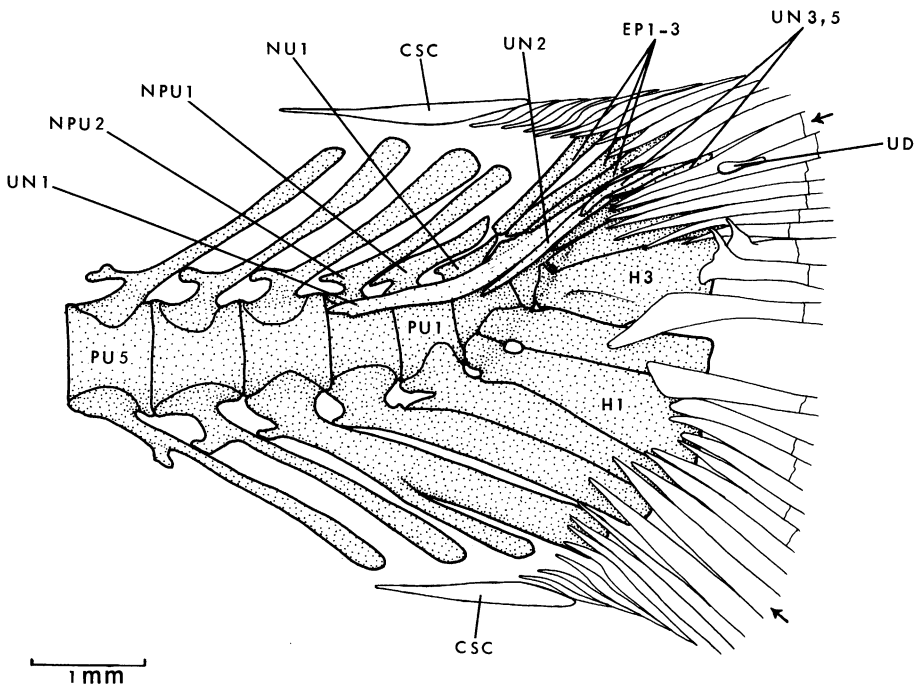


FIG. 50. *Leptolepides sprattiformis* (Blainville), caudal skeleton of BMNH P.926, reversed and slightly restored. Kimmeridgian, Solnhofen, Bavaria.

specimens, and the second ural neural arch, represented by the outgrowth on the anterodorsal surface of the bone. He also interpreted the second uroneural, which is shorter in his drawing than in ours, as the third (numbered "4" because of his belief that the first is compound) and the third as the second (numbered "3").

Leptolepides has, so far as it is known, all the derived characters of *Tharsis dubius* (nos. 1-35 in the preceding section), and also numbers 37 (AMNH† 1441 shows that there are seven hypurals), 38, 39, 40. These features place the genus in the Elopocephala. In the lower jaw (fig. 32G), the articular and angular are completely fused, in the same way as in clupeocephalans (number 41), but the retroarticular is not excluded from the joint surface (number 42). Similarly, there is a membranous outgrowth on the first uroneural (larger and more digitate in Nybelin's drawing than in ours; number 43), but the neural arch on U1 is not reduced or modified (number 44). These characters indicate that *Leptolepides* is a member of the Clupeocephala, but is not assignable to either of its subgroups (Clupeomorpha, Euteleostei). Other features suggestive of clupeocephalan relationships are the comma-shaped antorbital, without enclosed sensory canal (cf. Nelson, 1969b), and the flattened, membranous form of the posterior neural and hemal spines (fig. 48, cf., for example, Nybelin, 1971, pls. 5, 6). There are striking resemblances between the skull of *Leptolepides* and that of the Cretaceous salmoniform *Gaudryella* (cf. fig. 49 and Patterson, 1970b, fig. 31A) and between the mandibular dentition of *Leptolepides* and that of the salmoniform *Humbertia* (cf. fig. 32G and Patterson, 1970b, fig. 22A), which is contemporary with *Gaudryella*. But we do not construe these resemblances as evidence of relationship. One other feature of interest is the basihyal tooth-plate of *Leptolepides* (BMNH P.263, AMNH† 8686). This is an ovoid bone with teeth only around its periphery, as in searsiid argentinoids (Greenwood and Rosen, 1971) and some salmonoids (Rosen, 1974). But again we do not believe that this resemblance can be regarded as indicative of relationship. Our analysis indicates that *Leptolepides* is a member of the Clupeocephala, best placed as the sister-group of the two extant subtaxa of that group (fig. 54), the latter group being characterized by three features (nos. 42, 44, 45), and the Clupeocephala as a whole by two features (nos. 41, 43).

Pachythrissops. The genus *Pachythrissops* Woodward (1919, p. 128) is known from the type-species, *P. laevis* Woodward (Purbeckian, Dorset, England), *P. vectensis* Woodward (Weald Clay, Neocomian, Isle of Wight, England), and *P. propterus* (Wagner) (Kimmeridgian of Solnhofen, Germany). *Pachythrissops laevis* and *P. propterus* are from Upper Jurassic deposits, and *P. vectensis* is Lower Cretaceous. *Parathrissops furcatus* Eastman is doubtfully included in this genus. Nybelin (1971, pp. 39-41) analyzed the caudal skeleton and lower jaw of *Pachythrissops propterus* and, on the basis of shared primitive characters, proposed that *P. propterus* "could stand in rather near relation to the ancestors of *Megalops.*" Forey (1973a) reviewed the general case for a *Pachythrissops*-megalopid relationship, including Nybelin's proposal, and concluded that although all of their resemblances are in primitive features this superficial similarity warrants placing *Pachythrissops* within the Megalopidae. Nybelin (1971, p. 40, fig. 6D) correctly illustrated the specialized PU1-U1 neural arch complex in *Megalops*, a structure diagnostic of and unique for tailed elopomorphs, and in his comparative figure of *P. propterus* showed this structure not to be present. Neither of our specimens of *P. laevis* shows this characteristic elopomorph caudal feature (fig. 51). The two rudimentary neural arches that can be seen on U1 in *P. laevis* are of a generalized type. Further, in our material of *P. laevis* and Nybelin's illustration of *P. propterus* uroneural structure cannot be distinguished from that of *Leptolepis coryphaenoides*, and clearly is more primitive than that of *Tharsis dubius* in which the uppermost three small uroneurals lie at an angle to and overlap the lower uroneurals, as in extant forms (cf. figs. 33, 35). Relatively little is known about cranial and postcranial anatomy in the species of *Pachythrissops* but it is nevertheless possible to specify that *Pachythrissops laevis* shares characters C.21-24 with *Leptolepis coryphaenoides* and more apomorph groups and characters D.31, 33, and 34 with *Tharsis dubius* and extant teleosts. Whether or not it had a suborbital is unknown. But because uroneural structure in *Pachythrissops laevis* and *P. propterus* is more primitive than in *Tharsis dubius* (*Pachy-*

