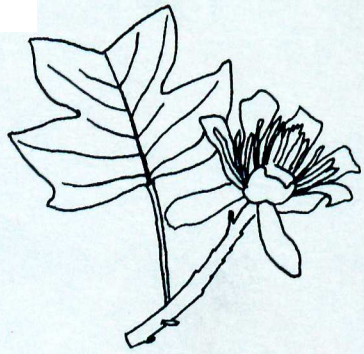
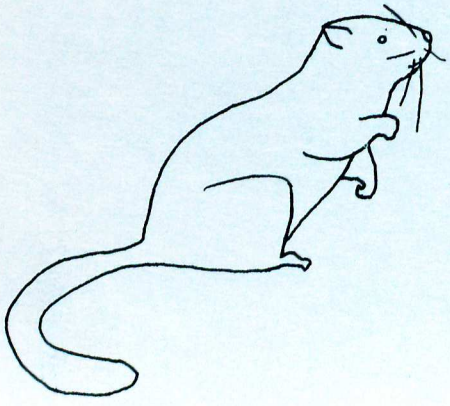
THE COMPARATIVE OSTEOLOGY AND PHYLOGENY OF THE BERYCIFORMES (PISCES: TELEOSTEI)

Steven J. Zehren





EVOLUTIONARY MONOGRAPHS

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THE COMPARATIVE OSTEOLOGY AND PHYLOGENY OF THE BERYCIFORMES (PISCES: TELEOSTEI)

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ABSTRACT

A comparative osteological examination of the living members of the Order Beryciformes is performed in order to determine their phylogenetic relationships. The degree of phylogenetic relationship among taxa is determined by measuring the amount of similarity in derived character states.

26 species (representing 24 genera and 11 families) of beryciforms were cleared and stained for examination. Complete osteological descriptions and numerous illustrations of eight of these species [Polymixia lowei (Family Polymixiidae), Anoplogaster cornuta (Anoplogasteridae), Diretmus argenteus (Diretmidae), Centroberyx affinis (Berycidae), Photoblepharon palpebratus (Anomalopidae), Monocentris japonicus (Monocentridae), Paratrachichthys sp. (Trachichthyidae) and Ostichthys trachypoma (Holocentridae)] are included.

70 characters, representing all parts of the skeleton, are selected for analysis. For each character numerical states are assigned to represent the categories of phenetic expression present in the members of the Beryciformes. In addition to the 26 Recent species examined, the phenotype of numerous fossil beryciforms is taken into consideration when designating character states (the data for the fossils are taken from the literature).

After defining the states present in a character, it is necessary to construct a character state tree showing the sequence of change in states. The method which is used to determine the primitive states of characters (i.e., the states from which the sequences of change began) involves making "out-group" comparisons. The Beryciformes compose the "in-group" while all other teleosts constitute the "out-group". By examining members of the "out-group" both below (more primitive than) and above (more advanced than) the Beryciformes in terms of their level of structural organization, it is usually possible to determine which state represents the primitive beryciform condition. A wide variety of teleosts, including members of the Myctophoidei, Ctenothrissiformes and Pattersonichthyiformes, is selected to represent the "out-group". A detailed analysis reveals that although there is no strong evidence to suggest that any one of the three groups noted above is particularly closely related to the ancestor(s) of the Beryciformes, all three groups lie closer to this ancestry than any of the other members of the "out-group" examined. Emphasis is therefore placed on the character states present in myctophoids, ctenothrissiforms and pattersonichthyiforms when attempting to determine the primitive vs. derived nature of the states present in beryciforms.

For multiple state characters (characters with three or more states), it is also necessary to determine the correct sequence of change in

the derived states. This is done by ordering the states such that the least complex evolutionary pathway is assumed (i.e., the states are ordered in a logical numerical or phenetic sequence after the primitive state is determined).

A computer program, the Combinatorial Method, is used to investigate the phylogenetic relationships of the Beryciformes. The Combinatorial Method utilizes the phylogenetic information contained in the character state trees. It does this by generating a list of all of the nonredundant, monothetic combinations of OTUs (operational taxonomic units). A nonredundant, monothetic combination is the largest combination of OTUs sharing a given set of derived character states. The combinations in the list are ordered according to the number of derived states which their OTUs possess, beginning at the highest level. The degree of phylogenetic relationship among OTUs is considered to be proportional to the number of derived states which they share. Thus, combinations whose OTUs share more derived states are selected in favor of those with fewer states. In those cases where an OTU appears in two different combinations at the same level of shared states, additional criteria are applied in order to choose between the combinations.

By using the Combinatorial Method, a dendrogram showing the phylogenetic relationships within the Beryciformes is constructed. The relationships shown in this dendrogram are discussed in detail. A second dendrogram showing the possible relationships within the Beryciformes is also included. A comparison reveals that although many of the groups present in the two dendrograms are identical, the second dendrogram is a better representation of the phylogenetic relationships of the 26 species examined in terms of 1) the number of groups defined by the presence of unique, derived states and 2) the consistency of the arrangement of the groups with respect to additional morphological data.

Some of the more important systematic conclusions resulting from this study are as follows. 1) With regard to the 26 species examined, it is possible to identify derived character states which are unique to each of the families represented (except the Trachichthyidae) 2) Polymixia should not be included in the Order Beryciformes 3) Anoplogaster is more closely related to "typical beryciforms" (in particular, to trachichthyids, monocentrids and anomalopids) than to stephanoberyciforms (stephanoberycids, gibberichthyids and melamphaeids) 4) Stephanoberyciforms constitute a monophyletic group, but should not be placed in an order separate from the Beryciformes and 5) The Order Beryciformes (even after the removal of Polymixia) may not constitute a monophyletic group.

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CHAPTER I

INTRODUCTION

Objective and Nature of Investigation

The objective of this investigation is to determine the evolutionary relationships among the living members of the Order Beryciformes, a group of marine teleostean fishes, on the basis of the comparative anatomy of the skeletal system.

There are, of course, numerous aspects of the evolution of any group of organisms: relative and absolute times of origin of various lineages in the geological record, rates of evolution, morphological trends, degrees of environmental adaptation in different lineages, etc. This investigation is primarily concerned with only one aspect of the evolution of the Beryciformes: determination of the relative recency of common ancestry among the species examined. In this investigation, relative recency of common ancestry is determined by measuring the amount of morphological similarity in derived (specialized) character states.

General Remarks Concerning the Order Beryciformes, with an Introduction to Each of the Families

In a recent classification of the teleostean fishes [that of Greenwood et al. (1966)], the Order Beryciformes was divided into three suborders (Stephanoberycoidei, Polymixioidei, Berycoidei) and twelve families (Stephanoberycidae, Melamphaeidae, Gibberichthyidae, Polymixiidae, Diretmidae, Trachichthyidae, Korsogasteridae, Anoplogasteridae, Berycidae, Monocentridae, Anomalopidae, Holocentridae) (fossil taxa were not included in this classification). The total number of species (excluding fossils) contained in the order is about 141 (table 9).

The Order Beryciformes is well-represented in the geological record. Patterson (1964, 1967, 1968), Gaudant (1969) and Radovčić (1975a) have described approximately 52 species of beryciforms from the Mesozoic. According to Patterson (1964), the earliest known members of the order appeared at the base of the Upper Cretaceous (Cenomanian).

Taxonomically, the Order Beryciformes is placed in the Superorder Acanthopterygii because its members possess spines in the paired and/or unpaired fins. Beryciforms are generally considered to represent the basal stock from which many of the more advanced acanthopterygians, such as the very large and diverse order, the Perciformes, have evolved (e.g., Jordan, 1905; Patterson, 1964; Greenwood et al., 1966; Gosline, 1968; McAllister, 1968). There are three main features in which the Perciformes are more advanced than their beryciform relatives. These are: (1) absence of the orbitosphenoid in

the neurocranium (2) reduction of the number of soft pelvic rays to five and (3) reduction of the number of principal caudal rays to 17 (Patterson, 1964, p. 466) (a few exceptions do occur, however--the orbitosphenoid is absent in the beryciform families Gibberichthyidae, Melamphaeidae and Stephanoberycidae, and the pelvic fins in the Gibberichthyidae and Monocentridae contain five or fewer soft rays). According to Patterson (1964, p. 472), the functional or adaptive significance of these three features is unknown.

In the following introduction to the families of beryciform fishes, the taxonomic content, horizontal and vertical distribution, and prominent morphological characteristics of each are noted. Information pertaining to habits and behavior, food, development and growth, and economic importance is also provided when possible.

The Family Trachichthyidae [figs. 66-69 (appendix III, p. 367)] contains five genera (Gephyroberyx, Hoplostethus, Paratrachichthys, Trachichthys, Optivus) and 26-28 species (table 9). Trachichthyids range from 31°S-45°N in the western Atlantic, from 40°S - 53°N in the eastern Atlantic, and from about 33°S - 7°N in the eastern Pacific (Menezes, 1971, p. 143; Woods and Sonoda, 1973, p. 299). Species also occur in the Mediterranean, Indian Ocean and western Pacific (Japan, Philippines, Tasmania, New Zealand) (Woods and Sonoda, 1973, p. 299). Trachichthyids are predominantly a deep-water group, although Paratrachichthys argyrophanus may occur at a depth of only 115 meters (Woods and Sonoda, 1973, p. 327).

The body of trachichthyids is deep and compressed (except in Paratrachichthys and Optivus, where it is more elongate). The head bears a series of deep mucous cavities for the lateral line. The mouth is large and oblique. Unlike many other beryciforms, trachichthyids typically bear a large spine at the angle of the preopercle.

Within the Trachichthyidae, luminescence is known to occur in some species of Paratrachichthys and in Hoplostethus metallicus (Woods and Sonoda, 1973, p. 267). In Paratrachichthys argyrophanus there are shiny, striated areas on the sides of the isthmus, on the bases of the pectoral fins, and along the lower sides of the body (see Woods and Sonoda, 1973, p. 326, figs. 29-30). The functional significance of the striated light organs was not discussed by Woods and Sonoda.

Trachichthyids apparently feed primarily on fish and crustaceans. Thus, Woods and Sonoda (1973) report the presence of small shrimp and gonostomatid fish in the stomachs of Gephyroberyx darwini, small fish in Paratrachichthys argyrophanus, small crustaceans in Hoplostethus mediterraneus and H. occidentalis, and iniomid fish in H. atlanticus.

The Family Monocentridae (pinecone fishes, figs. 70-71) includes only two genera (Monocentris, Cleidopus) and three or four species (table 9). Monocentrids are found in the waters off South Africa, Japan and Australia, as well as in the southeastern Pacific (Woods and Sonoda, 1973, p. 281). In addition, Kropach (1975, p. 194) reported the capture of a live specimen of Moncentris japonicus in the Red Sea. Although Herald (1961, p. 158) stated that M. japonicus lives on the bottom in deep water, the specimen from the Red Sea mentioned above was taken at a depth of only three m (Kropach, 1975, p. 194). M. reedi may also occur in shallow water (25-35 feet deep) (Woods, personal communication). Cleidopus gloriae-maris occurs on the east and west coasts of Australia in benthic habitats from 5 to 150 m (Paxton, 1973, p. 521).

Monocentrids are perhaps the most bizarre of all beryciforms in terms of external morphology. The popular name, pinecone fish, is indeed very apt,

for the body is covered with large, heavy, plate-like scales. The spinous portion of the dorsal fin in monocentrids is highly modified. When fully erected, the spines project strongly in opposite directions (not in the sagittal plane as in other fishes). The pelvic fin is also unusual in that it contains an enormous spine and only two or three rudimentary soft rays. A distinct groove in the armor covering the lower portion of the body receives the pelvic spine when the fin is not extended. As in trachichthyids and anomalopids, pinecone fishes possess luminous organs. These are located on or between the lower jaws, and produce phosphorescence by means of the activity of symbiotic phosphorescent bacteria (Herald, 1961, p. 158; Woods and Sonoda, 1973, p. 267).

Monocentris japonicus is a schooling species which may attain a length of 127 mm (Herald, 1961, p. 158). When alive, it is bright yellow with black patches that cover most of the body and eye (Kropach, 1975, p. 194). In southern Japan, M. japonicus is eaten with vinegar--either fried, roasted, or in soya bean soup (Herald, 1961, p. 158). Both M. japonicus (Kropach, 1975, p. 194) and Cleidopus gloriae-maris (Paxton, 1973, p. 521) are nocturnal. The adults of C. gloriae-maris feed primarily on prawns (Paxton, 1973, p. 521).

The Family Anomalopidae (lantern-eye fishes, figs. 72-73) consists of three genera (Anomalops, Photoblepharon, Kryptophaneron) and four species (table 9). Anomalops katopteron and Photoblepharon palpebratus occur in the Indo-West Pacific (Rosenblatt and Montgomery, 1976, p. 510). A subspecies of P. palpebratus has also recently been described from the Red Sea (Abe and Haneda, 1973). Kryptophaneron alfredi is known from only one specimen, found floating on the surface of the sea off Kingston Harbor, Jamaica (Silvester and Fowler, 1926, p. 247). This specimen is presumed to have been destroyed (Woods and Sonoda, 1973, p. 329). It was, therefore, of great interest when another specimen of Kryptophaneron was captured on May 18, 1972, in the southern portion of the Gulf of California. This specimen was found to represent a new species of Kryptophaneron (K. harveyi) and has been described by Rosenblatt and Montgomery (1976).

Rosenblatt and Montgomery (1976, pp. 512-513) have presented evidence which suggests that both species of Kryptophaneron, like those of Anomalops and Photoblepharon, live on high relief bottom, but in considerably deeper water. A habitat of this sort is unworkable with nets and almost inaccessible to conventional scuba divers because of depth, and could, therefore, account for the absence of Kryptophaneron from collections. Furthermore, although the trawl in which K. harveyi was captured was pulled across rather level bottom at 32-36 meters, the track lay near a steep drop-off, and approached the head of a submarine canyon. Certain species taken along with K. harveyi are suggestive of the proximity of rocky substrate. These circumstances suggest that the individual of K. harveyi strayed from a rocky habitat out (and perhaps up) onto the level-bottom area where it was captured.

Most anomalopids are small fishes, the largest species being Anomalops katopteron, which may reach a length of 305 mm (Herald, 1961, p. 158). Anomalopids are characterized by the possession of a slender to moderately deep body, an oblique mouth, a blunt snout (especially in Anomalops and Photoblepharon), fleshy tubercles on the posterior border of the orbit (single tubercle in Kryptophaneron and Photoblepharon, eight or nine in Anomalops), and small, rough scales (Woods and Sonoda, 1973, p. 328; Rosenblatt and Montgomery, 1976, p. 510 and p. 513). Kryptophaneron resembles

Photoblepharon in that the lateral line scales are enlarged and conspicuous, but agrees with Anomalops in the presence of a distinct spinous dorsal fin (Rosenblatt and Montgomery, 1976, p. 513).

The most prominent feature of anomalopids is the presence of a well-developed subocular light organ. According to Harvey (1952, p. 524), the light organ retains its ability to light for a long time after removal, so that the natives of the Banda Islands are able to make use of it as bait when fishing at night. The light organ is composed of a series of tubes containing luminous bacteria, and the structural mechanism for controlling the pattern of light emission is different in each of the three genera (Harvey, 1925; Herald, 1961, p. 158; Rosenblatt and Montgomery, 1976, p. 514). In Anomalops there is a muscular attachment which allows the light organ to be rotated into a black pocket. In Photoblepharon the light organ is occluded by a dark, movable membrane, which is drawn up over the gland. In Kryptophaneron the organ is rotatable, but a membrane is also present (although not as well-developed as in Photoblepharon).

Rosenblatt and Montgomery (1976, p. 514) have attempted to explain the differences in the mechanisms for controlling light emission in terms of habitat and behavior. They suggest that anomalopids are derived from a deep-water ancestor, and that the light organ originated in this twilight zone habitat. Kryptophaneron, with both mechanisms of light control (the primitive condition according to Rosenblatt and Montgomery), has remained in or near the ancestral habitat, while the lineages leading to Photoblepharon and Anomalops invaded shallow water. However, Photoblepharon retained the ancestral habit of staying near the substrate (shelter), whereas Anomalops became a nocturnal, pelagic planktivore. Photoblepharon relied on the shutter mechanism, which allowed enlargement of the light organ. The shutter in Photoblepharon is used to produce rapid blinks. The frequency of blinking is irregular, and may be evoked by social interactions or as a startle response. When frightened, Photoblepharon occludes the light organ briefly and makes a quick dart to shelter. Anomalops, on the other hand, has relied on the rotational mechanism, which allows the organ to be occluded for a relatively long period. Since Anomalops feeds in clear water, near the surface, and away from the obstructions of a reef, a predator would be able to see the light organ and begin its rush from a considerable distance. A rapid blink and a short dash would be ineffectual in this instance, since the predator would only be required to make a small course correction when the light came back on. Rosenblatt and Montgomery suggest that the relatively long period of occlusion of the light organ in Anomalops, in addition to the fact that all members of the school are blinking, provides an effective mechanism for lessening the opportunity of a predator to fixate visually on a single individual.

Ichthyologists may soon learn more about the biology of this interesting group of fishes, for Mr. David Fridman (personal communication) is making observations on live specimens of Photoblepharon palpebratus steinitzi (the new subspecies from the Red Sea), both in the field and in aquaria. According to Fridman, P. p. steinitzi uses its light organ to attract prey, which consist of copepods and small fish larvae.

The Family Melamphaeidae (bigscale fishes, figs. 74-77) contains five genera (Melamphaes, Sio, Scopelogadus, Scopeloberyx, Poromitra) and 31 or 32 species (table 9). Although the family is mainly circumtropical, at least one representative of each genus is partly or wholly temperate (or occasionally even higher) (Ebeling and Weed, 1973, p. 422). Adult and half grown

melamphaeids are usually bathypelagic below 100-200 m, but larvae and young may occur in more shallow water (Ebeling and Weed, 1973, p. 422).

Melamphaeids are small fishes (usually 40-130 mm) and are generally blackish or dark brown in color (Ebeling, 1962, p. 14 and p. 93). Although small, melamphaeids are apparently actively swimming predators (Cohen, 1973, p. 461). Important morphological features present in this group include the following (Ebeling, 1962, pp. 11-13): (1) rather streamlined body which is blunted anteriorly by the head (2) cranium compressed and with a greatly restricted interorbital space, which, in all species except Poromitra megalops, is correlated with the presence of relatively small eyes (3) cleft of mouth moderately wide and oblique (4) circumorbital bones very wide (completely covering the cheek) and deeply channeled (5) presence of moderate to very large cycloid scales, which appear to be frequently lost and replaced (6) vestigial lateral line (7) sensory-canal system of the head very well-developed, the canals covered only by head epidermis which is stretched between paper-thin bony partitions (8) head epidermis decorated with narrow embossed dashes and lines which resemble parallel folds, and which are presumably sensory in function and (9) presence of two light-colored patches, possibly of luminous tissue, beneath the gill cover.

Ebeling (1962) has studied the systematics and zoogeography of Melamphaes. He divided the 19 species of this genus into six species groups, one of which (the M. simus group) contains only "dwarf species." Whereas the adults in all of the other species groups are usually 40-130 mm, the dwarf individuals in the M. simus group are less than 25-28 mm in standard length (Ebeling, 1962, p. 93). Ebeling (1962, p. 145) found that whereas the four dwarf species of the M. simus group usually inhabit central waters of low food supply, most of the species that contain large individuals occur in the productive Subarctic, transitional, Indonesian, and eastern equatorial waters, all of which contain a larger supply of food (possibly comprising larger items). Another melamphaeid genus, Scopeloberyx, also contains species with large and small (dwarf) adults (Ebeling and Weed, 1973, p. 445). In general, however, there is no clear-cut segregation of dwarf species into central water masses of low organic productivity and of "giants" into highly productive peripheral water masses, like that shown for Melamphaes (Ebeling and Weed, 1973, p. 445).

Ebeling (1962, p. 151) believes that speciation within the Melamphaeidae probably occurs across physico-biologically defined water-mass boundaries which filter through mutants preadapted to new environmental regimens. Subsequent competition with contiguous populations of closely related forms would reinforce the initial partial isolation of the new population, therefore accelerating its evolutionary divergence (Ebeling, 1962, p. 151). Ebeling (1962, p. 151) suggests, for example, that in the Pacific, the Equatorial Counter Current and Equatorial Undercurrent may have repeatedly transported such preadapted waifs eastward to the highly productive Eastern Pacific Equatorial water mass, where, isolated from their western relatives, they evolved into the endemic melamphaeid fauna of the eastern tropical Pacific.

The Family Gibberichthyidae (gibberfishes, fig. 78) is represented by only two species: Gibberichthys pumilus from the western Atlantic, and G. latifrons from the Indian Ocean and the western and southwestern parts of the Pacific Ocean (de Sylva and Eschmeyer, 1977). While it appears that the depth range of adult G. pumilus is roughly 300-1000 m, one adult of G. latifrons was collected at a depth of only 58 m (de Sylva and Eschmeyer, 1977, pp. 228-229). The prejuveniles of G. pumilus are epipelagic, although

there is some evidence to suggest that they migrate to a lower level during daylight hours (de Sylva and Eschmeyer, 1977, p. 228). De Sylva and Eschmeyer (1977, p. 227) report that the largest specimen of G. latifrons is 124 mm SL, while the largest specimen of G. pumilus which they measured was 91.5 mm SL.

Gibberichthys possesses two very unusual features: 1) preceding the soft portion of the dorsal and anal fin is a series of short (but strong) spines, all but the last of which are firmly fused to the underlying radial elements and 2) the lateral line consists of a wide band of vertical rows of papillae (six to eight in a column) along the sides of the body (Ebeling and Weed, 1973, pp. 412-413). A number of investigators have noted that the lateral line in Rondeletia (Order Cetunculi--the whalefishes) is similar to that of Gibberichthys, and suggested that these two forms may be related (e.g., Herald, 1961, p. 159; Rosen, 1973, p. 492; Ebeling and Weed, 1973, p. 399).

In 1965, Robins and de Sylva described a new species of fish, Kasidoron edom, representing a new family, the Kasidoroidae. De Sylva and Eschmeyer (1977, pp. 219-226) later showed, however, that K. edom actually represents the prejuvenile stage of Gibberichthys pumilus.

The prejuveniles of G. pumilus [K. edom] possess a number of interesting features, including: (1) development on the third ray of the pelvic fin of a spectacular arborescence (the "pelvic tree") whose terminal hollow sacs may possess a luminous substance (see Robins and de Sylva, 1965, p. 191, fig. 1) (2) absence of spines in the fins (3) body scaleless (except for a few cycloid scales along the lateral line), the skin being provided, instead, with numerous small papillae which lend a velvety texture to the fish (4) presence of only a single row of very fine teeth in both jaws (5) enormously developed eyes and (6) absence of ridges and spines on the top of the head (Robins and de Sylva, 1965, pp. 189-195). These features are not present in the adults of G. pumilus (personal observation). Other ontogenetic changes which occur in G. pumilus are discussed by de Sylva and Eschmeyer (1977), who provide an excellent series of illustrations of developmental stages ranging from small prejuveniles (7.5 mm SL) to large adults (82 mm SL) [note: de Sylva and Eschmeyer (1977, p. 221, fig. 7, and p. 228, fig. 16) also include illustrations of the osteology of an 87 mm SL specimen]. Among the changes noted by de Sylva and Eschmeyer are the shift in the position of the maxilla to accommodate a posterior displacement of the angle of the preopercle and opercle, and the growth of the circumorbital bones so that the maxilla becomes partially sheathed.

Fortunately, one of the prejuveniles of G. pumilus described by Robins and de Sylva (1965) was kept alive for a short time in an aquarium while photographs and a short motion picture sequence were taken. These observations enabled Robins and de Sylva to speculate on the functional significance of the "pelvic tree". Its use as a lure to attract food seems impossible, since it trailed below and behind the animal during swimming (Robins and de Sylva, 1965, p. 199). Rather, the authors suggest that the function of the "pelvic tree" is one of camouflage, and that the fish is imitating a siphonophore or perhaps some other coelenterate, thus gaining predator immunity (Robins and de Sylva, 1965, p. 199).

Young gibberfishes also appear to be poor swimmers. Robins and de Sylva (1965, p. 199) state that even though the animal swam rather strongly when placed in the aquarium, a great deal of effort appeared to be required to accomplish small movements. Swimming was accomplished by rapid lateral movements of the pectoral and caudal fins and the caudal peduncle (Robins and

de Sylva, 1965, p. 199). The posterior rays of the dorsal and anal fins appeared to be used only to a small extent, if at all; these fins seemed to be more important as keels (Robins and de Sylva, 1965, p. 199).

Based on an examination of the stomach contents of 13 specimens, de Sylva and Eschmeyer (1977, p. 229) found that the adults of G. pumilus feed primarily on the amphipod Cyphocaris johnsoni (some species of copepods were also found, however). De Sylva and Eschmeyer (1977, pp. 229-230) noted that since previous work has shown that this amphipod is scarce in the total plankton mass above 3000 m, and because other plankters in the stomachs were few, G. pumilus is probably selective in its food.

The Family Stephanoberycidae (pricklefishes, fig. 79) contains three genera (Stephanoberyx, Acanthochaenus, Malacosarcus), each with a single species (table 9). Stephanoberycids occur in the western tropical Atlantic (including the Caribbean Sea and the Gulf of Mexico), the western tropical Indian Ocean, and the western tropical Pacific (Ebeling and Weed, 1973, p. 415). All three species are bathypelagic or abyssal benthic (Ebeling and Weed, 1973, p. 415).

The pricklefishes receive their name from the fact that, in two of the genera, Stephanoberyx and Acanthochaenus, the body is covered with small, firmly fixed, ctenoid scales, which bear from one to six large, sharp, outwardly projecting spines at their centers or posterior fields (Ebeling and Weed, 1973, p. 415). The rare genus Malacosarcus (as far as known, only four specimens, all in very poor condition, have been collected) differs radically from the other two genera in its squamation (Ebeling and Weed, 1973, pp. 415-416). The body scales of Malacosarcus are moderate in size, irregular, unsculptured, extremely thin, and deciduous (Günther, 1887, p. 30). Although the spines in the dorsal and anal fins of stephanoberycids are only feebly developed (or, in some cases, absent), there is a long series (8-11) of procurrent spines in front of the upper and lower lobes of the caudal fin (Ebeling and Weed, 1973, pp. 415-417). As in many other beryciforms, stephanoberycids possess a series of well-developed sensory head canals (Ebeling and Weed, 1973, p. 415).

The largest specimen of Malacosarcus examined by Ebeling and Weed (1973, p. 416) was 45 mm. The largest specimen of Stephanoberyx measured was 94 mm (two specimens, 81 mm in length, were reported to be sexually mature) (Ebeling and Weed, 1973, pp. 418-419). The largest Acanthochaenus examined was 131 mm (one specimen, 118 mm, was reported to be sexually mature) (Ebeling and Weed, 1973, pp. 420-421).

The Family Berycidae (alfonsinos, figs. 80-81) contains only two genera (Beryx, Centroberyx) and six species (table 9). Berycids are found from Newfoundland to Cuba and the Gulf of Mexico in the western Atlantic, from Iceland to the Cape of Good Hope in the eastern Atlantic, from the Natal coast of South Africa and from southern and western Australia in the Indian Ocean, and from Japan, New Zealand and Hawaii in the Pacific Ocean (Woods and Sonoda, 1973, p. 281). Berycids live in deep water [Beryx splendens is usually found at depths of 548-732 m (Herald, 1961, p. 158)].

Distinctive features of this family include an ovate and compressed body, a deeply forked caudal fin with pointed lobes, a large and obliquely oriented mouth, large eyes, and the presence of small, adherent, shield-shaped scales (Woods and Sonoda, 1973, p. 281). The pelvic fin may contain up to 13 rays (many more than in other beryciforms), in addition to the well-developed spine. Beryx splendens is bright red in color and reaches a length

of about 610 mm (Herald, 1961, p. 158).

Beryx is considered an excellent food fish in Japan and Madeira, where considerable numbers are taken on long lines (Herald, 1961, p. 158; Woods and Sonoda, 1973, p. 285). Although no information on the type of food eaten by berycids is provided, Woods and Sonoda (1973, p. 289) report that a 27 mm specimen of Beryx splendens was taken from the stomach of Alepisaurus ferox.

The Family Holocentridae (squirrelfishes or soldierfishes, figs. 82-86) comprises seven genera (Myripristis, Ostichthys, Plectrypops, Corniger, Holocentrus, Adioryx, Flammeo) and 58-59 species (table 9). Holocentrids have a world-wide distribution in tropical marine waters (Herald, 1961, p. 157). Although many squirrelfishes live in association with coral reefs, some species are found in rocky areas (Woods and Sonoda, 1973, p. 332). Most holocentrids are shallow water inhabitants. However, some species, such as those of the genus Ostichthys, live in much deeper water [Woods and Sonoda (1973, p. 332) report that O. trachypoma may occur at depths up to 503 m].

Holocentrids are characterized by the presence of well-developed spinous dorsal fins, sharp scales and large, squirrel-like eyes. The anal fin contains four spines, the third of which is enlarged. The body tends to be elongate, the sides are compressed, and the caudal peduncle is slender (Woods and Sonoda, 1973, p. 331). The mucous cavities on the head are only moderately developed, and the mouth is nearly horizontal (Woods and Sonoda, 1973, p. 331). In many species, the swim bladder is well-developed and makes an intimate connection with the auditory bulla of the skull (Nelson, 1955). Squirrelfishes are often brightly colored, usually some shade of red (Herald, 1961, p. 157). The largest species in the family is Adioryx spinifer, which reaches a length of about 610 mm (Woods, personal communication).

Holocentrids are nocturnal, hiding in the cracks and crevices of reefs during the day, but coming out at night to forage (Herald, 1961, p. 157). Woods and Sonoda (1973) report that Holocentrus rufus feeds on small gastropods and crustaceans, Adioryx vexillarius on crawling or sessile bottom-dwellers, and A. coruscus on small shrimps and crabs.

A number of species of squirrelfish, including Holocentrus ascensionis (Moulton, 1958), H. rufus (Gainer et al., 1965) and H. xantherythrus [= Adioryx xantherythrus] (Herald, 1961, p. 157), are capable of producing sounds. Herald (1961, p. 157) reports that a series of faint intermittent sounds was produced by a pair of A. xantherythrus while engaged in courting activity. The pair held their tails close together with the forward parts of the body apart, so that a V or Y was formed between them (Herald, 1961, p. 157).

Squirrelfishes have larvae which are very peculiar in appearance (see Greenfield, 1966, p. 9, fig. 2). The snout is long and pointed, and the head bears several spines which probably serve as flotation devices (Greenfield, 1966, p. 7). Instead of remaining near the bottom, larval squirrelfishes become a part of the floating plankton and are apt to be swept for many miles by surface currents (Herald, 1961, p. 157). These larvae are of some importance as forage fishes for offshore tuna (Herald, 1961, p. 157; Woods and Sonoda, 1973, p. 344). When holocentrids transform from the pelagic larval stage to the sedentary adult stage, they lose their head spines and change their body colors (Woods and Sonoda, 1973, p. 267). In Plectrypops retrospinis this transformation occurs when the fish is about

40 mm SL (Woods and Sonoda, 1973, p. 385).

Economically, Myripristis contains the most important species of the Family Holocentridae (Herald, 1961, p. 157). In Hawaiian fish markets, fishes of this genus are known as "menpachi" and command a premium price (Herald, 1961, p. 157). Woods and Sonoda (1973, p. 344) report that Holocentrus rufus and H. ascensionis are also sold in markets for local use throughout the Caribbean area. Plectrypops retrospinis (the cardinal squirrelfish) is not known to be used as food because of its relatively small size and scarcity, but its bright red color makes it a desirable species for the aquarium (Woods and Sonoda, 1973, p. 385).

The Family Diretmidae (spinyfins, fig. 87) comprises one genus (Diretmus) and two or three species (table 9). In the Atlantic, Diretmus ranges from Nova Scotia south to the Gulf of Mexico and the southern Caribbean Sea, and from Iceland south to the Gulf of Guinea (Woods and Sonoda, 1973, pp. 290-291). It is also found in both the Atlantic and Indian Oceans off South Africa, and in the Arabian Sea (Woods and Sonoda, 1973, p. 291). In the Pacific, Diretmus is found from the coast of Oregon to the Marquesas Islands, as well as from northern Japan, the Philippines, New Zealand and southeastern Australia (Woods and Sonoda, 1973, p. 291). The bathymetric range is 229-2195 m for Diretmus argenteus and 293-732 m for D. pauciradiatus (Woods and Sonoda, 1973, p. 295 and p. 298).

The body of small specimens of Diretmus (up to 100 mm) is compressed, thin, and nearly round, whereas in larger individuals it becomes heavier and more elongate (Woods and Sonoda, 1973, p. 290). The bones of the head are ornamented with thin, delicate ridges. The mouth is very oblique. The eyes are enormous (the interorbital area of the skull is, therefore, very narrow). The dorsal and anal fins (which are rather long) lack spines, although the lateral edges of the anterior rays are distinctly serrated (hence the popular name, spinyfins). A series of ventral ridge scales (scutes) is present both before and behind the anal opening. The body scales are small and shield-shaped, as in the Berycidae (Woods and Sonoda, 1973, p. 281 and p. 290). In contrast to other beryciforms, the lateral line is absent in adult diretmids. Specimens of Diretmus argenteus may reach 370 mm SL (Barnard and von Bonde, 1944, p. 237). The largest specimen of D. pauciradiatus measured by Woods and Sonoda (1973, p. 298) was 124.5 mm SL.

The larvae of D. argenteus have been briefly described and figured by Parr (1933, p. 8). Parr noted that the well-developed cephalic and preopercular spines of larval Diretmus are very similar to those of young Anoplogaster. The spines of Diretmus larvae are pelagic adaptations and are lost with maturity (adult diretmids are evidently benthic) (Woods and Sonoda, 1973, p. 267).

The Family Anoplogasteridae (fangtooth or ogrefish, fig. 88) contains only one species, Anoplogaster cornuta (table 9). Anoplogaster occurs in the Atlantic and Pacific Oceans from 45° 56' N to 46° 56' S, and in the Indian Ocean from the equator to 22°S (Woods and Sonoda, 1973, p. 387). The bathymetric range is from 45 to 3084 m for the young and from 900 to 4900 m for the adults (Grey, 1955, p. 296).