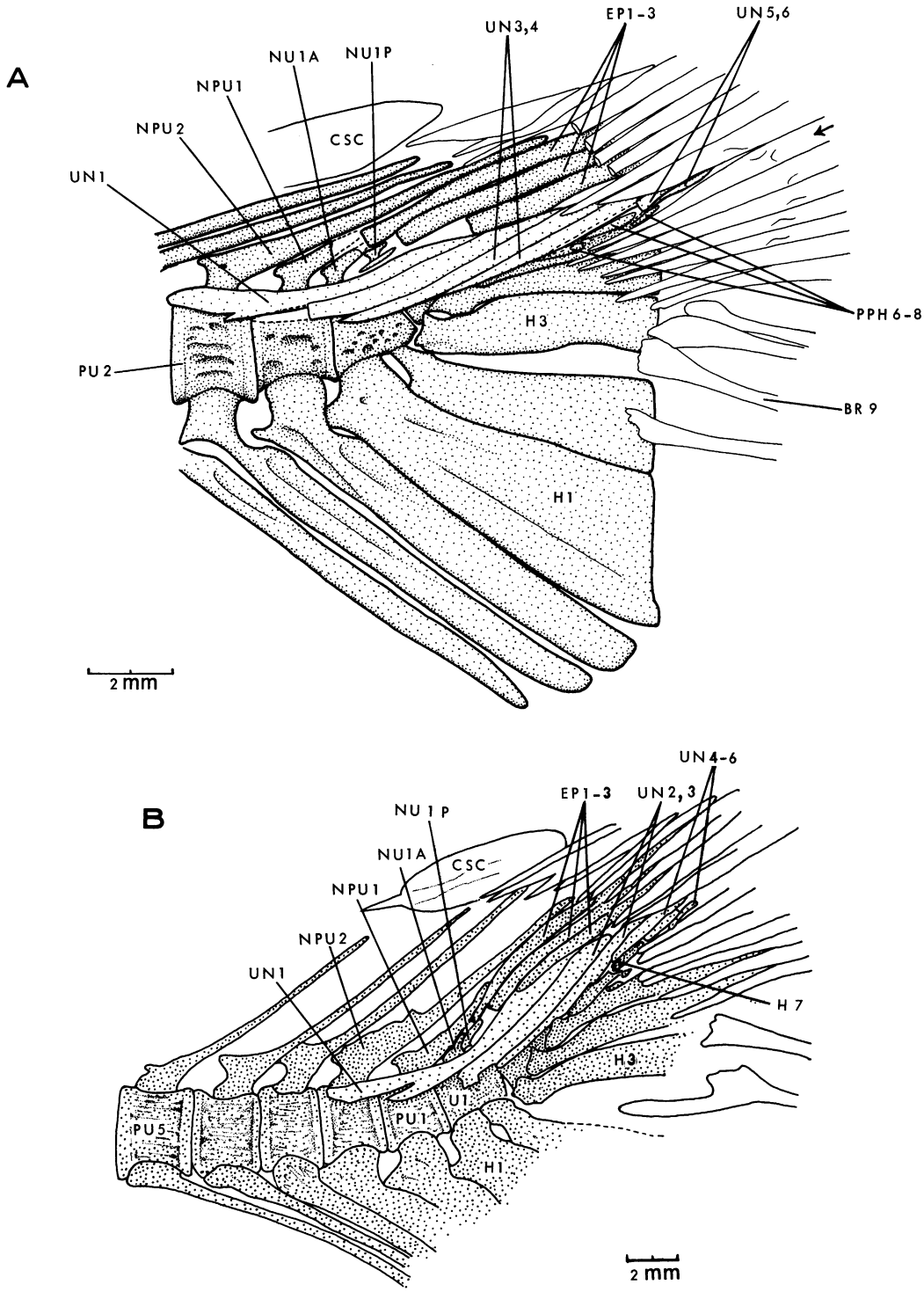


FIG. 51. *Pachythrissops laevis* Woodward, caudal skeleton of A, holotype, BMNH 40333, slightly restored; and B, BMNH P.29392, reversed. Upper Jurassic (Purbeckian), Purbeck Beds, Swanage, Dorset.

thrissops does not share D.35), the sister-group of these species of *Pachythrissops* may lie between ichthyodectiforms and *Tharsis* in our cladogram in the same way as *Leptolepis talbragarensis.* That species lacks a suborbital and epipleural bones, whereas *Pachythrissops* has epipleurals and the suborbital condition is unknown, so the two forms occupy the same position in the cladogram for slightly different reasons.

Ascalabos. Ascalabos voithii Münster (1839, p. 112), the only recognized member of its genus, is a small Upper Jurassic fish with many distinctive characteristics including a large head, deep abdominal region, and relatively few vertebrae (38 to 40; fig. 52). The trivial name *voithii* had been included in *Leptolepis* by Agassiz, but was returned by Nybelin (1974) to *Ascalabos* on the grounds that "*Ascalabos voithi* is a very characteristic species, quite different from the leptolepids." Nybelin published restorations of the skull and caudal skeleton of *A. voithii*, and discussed the axial skeleton and fins, but reached no conclusions about relationships. Taverne (1975e) published a restoration of the whole fish and caudal skeleton. He concluded that the species is a leptolepid, and treated *Ascalabos* as a subgenus of *Leptolepis.* Little of the skull and shoulder girdle is preserved in the specimens examined by Nybelin, Taverne, and us; the few distinctive characters that can be discerned do not suggest to us, nor did they to Nybelin or Taverne, the affinities of this paleospecies. Nybelin's restoration of the caudal skeleton, presumably based on the five specimens selected by him for detailed analysis, and Taverne's restoration of the caudal skeleton of a specimen 55 mm. in total length, correspond fairly well with the caudal structure of a relatively large (115 mm. total length) acid-prepared Solnhofen specimen examined by us (fig. 53). Certain differences are noteworthy: in our fish, 1) the anterior two uroneurals extend forward onto PU3, rather than PU2 (Nybelin), or PU3 and PU2 (Taverne), and there are three uroneurals extending beyond U2, rather than four (Taverne); 2) the uroneurals form a more or less evenly graded antero-posterior series of large to small elements, rather than having the anterior three (Nybelin) or four (Taverne) elements distinctly larger than the posterior ones; 3) there are seven well-formed uroneurals, rather than six

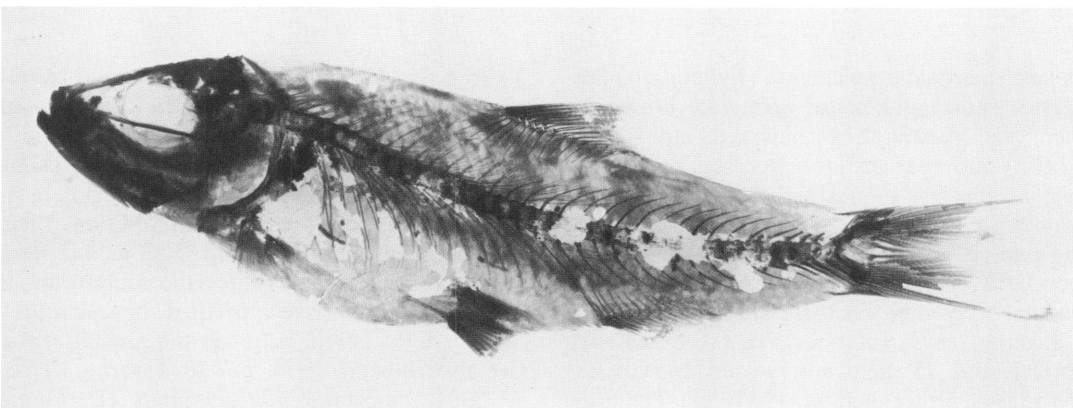


FIG. 52. *Ascalabos voithii* Münster, positive print from radiograph of BMNH 37062, a transfer preparation, Kimmeridgian, Solnhofen, Bavaria. ×1.5 approx.

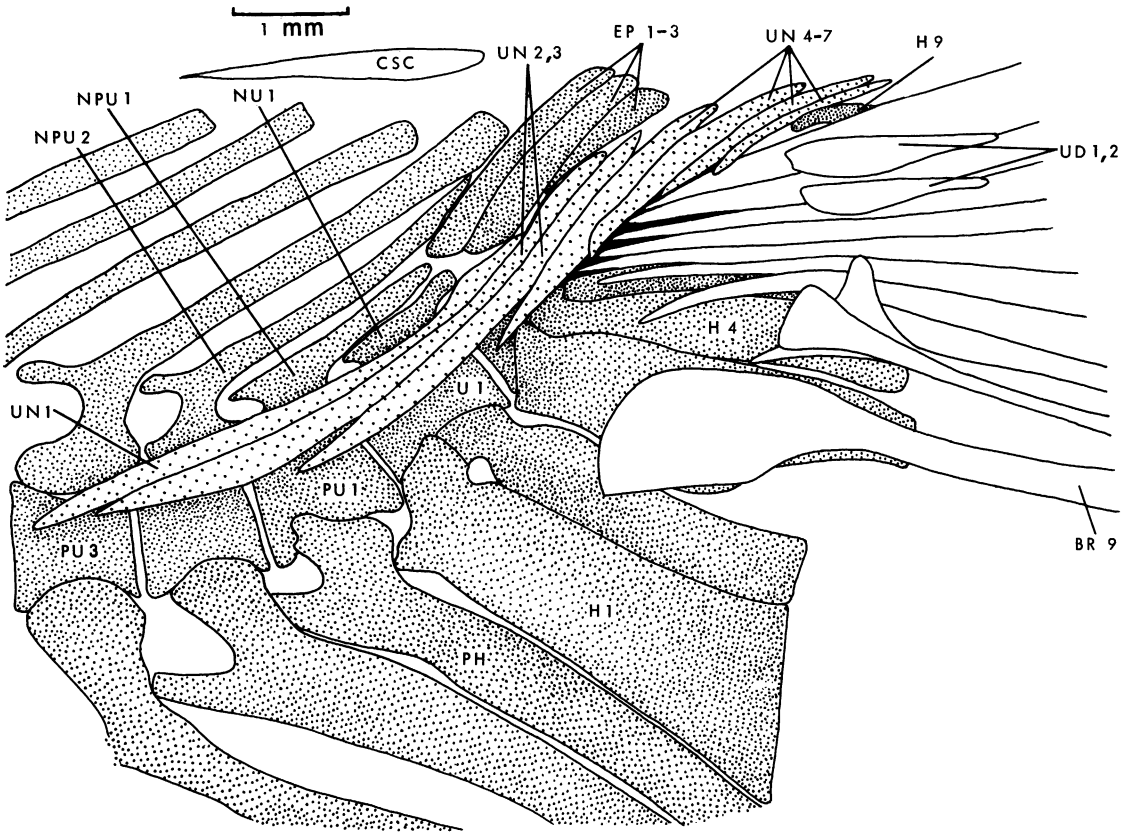


FIG. 53. *Ascalabos voithii* Münster, caudal skeleton as preserved in BMNH 37062 (same specimen as in fig. 52).

plus two rudimentary elements (Nybelin); 4) the posterior neural and hemal spines are crowded, rather than separated by marked interspaces (Nybelin) and bear distinct processes near their bases; 5) the last neural arch is a single rudimentary element over U1, rather than there being two elements in this position (Nybelin), or fusion between the second element and the first uroneural (Taverne); 6) there are nine hypurals, as Taverne says (number not specified by Nybelin); and 7) there are two urodermals, as Taverne says, rather than one (Nybelin). The uroneural series is undifferentiated as in *Pachythrissops* and, indeed, *Ascalabos voithii* stands in the same relation to other teleosts as does *Pachythrissops.* That is, it also shares characters C.21-24 with *Leptolepis coryphaenoides* and more apomorph groups and characters D.33 and 34 (see fig. 48) with *Tharsis dubius* and extant teleosts. As in *Pachythrissops*, the condition of the suborbital is not known. *Pachythrissops* also shares D.31, "no middle pitline groove crossing dermopterotic," but the comparable region in *A. voithii* is not well preserved. In addition, there may be some question about D.33 in *A. voithii* (sculptured autocentra) since the sculpturing, if that is what we have identified, is represented entirely by a lateral ridge on the preural centra (see also Nybelin, 1974, p. 178, Taverne, 1975e, p. 239). Epipleural intermusculars (D.34) are clearly present in our specimens in the region above and just forward of the anal fin insertion (fig. 52), but are said to be absent in Taverne's small specimen. We conclude, therefore, as we did for *Pachythrissops*, that the sister-group of *A. voithii* may be expected to lie somewhere be-

tween ichthyodectiforms and *Tharsis* in our cladogram of teleostean relationships (fig. 54).