The young of Anoplogaster (Anoplogaster stage, up to 88 mm SL) differ strikingly from the adults (Caulolepis stage, 83-160 mm SL) (Grey, 1955, pp. 293-296; Woods and Sonoda, 1973, pp. 389-392). This accounts for the fact that young and adult Anoplogaster were placed in separate genera (Anoplogaster and Caulolepis) by early investigators. The most important

differences between juveniles and adults are as follows (Grey, 1955, pp. 293-294; see also p. 295, fig. 53). (1) The body is triangular in cross section in very young specimens but becomes evenly compressed with growth. (2) The long cephalic and preopercular spines typical of young examples become short and stubby in adults. (3) In the young, there is a single row of small uniform teeth in both jaws. As growth proceeds, a few slightly larger teeth appear until, eventually, the characteristic fangs develop. At first appearance, these fangs are depressible, but they become firmly fixed in full adults. Most of the small teeth disappear in time, but a few may persist in adult specimens. (4) Young Anoplogaster are silvery in color while the adults are uniformly blackish brown.

Other distinctive features of Anoplogaster (common to both young and adults) include the presence of a large, oblique mouth, and the absence of spines in the dorsal, anal and pelvic fins. The head is large in all specimens although Parr (1933, p. 12, fig. 4) has shown that the relative size of the head decreases as the absolute length of the individual increases.

The scales of Anoplogaster are of a peculiar structure. They are in the form of very thin plates which lie embedded in the skin. Each scale bears a short pedicel and a thin cup. The lateral line is an open groove whose floor is bridged at regular intervals by two scales which have fused together (Woods and Sonoda, 1973, p. 390, fig. 64).

The stomachs of juvenile specimens of Anoplogaster are generally greatly extended by quantities of larval crustaceans (Woods and Sonoda, 1973, p. 392). Juveniles are also an important source of food for other fishes, for they are often found in the stomachs of several species of tuna, albacore, marlin, Alepisaurus and Aphanopus (Woods and Sonoda, 1973, p. 392).

The Family Polymixiidae (barbudos or beardfishes, fig. 89) contains only a single genus, Polymixia, with five species (table 9). In the western Atlantic, Polymixia is found off New Jersey, in the Gulf of Mexico and in the Caribbean Sea, while in the eastern Atlantic, it ranges from Madeira to St. Helena (Woods and Sonoda, 1973, p. 269). Polymixia also occurs in the Indian Ocean and in the Pacific Ocean off Japan and Hawaii (Woods and Sonoda, 1973, p. 269). Polymixia usually lives in depths between 183 and 366 m (Herald, 1961, p. 158).

Polymixia possesses a number of distinctive features, the most peculiar of which is the presence of a pair of barbels ("whiskers") beneath the chin (hence, the name beardfishes). These fleshy barbels are supported by modified branchiostegal rays of the hyoid arch. The snout of Polymixia is blunt, rounded and adipose. The mouth is nearly horizontal and the lower jaw is shorter than the upper. The V-shaped caudal fin has a black margin (Herald, 1961, p. 158) and contains only 18 principal rays (nearly all other beryciforms have 19 principal rays). Polymixia nobilis appears to grow larger than the other species, reaching 280 mm SL (Woods and Sonoda, 1973, p. 269).

Polymixia lowei feeds on crustaceans and small fish, for the remains of these organisms have been removed from the stomachs (which are thick-walled and muscular) of several specimens (Woods and Sonoda, 1973, pp. 278-279). Although Herald (1961, p. 158) reports that the flesh of Polymixia is nonedible, Woods and Sonoda (1973, p. 273) state that P. nobilis is commonly found in the fish markets of Madeira.

An Historical Review of the Systematic Work on the Beryciform Fishes

In the following review of the systematic work on the beryciform fishes, attention is focused on only a few of the many problems which exist. Several terms are used in the discussion which must be clarified at this point The term beryciform fishes (or beryciforms) is employed rather freely, and, with respect to the particular classification under discussion,[1] refers to all of the fishes included in that classification. The term staphanoberyciform refers only to fishes belonging to the families Stephanoberycidae (Stephanoberyx, Acanthochaenus, Malacosarcus), Gibberichthyidae (Gibberichthys) and Melamphaeidae (Poromitra,[2] Melamphaes,[3] Sio, Scopeloberyx, Scopelogadus). Finally, the term "typical beryciform" refers to all of the fishes included in the classification under discussion except the stephanoberyciforms and the families Rondeletiidae, Barbourisiidae, Cetomimidae (the three families of whalefishes), Mirapinnidae, Eutaeniophoridae and Megalomycteridae.

The particular problems in beryciform systematics which are emphasized in the following discussion are: (1) the relationship of Polymixia (Family Polymixiidae) to the other beryciform fishes [i.e., whether Polymixia is included within or excluded from the Order Beryciformes (or its equivalent)] (2) the relationship of Anoplogaster [= Caulolepis (Woods and Sonoda, 1973, p. 387)] (Family Anoplogasteridae) to the other beryciform fishes [i.e., whether Anoplogaster is included with some (or all) of the stephanoberyciforms in a separate group, or whether it is associated with the more "typical beryciforms"] and (3) the relationship of the stephanoberyciforms to the "typical beryciforms" [i.e., whether some (or all) of the stephanoberyciforms (with or without Anoplogaster) are placed in a separate order (termed the Stephanoberyciformes or Xenoberyces), or whether they are included with the "typical beryciforms" in the Order Beryciformes (or its equivalent)].

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[1] The classification of the beryciform fishes (down to the generic level when possible) which is presented by each of the authors cited in the following discussion [except Regan (1912), Parr (1929, 1933), Nelson (1955), Patterson (1967, 1968), Gaudant (1969, 1973) and Radovčić (1975a)] is included in table 1. None of the authors mentioned above presents a formal classification of the beryciform fishes. Neither do Starks (1904) or Rosen (1973). However, in the latter two cases, the composition and/or relationships of the beryciform fishes are expressed rather clearly by the authors. For the sake of completeness, I have, therefore, made an attempt to express the systematic conclusions of Starks (1904) and Rosen (1973) in the form of taxonomic classifications.

[2] Poromitra (= Lophocephalus, Poromitrella) (Ebeling and Weed, 1973, p. 432).

[3] Melamphaes (= Plectromus, Metopias) (Ebeling and Weed, 1973, p. 451).

Cuvier (1829) divided the "ordinary fishes" (all fishes except cyclostomes, chondrichthyans and sturgeons) into two large orders, the Malacopterygians and the Acanthopterygians, on the basis of the presence or absence of fin spines. Several of the genera (Holocentrum, Myripristis, Beryx, Trachichthys and Monocentris) which were to be assigned to the Order Beryciformes (or its equivalent) by later workers were placed by Cuvier in the acanthopterygian families Percoides and Joues Cuirassées (armored cheek). Cuvier's Percoides included, in addition to the first four genera listed above, many forms which are usually placed in the Suborder Percoidei (Order Perciformes) by recent workers. Monocentris was assigned to the Joues Cuirassées, a family containing many species belonging to the Family Triglidae (Order Scorpaeniformes) of recent investigators. In his classification, Cuvier noted several of the most important features for each of these "beryciform" genera.

Lowe (1843) established the Family Berycidae to contain all of the beryciform genera of Cuvier (1829). A new form, Polymixia, was also included. In his characterization of the Berycidae, Lowe (1843, p. 47) noted the presence of an "anormal number of ... rays in the ventral [pelvic] fins." Numerous authors have followed Lowe by including this feature in their characterization of the beryciform fishes. Lowe described the superficial morphology of Beryx splendens and Trachichthys pretiosus [= Hoplostethus mediterraneus (Woods and Sonoda, 1973, p. 318)] in some detail. Lowe also described (more briefly) the visceral anatomy of these two species.

Günther (1859) followed Lowe (1843) in recognizing only a single family (Berycidae) for the beryciform fishes. In addition to Lowe's genera, three new forms (one of which was Anoplogaster) were included. Günther provided a list of the superficial morphological features for the Family Berycidae (one feature being the presence of usually more than five soft rays in the pelvic fin) and for each of the contained genera.

Gill (1872) assigned the beryciform fishes to three separate families--the Polymixiidae, Monocentridae and Berycidae. Gill recognized the distinctness of the Family Polymixiidae (Polymixia), for it was placed in a separate superfamily, the Polymixoidea. The Monocentridae and Berycidae were assigned to the Superfamily Berycoidea, which was placed directly after the Polymixoidea. The genera included in the latter two families were not listed by Gill.

Goode and Bean (1895), in their treatise on the deep-sea and pelagic fishes of the world, associated a number of new genera (some representing new families) with the beryciform fishes of previous investigators. Polymixia and Diretmus (a genus included in the Beryciformes by many later workers) were placed in separate families, both of which were widely separated from the others (six families intervene between the Diretmidae and the Anomalopidae; twenty-three between the Polymixiidae and the Anomalopidae). Anoplogaster (Subfamily Anoplogastrinae) was grouped with both "typical beryciforms" [i.e., Beryx (Subfamily Berycinae)] and stephanoberyciforms [i.e., Melamphaes, etc. (Subfamily Melamphainae)] in a single family, the Berycidae. Although most of the stephanoberyciform genera recognized by Goode and Bean were grouped together in a single taxon (the Subfamily Melamphainae), one form, Stephanoberyx, was excluded. Stephanoberyx was placed in its own family, the Stephanoberycidae.

Jordan and Evermann (1896), in their study of the fishes of North and Middle America, presented a classification which was very similar to that of Goode and Bean (1895). There are, however, two noteworthy differences. First, the various beryciform families were united in a single taxon, the

Group Berycoidei [Goode and Bean (1895) did not recognize any taxonomic categories between the ordinal and familial levels, so that the various beryciform families (except the Diretmidae and Polymixiidae) were associated only in the sense that they were listed consecutively]. Second, the Polymixiidae (as well as another family, the Mullidae) was closely associated with the other beryciform families (i.e., the Polymixiidae and Mullidae were included in the Group Berycoidei).[1] Like many other workers, Jordan and Evermann characterized their Group Berycoidei by the retention of archaic features, such as presence of a duct connecting the swim bladder with the gut and the presence of an increased number of pelvic fin rays.

In the classification of Boulenger (1904), most of the beryciform genera recognized by previous workers (including Polymixia, Anoplogaster and a number of stephanoberyciforms) were grouped together in the Family Berycidae (like other workers, Boulenger stressed the presence of primitive features when characterizing this group). Although Boulenger did not use the category of Superfamily in his classification, the families Berycidae, Monocentridae and Pempheridae [a family whose members show a striking resemblance to Beryx (Berycidae) according to Boulenger (1904, p. 656)] were placed consecutively at the base of the Division Perciformes of the Suborder Acanthopterygii. While several stephanoberyciform genera were placed in the Family Berycidae, as noted above, Stephanoberyx and Malacosarcus were far removed, being placed in the Family Stephanoberycidae of the Suborder Haplomi (a total of four suborders, containing 31 families, separates the Haplomi and the Acanthopterygii in Boulenger's classification). Finally, it should be noted that Boulenger's classification differed from previous ones in that fossil taxa were included.

Starks (1904) was the first to undertake a detailed anatomical investigation of the beryciform fishes (termed the Berycoidea by Starks). He described the osteology (except the caudal skeleton) of six species, representing five different families [Hoplostethus japonicus (Trachichthyidae), Beryx splendens (Berycidae), Holocentrus ascensionis and Myripristis occidentalis (Holocentridae), Polymixia japonica (Polymixiidae) and Monocentris japonicus (Monocentridae)]. Starks, like previous investigators, was impressed with the primitive features shared by the members of these five families. Thus, he states that "[t]hese families are held together by some very constant characters, the most important of which, aside from the increased number of ventral rays, is the presence of well-developed orbitosphenoids. When such diverse families as these possess so important a character, seconded as it is by several minor ones, it seems justifiable to base a group upon it" (Starks, 1904, p. 601). Starks also presented evidence for the removal of several families [including the Mullidae of Jordan and Evermann (1896) and the Pempheridae of Boulenger (1904)] from the Berycoidea.

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[1]It should be noted, however, that Jordan and Evermann (1896, p. 834) stated that the pertinence of the Polymixiidae and Mullidae to the Group Berycoidei was questionable. The Mullidae was associated with the Polymixiidae because the members of both families possess a reduced number of branchiostegal rays and a pair of long barbels beneath the throat (Jordan and Evermann, 1896, p. 855). The Polymixiidae was, in turn, linked to the other beryciform families by the presence of a large number of pelvic rays and the structure of the fins (Jordan and Evermann, 1896, p. 854).

Phylogenetic relationships among the beryciform species examined were not discussed by Starks.

Regan (1911) divided the beryciform fishes of earlier investigators into two orders--the Berycomorphi and the Xenoberyces. Polymixia and three fossil genera were placed in the Polymixiidae, which, along with seven other families, constituted the Order Berycomorphi. Anoplogaster was united with several stephanoberyciform genera in the Family Melamphaidae. The Stephanoberycidae, containing the remaining stephanoberyciform genera, was closely associated with the Melamphaidae (these two families constituted the Order Xenoberyces). Thus, Regan was the first to group all of the stephanoberyciform genera into a single taxon which was exclusive of all other beryciforms (except Anoplogaster). Although Regan (1911, p. 8) noted a number of features in which the Xenoberyces differ from the Berycomorphi (toothless palate, absence of a subocular shelf, triangular shape of the single supramaxilla, absence of an orbitosphenoid), he believed that the Xenoberyces were probably derived from the same stock as the Berycomorphi because of the similarity in the structure of the protractile mouth and caudal fin.

In 1912, Regan added another family, the Caristiidae, to his Order Berycomorphi. According to Regan (1912, pp. 637-638), the Caristiidae (containing Caristius japonicus and the possibly conspecific Platyberyx opalescens) is most closely related to the Diretmidae, although a number of morphological differences between the two families was noted.

Jordan (1923) presented a classification[1] which was very similar to that of Regan (1911). Like Regan, Jordan divided the beryciform fishes into two orders, the Berycoidei and the Xenoberyces; the former contained 12 families (including the Polymixiidae and Caristiidae), while the latter comprised only two [the Stephanoberycidae and Melamphaidae (including Anoplogaster)]. The stephanoberyciform genus Acanthochaenus was included (in the Family Stephanoberycidae) for the first time. Although Jordan did not discuss phylogenetic relationships in any detail, he noted that the Family Melamphaidae was a small group of deep-sea fishes which was "not altogether homogeneous" (Jordan, 1923, p. 172). While there is, unfortunately, no way to be certain as to why Jordan considered the Melamphaidae to be somewhat heterogeneous, his inclusion of Anoplogaster in this family may have been partially responsible. A final point worth noting is that the Family Ctenothrissidae, a group believed by many later investigators to be close to the ancestry of the beryciform fishes, was placed within the Order Berycoidei by Jordan.

Parr (1929) was the first to suggest a relationship between some of the whalefishes (families Cetomimidae, Barbourisiidae and Rondeletiidae) and the beryciform fishes. He described and figured the osteology of Cetomimus regani (Cetomimidae) and Rondeletia bicolor[2] (Rondeletiidae). Parr placed

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[1] Jordan (1923, p. 79) states that no effort was made to distinguish between valid names, preoccupied names and synonyms in his classification.

[2] Parr (1929) also illustrated and briefly described the viscera of Rondeletia bicolor.

the Cetomimidae in the Order Iniomi, but concluded that Rondeletia was "a typical representative of the order Xenoberyces" as defined by Regan (1911) (Parr, 1929, p. 38). Parr felt, however, that the justification of separating the Xenoberyces from the Berycomorphi was rather doubtful. Thus, he states that in "addition to the points of resemblance [between the Xenoberyces and Berycomorphi] already mentioned by Regan one may . . . also call attention to such a great number of other osteological characters in which Rondeletia shows a perfect concordance with the true Berycomorphi, that the justification of maintaining two entirely separate orders seems rather problematical" (Parr, 1929, pp. 38-39).

In 1933, in his paper on the deep-sea beryciform and perciform fishes from the waters around the Bahama and Bermuda Islands, Parr no longer recognized the Xenoberyces of Regan (1911) and Jordan (1923) as a distinct order. Furthermore, Regan's (1911) Family Melamphaidae was split into the Melamphaidae sensu stricto, embracing Melamphaes, Plectromus and Scopelogadus, and the Caulolepidae, embracing Caulolepis and Anoplogaster [recall (p. 16) that Caulolepis is a synonym of Anoplogaster]. In contrast to Regan, Parr believed that Anoplogaster was closely related to the more "typical beryciforms" (in particular, to the families Diretmidae and Trachichthyidae). Parr also described three new species of beryciforms--Gibberichthys pumilus, Korsogaster nanus and Melamphaes opisthopterus. The lack of resemblance between Gibberichthys pumilus and other beryciforms induced Parr to recognize a new family for this species (the Gibberichthyidae). Korsogaster nanus was placed with the genus Leiogaster in another new family, the Korsogasteridae. Parr (1933, p. 4) stated that the Korsogasteridae is apparently nearly related to the Trachichthyidae, but that its members do not possess the keeled abdominal scales characteristic of the latter family.