Our purpose in commenting on the phylogenetic placement of selected species of "*Anaethalion*," "leptolepids," and *Pachythrissops* is twofold. We would like to demonstrate, on the one hand, that prior taxonomic assignment of many fossil teleosts has been done very casually, and that these unsupported assignments have been made the basis for sometimes extended, and invariably spurious, discussions of early teleostean evolution. Our other purpose in presenting these brief comments is to show that even an *incertae sedis* placement of a fossil, when formulated on some definite anatomical evidence of shared derived characters, constitutes a definite, and supported, taxonomic assignment that can be used with confidence in discussing the evolution of the group or division to which it has explicit affinity.

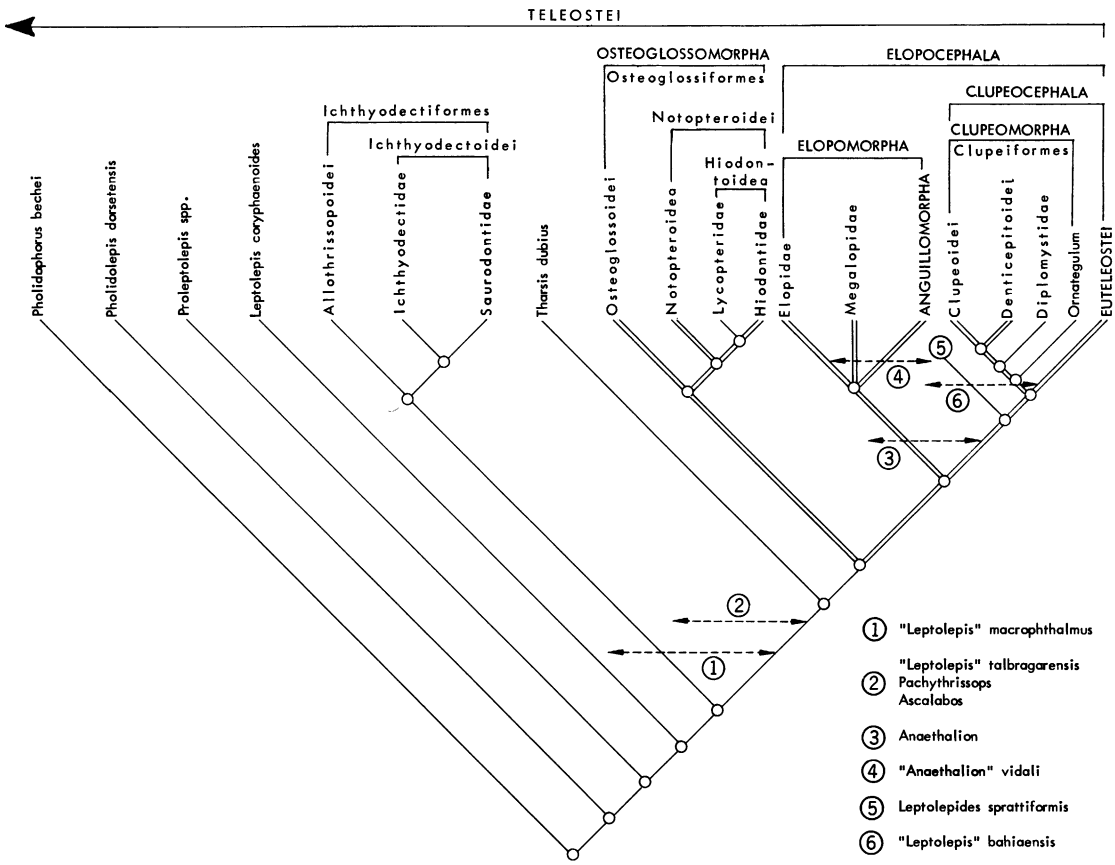


FIG. 54. A theory of relationships of extant teleosts (double lines) and the fossil forms (single lines) dealt with here. Certain groups *incertae sedis* (double-headed, horizontal, dashed arrows) are included to show the limits within which their exact sister-group positions may be expected to occur in the cladogram when new information or better fossils become available; the arrows, therefore, represent precise statements of what is currently known about the relationships of these fossils (see text). Unresolved questions of relationship among extant organisms are represented by polychotomies (e.g., the trichotomy for elopids, megalopids, and anguillomorphs). According to this scheme the Osteoglossomorpha and the Osteoglossiformes are coextensive, as are the Clupeomorpha and the Clupeiformes.

CLASSIFICATION OF FOSSILS IN RELATION TO MESOZOIC AND RECENT TELEOSTS

The theoretical difficulties in classifying fossils with extant organisms that have been pointed out by Hennig (1966, pp. 71, 191), Brundin (1966, p. 21), Crowson (1970, p. 250), and Griffiths (1974), among others, arise from two sources: the impossibility of classifying ancestral species in the same hierarchy as their descendants (since the ancestral species is equivalent to the higher taxon containing its descendants), and the impossibility of ranking ancient fossil species or groups in a Linnaean hierarchy in which absolute age is the ranking criterion (where categories are age classes, in Griffiths's terminology). In our opinion, both these theoretical problems are circumvented by treating fossil species as terminal taxa, i.e., as sister-groups of other taxa. This procedure is no more complicated or novel than regarding all fossil and Recent species as equivalent analytical units with comparable biological properties. It also entails arguments consistent with the ideas that specimen age cannot settle questions about age of the taxa to which fossils are assigned and that specimen age can never falsify theories of relationship based on biological evidence. An ancestral taxon, if it is not to be arbitrary, must be a species, and its identification as ancestral must be preceded by a comparative analysis to determine the nature of its relatedness. No one, for example, would previously have proposed that any "pholidophorid" is ancestral to teleosts if comparative study had not first shown all "pholidophorids" to be halecostomes.

Concerning only the practice of identifying ancestors, as distinct from the theoretical justification for such an undertaking, it is evident, therefore, that looking for ancestors involves a secondary, and negative, concept, i.e., after finding a taxon to have membership in a more inclusive taxon its ancestral status is decided secondarily on the basis of what it does not have. Hence, any species found to be more primitive with respect to all known or analyzable characters than other members of its group is a priori ancestral to the other included members of its group. Even allowing this procedure, with its inevitable consequence, one may ask: What is learned by discovering that a taxon, assigned to a group on the basis of one or more synapomorphies with all members of the group, shares no other apomorphies with any part of the group? The answer manifestly is that the taxon deserves membership in the group and that its relationship to any part of the group is equivalent to its relationship to the whole group, i.e., it is not more closely related to one than to any other member. That is a statement of cladistic relationship which cannot distinguish whether the taxon in question shared a common ancestor with the other members of the group or was ancestral to them. How, then, does one go from such statements to conclusions about ancestry? This question has never been answered, and little wonder, for the fact is, in phylogenetic investigation, we are simply assuming the appropriateness of the *concept* of ancestry and descent (or genealogy) as an axiom for the interpretation of a pattern of character distributions. There is good reason to use this genealogical axiom, because it gives order and direction to comparative biological data and because genetic studies have revealed no other mechanisms for genetic continuity and change (evolution) than that provided by the consequences of ancestry and descent (genealogy). But this axiom does not in turn justify the extrapolation that the patterns formed by character distributions (the empiric data) are themselves direct evidence of genealogy. If we allow such an extrapolation, we are in effect declaring that the patterns are evidence of genealogy because they are most easily understood in terms of the axiom that they have resulted from the genealogical process. We find it hard to believe that many of our colleagues would entertain this tautology as a sufficient basis for their work. If we disallow such an extrapolation, it follows that patterns of

character distribution may be explained tautologically as the results of the genealogical process but cannot provide direct, empirical evidence for a particular ancestor. We conclude, therefore, that the systematics of fossil and recent taxa deals with the analysis of patterns derived from comparative biological investigations, that these patterns assume a phylogenetic meaning only when we interpret them within the framework of a concept of ancestry and descent (genealogy), and that its testable propositions lie entirely in the area of cladistic relatedness.

Løvtrup (1973) raised what, in his view, is a third theoretical difficulty (applying to evolutionary classifications as well as cladistic), the fact that fossils provide too few potential taxonomic characters for adequate testing of hypotheses on their relationships to living organisms. It is certain that no fossil can ever provide so many potential characters as a Recent organism, but there seems no theoretical limit to the number of potential characters offered by a fossil such as a fish skeleton, and Løvtrup's argument seems to us to raise a well-known practical difficulty rather than a theoretical one.

It is evident that as knowledge of the interrelationships of Recent organisms becomes more comprehensive and exact, our hierarchical cladistic classifications of them will become more complex to reflect the new information. Indeed, many new categories have been and are being erected to reflect the great increase in our phylogenetic understanding of fishes, insects, and tetrapods. It also is evident that the older a fossil is the greater the chances that it will represent a plesiomorph sister-group to a Recent assemblage. If we accord equal rank to sister-taxa, even a single paleospecies will have to be accorded a rank equal to its Recent sister-group and the two sister-groups together a still higher inclusive rank. Thus, the addition of fossils to the classificatory system, while according them taxonomic rank on an equal basis with Recent organisms, can only further compound the growing problem of nomenclatorially representing phylogenetic hypotheses. The problem raised particularly by the inclusion of older fossils is that they are likely to engender a procession of higher and higher ranks to express the relationships of increasingly plesiomorph sister-taxa.

These difficulties of or objections to incorporating fossils in the same system as Recent organisms are practical. In short, they stem primarily from the numerous categories of high rank which must be erected for fossils in a ranked sister-group system, and from the frequent changes in that system, including changes in the names and rank of extant taxa, which will result from the discovery or reinvestigation of fossils. Two main solutions or compromises have been proposed to meet these problems.

I. *Fossils should not be classified with Recent organisms.*

Crowson (1970, p. 250), elaborating a suggestion first made by Bigelow (1961; see also Brundin, 1966, p. 21; Tuomikoski, 1967), proposed that we should "abandon the attempt to fit fossils and modern organisms into one and the same system." Crowson suggested that the geological past should be divided into several roughly equal periods of time, and that separate classifications should be written for each of these periods. Crowson's ideas have been quoted with approval by several writers on cladistics, but so far as we are aware they have not yet been tried out in practice. We have experimented with this scheme, attempting to write classifications of Jurassic and Cretaceous teleosts, and we find that these attempts raise more problems than they solve. Adopting Crowson's suggestion of separate classifications for the Neogene, Palaeogene, Upper Cretaceous, Lower Cretaceous, Jurassic, Upper Trias, Lower Trias (and so on), and of upgrading persistent lineages by one category in each successive classificatory system, the main categories in use in fishes might fall out as in the table below (gaps are left in the table in order to allow flexible usage of supra- and infra- categories: the categories do not follow the downgrading with age recommended by Crowson in his table 1, since the categories in use for extant fishes and other vertebrate groups have not yet undergone the demotion necessary to bring them into line with invertebrate groups, which form the basis of Crowson's table).

Recent	Tribe	Family	Order	Cohort	Class
(1) Neogene					
(2) Palaeogene	genus	Tribe	Family	Order	Cohort
(3) U. Cretaceous					
(4) L. Cretaceous		genus	Tribe	Family	Order
(5) Jurassic					
(6) U. Trias			genus	Tribe	Family
(7) L. Trias					
(8) Permian				genus	Tribe

An immediate problem arises with the names to be used for "downgraded" taxa in earlier periods. For example, the extant Clupeomorpha are ranked here (p. 126) as a subcohort, and this contains an empty order, Clupeiformes, with two suborders. Clupeomorphs are represented in the Cretaceous by genera including *Diplomystus* (Upper and Lower Cretaceous, family Diplomystidae of Greenwood, 1968), *Spratticeps* (Lower Cretaceous, Patterson, 1970a) and *Ornategulum* (Upper Cretaceous, Forey, 1973c) which are clupeiforms (or clupeomorphs) unassignable to suborder. In an Upper Cretaceous classification the Clupeomorpha might rank as a superfamily, the Clupeiformes as a family, and since neither clupeiform suborder is yet recognized in the Cretaceous, this category may be omitted. There are then three ways in which a classification of Upper Cretaceous herrings might be written (the figure in parentheses is the notation suggested by Crowson to indicate "organisms of the third pre-Recent time segment"):

(a) superorder (3) Teleostei
  order (3) Elopocephala
    suborder (3) Clupeocephala
      superfamily (3) Clupeomorpha
        family (3) Clupeidae
          genera (3) *Diplomystus*, *Ornategulum*

(b) superorder (3) Teleostei
  order (3) Elopocephaliformes
    suborder (3) Clupeocephaloidei
      superfamily (3) Clupeomorphoidea
        family (3) Clupeiformidae
          genera (3) *Diplomystus, Ornategulum*

(c) superorder (3) Teleostei
  order (3) Elopiformes
    suborder (3) Clupeoidei
      superfamily (3) Clupeoidea
        family (3) Clupeidae
          genera (3) *Diplomystus*, *Ornategulum*

Of these three classifications, we believe that use of the extant group name, as in (a), introduces fewer ambiguities than the addition of the customary terminations for the appropriate categories, as in (b), or the formation of correct names, which have other meanings in the Recent classification, as in (c).

In the Lower Cretaceous, herring classification might be:

suborder (4) Teleostei
  superfamily (4) Elopocephala
    family (4) Clupeocephala
      subfamily (4) Clupeomorpha
        tribe (4) Clupeiformes
          genera (4) *Diplomystus, Spratticeps*

A problem arises here with *Diplomystus*, a "genus" that occurs in the Upper and Lower Cretaceous, and ranges up into the Eocene, and perhaps into the Oligocene and Miocene, according to the literature. Following Crowson's scheme, the Lower Cretaceous species of *Diplomystus* would represent a genus, those of the Upper Cretaceous a tribe, those of the Eocene and Oligocene a subfamily, and those of the Miocene a family. This is not simply a problem of nomenclature.

There is also a problem when extant taxa of relatively low rank are represented in remote geological periods. For example, the Upper Jurassic fish *Lycoptera* is a member of the extant superfamily Hiodontoidea (Greenwood, 1970b), and perhaps of the family Hiodontidae (the only extant family of that superfamily). A classification of Jurassic osteoglossomorphs might read:

superfamily (5) Teleostei
  family (5) Osteoglossomorpha
    subfamily (5) Osteoglossiformes
      tribe (5) Notopteroidei
        subtribe (5) Hiodontoidea
          genus (5) *Lycoptera*

The usual categories of the hierarchy are just sufficient to meet this case, but if it became necessary to communicate the information that *Lycoptera* is a member of the Hiodontidae (which would certainly be the most interesting piece of information about the fish), or if a more sophisticated analysis of the interrelationships of living osteoglossomorphs complicated the taxonomy, further categories would be needed.

As a final example, a partial phylogenetic classification of Jurassic teleosts, incorporating some information from our cladogram (fig. 54) and from Patterson (1973) might take this form:

superfamily (5) Teleostei
- group (5)—unnamed
  - family Pachycormidae
    - *Pachycormus*, *Hypsocormus*, *Sauropsis*, *Euthynotus*, *Saurostomus*, etc.
- group (5)—unnamed
  - subgroup (5)—unnamed
    - family Pleuropholidae
      - *Pleuropholis*, *Parapleuropholis*, *Austropleuropholis*
  - subgroup (5)—unnamed
    - section (5)—unnamed
      - *Pholidophorus bechei*
    - section (5)—unnamed
      - subsection (5)—unnamed
        - *Pholidolepis dorsetensis*
      - subsection (5)—unnamed
        - infrasection (5)—unnamed
          - *Leptolepis coryphaenoides*
        - infrasection (5)—unnamed
          - division (5)—unnamed
            - family Ichthyodectidae
              - subfamily Allothrissopinae *Allothrissops*
              - subfamily Ichthyodectinae *Thrissops*
          - division (5)—unnamed
            - subdivision (5)—unnamed
              - *Tharsis dubius*
            - subdivision (5)—unnamed
              - family (5) Osteoglossomorpha (see above for details)
              - family (5) Elopocephala
                - subfamily (5) Elopomorpha
                - "*Anaethalion*" sp.
                - subfamily (5) Clupeocephala
                - *Leptolepides sprattiformis*
              - Elopocephala *incertae sedis*: (5) *Anaethalion*
          - Teleostei *incertae sedis*: (5) Aspidorhynchidae (2 genera), (5) Pholidophoridae (*ca.* 10 genera), (5) *Galkinia*, (5) *Ligulella*, (5) *Majokia*, (5) *Catervariolus*, (5) *Ichthyokentema*, (5) *Ceramurus*, (5) "*Leptolepis*", (5) *Ascalabos*, (5) *Pachythrissops*, (5) *Mesoclupea*, (5) *Eoprotelops*, (5) *Luisichthys*

The advantages of such a classification compared with a cladistic classification of all teleosts, fossil and Recent, are that the fossils are removed from the Recent classification, increasing the tidiness of the latter (but decreasing its information content), and that in the fossil classification some groups or species, paraphyletic or *incertae sedis* in classifications of later periods, become monophyletic and classifiable in the classification of the period in which they first appear (for example, "*Anaethalion*" sp., *incertae sedis* at the supraordinal level in a classification of all teleosts, is classifiable in a Jurassic classification; the Pholidophoridae, a grade taxon in the Jurassic, is monophyletic and classifiable in a Triassic classification, since the pholidophorids are the most advanced teleosts known to be present in the Triassic). These advantages seem to us minimal. The disadvantages of such a scheme are evident: in order to accommodate those few Jurassic teleosts whose relationships can be reasonably inferred (a small proportion of those that have been named), it is necessary to name and rank 14 groups at seven categorical levels, and these categories must all be inserted between superfamily and family, since those two categories are established by the rank of extant Teleostei and its primary subdivisions. If other genera such as *Pholidophoroides* (Nybelin, 1966) and *Proleptolepis* (fig. 54) were included in the classification, as they could be on available information, four more group names and two categories would be necessary, and the complexity of the scheme will certainly be increased by investigation of the *incertae sedis* forms. These problems can be overcome by the use of a convention, discussed in the next section—a convention that allows the fossils to be classified with Recent organisms.