Berg (1940) followed Regan (1911) and Jordan (1923) by dividing the beryciform fishes into two orders, the Stephanoberyciformes and the Beryciformes. The Polymixiidae (Polymixia), Caulolepidae (Anoplogaster), Gibberichthyidae (Gibberichthys) and Melamphaidae (Melamphaes) were placed, along with 11 other families, in the Order Beryciformes. Since Berg did not recognize any taxonomic categories between the ordinal and familial levels, the relationships between the families of the Beryciformes are unclear. However, Berg evidently felt that Anoplogaster was more closely related to the "typical beryciforms" than to any of the stephanoberyciforms, since the Caulolepidae was separated from the Gibberichthyidae and Melamphaidae (which were placed next to one another) by five other families. Berg's other order, the Stephanoberyciformes, comprised only two families--the Stephanoberycidae and the monotypic Rondeletiidae.

An important work on beryciform systematics was J. R. Norman's paper entitled "A draft synopsis of the orders, families and genera of Recent fishes and fish-like vertebrates." This paper, which reviewed the literature up to 1938, and, as far as it was available to the author, from 1939-1944, was unfortunately never published. Norman provided keys for all of the suborders, families and genera which were recognized. Synonomies were also included. In Norman's classification, the beryciform fishes were once again united into a single group, the Order Berycomorphi. Two suborders, the Berycoidea and the Anoplogasteroidea, were recognized. The Berycoidea contained eight families, including the Polymixiidae (Polymixia). Anoplogaster (Anoplogasteridae) was grouped with the stephanoberyciforms (Stephanoberycidae and Melamphaidae) and Rondeletia (Rondeletiidae)

in the Suborder Anoplogasteroidea (note: Gibberichthys was not placed in a separate family, but was included in the Stephanoberycidae).

Nelson (1955) contributed to the understanding of the systematics of the Family Holocentridae (squirrelfishes) in his study on the morphology of the swim bladder and auditory bulla. Nelson presented evidence that the Holocentridae is composed of two distinct subfamilies: the Myripristinae, in which the swim bladder is in direct relationship with the auditory bulla, and the Holocentrinae, in which no connection is present (except in Holocentrus ascensionis and H. rufus, where a secondary connection, different from that present in the Myripristinae, has been effected) (Nelson, 1955, p. 126).

Lamber (1963) presented a classification of the beryciform fishes based on the comparative morphology of the otoliths (sagittae). In addition to a number of Recent species, Lamber examined many fossil beryciforms (primarily Tertiary), a large proportion of which represented new genera. Lamber, like Regan (1911), Jordan (1923) and Berg (1940), divided the beryciform fishes into two orders--the Beryciformes and the Stephanoberyciformes. The Beryciformes contained eight families arranged in three groups (A, B and C). Group A contained the Berycidae and Diretmidae while Group B contained the Trachichthyidae, Monocentridae and Anomalopidae. The subfamilies Myripristinae and Holocentrinae of Nelson (1955) were elevated to families which, along with a third family (designated as Family A, and containing but a single new genus from the Lower Cretaceous), constituted Group C. The Anoplogasteridae (Anoplogaster) was placed with the families Stephanoberycidae, Melamphaidae and Gibberichthyidae in the Order Stephanoberyciformes (it should be noted, however, that Lamber was uncertain as to the inclusion of the Gibberichthyidae in this order). In contrast to all previous investigators [with the possible exception of Goode and Bean (1895), who placed Polymixia in a family far removed from the other beryciform fishes--see p. 17], Lamber did not include Polymixia in either of his two orders.

Patterson (1964), in a distinguished monograph entitled "A review of Mesozoic acanthopterygian fishes, with special reference to those of the English chalk," described the osteology (except the caudal skeleton) of all the known genera of Cretaceous beryciforms. The osteology of the species belonging to the Order Ctenothrissiformes (extinct) was also described, and evidence was presented that this group lies close to the ancestry of at least some of the beryciform fishes. Like many earlier investigators, Patterson split the beryciform fishes into two orders, the Beryciformes and the Stephanoberyciformes [note: although Patterson (1964) did not present a formal classification of the Stephanoberyciformes, it is clear from his statements on page 473 that he considered this group to contain at least the families Stephanoberycidae and Melamphaidae]. Patterson followed Regan (1911) in his definition of the Order Beryciformes [Regan's definition included a number of primitive features, such as the presence of an orbitosphenoid and (typically) 19 principal caudal fin rays]. Three suborders were recognized within the Order Beryciformes--the Polymixioidei, Dinopterygoidei and Berycoidei. The Polymixioidei comprised two families, the Polymixiidae (including the Recent Polymixia and four fossil genera) and the Sphenocephalidae (containing one fossil genus, Sphenocephalus). The Dinopterygoidei contained four extinct families, each of which was represented by a single genus. The Berycoidei contained 11 families

(including the stephanoberyciform family Gibberichthyidae), all with living representatives.[1] According to Patterson, the only families of the Suborder Berycoidei which are present in the Mesozoic are the Trachichthyidae and Holocentridae. Each of the three suborders and all of the families with fossil representatives were defined osteologically. Patterson also noted similarities between certain Cretaceous beryciforms (polymixioids and dinopterygoids) and various groups of the Order Perciformes, and suggested that the Perciformes arose polyphyletically from the Beryciformes.

In the classification of Greenwood et al. (1966), the beryciform fishes were again united into a single group, the Order Beryciformes. The Stephanoberycidae, Melamphaeidae and Gibberichthyidae were grouped together into one suborder, the Stephanoberycoidei. The Polymixiidae constituted a second suborder, the Polymixioidei. The Anoplogasteridae was placed along with the more "typical beryciform" families in a third suborder, the Berycoidei. Greenwood et al. did not include exclusively fossil groups in their formal classification [thus, the Family Sphenocephalidae and the Suborder Dinopterygoidei of Patterson (1964) were omitted, even though the authors considered both of these groups as belonging to the Order Beryciformes (Greenwood et al., 1966, p. 390)].

In 1967, Patterson described three new genera of Cretaceous berycoids from Lebanon. He demonstrated that one of these genera, Lissoberyx, is a very primitive trachichthyid which possesses a mosaic of trachichthyid and holocentrid features, and suggested that these two families evolved from a common ancestor similar to Lissoberyx. Patterson (1967, p. 104) also stated that the Trachichthyidae "seem to be the stem group of a number of bathypelagic (Melamphaeidae, Stephanoberycidae, Gibberichthyidae, Korsogasteridae, Berycidae, Anoplogasteridae, Diretmidae) and neritic (Monocentridae, Anomalopidae) families," but he did not provide any evidence for these relationships.

The caudal skeletons of Cretaceous beryciforms were described and figured by Patterson in 1968. The evidence obtained in this investigation led Patterson to conclude that most of the beryciform-perciform lineages which he proposed in 1964 were incorrect, and that members of the Berycoidei, not the Dinopterygoidei or Polymixioidei, most closely approach the Perciformes with respect to the morphology of the caudal skeleton.

McAllister (1968) divided the Order Beryciformes into four suborders--the Polymixioidei, Dinopterygoidei, Berycoidei and Stephanoberycoidei. The Polymixioidei and Dinopterygoidei were identical in composition to the similarly named groups of Patterson (1964). The Anoplogasteridae (Anoplogaster) was included with nine families of "typical beryciforms" in the Berycoidei. The Stephanoberycoidei contained all three of the stephanoberyciform families, although McAllister (1968, pp. 101-102) noted that the inclusion of the Gibberichthyidae was questionable. McAllister (1968, p. 102) felt that there was good evidence, however, that the Melamphaeidae and Stephanoberycidae belong in the Order Beryciformes (this evidence involved similarities in the branchiostegal rays and hyoid arch).

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[1] Patterson (1964) did not list the Recent genera contained in each of the families of the Berycoidei. It is not clear, therefore, whether Patterson considered Anoplogaster to belong to one of the 11 families of the Berycoidei (a separate family, Anoplogasteridae, was not recognized), to the Order Stephanoberyciformes, or to neither.

Rosen and Patterson (1969) made several important changes in the classifications of Patterson (1964), Greenwood et al. (1966) and McAllister (1968). Thus, although the suborders Stephanoberycoidei and Berycoidei of Greenwood et al. (1966), and the Suborder Stephanoberycoidei of McAllister (1968), remained unchanged and were included in the Order Beryciformes by Rosen and Patterson, the Suborder Dinopterygoidei of Patterson (1964) and McAllister (1968), and the Suborder Polymixioidei of Patterson (1964), Greenwood et al. (1966) and McAllister (1968), were removed. With respect to the Dinopterygoidei, two of the families (the Aipichthyidae and Pharmacichthyidae) were placed in the Order Lampridiformes (the opah and ribbonfishes), while the other two (the Dinopterygidae and Pycnosteroididae) were assigned to a new order, the Polymixiiformes. In addition to the Dinopterygidae and Pycnosteroididae, the Polymixiiformes included all of Patterson's (1964) and McAllister's (1968) Polymixioidei except the Sphenocephalidae. Thus constituted, the Order Polymixiiformes was then far removed from the Order Beryciformes, being placed in a separate superorder, the Paracanthopterygii. The Sphenocephalidae was also removed to the Paracanthopterygii, but was placed in a different group than the Polymixiiformes.

Although certain groups previously associated with the beryciform fishes were removed by Rosen and Patterson (1969), the concept of the Order Beryciformes was expanded by their inclusion of all three of the whalefish families--the Cetomimidae, Barbourisiidae and Rondeletiidae [up to this point, only the Family Rondeletiidae had been assigned to the Order Beryciformes or Xenoberyces (Parr, 1929, 1933; Berg, 1940; Norman, unpublished manuscript)]. Of the three families, Rosen and Patterson (1969, pp. 456-457) concluded that the Rondeletiidae was the most generalized and showed the strongest indication of a relationship with other beryciforms (especially Gibberichthys).

Gaudant (1969) contributed to our knowledge of fossil beryciforms by describing and illustrating six new species of Cretaceous berycoids from Lebanon. Four of these species represented new genera--Serratocentrus, Ctenocephalichthys and Holocentropsis. All three genera were placed in the Family Holocentridae (Holocentropsis was believed to be related to the living genus Holocentrus) (Gaudant, 1969, p. 282). Gaudant (1969, p. 275 and p. 278) also established two new genera (Stichopteryx and Alloberyx) to contain certain species which had previously been placed in the fossil genus Hoplopteryx. Although Stichopteryx was placed in the Family Trachichthyidae, Gaudant (1969, p. 275) noted that this form possesses some features seen in the fossil holocentrid Stichocentrus. Alloberyx was placed (somewhat questionably) in the Family Holocentridae. According to Gaudant (1969, p. 278), the structure of the opercular apparatus, the form of the maxilla and the composition of the unpaired fins in Alloberyx seem to indicate some affinities with the Cretaceous holocentrids Caproberyx pharsus and Stichocentrus.

In the classification of Gosline (1971), the Order Beryciformes was divided into 11 families. His definition of the order included a number of primitive features, such as the usual presence of an orbitosphenoid. Gosline (1971, pp. 147-148) noted that because the osteology of some of the living forms is almost unknown, it would be premature to assign the families to any formal suborders within the Beryciformes. Gosline (1971, p. 148) also remarked on the difficulty in coordinating the classification of modern beryciforms with those of the Cretaceous due to the lack of adequate osteological studies. Included among the 11 families recognized

by Gosline are the Polymixiidae, Anoplogasteridae, Stephanoberycidae and Melamphaeidae. The stephanoberyciform family Gibberichthyidae was not included in the Beryciformes--rather, it was placed (along with the families Kasidoroidae, Barbourisiidae and Rondeletiidae) in a group (termed Group 3) of the Order Cetomimiformes. Gosline (1971, p. 148) did note, however, that further study may prove that Group 3 of his Cetomimiformes should be transferred to the Beryciformes.

Gaudant (1973) performed an interesting statistical analysis on two species of the fossil beryciform genus Acrogaster (A. daviesi and A. heckeli). She presented evidence suggesting that these two forms, present in the same geological deposit, are actually representatives of the same species, and that the morphometric and meristic characters which separate them are attributable to sexual dimorphism.

In the classification of Woods and Sonoda (1973), the stephanoberyciform families Stephanoberycidae, Gibberichthyidae and Melamphaeidae were again removed from the Order Beryciformes (termed Berycomorphi by Woods and Sonoda), while the Family Polymixiidae was once again included. Woods and Sonoda divided the Berycomorphi into three suborders--the Polymixioidei, Berycoidei and Anoplogasteroidei. The Polymixioidei and Anoplogasteroidei each contained but a single family and genus (Polymixia and Anoplogaster, respectively) (note: Woods and Sonoda did not include fossil groups in their classification). The Berycoidei, the central group of the Order Berycomorphi, contained seven families.

Woods and Sonoda's work (1973) was an important contribution to our knowledge of the beryciform fishes. Descriptions of all of the beryciform species (including two new species--Diretmus pauciradiatus and Hoplostethus occidentalis) from the Western North Atlantic were included. In the descriptions, emphasis was placed on characters of the scales, fins and teeth. Information concerning the size, morphological variation, economic importance, habits, food, development and growth, and range and abundance of the species was also included. Finally, the morphology of the pelvic girdle in a number of forms was described and illustrated.

Ebeling and Weed (1973) studied the families Stephanoberycidae, Gibberichthyidae and Melamphaeidae. According to these authors, these three families constitute a separate, although rather diverse, order--the Xenoberyces. Thus, Ebeling and Weed state that the "fishes of the order Xenoberyces make up a heterogeneous deep-sea assemblage, whose members are more or less intermediate in structure between the Beryciformes . . . and the Cetunculi [whalefishes]" (Ebeling and Weed, 1973, pp. 397-398), and that the "xenoberycoid families are best left together as one motely group, more because of their joint disagreement with typical Beryciformes on one side and with typical Cetunculi on the other, than because of their close morphological resemblance to one another" (Ebeling and Weed, 1973, p. 399).

Ebeling and Weed (1973) investigated both the intraordinal relationships of the Xenoberyces and the relationship of the Xenoberyces to the Cetunculi. In order to accomplish this, 23 characters, "probably of phylogenetic significance," were selected, and then coded into three or four states (state one being the most primitive and the higher states the

more specialized)[1] (Ebeling and Weed, 1973, pp. 400-401). For each species examined, the sum of the coded states for all 23 characters was calculated. This sum, which was termed the "index of primitiveness," expresses the degree of specialization exhibited by each species, with the lower values indicating the more primitive forms (Ebeling and Weed, 1973, p. 401). On this basis, Ebeling and Weed (1973, p. 401) concluded that the Xenoberyces are more primitive than the two cetunculans (Rondeletia and Cetostoma) which were examined. Then, in order to group the species by their relationships with one another, Ebeling and Weed compared each species with every other by simply summing the number of character states held in common by each species pair[2] (Ebeling and Weed, 1973, pp. 402-403). This analysis revealed a close relationship between Rondeletia and Cetostoma on one hand and between Rondeletia and some xenoberycoids on the other [note: although Ebeling and Weed placed Rondeletia in the Cetunculi, they considered it to constitute "a true missing link between the Xenoberyces and Cetunculi" and stated that it might well be included in the Xenoberyces (as suggested by Parr, 1929, and Berg, 1940) pending further investigation of its affinities (Ebeling and Weed, 1973, p. 399)]. The analysis also led Ebeling and Weed (1973, p. 404) to conclude that "[w]hereas Stephanoberyx . . . , Malacosarcus . . . , and Poromitra . . . are all relatively closely interrelated, Gibberichthys . . . might best be considered a primitive xenoberycoid, somewhat apart from these others, but most similar to Stephanoberyx."

Rosen (1973) investigated the evolutionary relationships among the families of beryciform fishes (including stephanoberyciforms) primarily on the basis of the morphology of the jaw musculature, upper pharyngeal apparatus and caudal skeleton. Comparisons between various beryciform and certain non-beryciform groups [such as zeoids (John Dories and their relatives) and lampridiforms (opah and ribbonfishes)] were also made. Rosen, unlike most previous investigators, utilized only derived features for assessing phylogenetic affinities. According to Rosen (1973, p. 397), the "beryciform grade appears to contain three groups: a monophyletic group including the trachichthyoids [Trachichthyidae, Anomalopidae, Monocentridae, Diretmidae, Paradiretmidae, Korsogasteridae and Sorosichthyidae], stephanoberycoids [Stephanoberycidae, Gibberichthyidae, Melamphaeidae, Anoplogasteridae, Rondeletiidae, Barbourisiidae, Cetomimidae, Mirapinnidae, Eutaeniophoridae and Megalomycteridae] and probably also the berycids, zeoids, lampridiforms and the Cretaceous dinopterygoids; the Holocentridae; and the Polymixioidei." Rosen used the phrase "beryciform grade" because "no strong advanced features, and discouragingly few weak ones, were found to indicate that the beryciforms constitute a monophyletic taxon" (Rosen, 1973, p. 505). In particular, Rosen (1973, p. 502) noted that "there are very scant data on derived character states to relate the Polymixiidae [emphasis mine] and

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[1] Ebeling and Weed (1973) did not state why these 23 characters are probably phylogenetically significant, and they did not provide any indication of the method used to determine which states are the most primitive.

[2] The number of coincident character states for each species pair included both primitive and specialized states.

Holocentridae to other beryciforms."

The strength of Rosen's work (1973) is that only derived character states are used for relating taxa [the importance of utilizing only derived character states for determining evolutionary relationships is discussed by Hennig (1966)]. Nevertheless, Rosen's work more than any other, reveals the great need for further study of the relationships of the beryciform fishes. Thus, one finds in his paper such statements as "there seems to be a community of relationship among trachichthyoids, berycids, zeoids, lampridiforms and the Cretaceous Dinopterygoidei, but working out possible sister-group [cladistic] relationships among them requires a more thorough review of their anatomy" and "[t]here is thus some reason to agree with the proposals . . . that all the above fishes are somehow interrelated and bear the designation 'stephanoberycoids,' although the nature of these relationships is far from clear" (Rosen, 1973, p. 486 and p. 498, resp.).

Radovčić (1975a) described and illustrated five species of fishes (Omosoma croatica sp. nov., Berycopsia inopinnata gen. et sp. nov., Dalmatichthys malezi gen. et sp. nov., Erugocentrus illyricus gen. et sp. nov. and Adriacentrus crnolataci gen. et sp. nov.) from the Upper Cretaceous (Turonian and Senonian) of Yugoslavia. Radovčić placed Omosoma and Berycopsia in the Family Polymixiidae, while Dalmatichthys was made the type of a new family, the Dalmatichthyidae. Both the Polymixiidae and Dalmatichthyidae were assigned to the Order Polymixiiformes (of the Superorder Paracanthopterygii). Erugocentrus and Adriacentrus were placed in the Family Holocentridae of the Order Beryciformes (Superorder Acanthopterygii). Radovčić also discussed the affinities of his five new species with certain of the Cretaceous beryciforms described by Patterson (1964, 1967, 1968) and Gaudant (1969). One of the conclusions reached by Radovčić (1975a, p. 39) was that Dalmatichthys is closely related to the polymixiiform Pycnosteroides. Radovčić (1975a, p. 39) also expressed the opinion that future studies will show the need for splitting the Family Polymixiidae as defined by Patterson (1964).

Nelson (1976), in his book entitled "Fishes of the World," divided the Order Beryciformes into three suborders--the Stephanoberycoidei, Berycoidei and Cetomimoidei. The Stephanoberycoidei contained all three of the stephanoberyciform families, as well as the Family Kasidoroidae [recall (p. 11), however, that the Kasidoroidae has been shown to be based on the prejuveniles of Gibberichthys]. Like Rosen and Patterson (1969) and Rosen (1973), Nelson included all three families of whalefishes (Rondeletiidae, Barbourisiidae and Cetomimidae) in the Beryciformes (in this case, in the Suborder Cetomimoidei). The Anoplogasteridae (Anoplogaster) was placed with nine families of "typical beryciforms" in the Berycoidei. Polymixia was excluded from the Beryciformes by Nelson, being placed instead in the Order Polymixiiformes (of the Superorder Paracanthopterygii). For each of the beryciform families (except the Sorosichthyidae and Paradiretmidae) recognized, Nelson briefly discussed the distribution, taxonomic content and major morphological characteristics.

In reviewing the previous systematic work on the Beryciformes, it is evident that certain groups have repeatedly been included and excluded from the order. The Polymixiidae (Polymixia), Anoplogasteridae (Anoplogaster) and Stephanoberyciformes (Xenoberyces) are particularly problematical groups. Thus, Polymixia is included in the Order Beryciformes (or its equivalent) by Lowe (1843), Günther (1859), Jordan and Evermann (1896), Boulenger (1904), Starks (1904), Regan (1911), Jordan (1923), Berg (1940),

Norman (unpublished manuscript), Patterson (1964), Greenwood et al. (1966), McAllister (1968), Gosline (1971) and Woods and Sonoda (1973), but excluded from the order by Goode and Bean (1895), Lamber (1963), Rosen and Patterson (1969), Rosen (1973)[1], Radovčić (1975a) and Nelson (1976). The relationship of Anoplogaster is also uncertain. Thus, Anoplogaster is: (1) included in the same group with some (or all) of the stephanoberyciforms by Regan (1911), Jordan (1923), Norman (unpublished manuscript), Lamber (1963) and Rosen (1973) (2) included in the same group with some (or all) of the "typical beryciforms" by Günther (1859), Parr (1933), Greenwood et al. (1966), McAllister (1968), Rosen and Patterson (1969), Woods and Sonoda (1973), Ebeling and Weed (1973) and Nelson (1976) and (3) included in a group with both stephanoberyciforms and "typical beryciforms" by Goode and Bean (1895), Jordan and Evermann (1896), Boulenger (1904) and Berg (1940). Finally, it has been shown that the distinctness of the stephanoberyciforms (with or without Anoplogaster) with respect to the "typical beryciforms" is also controversial. Thus, Regan (1911), Jordan (1923), Berg (1940), Lamber (1963), Patterson (1964), Woods and Sonoda (1973) and Ebeling and Weed (1973) place some (or all) of the stephanoberyciforms in an order separate from the "typical beryciforms," whereas Goode and Bean (1895), Jordan and Evermann (1896), Boulenger (1904)[2], Parr (1933), Norman (unpublished manuscript), Greenwood et al. (1966), McAllister (1968), Rosen and Patterson (1969), Rosen (1973) and Nelson (1976) do not.

The present investigation will attempt to solve the particular problems discussed above. In addition, the study will address itself to a more fundamental question--namely, do the Beryciformes (with or without the stephanoberyciforms) constitute a natural (monophyletic) group?

Rosen (1973) is one of the few investigators who has suggested that the Beryciformes may not be monophyletic. A review of the history of the classification of the beryciform fishes reveals that Rosen's suggestion is well-founded. It has been shown above that previous investigators [Lowe (1843), Günther (1859), Jordan and Evermann (1896), Boulenger (1904), Starks (1904), Regan (1911), Berg (1940), Patterson (1964), Gosline (1971) and Woods and Sonoda (1973)] have often included primitive features (especially the presence of a large number of pelvic and caudal fin rays, and the possession of an orbitosphenoid) in their definitions of the group. Hennig (1966) has shown that primitive features do not provide valid evidence for demonstrating the monophyletic nature of a group.

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[1]Although Rosen (1973) did not present a formal classification of the Beryciformes, his statement (p. 502) that "there are very scant data on derived character states to relate the Polymixiidae . . . to other beryciforms" suggests that this group should be removed from the order.

[2]In the classification of Boulenger (1904), however, two stephanoberyciform genera (Stephanoberyx and Malacosarcus) are far removed from the other beryciform fishes, and are placed in a separate suborder (the Haplomi).

The possibility that the Order Beryciformes is not monophyletic must, therefore, be kept in mind. Various groups within the Beryciformes may actually be most closely related to certain non-beryciform fishes, such as members of the Order Perciformes [recall that Patterson (1964) presented evidence for the existence of a number of beryciform-perciform lineages]. However, regardless of whether the Beryciformes are shown to be monophyletic or not, the knowledge gained through a comprehensive anatomical study such as this should provide a very solid foundation from which future investigators can progress in their studies of beryciform--non-beryciform (e.g., zeiform, lampridiform, cetomimiform, perciform) relationships.

TABLE 1

HISTORY OF THE CLASSIFICATION OF THE BERYCIFORM FISHES
FROM THE YEARS 1829-1976
(+ denotes fossil taxon)

Cuvier (1829)

Les Acanthoptérygiens (1er ordre)
Les Percoides (1er famille)
Holocentrum
Myripristis
Beryx
Trachichthys
Les Joues Cuirassées (2me famille)
Monocentris

Lowe (1843)

Division I (Series I). Acanthopterygians
Family Berycidae
Beryx
Trachichthys
Polymixia
Holocentrum
Myripristis
Monocentris

Günther (1859)

Order Acanthopterygii
Family Berycidae
Monocentris
Hoplostethus
Trachichthys
Anoplogaster

TABLE 1--cont.

Beryx
Polymixia
Myripristis
Holocentrum
Rhynchichthys

Gill (1872)

Order Teleocephali
Sub-order Acanthopteri
Superfamily Polymixoidea
Family Polymixiidae
Superfamily Berycoidea
Family Monocentridae
Family Berycidae

Goode and Bean (1895)

Order Teleocephali
Family Berycidae
Subfamily Berycinae
Beryx
Subfamily Melamphainae
Melamphaes
Plectromus
Scopelogadus
Malacosarcus
Poromitra
Subfamily Anoplogastrinae
Anoplogaster
Caulolepis
Family Stephanoberycidae
Stephanoberyx
Family Trachichthyidae
Trachichthys
Hoplostethus
Family Bathyclupeidae
Bathyclupea
Family Anomalopidae
Anomalops
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Family Diretmidae
Diretmus

TABLE 1--cont.

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Family Polymixiidae
Polymixia

Jordan and Evermann (1896)

Order Acanthopteri
Suborder Rhegnopteri
Group Berycoidei
Family Bathyclupeidae
Bathyclupea
Family Stephanoberycidae
Stephanoberyx
Family Trachichthyidae
Hoplostethus
Family Berycidae
Subfamily Anoplogastrinae
Caulolepis
Anoplogaster
Subfamily Melamphainae
Poromitra
Plectromus
Subfamily Berycinae
Beryx
Family Holocentridae
Myripristis
Holocentrus
Flammeo
Plectrypops
Family Polymixiidae
Polymixia
Family Mullidae
Mullus
Mulloides
Upeneus

Boulenger (1904)

Order Teleostei
Suborder Haplomi
Family Stephanoberycidae
Stephanoberyx
Malacosarcus

.
.
.

TABLE 1-cont.

Suborder Acanthopterygii
Division Perciformes
Family Berycidae
Beryx
Polymixia
Aphredoderus
Melamphaes
Plectromus
Scopelogadus
Anoplogaster
Caulolepis
Trachichthys
Paratrachichthys
Gephyroberyx
Myripristis
Holocentrum
+Sphenocephalus
+Acrogaster
+Pycnosterinx
+Hoplopteryx
+Asineops ?
Family Monocentridae
Monocentris
Family Pempheridae
Pempheris
Parapriacanthus
Neopempheris
Bathyclupea

Starks (1904)[a]

Group Berycoidea
Family Trachichthyidae
Hoplostethus
Family Berycidae
Beryx
Family Holocentridae
Holocentrus
Myripristis
Family Polymixidae
Polymixia
Family Monocentridae
Monocentris

Regan (1911)

Order Berycomorphi
Family Polymixiidae
Polymixia
+Platycormus

TABLE 1--cont.

+Omosoma ?
+Pycnosterinx ?
Family Berycopsidae
+Berycopsis
Family Berycidae
Beryx
Hoplopteryx
Family Diretmidae
Diretmus
Family Trachichthyidae
Trachichthys
Hoplostethus
Paratrachichthys
Gephyroberyx
+Aipichthys ?
+Acrogaster ?
+Sphenocephalus ?
Family Monocentridae
Monocentris
Family Anomalopidae
Anomalops
Photoblepharon
Family Holocentridae
Adioryx
Holocentrus
Myripristis
Ostichthys
+Homonotus
+Trachithyioides
+Dinopteryx ?
+Caproberyx
Order Xenoberyces
Family Stephanoberycidae
Stephanoberyx
Malacosarcus
Family Melamphaidae
Melamphaes
Plectromus
Scopelogadus
Anoplogaster
Caulolepis

Jordan (1923)

Order Xenoberyces
Family Stephanoberycidae
Stephanoberyx
Acanthochaenus
Malacosarcus

TABLE 1--cont.

Family Melamphaidae
Metopias
Anoplogaster
Melamphaes
Poromitra
Caulolepis
Plectromus
Scopelogadus
Lophocephalus
Scopeloberyx
Poromitrella
+Aulolepis

Order Berycoidei
Family Polymixiidae
Polymixia
Nemobrama
Dinemus
+Pycnosterinx
+Imogaster
+Platycormus
Family Berycopsidae
+Berycopsis
+Stenostoma
Family Berycidae
Beryx
Centroberyx
Trachichthodes
Austroberyx
+Pristigenys
+Macrolepis
+Heterolepis
+Hemigonolepis
+Prionolepis
+Goniolepis
+Hemicyclolepis
+Spinacites
+Electrolepis
+Lobopterus
+Bradyurus
Family Hoplopterygidae
+Hoplopteryx
Family Diretmidae
Diretmus
Discus
Family Monocentridae
Monocentris
Lepisacanthus
Ericius
Lepicantha
Cleidopus

TABLE 1--cont.

Family Anomalopidae
Heterophthalmus
Anomalops
Photoblepharon
Family Trachichthyidae
Trachichthys
Hoplostethus
Paratrachichthys
Gephyroberyx
Leiogaster
+Acrogaster
+Sphenocephalus
+Aipichthys
+Acanthophoria
Family Holocentridae
Holocentrus
Corniger
Myripristis
Rhynchichthys
Plectrypops
Rhinoberyx
Rhamphoberyx
Neomyripristis
Holotrachys
Neoniphon
Harpage
Ostichthys
Flammeo
Howella
Beanea
Sargocentron
Adioryx
+Homonotus
+Trachichthyoides
+Caproberyx
Family Dinopterygidae
+Dinopteryx
Family Ctenothrissidae
+Aulolepis
+Ctenothrissa
Family Caristiidae
Caristius
Platyberyx

Berg (1940)

Order Stephanoberyciformes (Xenoberyces)
Family Stephanoberycidae
Stephanoberyx
Acanthochaenus
Malacosarcus

TABLE 1--cont.

Family Rondeletiidae
Rondeletia
Order Beryciformes (Berycomorphi)
Family Polymixiidae
Polymixia
Family Berycopsidae
+Berycopsis
Family Berycidae (including Hoplopterygidae)
Beryx
Hoplopteryx
Family Diretmidae
Diretmus
Family Caristiidae (Elephenoridae)
Caristius
Platyberyx
Family Trachichthyidae
Family Ostracoberycidae
Ostracoberyx
Family Caulolepidae
Caulolepis
Anoplogaster
Family Korsogasteridae
Korsogaster
Leiogaster
Family Monocentridae
Monocentris
Family Anomalopidae
Photoblepharon
Family Holocentridae
Myripristis
Holocentrus
Adioryx
Family Dinopterygidae
+Dinopteryx
Family Gibberichthyidae
Gibberichthys
Family Melamphaidae
Melamphaes

Norman (unpublished manuscript)

Order Berycomorphi
Suborder Berycoidea
Family Polymixiidae
Polymixia
Family Berycidae
Beryx
Hoplopteryx
Family Diretmidae
Diretmus

TABLE 1--cont.

Family Caristiidae
Caristius
Family Trachichthyidae
Trachichthys
Hoplostethus
Paratrachichthys
Gephyroberyx
Family Monocentridae
Monocentris
Cleidopus
Family Anomalopidae
Anomalops
Kryptophanaron
Photoblepharon
Family Holocentridae
Adioryx
Holocentrus
Beanea
Myripristis
Holotrachys
Ostichthys
Plectrypops
Suborder Anoplogasteroidea
Family Stephanoberycidae
Acanthochaenus
Stephanoberyx
Malacosarcus
Gibberichthys
Family Melamphaidae
Poromitra
Melamphaes
Family Anoplogasteridae
Caulolepis
Anoplogaster
Family Rondeletiidae
Rondeletia

Lamber (1963)

Order Beryciformes
Group A
Family Berycidae
Beryx
+Genus A
Family Diretmidae
Diretmus
+Genus B
Group B
Family Trachichthyidae

TABLE 1--cont.

Gephyroberyx
Hoplostethus
Paratrachichthys
Trachichthys
+Genus C
+Genus D
+Genus E
+Genus F

Family Monocentridae
Monocentris
Cleidopus
+Genus G
+Genus H
+Genus I

Family Anomalopidae
Anomalops
Kryptophanaron
Photoblepharon

Group C

Family A
+Genus J

Family Holocentridae
+Holocentrites
+Holocentroides ?
Holocentrus

Family Myripristidae
+Caproberyx ?
Corniger
+Homonotus ?
Myripristis
Ostichthys
Plectrypops
+Stintonia
+Trachichthyioides ?
+Weileria

Order Stephanoberyciformes

Family Stephanoberycidae
Stephanoberyx
Acanthochaenus
Malacosarcus

Family Anoplogasteridae
Anoplogaster
Petropolichthys ?

Family Melamphaidae
Melamphaes
Poromitra
Poromitrella

Family Gibberichthyidae ?
Gibberichthys

TABLE 1--cont.