II. *Fossils should be classified with Recent*

organisms, but should be treated in a different way.

Schemes of this sort have been proposed and discussed by Hennig (1969) and Nelson (1972, 1974), from different points of view.

Hennig's (1969) discussion is worth summarizing, with substitution of teleostean fishes for the entomological example used in the original. He starts from the proposition that a Recent monophyletic group (Teleostei) has been recognized, because of autapomorphous features that are assumed to have been present in the latest common ancestor of that group. Obviously, all these characters did not appear at once, but must have been acquired in sequence during the time-span between the period when the latest common ancestor of the group lived, and the time when the group separated from its sister-group (halecomorphs). Within this theoretical framework, Hennig asks how, in practice, fossils should be ascribed to the group in question.[1] Hennig would propose that the teleosts in the narrow sense of "descendants of the latest common ancestor of all extant teleosts" should be referred to as *Teleostei, and that the name Teleostei should be applied to all those fossils that are more closely related to extant teleosts than to *Amia*. Those members of the Telostei, which are not ascribable to the *Teleostei, Hennig refers to as the stem-group (*Stammgruppe*). He admits that this stem-group concept is in part typological, but adopts it as a compromise which brings practical advantages in investigations of the history of the extant group. He also admits that the concept is unsatisfactory in those groups where the time-span between the origin of the group and the origin of its extant subgroups is long (in teleosts the present estimate of this time-span is from the base of the Trias to the Upper Jurassic), and in which there are numerous stem-group fossils, some of which are known to be more closely related than others to the Recent species of the entire group: that is the case in teleosts. In such circumstances, Hennig suggests that the relationships of the fossils might be expressed by inserting intermediate categories (*Zwischenkategorien*) in the system, but that these should not entail changing the names of Recent groups, and should not be considered in a system that is only concerned with Recent groups.

Nelson (1972, 1974) provided a convention which meets the needs expressed by Hennig. Nelson pointed out that the Linnaean hierarchy has only two resources which might be used to express phylogenetic relationship, subordination (division of one taxon into subtaxa of equal rank) and sequencing (the order in which such subtaxa are listed). In classifications based on theories of common ancestry relationship (not ancestor-descendent relationship), subordination alone is sufficient to produce an efficient classification, where the test of efficiency is whether the theory of relationships is recoverable from

[1] There are three possibilities: (1) Limit the group to those species that can be assumed to be descendants of the latest common ancestor of Recent teleosts. We should then include in the Teleostei only those fossils that show all the synapomorphies of all Recent teleosts. In practice, this would mean including in the system only those forms that can be ascribed to extant subgroups of the Teleostei, since it will hardly ever be possible to demonstrate the presence of all teleostean synapomorphies, even if they are confined to the skeleton, in a particular paleospecies (see examples in Rosen, 1973, pp. 442-451, 455-467).

(2) Ascribe to the teleosts all those fossils which have at least one synapomorphy with all extant teleosts, implying that they are more closely related to teleosts than to *Amia*, the extant sister-group of teleosts. This is the approach adopted by Patterson (1973).

(3) Decide that certain teleostean synapomorphies are "essential" features of the group, and ascribe to the group only those fossils that possess these features, excluding more primitive teleost-like fossils. This is the approach that has previously been adopted, although not usually explicitly (see summary in Patterson, 1967a), and which is explicitly adopted by Patterson (1968, uroneurals and compound first ural centrum as essential features) and Nybelin (1971, supraoccipital bone as essential feature). It is also the approach currently used in many other vertebrate groups (mammals–dentary/squamosal joint as essential feature; birds–feathers as essential feature; reptiles–absence of cranial sensory canals as essential feature). Hennig pointed out, and we agree, that by this approach phylogenetic problems are not solved but set aside, and he therefore rejects it.

Hennig concluded that each of the first two methods is compatible with a phylogenetic system, but that the first has the disadvantage of requiring a name for those teleost-like fossils that do not belong to any Recent teleostean subgroup (e.g., Prototeleostei), and another name (e.g., Teleosteodea) for Teleostei plus Prototeleostei: the same condition will apply to each teleostean subgroup, to the Halecomorphi, to the Halecostomi, and so on, leading to extraordinary complications.

the classification without loss of information. This leaves the other resource of the hierarchy, sequencing, unused, and Nelson suggests that it may be used to incorporate fossils in a classification, with the aim of minimizing changes in the classification (naming or ranking) of Recent groups: this convention seems precisely to meet the need for *Zwischenkategorien* which Hennig proposed.

With such a convention it is necessary to signify (†) fossil groups or species, and to explain that the sequence of such taxa within a higher taxon indicates that each is the sister-group of all those succeeding it. The convention results in giving extinct groups (or species) the same rank as the primary subdivisions of their extant sister-group. This system seems to us to be satisfactory, and we propose to employ it, noting also Hennig's recommendation that such fossil groups or species need not be considered in treatments devoted to Recent organisms alone.

But when we come to apply this convention in practice, another problem arises. Fossils are, of course, named in the way demanded by the "Code"—they are given a trivial name and ascribed to a genus. Many extinct genera have been collected into extinct families and other higher taxa such as Pholidophoridae, Leptolepididae, and so on, and discussion of fossils would hardly be possible without such collective terms. In a phylogenetic classification it becomes clear that many such extinct higher taxa are not demonstrably monophyletic: some appear to be paraphyletic, others to be polyphyletic, whereas some are so poorly characterized that their status is unknown (see Patterson, 1973, p. 298, for an assessment of the status of extinct nominal families of higher actinopterygians). Our investigation of the Leptolepididae *sensu stricto* shows it to be polyphyletic, and our investigation of *Anaethalion* shows that it is certainly paraphyletic, whereas Forey (1973b) suggested that it is polyphyletic. In *Pholidophorus* we know of no grounds for the assertion, implied by the name, that *P. bechei*, for example, is more closely related to the Triassic *P. latiusculus* than it is to *Pholidolepis* or *Elops*, and Nybelin's (1966) figure 16 implies that it is not. With existing material, there seems to be no way of testing Nybelin's tentative conclusion that *P. bechei* is more closely related to teleosts than to *P. latiusculus*, since the latter is so poorly known. If we wish to classify *P. bechei*, as a relatively well-known fish whose relationships can be established with some precision, it is only this species that can be classified, not *P. latiusculus*, which might, for example, be the sister-group of *P. bechei* and all more advanced teleosts. *P. bechei* happens to be the type-species of *Pholidophorus* so that we are justified in taking it to be representative of the genus, whatever the relationships of many other nominal species currently placed in *Pholidophorus* may be (the relationships of many of these will probably never be known). Similarly, *Leptolepis coryphaenoides*, whose relationships we wish to express, is the type-species of the genus, but in classifying it, we do not mean to say anything precise about the remaining nominal species of *Leptolepis*. The fossils whose relationships we wish to express are thus often single "species," abstracted from extinct "genera" of unknown status, and only when the species in question are the type-species of the genera, or when the genera are monotypic, can generic names legitimately be used. The relationships of such species can be expressed in a classification, using Nelson's convention of sequencing. But that convention requires that all sequenced groups or species be given the same rank as the primary subgroup of their extant sister-group, which in Teleostei is supercohort (p. 126). Such a category requires a name, and convention demands that it contain at least the mandatory categories, family and order. A monotypic and named supercohort, order and family for *Pholidophorus bechei* or *Leptolepis coryphaenoides* is not an efficient way to communicate the theory of relationships. That opinion is influenced by our belief that the taxa in question, because of their basis in fragmentary fossils, are particularly vulnerable to realignment and further multiplication of categories when new information is obtained.[1] Where the fossil group

[1] The most extensive application of the alternative approach, ranking and naming each sister-group pair produced by the addition of fossils to the system, is McKenna's (1975) draft classification of mammals. The proliferation of categories caused by the incorporation of relatively few fossil taxa is evident there. In our view, McKenna has yet to confront the most serious problems since he treats Mammalia in the traditional way, excluding the "mammal-like reptiles." This means that McKenna deals only with extant subgroups of mammals

is more extensive and is already furnished with ordinal and family names, like the Ichthyodectiformes, naming of a supercohort might seem less inefficient, but neither is it obviously advantageous.

We therefore propose that fossil groups or species, sequenced in a classification according to the convention that each such group is the (plesiomorph) sister-group of all those, living and fossil, that succeed it, should be called "*plesions.*" Plesions may be inserted anywhere (at any level) in a classification, without altering the rank or name of any other group. They may bear a categorical name representing any conventional rank, from genus and species upward [e.g., plesion *Pholidophorus bechei*, plesion (family) Pachycormidae, plesion (order) Ichthyodectiformes, plesion (class) Acanthodii], these ranks being those already existing in the literature, used only for reference and to avoid ambiguity. In effect, our proposal is that it should no longer be necessary to rank fossils formally, except within extinct monophyletic groups, where self-contained phylogenetic classifications may be built up as among ichthyodectiforms, pp. 115. Plesions need not be included in systematic work dealing only with living organisms: their place is in general classifications, in works concerned with the history or biogeography of particular groups, and in paleontological work.

The final question that arises concerns the status of such "groups" as the Pholidophoridae and Leptolepididae, after the removal of certain species or monotypic genera (*Pholidophorus bechei*, *Tharsis*, etc.) as plesions. The remaining nominal species are, of course, *incertae sedis.* Nelson (1972) has discussed usage of the term *incertae sedis*, and recommended that it be reserved for fossil species and groups of unknown or uncertain relationships, similar uncertainties with Recent groups being expressed in classifications by inclusion of more than two subtaxa in a taxon, and in cladograms by multiple furcations, as with the Elopomorpha in figure 54 and in our classification (p. 163).[1] We think this is a sound proposal, for it emphasizes the real difference between uncertainties arising from deficient theories of relationships (with Recent taxa, where the whole organism is available for study) and from deficient specimens (with fossils, where doubts about relationships are due to lack of anatomical information). A few Recent taxa are *incertae sedis* in the same way as fossils, presumably temporarily (e.g., the fish *Therobromus callorhini* Lucas, based on bones from fur-seal stomachs).

and their fossil relatives (the mammalian equivalent of the area indicated by double lines in our fig. 54), and has not yet encountered the problem of series of fossil taxa which are each the sister-group of the entire Recent assemblage plus one or more fossil species or groups, the situation we have had to tackle.

[1] Our reason for treating the extant subtaxa of the Elopomorpha as an unresolved trichotomy, rather than as a dichotomy (between the Elopomorpha and Anguillomorpha of Nelson, 1973b, or the Megalopidae and the remaining elopomorphs, as in Forey, 1973b, fig. 1), is that in our opinion no derived characters have yet been offered to validate such a dichotomy. Nelson (1973b, p. 346) cited two supposed synapomorphies of Elopidae and Megalopidae, the medial position of the posterior opening of the mandibular sensory canal, and the ramified cephalic sensory canals. We have argued above (p. 101, fig. 32) that the mandibular sensory canal opening does not have this significance, and we do not believe that the bone-enclosed parts of the sensory canals of elopids and megalopids (the only parts comparable with fossils) show any specialization when compared with those of pholidophorids and leptolepids. Forey's scheme of relationships is not based on synapomorphies, but on supposed relative ages of the groups, with *Pachythrissops* included in the Megalopidae, an assignment which we do not uphold (p. 149). The names given to the three elopomorph subtaxa in figure 54 are those in current use, but in our classification we have followed the convention (Nelson, 1972) that Recent monophyletic groups of uncertain sister-group relationships be considered to form part of a polychotomy or series of unresolved dichotomies, and be classified as taxa of equal rank to the other members of the polychotomy. The most conservative solution to the elopomorph trichotomy is to adopt past usages at the ordinal level for the Elopidae (Elopiformes) and Anguilliformes (including the components of Nelson's [1973b] Anguillomorpha, his "albuloids" and "anguilloids," here ranked as suborders), and to make the third monophyletic group, Megalopidae, coordinate with those as the order Megalopiformes (new). Those who are bothered by the creation of this new higher category should reflect that our action is the most conservative available to us that is consistent with the classificatory method we advocate; that the three elopomorph subtaxa and their components were previously ranked on arbitrary or unstated grounds; and that according to the ranking criterion proposed by Hennig (1966, p. 160), age, our classification is consistent with the known minimum ages of the three groups.

Placing a fossil group or species *incertae sedis* within an extant taxon only sets a lower limit on its possible relationships, and in a sequenced classification this level may be well below that currently established (see below). In many cases, we can also place an upper limit on the zone of uncertainty. For example, *Pachythrissops* (p. 149) includes tolerably well-known fishes that must be classed as Teleostei *incertae sedis.* Yet these fishes show a suite of relatively advanced characters which indicate that their relationships lie in the region of ichthyodectiforms, that is, the area of uncertainty is between ichthyodectiforms and *Tharsis dubius* (see fig. 54). In a ranked sister-group system it would be possible to indicate the lower limit of this area quite precisely, by placing *Pachythrissops incertae sedis* in a taxon containing ichthyodectiforms and higher teleosts, but in a sequenced system this is not possible, and it must be placed as Teleostei *incertae sedis.* One anomalous consequence of a sequenced system is therefore that some of the taxa placed as *incertae sedis* are, in the present state of knowledge of their anatomy, interchangeable with plesions: we could exchange *Pachythrissops* for *Tharsis dubius* or "*Leptolepis*" *macrophthalmus* for ichthyodectiforms in our system, for example. We choose to include the Ichthyodectiformes and *Tharsis dubius* as plesions because we have reason to believe that ichthyodectiforms are monophyletic and because the structure of both is well known. Even in a ranked sister-group system, there is no device capable of showing the upper limit of the area of uncertainty about an *incertae sedis* group or species, and this is best done in a cladogram (fig. 54). In our opinion, the one advantage that a cladogram has over a classification is not that the diagram is more precise in expressing relationships (the claim that is usually made), but that it is more precise in expressing uncertainties about relationships.

We have approached the problem of the identification, phylogeny, and classification of certain Mesozoic teleosts by trying to satisfy a number of analytical requirements, and these are set out below:

1. To treat fossil and Recent species as coequal in phylogenetic investigation, i.e., to impose on the study of each the same requirements for gathering and assessing phylogenetic evidence.
2. To attempt phylogenetic placement of only those fossil groups satisfying the cladistic meaning of monophyly, i.e., a group which includes all the descendants of a hypothesized stem species. Often, this requirement means placing in the hierarchy only a single member (species) of a genus or phenetic group, the other members of which are imperfectly known or for which synapomorphies cannot be stated precisely. It also means that when two or more fossil taxa are found to occupy interchangeable positions in a hierarchy or cladogram, only the most complete and well-studied taxon is selected for detailed phylogenetic comparison.
3. To allocate to an *incertae sedis* category fossil taxa that cannot be placed precisely in a hierarchy or cladogram because they do not "use up" one or more synapomorphies in a specified hierarchy of derived character states: that is, their sister-group relationships cannot be guessed without ambiguity. This may be because they are a) imperfectly known, b) interchangeable with other such taxa in the system because of (a), or c) do not satisfy a strict definition of monophyly.

The *incertae sedis* category is applicable at all hierarchical levels that are generated by the study of extant organisms. Thus, in the following classification, we show *incertae sedis* groups at the halecostome hierarchical level, within the category Teleostei, the Elopocephala and among Elopomorpha. The included taxa *incertae sedis* are precisely placed, according to synapomorphies that they share with members of the hierarchical level to which they are assigned. In effect, this precise placement means that the *incertae sedis* category is not merely a catch basket for fossil fragments or incompletely studied whole fossils but is the most parsimonious statement of the phylogenetic position of a taxon that can be made with available information. It is obviously important and desirable for us to know that although "*Anaethalion*" *vidali* can be assigned to the Cohort Elopomorpha, other forms of *Anaethalion* are at present only precisely assignable to the Supercohort Elopocephala. But the latter assignment also means that future investigations into more detailed statements of *Anaethalion* relationships might be most promisingly pursued within or in relation to the elopocephalans. It is therefore evident that a cladogram is able to express the

potential relationships of *incertae sedis* taxa more completely than a formal classification unless the classification were to incorporate a complex analytical notation—an added complication which we judge to be undesirable.

It is evident to us and to those familiar with the controversy between cladal versus gradal schools of phylogenetic reconstruction and classification that the various questions raised above are problems of real concern only to the precise requirements of the cladistic method. Traditional evolutionary classifications, in contrast, are capable of absorbing all manner of grade categories, such as the "Pholidophoridae" and "Leptolepididae," multiple furcations as final statements of relationship, ancestor-descendent relationships (as opposed to sister-group relationships), and nonphyletic measures such as "degrees of adaptational divergence" and "adaptive zones" as valid representations of evolutionary history. Although evolutionary classifications are simpler to construct, because they depend so heavily on authoritative judgments and opinions, little of the informational input is retrievable from the formal hierarchy (Nelson, 1974; Cracraft, 1974; Rosen, 1975; Hennig, 1975). All that cannot be retrieved from the formal cladistic hierarchy as used here are the details of the analytical constraints, or guidelines, for future investigation of *incertae sedis* taxa.