Patterson (1964)

Order Beryciformes
- Suborder Polymixioidei
  - Family Polymixiidae
    - Polymixia
    - +Berycopsis
    - +Homonotichthys
    - +Omosoma
    - +Pycnosterinx
  - Family Sphenocephalidae
    - +Sphenocephalus
- Suborder Dinopterygoidei
  - Family Dinopterygidae
    - +Dinopteryx
  - Family Pycnosteroididae
    - +Pycnosteroides
  - Family Aipichthyidae
    - +Aipichthys
  - Family Pharmacichthyidae
    - +Pharmacichthys
- Suborder Berycoidei
  - Family Berycidae
  - Family Trachichthyidae
    - +Hoplopteryx
    - +Acrogaster
    - +Tubantia
  - Family Anomalopidae
  - Family Caristiidae
  - Family Diretmidae
  - Family Gibberichthyidae
  - Family Korsogasteridae
  - Family Monocentridae
  - Family Sorosichthyidae
  - Family Paradiretmidae
  - Family Holocentridae
    - +Caproberyx
    - +Trachichthyoides
    - +Kansius

Greenwood et al. (1966)

Order Beryciformes
- Suborder Stephanoberycoidei
  - Family Stephanoberycidae
  - Family Melamphaeidae (Melamphaidae, Melamphasidae)
  - Family Gibberichthyidae
- Suborder Polymixioidei
  - Family Polymixiidae

TABLE 1-cont.

Suborder Berycoidei
Family Diretmidae
Family Trachichthyidae (including Hoplopterygidae, Sorosichthyidae)
Family Korsogasteridae
Family Anoplogasteridae (Caulolepidae)
Family Berycidae
Family Monocentridae
Family Anomalopidae
Family Holocentridae (Holocenthridae)

McAllister (1968)

Order Beryciformes (Stephanoberyciformes)
Suborder Polymixioidei
Family Sphenocephalidae
+Sphenocephalus
Family Polymixiidae (Berycopsidae)
Polymixia
+Homonotichthys
+Pycnosterinx
+Berycopsis
+Omosoma
Suborder Dinopterygoidei
Family Dinopterygidae
+Dinopteryx
Family Pycnosteroididae
+Pycnosteroides
Family Aipichthyidae
+Aipichthys
Family Pharmacichthyidae
+Pharmacichthys
Suborder Berycoidei
Family Berycidae
Beryx
Family Holocentridae (Myripristidae)
Holocentrus
+Caproberyx
Myripristis
+Trachichthyoides
Family Trachichthyidae (Korsogasteridae)
+Hoplopteryx
+Acrogaster
Hoplostethus
Gephyroberyx
Korsogaster
Trachichthys
Family Anoplogasteridae (Caulolepidae)
Anoplogaster

TABLE 1--cont.

Family Diretmidae
Diretmus
Family Sorosichthyidae
Sorosichthys
Family Paradiretmidae
Paradiretmus
Family Caristiidae (Elephanoridae)
Platyberyx
Caristius
Family Anomalopidae
Anomalops
Photoblepharon
Family Monocentridae
Monocentris
Suborder Stephanoberycoidei
Family Melamphaidae
Melamphaës
Scopelogadus
Scopeloberyx
Poromitra
Sio
Family Stephanoberycidae
Stephanoberyx
Malacosarcus
Family Gibberichthyidae

Rosen and Patterson (1969)

Order Beryciformes
Group[b] Stephanoberycoidei
Family Stephanoberycidae
Family Melamphaeidae
Family Gibberichthyidae
Group Berycoidei
Family Diretmidae
Family Trachichthyidae
Family Korsogasteridae
Family Anoplogasteridae
Family Berycidae
Family Monocentridae
Family Anomalopidae
Family Holocentridae
Group Cetomimoidei
Family Cetomimidae
Family Barbourisiidae
Family Rondeletiidae
Group_____ (unnamed)
Family Kasidoroidae

TABLE 1--cont.

Gosline (1971)

Order Beryciformes
- Family Polymixiidae
- Family Caristiidae
- Family Berycidae
- Family Trachichthyidae
- Family Diretmidae
- Family Monocentridae
- Family Anomalopidae
- Family Holocentridae
- Family Anoplogasteridae
- Family Stephanoberycidae
- Family Melamphaidae

Woods and Sonoda (1973)

Order Berycomorphi (Beryciformes)
- Suborder Polymixioidei
  - Family Polymixiidae
    - Polymixia
- Suborder Berycoidei
  - Family Trachichthyidae
    - Gephyroberyx
    - Paratrachichthys
    - Trachichthys
    - Hoplostethus
    - Optivus
  - Family Anomalopidae
    - Anomalops
    - Photoblepharon
    - Kryptophaneron
  - Family Berycidae
    - Beryx
    - Centroberyx
  - Family Diretmidae
    - Diretmus
  - Family Monocentridae
    - Monocentris
  - Family Holocentridae
    - Myripristis
    - Ostichthys
    - Plectrypops
    - Corniger
    - Holocentrus
    - Adioryx
    - Flammeo
  - Family Sorosichthyidae
    - Sorosichthys

TABLE 1--cont.

Suborder Anoplogasteroidei
Family Anoplogasteridae
Anoplogaster

Ebeling and Weed (1973)

Order Xenoberyces (Stephanoberyciformes)
Family Gibberichthyidae
Gibberichthys
Family Stephanoberycidae
Malacosarcus
Stephanoberyx
Acanthochaenus
Family Melamphaidae
Scopelogadus
Poromitra
Scopeloberyx
Melamphaes
Sio

Rosen (1973)[c]

Grade Beryciformes
Group 1
Trachichthyoidea
Family Trachichthyidae
Family Anomalopidae
Family Monocentridae
Family Diretmidae
Family Paradiretmidae (probably)
Family Korsogasteridae (probably)
Family Sorosichthyidae (probably)
Stephanoberycoidea
Family Barbourisiidae
Family Rondeletiidae
Family Gibberichthyidae
Family Melamphaeidae
Family Stephanoberycidae
Family Anoplogasteridae
Family Cetomimidae
Family Mirapinnidae
Family Eutaeniophoridae
Family Megalomycteridae

Other taxa probably belonging to Group 1
Family Berycidae
Group Zeoidea
Order Lampridiformes
+Group Dinopterygoidei

TABLE 1--cont.

Group 2
Family Holocentridae

Group 3
Family Polymixiidae

Nelson (1976)

Order Beryciformes
Suborder Stephanoberycoidei
Family Stephanoberycidae
Acanthochaenus
Malacosarcus
Stephanoberyx
Family Melamphaeidae
Melamphaes
Poromitra
Scopeloberyx
Scopelogadus
Family Gibberichthyidae
Gibberichthys
Family Kasidoroidae
Kasidoron
Suborder Berycoidei
Family Sorosichthyidae
Sorosichthys
Family Paradiretmidae
Paradiretmus
Family Trachichthyidae
Gephyroberyx
Hoplostethus
Optivus
Paratrachichthys
Trachichthys
Family Diretmidae
Diretmus
Family Korsogasteridae
Korsogaster
Family Anoplogasteridae
Anoplogaster
Family Berycidae
Beryx
Centroberyx
Family Monocentridae
Monocentris
Family Anomalopidae
Anomalops
Kryptophanaron
Photoblepharon

TABLE 1--cont.

Family Holocentridae
Holocentrus
Adioryx
Flammeo
Beanea
Myripristis
Ostichthys
Plectrypops
Holotrachys
Corniger
Suborder Cetomimoidei
Family Rondeletiidae
Rondeletia
Family Barbourisiidae
Barbourisia
Family Cetomimidae
Cetomimus
Cetostomus
Ditropichthys
Gyrinomimus

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[a]Starks (1904) did not present a classification of the beryciform fishes. The classification presented here merely represents an attempt to formalize the systematic conclusions of Starks.

[b]In their classification, Rosen and Patterson (1969, pp. 460-461) indicated only that the Order Beryciformes includes the Stephanoberycoidei, Berycoidei, Cetomimoidei and Mirapinnatoidei [in part (Family Kasidoroidae)] of Greenwood et al. (1966). Although the Stephanoberycoidei, Berycoidei, Cetomimoidei and Mirapinnatoidei are all assigned subordinal rank by Greenwood et al. (1966), it is not clear whether Rosen and Patterson (1969) continue to recognize these groups as suborders in their classification. For this reason the neutral term "group" is used in the classification presented here.

[c]Rosen (1973) did not present a classification of the beryciform fishes. The classification presented here merely represents an attempt to formalize the systematic conclusions of Rosen.

CHAPTER II

MATERIALS AND METHODS

Materials

The material which was cleared and stained for examination is listed in table 8. In some cases, the availability and abundance of material dictated which species were examined. In general, small specimens were selected. There were several reasons for this: (1) small specimens clear more rapidly and usually more satisfactorily (2) small specimens are more convenient to handle (in terms of both dissection and storage) and (3) small specimens present fewer problems when using a camera lucida to make illustrations. It should be noted that the relationship between specimen size and nature of character state expression was usually not known. In those cases where character states were known to be size dependent [e.g., the presence of a long preopercular spine in juvenile specimens of Anoplogaster; the presence of a short and stubby spine in adults (Grey, 1955, p. 294)], the states present in adult individuals were taken to represent the species. In addition to the cleared and stained material, a number of specimens preserved in 70% ethanol was partially dissected to examine details of the soft anatomy, such as the attachment of muscles and ligaments and the passage of nerves and blood vessels. Extensive use was also made of the dried skeletal material in the collection at the Field Museum of Natural History in Chicago.

Methods

This investigation consisted of six major steps:

(1) collection of comparative osteological data through dissection of specimens
(2) selection of characters for analysis
(3) differentiation of character states
(4) determination of derivativeness of character states
(5) determination of the sequence of change in states in multiple state characters (characters with three or more states)
(6) use of a computer program (Combinatorial Method) for clustering taxa into natural (monophyletic) groups.

The first five steps constitute the construction of the data set. The sixth step involves the analysis of the data set in order to produce a phylogeny. Steps 2-6 are discussed in detail following the chapters on descriptive osteology. At this juncture, it is necessary only to discuss step 1 and certain points concerning steps 2 and 4.

Collection of Comparative Osteological Data

Specimens were cleared with trypsin and stained with alizarin using the technique developed by Taylor (1967). They were then completely dissected

under a Spencer AO microscope at 10 to 30 power. X-rays of some of the material were taken when dissection of additional specimens was not possible. The illustrations of the bones were made with a camera lucida attached to a Wild dissecting microscope. It was not possible to make drawings of the bones for all of the species examined. However, for most of the species which are described in detail, all of the bones except those of the branchial arches, vertebral column, and dorsal and anal fins are illustrated.

Species representing most of the genera belonging to all of the Recent families of the Beryciformes (except the Korsogasteridae) recognized by Greenwood et al. (1966, p. 398) were examined (see table 9) [note: according to Woods and Sonoda (1973, p. 316), Korsogaster nanus, the only member of the Korsogasteridae, is synonymous with Hoplostethus mediterraneus (Family Trachichthyidae)]. Complete osteological descriptions were written for all of the beryciform genera examined except those belonging to the Suborder Stephanoberycoidei (families Stephanoberycidae, Melamphaeidae and Gibberichthyidae) and Adioryx and Plectrypops (Family Holocentridae). For these forms, as well as for the non-beryciform teleosts which were examined (for the purpose of character analysis), only the states of the characters used in this investigation were recorded.

Selection of Characters for Analysis

Ideally, conclusions concerning evolutionary relationships are based on a wide variety of data. Simpson (1961, p. 71) states:

> It is a corollary of the fact that organisms are to be classified, not their characters, that the whole organism should be considered in all its parts and all its aspects. There are, of course, practical limits as to what can be observed... Nevertheless it is an axiom of modern taxonomy that variety of data should be pushed as far as possible toward the limits of practicability.

In this investigation, only osteological characters were utilized. There were three reasons for this. First, it was not feasible, in the time allotted for this investigation, to consider all aspects of the anatomy. Second, a great deal more is known about the comparative anatomy of the teleostean skeleton than the morphology of any other anatomical system. Investigators have only recently been turning their attention to other morphological systems in an effort to ascertain phylogenetic affinities [e.g., studies by Freihofer (1963), Greenwood (1971) and Nelson (1972a)]. Third, beryciforms are relatively well-known in the fossil record. It was therefore desirable to use osteological characters so that the morphology of the fossils could be taken into account.

Determination of Derivativeness of Character States

The basic methodology utilized in this investigation for determining phylogenetic relationships among taxa is that of Hennig (1966). The most fundamental principle embodied in this methodology is that only the common possession of derived or advanced states of characters among organisms provides valid evidence for phylogenetic relationship [note: although Hennig

(1966) is the first investigator to stress the importance of utilizing only derived character states for ascertaining phylogenetic affinities, he is by no means the only one to do so--see also Brundin (1966, 1972), Throckmorton (1968) and Nelson (1969b, 1970a)]. For a complete discussion of the methodological principles of phylogenetic systematics, the reader should consult Hennig (1966). The discussion which follows will concern only the definitions of several terms which are essential for a thorough understanding of the material presented in later chapters.

Morphological character states are progressively modified or transformed during evolution. The transformation stages of a single character constitute a transformation series (Hennig, 1966). The character state from which transformation started is the primitive state, while all other states of the transformation series are derived (Hennig, 1966, p. 89; note: Hennig uses the terms plesiomorphous and apomorphous instead of primitive and derived). It is important to note that the terms primitive and derived are relative: for example, in a transformation series which consists of three states related in a linear fashion (i.e., a → a' → a''), states a' and a'' are derived relative to a, but a' is primitive relative to a''.

The terms phylogenetic relationship and monophyletic group have different meanings among systematists [Nelson (1972b) discusses the meaning of the term phylogenetic relationship as used by Mayr, Simpson and Hennig]. The definitions of phylogenetic relationship and monophyletic group adopted in this work are those of Hennig. Hennig (1966, p. 74) defines phylogenetic relationship as follows:

> A particular taxon B is more closely related to another taxon C than to a third taxon A if, and only if, it has at least one stem [ancestral] species in common with C that is not also a stem species of A.

A monophyletic group is defined by Hennig (1966, p. 73) as:

> a group of species in which every species is more closely related to every other species than to any species that is classified outside this group.

The phrase "more closely related" in the definition of a monophyletic group means closer phylogenetic relationship (as defined above).

Finally, it is necessary to briefly discuss the concept of sister groups.

> Species groups that arose from the stem species of a monophyletic group by one and the same splitting process may be called "sister groups" (Hennig, 1966, p. 139).

In order to construct a dendrogram showing the phylogenetic relationships among a group of organisms, the phylogenetic systematist must first establish the monophyletic nature of a group (by demonstrating the presence of at least one derived character state common to all of its members), and then search for its sister group (which must also be monophyletic) (Hennig, 1966, p. 139; Brundin, 1972, p. 116). The sister groups are then united into a monophyletic group of higher taxonomic rank. The search for the sister groups of these higher ranking monophyletic groups is then repeated until all of the taxa under consideration are accounted for.

CHAPTER III

THE OSTEOLOGY OF THE BERYCIFORMES

(GENERAL DESCRIPTION)

The purpose of this chapter is twofold: (1) to provide the reader with a knowledge of the general pattern of construction of the skeleton in the Beryciformes and (2) to avoid repetition in the following chapter (detailed descriptions of the osteology of the Beryciformes). In this chapter, the morphological features shared by most or all of the beryciform species examined (table 8) are stressed.

For clarity, the descriptions are in sections which correspond to the major morphological components of the skeleton. The bones described in each section have a structural or topographical relationship to one another and do not necessarily constitute a functional unit.

Illustrations of the bones of a hypothetical beryciform, showing only the anatomical features which are common to all of the species, are not included. Rather, the references which are provided at the beginning of each descriptive section in this chapter are, for the most part, to anatomical illustrations of certain beryciform species which were examined in this investigation [the anatomical illustrations (figs. 6-65) may be found in appendix II (p. 302), and an explanation of the abbreviations used in these illustrations is given in table 83 (p. 364)]. However, since the vertebral column, ribs, and bones of the dorsal and anal fins are not illustrated for any of the beryciform species examined, references to appropriate illustrations in the literature are included. In these latter cases, the illustrations which are cited are of the bones of the generalized characid, Brycon meeki. Although Brycon meeki is not a member of the Order Beryciformes, it exhibits many of the features of the axial skeleton and dorsal and anal fins described in this chapter.

The nomenclature of the bones generally follows that of Patterson (1964). The following exceptions should be noted (Patterson's terminology is given in parentheses): pterosphenoid (pleurosphenoid), angulo-articular (articular), retroarticular (angular), infraorbitals (suborbitals), epihyal (proximal ossification of ceratohyal), ceratohyal (distal ossification of ceratohyal), extrascapular (supratemporal) and actinost (pectoral radial). The nomenclature of the bones of the dorsal and anal fins follows that of Smith and Bailey (1961) and Weitzman (1962), while that of the caudal skeleton follows Patterson (1968).

The Neurocranium

The neurocranium is composed of dermal and endoskeletal elements, and serves to protect the brain and major sense organs. For descriptive purposes, the neurocranium may be divided into five regions: the skull roof, the ethmoid region, the orbital region, the otic region and the occipital region.

The Skull Roof (Figs. 49-50)

The skull roof is composed of a longitudinal series of three pairs of dermal bones, plus the epiotics and supraoccipital. The dermosphenotics also form a tiny portion of the skull roof, but are described with the circumorbital bones because they carry part of the infraorbital lateral line. The paired series of dermal elements of the skull roof includes the nasals, frontals and parietals (from anterior to posterior). These bones are often highly ornamented with spinous or serrated crests and ridges. The nasals overlie the olfactory organs and the frontals form the bony roofs over the orbits. Each frontal bears a thin sheet of bone (orbital lamina) which extends ventrally into the dorsal portion of the orbit. The epiotics are ossifications of the otic capsules (Goodrich, 1958, pp. 376-377), but are described with the bones of the skull roof because they are involved in the formation of the supratemporal and posttemporal fossae. The epiotics usually form the posterodorsal corners of the neurocranium. Each usually bears a facet on its dorsal surface for articulation with the dorsal limb of the posttemporal bone. The supraoccipital is a relatively large bone which, in contrast to primitive teleosts, separates the parietals completely. The supraoccipital contributes to the formation of the supratemporal fossae.