The formal classification setting out the conclusions expressed in figure 54, and our method of incorporating them in a hierarchy, is given below. In order to exemplify that method, the classification is extended to cover the division Halecostomi, using information from Patterson (1973). The boxed part of the classification corresponds with figure 54 and with the groups discussed in the present paper.

SUMMARY

The objectives of this study were to review evidence pertaining to the cladistic relationships of Mesozoic fishes previously grouped as the Ichthyodectiformes, to resolve the relationships of the major groups of extant teleosts and selected Mesozoic teleosts, and to place the ichthyodectiforms within the resulting cladogram of halecostome interrelationships.

The primary purpose of the survey of ichthyodectiform structure was to decide, on the basis of shared derived characters (synapomorphies), whether the group is monophyletic, what subgroups it contains, and what each subgroup comprises. Structural complexes surveyed include all parts of the skeleton, except parts of the gill arches. On the basis of skeletal characters an order Ichthyodectiformes is defined to include the suborder Allothrissopoidei (new) for the forms of *Allothrissops*, the suborder Ichthyodectoidei for the families Ichthyodectidae (*Ichthyodectes*, *Xiphactinus*, *Gillicus*, *Cladocyclus*, *Eubiodectes*, *Proportheus*, *Chirocentrites*, *Thrissops*, *Spathodactylus*), and Saurodontidae (*Saurodon and Saurocephalus*). Most of the nominal species of ichthyodectoid genera are at present defined only on stratigraphic or geographic evidence, or both, and distinctions between some of the genera are equally weak. As a unit, the Ichthyodectiformes are defined by two derived features, an endoskeletal ethmo-palatine bone in the floor of the nasal capsule, and uroneurals that cover the lateral faces of the preural centra. The analysis also supports the exclusion of the Chirocentridae (and by implication, other clupeomorphs) from this Mesozoic assemblage, and reveals no evidence of synapomorphies to unite ichthyodectiforms with osteoglossomorphs or other extant teleostean subgroups. This survey also redescribes *Cladocyclus* from acid-prepared new material.

The discussion of the interrelationships of the major groups of teleosts reviews each of the principal hypotheses advanced by previous workers. Many of these hypotheses are rejected as being based on symplesiomorphies, concepts of overall similarity, or questionable evidence of synapomorphy. In the consideration of the composition and interrelationships of extant teleosts the discovery of a hitherto unrecognized skeletal feature, a synapomorphy of all tailed elopomorphs that permits positive identification of some elopomorph fossils, is reported. It is also concluded that:

1) The evidence is sufficient to infer that

INFRACLASS Neopterygii
DIVISION Ginglymodi
DIVISION Halecostomi
Halecostomi *incertae sedis* †"Semionotidae,"[1] †"Macrosemiidae," †"Oligopleuridae"
plesion †*Dapedium*
SUBDIVISION Halecomorphi
Halecomorphi *incertae sedis* †"Parasemionotidae," †"Caturidae"
ORDER Amiiformes
plesion †*Ospia*
plesion †*Caturus*
plesion †*Liodesmus*
plesion †Sinamiidae
FAMILY Amiidae
SUBDIVISION Teleostei
Teleostei *incertae sedis* †*Catervariolus*, †*Ceramurus*, †*Galkinia*, †*Ligulella*, †*Majokia*, †*Paleolabrus*, †Pleuropholidae, †"Pholidophoridae," †"Leptolepididae," †*Pachythrissops*, †*Ascalabos*, †Crossognathidae
plesion †Pachycormidae
plesion †Aspidorhynchidae
plesion †*Ichthyokentema*
plesion †*Pholidophorus bechei*
plesion †*Pholidolepis dorsetensis*
plesion †*Proleptolepis*
plesion †*Leptolepis coryphaenoides*
plesion †Ichthyodectiformes
SUBORDER †Allothrissopoidei, new
FAMILY †Allothrissopidae, new
SUBORDER †Ichthyodectoidei
FAMILY †Ichthyodectidae
FAMILY †Saurodontidae
plesion †*Tharsis dubius*
SUPERCOHORT Osteoglossomorpha
ORDER Osteoglossiformes
SUBORDER Osteoglossoidei
SUBORDER Notopteroidei
SUPERFAMILY Hiodontoidea
plesion †Lycopteridae
FAMILY Hiodontidae
SUPERFAMILY Notopteroidea
SUPERCOHORT Elopocephala
Elopocephala *incertae sedis* †*Anaethalion*
COHORT Elopomorpha
Elopomorpha *incertae sedis* †"*Anaethalion*" *vidali*
ORDER Elopiformes
ORDER Megalopiformes, new
ORDER Anguilliformes
SUBORDER Albuloidei
SUBORDER Anguilloidei
COHORT Clupeocephala
Clupeocephala *incertae sedis* †"*Leptolepis*" *bahiaensis*
plesion †*Leptolepides sprattiformis*
SUBCOHORT Clupeomorpha
ORDER Clupeiformes
plesion †*Ornategulum*
plesion †Diplomystidae
SUBORDER Denticipitoidei
SUBORDER Clupeoidei
SUBCOHORT Euteleostei

[1] The use of quotation marks signifies either that the taxon is nonmonophyletic, or that the taxon no longer contains its type genus, or both, e.g., "Semionotidae" (nonmonophyletic), "Leptolepididae" (nonmonophyletic and now excluding its type genus by virtue of the exclusion of the type species of *Leptolepis*, *L. coryphaenoides*).

osteoglossomorphs and elopomorphs are definable monophyletic groups.

2) Clupeomorphs and euteleosts form a single monophyletic group (Clupeocephala, new usage) on the basis of two synapomorphies in the lower jaw, the derived fusion of tooth plates with the first three pharyngobranchials and fifth ceratobranchial, and possibly also one feature of the caudal skeleton.

3) Elopomorphs are the sister-group of clupeocephalans on the basis of synapomorphies of the uroneural elements in the caudal skeleton, and osteoglossomorphs are the sister-group of those three on the basis of all those synapomorphies that distinguish living teleosts from *Amia*.

An analysis is presented that combines two of the better known members of the "Pholidophoridae" and three of the better known members of the "Leptolepididae" with extant teleosts into a single theory of relationships. A hierarchy of shared derived features is given, representing the comparative series *Pholidophorus bechei*, *Pholidolepis dorsetensis*, *Proleptolepis* spp., *Leptolepis coryphaenoides*, *Tharsis dubius*, osteoglossomorphs, elopomorphs, clupeomorphs and euteleosteans, involving 48 characters, each of which is a synapomorphy at some point in the sequence. Hence, *Pholidolepis* is shown to differ from *Pholidophorus* and resemble the three "Leptolepididae" and extant teleosts in three synapomorphies;

Proleptolepis to differ from the two "Pholidophoridae" and resemble the other forms in nine synapomorphies;

Leptolepis to differ from *Proleptolepis* and "pholidophorids" and resemble *Tharsis* and extant teleosts in 12 synapomorphies;

Tharsis to differ from the preceding four species and resemble extant teleosts in 11 synapomorphies;

osteoglossomorphs to differ from the paleospecies and resemble other extant teleosts in four synapomorphies;

elopomorphs to differ from osteoglossomorphs and the paleospecies and resemble clupeomorphs and euteleosts in one synapomorphy;

and clupeomorphs and euteleosts to differ from all other members of the series but resemble each other in four, possibly five, shared derived features.

In referring to the cladistic analysis of five paleospecies and four Recent cohorts, it can be seen that ichthyodectiforms possess all the derived features of *Pholidophorus*, *Pholidolepis*, *Proleptolepis*, *Leptolepis coryphaenoides*, and all but three of the 11 features specified for *Tharsis*. Hence, ichthyodectiforms are shown to share eight derived features (of the skull and vertebrae) with *Tharsis* and extant teleosts and are thus identified as the sister-group of *Tharsis* plus extant groups in this particular theory of relationships.

Other Mesozoic teleosts were then compared with the phylogenetic theory that includes ichthyodectiforms, with the following results:

1) Some fossils assigned to the genus *Anaethalion* are members of the group (Elopocephala, new usage) including Elopomorpha, Clupeomorpha, and Euteleostei. On caudal and lower jaw evidence *A. vidali* from the Cretaceous is referable to the Elopomorpha, as are an unnamed Jurassic specimen assigned to *Anaethalion* and possibly also *A. angustissimus* on caudal evidence. *Anaethalion angustus*, *A. knorri*, and *A.* cf. *subovatus* are precisely referable only as Elopocephala *incertae sedis*.

2) *Leptolepis macrophthalmus* is precisely assignable *incertae sedis* to a group including ichthyodectiforms, *Tharsis dubius* and extant teleosts.

3) *Leptolepis talbragarensis* has all the derived features except two that unite *Tharsis dubius* with extant teleosts, and is therefore *incertae sedis* in the group comprising *Tharsis* and extant teleosts.

4) *Leptolepis bahiaensis* is assignable *incertae sedis* to the group including Clupeomorpha and Euteleostei (Clupeocephala, new usage).

5) *Leptolepides sprattiformis* is presently assignable as the sister-group of the Clupeocephala.

6) *Ascalabos voithi* and the forms of *Pachythrissops* may have their sister-group relationships somewhere between ichthyodectiforms and *Tharsis dubius* in our cladogram of teleostean relationships, that is, are *incertae sedis* in a group including *Tharsis dubius* and extant teleosts.

7) The Crossognathidae, a nominal family including *Crossognathus* and *Apsopelix*, are *incertae sedis* in the group containing *Tharsis dubius* and extant teleosts.

It is noted that the various *incertae sedis* placements of fossils, when formulated on some definite anatomical evidence of shared derived characters, constitute definite and supported taxonomic assignments that can be used with confidence in discussions of the evolution of the group or division to which they have explicit affinity. It is also noted that the *incertae sedis* category is applicable at all hierarchical levels recognized in a given classification.

Prior to attempting a formal classification based on the proposed relationships, consideration is given to theoretical difficulties in classifying fossils with extant organisms. Among these difficulties, the chief ones are seen as the impossibility of classifying ancestral species in the same hierarchy as their descendants and of ranking ancient fossil species or groups in a Linnaean hierarchy in which absolute age is the ranking criterion. These theoretical difficulties are circumvented 1) by treating all fossil species as terminal taxa with potential sister-group relationships to other taxa and thereby treating fossil and Recent species as equivalent analytical units; and 2) by recognizing that specimen age can neither settle questions of the absolute age of taxa (species, genus, family, etc.) nor falsify theories of relationship based on biological evidence. It is also remarked that the systematic study of fossil and Recent taxa deals with the analysis of patterns derived from comparative biological investigations, that these patterns assume a phylogenetic meaning only when interpreted within the framework of a concept of ancestry and descent (genealogy), and that the testable propositions of such study, therefore, lie wholly in the area of cladistic relatedness. That conclusion is developed from an argument to show that the identification of particular specimens, species, or higher taxa as ancestors is tautological—a tautology that arises from a failure to distinguish between the study of biological patterns and the interpretive foundation provided by genetics.

A hierarchy that includes fossil and Recent species based on a ranked sister-group system is itself shown to present problems. These problems stem primarily from the numerous categories of high rank that must be erected for fossils in a ranked sister-group system, and from the frequent changes in that system, including changes in the names and ranks of extant taxa, which will result from the discovery or reinvestigation of fossils. Alternatives to this practice are reviewed:

(1) Fossils should not be classified with Recent organisms.

(2) Fossils should be classified with Recent organisms, but should be treated in a different way.

The advantages of (1), above, are that fossils are removed from the Recent classification, increasing the tidiness of the latter (but decreasing its information content), and that in the fossil classification some groups or species, nonmonophyletic or *incertae sedis* in classifications of later periods, become monophyletic and classifiable in the classification of the period in which they first appear. These advantages are considered minimal, especially in view of complex ranking problems that arise if categorical levels are determined, as proposed by advocates of such systems, by absolute age of taxa.

The disadvantages of the above system can be overcome by adopting a convention, as given in (2), above, which treats fossils in a special way in classifications combining fossil and Recent species and groups. This convention recognizes that the Linnaean hierarchy has only two resources that might be used to express phylogenetic relationships, subordination (division of one taxon into subtaxa of equal rank) and sequencing (the order in which such subtaxa are listed). In classifications based on theories of common-ancestry relationship (sister-group relationship as opposed to ancestor-descendent relationship) subordination alone is sufficient to produce an efficient classification (the cladistic relationships are completely recoverable from the classification). The unused resource, sequencing, may thus be employed to include fossils in the hierarchy without necessitating changes in ranking or naming of extant taxa. The sequence of such fossil taxa within a higher taxon based on extant species indicates that each is the sister-group of all those succeeding it in the classification, i.e., its position conforms to the sequence of branches in the cladogram. It is proposed that fossil groups or species, sequenced in a classification according to the convention that each such group is the plesiomorph sister-group of all those, living and fossil, that succeed it, should be called "plesions." Plesions may be inserted any-

where in a classification, without altering the rank or name of any other group. A plesion may also retain a categorical name representing any conventional rank that it bore prior to its inclusion in the classification, both for reference to the literature and to avoid ambiguity. In effect, the proposal is that it should no longer be necessary to rank fossils formally, except within extinct monophyletic groups where self-contained subordinated classifications may be built up (as within the Ichthyodectiformes). The ichthyodectiforms are sequenced, however, as plesion Ichthyodectiformes (rather than order Ichthyodectiformes) preceding plesion *Tharsis dubius* in the hierarchy.

If fossils are sequenced as plesions within named extant groups of specified rank, it is evident that no categorical name can exist to identify a group consisting of an extant taxon and one or more plesions (e.g., plesion *Tharsis dubius* plus extant teleosts). That this poses an inconvenience in discussions of such a group, we acknowledge, requiring use of statements such as: "plesion Ichthyodectiformes, the sister-group of plesion *Tharsis dubius* and extant teleosts," or "plesion *Pholidophorus bechei*, the sister-group of five plesions (which may be specified or not) and extant teleosts." Such inconvenience, however, must be weighed against the bother of having to adjust the level of existing ranks, or of creating categorical levels to intercalate within existing ranks, and of naming each new sister-group pair and empty categories within such taxa, as would be necessary if fossils entered the ranking procedures. The ultimate justification for the compromise and convention proposed here is that fossils have a place only in comprehensive classifications and in detailed analyses concerned with the phylogeny or biogeography of particular groups. Plesions need not be included in classifications dealing only with living organisms or in those being presented to general audiences.

Another convention has also been adopted concerning fossil and Recent species or groups whose cladistic relationships cannot be specified. Fossil groups of uncertain sister-group position in a cladistic hierarchy are inserted in the classification *incertae sedis* at the level of the hierarchy to which they can be assigned on present evidence. Recent monophyletic groups of uncertain sister-group position are considered to form part of a polychotomy (series of unresolved dichotomies), and are included in the classification as taxa of equal rank with the other members of the polychotomy. Such a convention has the advantage of specifying what is currently known about the relationships of a fossil (although a cladogram can express this even more precisely) and of identifying unresolved problems in phylogenetic analysis among extant species or groups.

A formal hierarchical classification of the teleosts is given, incorporating the various theoretical points and conventions that apply to fossils, and this is placed within the perspective of an over-all classification of some of the main groups of neopterygian fishes.

Because the reorganization of fish classification has been proceeding at a rapid pace in the hands of many different persons during the last decade, it seems in order to conclude with a word about our proposed new classification—a proposal that may appear to some researchers and teachers in ichthyology as yet another affront to the traditional view of biological classification as a stable reference system that serves all subdisciplines of biology. The first point to recognize is that most investigators in taxonomy operate with the reasonable assumption that their studies will bring a greater order to taxonomic expressions of phyletic relatedness, even though it may not seem so to those who have become comfortable with the taxonomic scheme being replaced or altered. But the reinvestigation of taxonomic problems is a weeding process that sorts out a few inappropriately placed forms. Sometimes these reinvestigations lead to the realization that the groups being restudied are composed almost entirely of weeds—as would be true of grade groups (polyphyletic groups that simply unite most or all the "primitive" members of a major phyletic unit). For example, the "Leptolepididae" and "Pholidophoridae" may previously have seemed to mean something fairly precise. This is not so. The difference between the Pholidophoridae as listed in standard textbooks, such as Romer (1966) or Lehman (1966), and Pholidophoridae *sensu stricto* as restated by Nybelin (1966) is profound, in content, stratigraphic range and "essence," but the difference could *only* be specified by listing *all* the named taxa (paleospecies) and trying to reach a decision, which would

have to be arbitrary, on which concept each fitted. Diagnoses of such taxa, even apparently comprehensive ones like that provided for the pholidophorids by Nybelin (1966), do not comprise characters of all the included species, but characters drawn from a few selected fossils and assumed to apply to all. As such, they are arbitrary and not subject to criticism. The general usage of these names, as "pholidophorid" or "pholidophoroid" (e.g., Greenwood et al., 1966, fig. 1; Patterson, 1968), is a further abstraction, even more immune to specification and criticism.

Our review of the anatomy of the better known leptolepids and pholidophorids, using the concepts of Hennig's (1966) *Phylogenetic Systematics*, has made it clear to us that the relationships of some of these paleospecies can be specified within a cladistic framework of Recent forms (as sister-groups of cohorts, orders or families of extant teleosts), whereas others are only specifiable at the level of their inclusion in the group as a whole. The question that arises in our minds, therefore, is whether having evidence that one "leptolepid" is a clupeocephalan, another, an elopocephalan, a third, the sister-group of all extant teleosts, a fourth, Teleostei *incertae sedis*, and so on, really represents a loss of order and stability when order and stability have only been lost from a group that cannot be defined precisely, that is demonstrably polyphyletic, that obscures relationship and thereby masks evolutionary sequences. If maintaining such groups as the "Leptolepididae" represents the interests of taxonomic order and stability, then it seems to us a matter of wanting to have order at the cost of testable theories of relationship, and stability at any cost.

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