The paired supratemporal and posttemporal fossae provide areas for the insertion of the epaxial musculature which extends onto the dorsal surface of the skull. The supratemporal fossa varies considerably in size. The supraoccipital crest forms the medial wall of the fossa and separates it from its fellow on the opposite side. The posttemporal fossa also varies in its degree of development. Vestiges of the bony roof of the posttemporal fossa of more primitive teleosts persist in some forms. The medial and lateral walls of the posttemporal fossa tend to converge anteriorly, so that there is often no distinct anterior wall. A small amount of cartilage is often present between the various elements of the posttemporal fossa.

The general pattern of the lateral line system on the skull roof is as follows. Two branches of the lateral line pass from the extrascapular of the pectoral girdle onto the skull. One branch, the supratemporal lateral line, passes onto the parietal. The other branch, the main cephalic lateral line, passes onto the lateral portion of the dorsal surface of the pterotic. Once on the pterotic, the lateral line immediately gives off the preopercular branch, which passes ventrally onto the dorsal limb of the preopercle. The main cephalic lateral line continues anteriorly (on the pterotic) until it reaches the region of the dermosphenotic (posterodorsal corner of the orbit). The lateral line then divides into the infraorbital branch, which passes ventrally onto the dorsalmost (fourth) infraorbital, and the supraorbital branch, which passes anteriorly onto the frontal. The supraorbital lateral line gives off small branches (twigs) as it courses anteriorly toward the nasal. The nasal carries the terminal portion of the supraorbital lateral line.

In many beryciforms, the various branches of the lateral line on the skull roof lie in deep cavities which are separated from one another by well-developed crests or ridges. These cavities are termed mucous cavities.

The Ethmoid Region (Fig. 50)

The ethmoid region is composed of the mesethmoid, lateral ethmoids and vomer, in addition to a variable amount of cartilage. The ethmoid cartilage

fills in the space between the medial portions of the lateral ethmoids and between the mesethmoid above and the vomer below. Posteriorly, the ethmoid cartilage may be continuous with cartilage in the orbital region.

The mesethmoid is a bone of variable size which lies in the midline. Dorsally it meets the anterior ends of the frontals and laterally it articulates with the medial edges of the lateral ethmoids. The anterior aspects of the mesethmoid and the ethmoid cartilage are often ridged or "keeled" in the midline. This ridge fits into a groove on the posterior aspect of the rostral cartilage of the premaxillae. The rostral cartilage thus glides upon the surfaces of the mesethmoid and ethmoid cartilage when the premaxillae are protruded.

The lateral ethmoids are plate-like elements lying on either side of the mesethmoid. They separate the olfactory organs in front from the orbits behind. The lateral ethmoid is notched or pierced by the olfactory nerve (I). The lateral ethmoid articulates with the anterior end of the frontal above and with the palatine and lacrimal below.

The vomer lies in the ventral midline of the ethmoid region. It is composed of a broad anterior portion (head), a tapered posterior portion (tail) and a pair of flanges (wings) which are often dorsolaterally-directed. The vomerine wings may contact the ventral portions of the lateral ethmoids and the vomerine head may bear teeth.

The Orbital Region (Fig. 50)

The orbital region is composed of the parasphenoid, orbitosphenoid, pterosphenoids and basisphenoid. Portions of the prootics and autosphenotics also contribute to the bony wall of the orbit, but these bones are more appropriately described with those of the otic region. The orbito- and pterosphenoids lie in the dorsal portion of the orbit, the basisphenoid in the posterior portion, and the parasphenoid in the ventral portion. The edges of the sphenoid bones provide a site for the attachment of the membranous interorbital septum.

The parasphenoid is a long bone which spans a considerable portion of the length of the neurocranium. Anteriorly it projects into the ethmoid region (where it lies dorsal to the tail of the vomer) and posteriorly into the otic and occipital regions (where it lies ventral to a variable portion of the ventral surface of the basioccipital). The anterior end of the parasphenoid is spatulate. Posteriorly, it expands into a broad, plate-like portion (otic region) before tapering (gradually or rapidly) to a point (occipital region). The posterior portion of the parasphenoid may be bent up at an angle (postorbital curvature). The central portion (shaft) of the parasphenoid lies in the orbital region of the neurocranium. The shaft may possess distinct, ventrolaterally-directed flanges, for articulation with the medial edges of the endopterygoids. Arising from the posterior portion of the shaft is a pair of ascending processes which flare upward to meet the prootics. The foramen for the internal carotid artery either pierces the ascending process or lies within the suture between the ascending process and the prootic.

The orbitosphenoid is usually V-shaped, consisting of two laminae which meet in the midline ventrally. However, in some forms a median process or plate (keel) projects ventrally from the fused edges of the laminae, thus providing a larger area for the attachment of the interorbital septum (Y-shaped). I exits from the cranial cavity between the laminae of the orbitosphenoid anteriorly or through a foramen located in the ventral midline

(where the laminae are fused). The orbitosphenoid is absent in some beryciforms.

The pterosphenoids are plate-like elements which usually fail to meet in the orbital midline. The ventral edges of the pterosphenoids usually form the lateral margins of the optic fenestra, through which the optic nerves (II) issue from the cranial cavity. The prootics may also enter into the lateral margins of the fenestra. The optic fenestra is usually closed off by the orbitosphenoid anteriorly and the arms of the basisphenoid posteriorly. The trochlear nerve (IV) may pierce the pterosphenoid or leave through the optic fenestra, close to the ventral edge of the pterosphenoid. The surface of the pterosphenoid may be grooved by the superficial ophthalmic nerves as they pass upward toward the orbital surface of the frontal.

The basisphenoid is Y-shaped. The "arms" of the basisphenoid form the upper limbs of the Y and the pedicel forms the lower limb. II usually issues through the optic fenestra just above and between the arms of the basisphenoid. The pedicel passes ventrally toward the parasphenoid shaft. The pedicel bisects the orbital opening of the myodome. The basisphenoid may be absent.

The myodome is a cavity which contains the extrinsic ocular muscles. The ascending processes of the parasphenoid and adjacent portions of the prootics form its lateral walls.

The Otic Region (Fig. 50)

The otic region is composed of the prootic, autosphenotic, pterotic and intercalar. The auditory bulla also lies in the otic region of the neurocranium.

The prootic is complex morphologically. It is involved in the formation of the myodome and the auditory bulla. The prootic usually forms the ventral part of the facet for the anterior head (or anterior portion of the head) of the hyomandibula. The prootic contains the trigemino-facialis chamber. This chamber is composed of two parts, separated by a bony septum. The inner portion, the pars ganglionaris, is a recess on the medial surface of the prootic. It contains the ganglia of the trigeminal (V) and facial (VII) nerves. The outer portion, the pars jugularis, contains a number of structures (orbital artery, jugular vein, and branches of V and VII). The pars jugularis possesses two to four external openings for the passage of these vessels and nerves. In those forms in which there are four openings, the orbital artery enters the pars jugularis separately (i.e., there is a separate foramen, the fourth opening, for the orbital artery). The other three openings, which are separated by two struts of bone (forming the lateral wall of the pars jugularis), are the posterior, lateral and anterior openings. The jugular vein enters the posterior opening and runs forward to leave the pars jugularis, along with the orbital artery, via the anterior opening. Branches of V and VII (see Patterson, 1964, p. 438, fig. 96B) may also leave through the anterior opening. The hyomandibular trunk of VII enters the pars jugularis through a foramen (the facial foramen) in its medial wall. The facial foramen is <u>not</u> one of the four external openings of the pars jugularis. The hyomandibular trunk of VII leaves the pars jugularis almost immediately through its lateral opening.

In those forms in which three openings (posterior, lateral and anterior) are present, the situation is as described above except that the orbital artery enters the pars jugularis through the posterior opening (along with

the jugular vein). In the condition where only two openings are present, the posterior strut of bone, which separates the posterior and lateral openings in other forms, is absent. In this case, the posterior and lateral openings have become confluent. When only two openings are present one may still refer to them as the anterior and "posterior" openings, but it is important to remember that the posterior opening is not entirely homologous with the posterior opening of other forms (with three or four openings). In forms with two external openings in the pars jugularis, the orbital artery and jugular vein enter the posterior and leave through the anterior opening, while the hyomandibular trunk of VII leaves via the posterior opening.

In addition to the openings described above, the prootic may bear foramina for the oculomotor (III) and glossopharyngeal (IX) nerves.

The autosphenotic forms the posterodorsal corner of the orbit. Its dorsal surface is overlain by the dermosphenotic and the posterolateral corner of the frontal. The autosphenotic usually bears a distinct postorbital process for the tendinous origin of the levator arcus palatini muscle. The autosphenotic usually forms the dorsal part of the facet for the anterior head (or anterior portion of the head) of the hyomandibula.

The pterotic forms the floor and lateral wall of the posttemporal fossa. The pterotic usually bears an elongate facet for reception of the posterior head (or posterior portion of the head) of the hyomandibula.

The intercalar is a thin bone which is tightly articulated to the surface of the neurocranium. It overlies the adjacent portions of the prootic, pterotic and exoccipital, thereby obscuring the sutures between these elements. The intercalar bears a thickened facet for articulation with the ventral limb of the posttemporal.

The auditory bulla, which contains the otoliths of the inner ear, is variably developed. Often it is large (inflated). The wall of the bulla is formed by the prootic, exoccipital and basioccipital. In addition to these bony elements, an area of cartilage or membrane is often present in the wall of the bulla. This cartilage or membrane may completely separate the prootic and basioccipital. In some forms the anterior end of the swim bladder contacts the wall of the auditory bulla.

The Occipital Region (Fig. 50)

The occipital region is composed of the exoccipitals and the basioccipital. The exoccipitals usually completely surround the foramen magnum (i.e., the exoccipital meets its fellow both above and below the foramen magnum). Near the margin of the foramen magnum, the exoccipital usually bears a number of tiny foramina for the occipital nerves. More anteriorly, the lateral surface of the exoccipital bears a larger foramen for the vagus nerve (X). The exoccipitals and basioccipital form a concave, tripartite occipital facet for articulation with the first vertebra. The dorsolateral portions of the facet are provided by the exoccipitals, and articulate with the "prezygapophyses" of the first vertebra. The ventromedial portion of the facet is formed by the posterior end of the basioccipital, and articulates with the centrum of the first vertebra.

The basioccipital forms the posteriormost portion of the ventral surface of the neurocranium. The ventral surface of the basioccipital often bears a shallow groove for reception of the posterior end of the parasphenoid. The basioccipital is thick and heavily ossified posteriorly (in the region

of the occipital facet), but is thin anteriorly, where it contributes to the wall of the auditory bulla. Baudelot's ligament is usually attached to the lateral surface of the posterior part of the basioccipital.

The Circumorbital Bones (Fig. 51)

The circumorbital bones consist of a series of seven elements which partially surround the margin of the orbit. From anterior to posterior these are: antorbital (accessory nasal), lacrimal, infraorbitals one through four, and dermosphenotic. All of the circumorbitals except the antorbital carry a portion of the infraorbital branch of the lateral line system. In more primitive teleosts, the antorbital carries the terminal portion of the infraorbital lateral line (Patterson, 1964, p. 340). The dorsal or anterior borders of the circumorbitals are reflected outward to form a groove or channel for the passage of the lateral line. The circumorbitals vary considerably in their size, shape and degree of ornamentation. The circumorbital series is incomplete in most forms, since the antorbital is usually absent.

A subocular shelf is usually present. The shelf is composed of flanges which project medially from the inner margins of the dorsal or anterior borders of the infraorbitals. The number of infraorbitals which contribute to the formation of the subocular shelf varies.

The Hyopalatine Bones (Fig. 51)

The hyopalatine series is composed of the hyomandibula, metapterygoid, quadrate, symplectic, endopterygoid, ectopterygoid and palatine. The hyopalatine bones form a large triangle whose corners are represented by the dorsal portion of the palatine, the head of the hyomandibula and the condyle of the quadrate. The palatine and the head of the hyomandibula articulate with the neurocranium above, while the quadrate condyle, which forms the apex of the triangle, articulates with the lower jaw. The hyopalatine bones, along with the preopercle, form a functional unit--the suspensory apparatus (K. Liem, 1970, pp. 23-25).

The hyomandibula usually consists of a broad, plate-like dorsal portion and a narrow, rather cylindrical ventral portion (the symplectic process). Projecting back from the dorsal portion is a process for articulation with the opercle. The head of the hyomandibula may be single or double. The head(s) of the hyomandibula is covered with cartilage for articulation with the otic region of the neurocranium. When the head is single it is usually narrow and elongate. In the double-headed condition the anterior head is spherical while the posterior head is rather elongate. The medial surface of the dorsal portion of the hyomandibula bears a foramen for the entrance of the hyomandibular trunk of VII. The tip of the symplectic process of the hyomandibula is separated from the dorsal ends of the symplectic and interhyal (of the hyoid arch) by a small amount of cartilage.

The metapterygoid is rather nondescript. Its anteroventral edge is usually convex and separated by a narrow space from the dorsal border of the quadrate.

The quadrate is triangular and has anterior, posterior and dorsal borders. The anterior border tightly articulates with the ventral limb of the ectopterygoid while the posterior border articulates with the dorsal edge of

the ventral limb of the preopercle. The medial surface of the quadrate is excavated for reception of the lower portion of the symplectic. The quadrate condyle is located at the apex of the bone, and is composed of medial and lateral heads.

The symplectic is a slender, rod-like bone. Its upper portion may be weakly expanded.

The endopterygoid is usually a large, thin, plate-like bone. The endopterygoid slopes slightly upward as it passes medially, forming the roof of the palate and the floor of the orbit as it does so. The endopterygoid may be toothed.

The ectopterygoid usually consists of distinct ventral and dorsal limbs. The dorsal limb of the ectopterygoid may bear teeth.

The palatine is irregular-shaped. The anterior end of the palatine bears a distinct maxillary process. The maxillary process projects anterolaterally, and its tip lies between the medial surface of the anterior end of the lacrimal (laterally) and the base of the maxillary head (medially). The palatine is usually toothed.

The Dermal Upper Jaw (Fig. 51)

The dermal upper jaw consists of the premaxilla, maxilla and a variable number of supramaxillae.

The premaxilla forms the major portion of the margin of the upper jaw. Ascending, articular and alveolar processes of the premaxilla are always present. The ascending and alveolar processes lie at approximately right angles to one another. The ascending process projects posterodorsally, and is firmly bound to its fellow in the midline. Projecting back from the posterior aspects of the ascending processes is a large block of cartilage--the rostral cartilage. The articular process projects posteriorly from the angle between the ascending and alveolar processes. Its convex border rests in the groove between the condyles of the head of the maxilla. The alveolar process of the premaxilla runs parallel to the maxillary shaft. The maxilla is sometimes expanded behind the tip (distal end) of the alveolar process. The alveolar process is always toothed. A postmaxillary process of the premaxilla, projecting back from the posterior edge of the alveolar process, is usually present. The postmaxillary process shows a considerable amount of morphological variation.

The maxilla is composed of two parts--the head and shaft. The head consists of two condyles. One condyle is dorsally-directed; the other is anteromedially-directed. The shaft of the maxilla is rather cylindrical except for its lower (distal) end, which tends to be broad and plate-like. The maxillary shaft may be ornamented. The dorsolateral surface of the lower portion of the maxillary shaft is surmounted by the supramaxilla(e). The maxilla is usually toothless.

The supramaxillae vary in number, size, shape and degree of ornamentation. The anterior end of the posterior supramaxilla almost always bears a slender process which projects anteriorly and which overlies the dorsal edge of the anterior supramaxilla when that bone is present.

The Lower Jaw (Fig. 51)

The lower jaw consists of three bones: the dentary, angulo-articular

and retroarticular. Meckel's cartilage may also be present. The bones of the lower jaw vary widely in their degree of ornamentation.

The dentary is large and forms the anterior portion of the jaw. The dentary is >- shaped, with the apex of the > pointing anteriorly. The upper limb of the > forms the ascending process. The ascending processes of the dentary and angulo-articular combine to form the coronoid process of the mandible, which varies in its degree of development. The ascending process of the dentary is always toothed. Posteriorly, the dentary is excavated or "hollowed out" (i.e., there are inner and outer plates of bone with a cavity between them). The anterior ends of the angulo-articular and Meckel's cartilage (if present) fit into this hollow. Anteriorly, the dentary meets its fellow in the midline, forming the mandibular symphysis.

The angulo-articular is thin and plate-like anteriorly, but is more heavily ossified posteriorly, in the region of the jaw articulation. Usually the upper edge of the posterior end of the angulo-articular bears a saddle-shaped facet for reception of the quadrate condyle. The angulo-articular usually possesses a distinct retroarticular process which forms part of this facet, and which strengthens the jaw articulation posteriorly.

The retroarticular is a small bone which forms the posteroventral corner of the lower jaw (it "caps" the posteroventral portion of the angulo-articular) The interoperculomandibular ligament is attached to the retroarticular.

The mandibular branch of the lateral line courses along the lower portions of the angulo-articular and dentary. The angulo-articular receives the lateral line from the ventral limb of the preopercle (preopercular lateral line) and passes it on to the dentary. The mandibular lateral line may be "open" or "closed." Open refers to the condition in which the lateral line is in broad communication with the surface, lying in a wide channel which is bridged only by relatively narrow struts of bone. Closed refers to the condition in which the lateral line is largely enclosed within bone, opening to the surface only through relatively small pores.

The Opercular Bones (Fig. 51)

The opercular series is composed of the opercle, subopercle, interopercle and preopercle. Functionally, the preopercle belongs to the hyopalatine series (suspensory apparatus), because it serves as the origin of the adductor mandibulae muscles and its motions correspond with those of the hyopalatine bones and are independent of those of the opercle, subopercle and interopercle (K. Liem, 1970, p. 30). The opercular bones may be highly ornamented.

The opercle is a plate-like bone of variable shape. The medial surface of the anterodorsal portion of the opercle bears a distinct, concave facet for articulation with the opercular process of the hyomandibula. Anteriorly the opercle is loosely bound to the dorsal limb of the preopercle; ventrally it overlaps and is tightly bound to the dorsal border of the subopercle.

The subopercle is a rather elongate, plate-like bone whose posterior portion is sometimes only feebly ossified (membranous). The anterior end of the subopercle usually bears a spike-like process which projects dorsally and which lies against the lower portion of the anterior border of the opercle. The subopercle is bound to the interopercle anteriorly by connective tissue.

The interopercle is usually plate-like and is often oval in shape. The interopercle is partially overlapped by the ventral portion of the

preopercle. The anterior end of the interopercle is attached to the retroarticular by the interoperculomandibular ligament.

The preopercle is L-shaped, with dorsal (vertical) and ventral (horizontal) limbs. The posteroventral corner of the preopercle (angle) may be drawn out into a prominent spine. The anterior border of the preopercle is reflected outward to form a flange which overhangs and partially protects the preopercular lateral line.

The Hyoid Arch and Branchiostegal Rays (Fig. 52)

The hyoid arch is composed of the hyomandibula, symplectic, interhyal, epihyal, ceratohyal, dorsal and ventral hypohyals, and basihyal. The hyomandibula and symplectic, which represent ossifications in the dorsal portion of the hyoid arch, are both topographically and functionally associated with the other bones of the hyopalatine series, and are described with them (above). The bones of the ventral portion of the hyoid arch are involved with the support of the branchiostegal rays, and show a number of features not seen in the more posterior branchial arches, which support the gills.

The interhyal is a small, rod-like bone. Dorsally it articulates with the cartilage between the tip of the symplectic process of the hyomandibula and the upper end of the symplectic. Ventrally it articulates with a shallow, concave facet on the posterodorsal corner of the epihyal.

The epihyal is triangular and articulates with the posterior edge of the ceratohyal anteriorly. The lateral surfaces of the epihyal and ceratohyal may be distinctly grooved for the hyoidean artery.

The ceratohyal is the largest bone of the hyoid arch (excluding the hyomandibula). The ceratohyal is variable in shape (although it is usually rather rectangular). It meets the dorsal and ventral hypohyals anteriorly. A small amount of connective tissue may separate the ceratohyal and dorsal hypohyal, however. The ceratohyal is usually perforated by a foramen which is spanned by a tough membrane. The size and shape of this foramen vary considerably.

There are always two hypohyals (dorsal and ventral). The hypohyals vary in shape, but the ventral hypohyal is usually deeper. The hypohyals may be partly cartilaginous. The dorsal hypohyal articulates with the first basibranchial.

The basihyal is an unpaired element lying in the ventral midline. The size of the basihyal is variable and it may be partly cartilaginous. The basihyal is sometimes completely absent (i.e., neither bone nor cartilage present). Posteriorly, the basihyal articulates with the anterior end of the first basibranchial.

Dermal tooth patches are only rarely associated with the elements of the hyoid arch.

The urohyal is described with the hyoid arch for convenience. The urohyal is plate-like and lies in the sagittal plane between the two sternohyoid muscles, beneath the other bones of the visceral skeleton. The size and shape of the urohyal vary. The anterodorsal corner of the urohyal may bear a process for the attachment of a ligament from the tips of the third hypobranchials. The urohyal-hypohyal ligaments run from the anterior end of the urohyal to the medial surfaces of the hypohyals.

The branchiostegal rays lie embedded in and provide support for the

branchiostegal membrane. The proximal ends (heads) of the rays articulate with the lower portions of the ceratohyal and epihyal. The number, size, shape, degree of ornamentation, and mode of articulation of the rays vary.

The Branchial Arches (Fig. 25)

Posterior to the hyoid arch are five branchial arches. The morphology and disposition of the skeletal elements of the branchial arches show many similarities among the species examined. The general pattern of the branchial skeleton is as follows.

Lying in the ventral midline are four basibranchials. The remaining elements of the branchial arches are paired. The first three branchial arches are complete. From ventral to dorsal, each consists of a hypobranchial, ceratobranchial, epibranchial and pharyngobranchial. The fourth arch is incomplete. A hypobranchial is never present, and the pharyngobranchial may be present or absent. The fifth arch is also incomplete, and consists only of a ceratobranchial. Thus, in addition to the four median basibranchials (BB1-BB4), there are three hypobranchials (HB1-3), five ceratobranchials (CB1-5), four epibranchials (EB1-4), and three or four pharyngobranchials (PB1-4) on each side.

Each branchial arch (except the fifth) is < - shaped. The ventral limb of the < is composed of the hypobranchial and ceratobranchial (or the ceratobranchial only in the fourth arch). The dorsal limb consists of the epibranchial and pharyngobranchial (or the epibranchial only in those forms in which PB4 is absent). Only the ventral limb of the < is represented in the fifth arch (CB5). The proximal end of any of the paired elements of the branchial skeleton is that which lies closest to the basibranchials. Thus, the angle of the < is formed by the articulation of the distal end of a ceratobranchial with the proximal end of an epibranchial.

A variety of dermal elements may be associated with the endoskeletal branchial arches. These dermal elements generally fall into one of two categories: (1) gill rakers and (2) tooth patches. Gill rakers are more strongly developed on the anterior branchial arches. Those on the posterior arches tend to become reduced and resemble tooth patches. Tooth patches vary widely in number, size and shape. Tooth patches may either lie embedded within the pharyngeal epithelium, being supported by (but not fused to) the underlying endoskeletal elements, or they may be fused to the underlying bones.

BB1-BB3 are always at least partially ossified. BB1 is deep and square-shaped. BB2 and BB3 are more shallow and elongate. BB4 is usually a small, block-like element, and is always entirely cartilaginous.

HB1 and HB2 are relatively short, rod-like bones. The proximal end of HB1 articulates with the suture between BB1 and BB2. Similarly, the proximal end of HB2 articulates with the suture between BB2 and BB3. HB3 is tapered proximally but broad and plate-like distally. The proximal portion of HB3 projects anteroventrally, and its tip closely approaches its fellow in the ventral midline, below the rest of the visceral skeleton. Connective tissue binds the tips of the third hypobranchials together. Distally, HB1-HB3 articulate with the proximal ends of CB1-CB3. The distal end of HB3 also articulates with BB4.

CB1-CB4 are long and rod-like. CB5 is shorter than the others and is usually not rod-like. The proximal end of CB4 articulates directly with

BB4. The proximal end of CB5 usually articulates indirectly with BB4 via a short ligament. The distal ends of CB1-CB4 articulate with the proximal ends of EB1-EB4. The distal end of CB5 does not articulate with any element. It lies embedded in the pharyngeal wall.

EB1-EB4 are triradiate (in the broad sense of the term). Thus, each epibranchial consists of proximal, distal and dorsal "limbs". The proximal and distal limbs constitute the main portion of the epibranchial. The dorsal limb is in the form of a flange or process which projects upward from the main portion. The dorsal limbs of EB1 and EB2 (but especially that of EB2) are usually rather poorly developed (hence, EB1 and EB2 are only weakly triradiate). EB3 and EB4 are very similar morphologically. They are truly triradiate since the dorsal limbs (which are flange-like) are well-developed and are approximately equal in length to the proximal and distal limbs.

The pattern of articulation of EB1-EB4 with the adjacent bones is as follows. The tips of the proximal limbs of EB1-EB4 articulate with the distal ends of CB1-CB4, as mentioned above. The tip of the distal limb of EB1 articulates with the proximal end of PB1. The tip of the distal limb of EB2 articulates with both the proximal limb of PB2 and with a facet on the dorsal surface of the lateral portion of PB3. The articulation with PB3 may be direct or indirect (in the indirect articulation, a short tract of ligamentous fibers connects the two elements). The tip of the distal limb of EB3 articulates with the proximal end of PB3. The tip of the distal limb of EB4 articulates with PB4 when the latter element is present. Usually PB4 is absent, in which case the distal limb of EB4 also articulates with the proximal end of PB3. The tip of the dorsal limb of EB1 articulates with the dorsal limb of PB2. The dorsal limb of EB2 fails to articulate with any element. The tips of the dorsal limbs of EB3 and EB4 articulate with each other.

PB1 is always slender and rod-like. Its distal end is attached to the neurocranium in the region of the articulation of the prootic with the ascending process of the parasphenoid. PB1 serves to suspend the branchial skeleton from the neurocranium. PB2 is rather triradiate, with proximal, distal and dorsal limbs. The distal limb usually fails to make contact with any element. The articulations of the proximal and dorsal limbs are described above. PB3 is large and plate-like. Its proximal end articulates with PB4 if that element is present. Its distal end does not usually articulate with any element. PB4 (when present) consists of a small cartilaginous block.

CB5, EB3 and PB2 usually have tooth patches fused to them. PB1 is always toothless and PB3 is always toothed (tooth patch fused to it). PB4 may be toothed or toothless. The dermal tooth patch underlies, but is not fused to, PB4. PB4 is unusual in that it may be absent while its tooth patch persists.

The Vertebral Column and Ribs

(See Weitzman, 1962, p. 70, Fig. 14)

There are two types of vertebrae--abdominal (precaudal) and caudal. The number of vertebrae may be expressed in a formula (e.g., the formula 12 + 17 = 29 indicates a total of 29 vertebrae, 12 of which are abdominal and 17 of which are caudal). The vertebral counts always include the terminal vertebra, the second ural centrum, if that element is autogenous

(i.e., not fused to the preceding vertebra). The first preural and first ural vertebrae are always fused. This compound vertebra is counted as one. The first caudal vertebra is the first vertebra which possesses a complete, unpaired hemal spine, and which does not possess pleural ribs. The proximal end of the first proximal radial of the anal fin is a useful landmark, since it usually lies just anterior to the hemal spine of the first caudal vertebra.

The first abdominal vertebra is modified for articulation with the occipital facet of the neurocranium. The neural arch of this vertebra may be autogenous or fused with respect to its centrum. The neural arches of the remaining vertebrae (up to and including that of the third preural vertebra) are fused to their centra. The hemal arches of all of the caudal vertebrae up to and including the fifth preural vertebra are also fused. The neural and hemal arches form canals for the spinal cord and caudal artery and vein.

The centra are bony, amphicelous cylinders. The centra of the abdominal vertebrae may bear projecting processes--the basapophyses. The basapophyses become progressively better developed as one passes posteriorly. The basapophyses of the first caudal vertebra are fused together to form a complete, unpaired hemal spine.

Three different types of ribs may occur. Pleural (ventral) ribs are always present, and are confined to the abdominal vertebrae. The pleurals extend downward and surround the abdominal cavity. Epineural and epipleural ribs (intermuscular bones) may also be present. The epineurals and epipleurals may extend into the caudal region.

The Pectoral Girdle and Fin (Fig. 55)

The pectoral girdle consists of a crescent-shaped chain of bones lying just posterior and dorsal to the opercular cavity. The girdle is composed of dermal and endoskeletal elements. The dermal bones (from dorsal to ventral) are the extrascapular, posttemporal, supracleithrum, cleithrum and one or two postcleithra. The dermal bones are frequently ornamented. The endoskeletal bones are the scapula and coracoid. A mesocoracoid arch is never present. The pectoral fin itself consists of a series of endoskeletal radials (proximal radials or actinosts, and sometimes distal radials), in addition to a variable number of dermal lepidotrichia. The pectoral fin is always inserted vertically, high up on the flank.

The extrascapular is a thin, plate-like bone of variable size and shape. The extrascapular usually partially overlaps the dorsal limb of the posttemporal bone, and usually lies embedded in the skin over the posttemporal fossa.

The posttemporal is forked. It possesses distinct dorsal and ventral limbs. Usually the dorsal limb articulates with the epiotic and the ventral limb with the intercalar. Short ligamentous fibers serve to strengthen these articulations. The posttemporal overlies the upper portion of the supracleithrum, and its medial surface (at the junction of the two limbs) usually bears a distinct facet for articulation with the dorsal end of that bone.

The supracleithrum is variable in shape. Below, it overlaps the upper portion of the dorsal limb of the cleithrum.

The cleithrum is the largest bone of the pectoral girdle. It possesses

two distinct limbs (dorsal and ventral). Projecting back from the dorsal limb is a plate of bone, the posterior lamina. The tips of the ventral limbs of the cleithra meet in the ventral midline (cleithral symphysis).

There are usually two postcleithra. The dorsal postcleithrum articulates against the medial surface of the posterior lamina of the cleithrum. The dorsal end of the ventral postcleithrum articulates against the medial surface of the dorsal postcleithrum. The postcleithra project posteroventrally into the body wall.

Some of the dermal bones of the pectoral girdle are modified in relation to the lateral line. The general pattern of the lateral line on the pectoral girdle is as follows. The dorsal end of the supracleithrum receives the lateral line from the anteriormost lateral line scale of the trunk. The lateral line usually runs through a short canal in the supracleithrum before passing onto the posttemporal. Once on the posttemporal, the lateral line proceeds anterodorsally to the extrascapular, where it divides into two branches (the supratemporal lateral line and the main cephalic lateral line). These branches then pass onto the skull (p. 49). The posttemporal and extrascapular usually bear crests or ridges which partially protect the lateral line.

The scapula articulates with the cleithrum anteriorly and dorsally and with the coracoid ventrally. A narrow strip of cartilage may separate the scapula and coracoid for a part of their length, however. The scapula is usually pierced by a single foramen. Dorsally, the posterior border of the scapula bears a distinct, concave facet for articulation with the condylar base of the first fin ray. More ventrally, the posterior border may possess one or more facets for articulation with the proximal ends of the actinosts.

The coracoid articulates with the scapula and cleithrum above. Anteriorly, the coracoid is prolonged into a distinct process--the coracoid process. The tip of the coracoid process often contacts the ventral limb of the cleithrum near the cleithral symphysis; the space between these elements is the coraco-cleithral fenestra.

There are always four actinosts, although the fourth is sometimes enlarged, suggesting that a fifth has become fused to it. The actinosts increase in size from the first (above) to the fourth (below). Proximally, the actinosts articulate with the endoskeletal portion of the girdle. Distally, they articulate with the distal radials (if present). The distal radials are small nodules of bone or cartilage which lie just beyond the ends of the actinosts and between the bases of the fin rays. One of the halves of the first fin ray is condylar at its base.

The Pelvic Girdle and Fin (Fig. 56)

The pelvic girdle consists of a single endoskeletal element, the pelvic bone or basipterygium, which lies in the ventral part of the body wall. The pelvic bones are usually plate-like, and are sometimes firmly united in the midline. A distinct crest or ridge, termed the rachis (K. Liem, 1970, p. 42), is usually present on the lateral surface of the pelvic bone. The posteromedial portion of the pelvic bone may possess a number of processes (anterior, medial and posterior processes, which project in the direction which their name implies). A fourth process, the lateral process, may also be present. It arises from the posterolateral portion of the pelvic bone,

just anteroventral to the point of articulation of the pelvic fin spine or outermost fin ray. The pelvic fin spine (if present) and rays articulate with the posterior border of the pelvic bone, which is usually covered with a small amount of cartilage. Short ligamentous fibers serve to bind the elements of the pelvic fin to the girdle.

It is necessary at this point to discuss the difference between fin spines and fin rays (lepidotrichia). Fin spines are modified lepidotrichia (Patterson, 1964, pp. 442-444). Fin spines are elements which (1) are not split longitudinally into two halves (2) are not transversely segmented and (3) are not branched distally. Lepidotrichia are always split longitudinally. The paired halves of each lepidotrichium are bound together by connective tissue. Lepidotrichia may or may not be segmented and branched distally.

The pelvic fin usually contains a spine. The number of fin rays varies. The number of spines and rays may be expressed in a formula (e.g., the formula I,6 indicates the presence of one spine and six rays).[1] A variable number of "free" (i.e., not fused) endoskeletal radial elements is usually present. One of the halves of the innermost fin ray is often condylar at its base. This condylar base probably represents a free radial of more primitive teleosts which has become fused to the innermost ray. The pelvic fins are thoracic or subthoracic in position. The pelvic fins are thoracic if they are inserted ahead of the tip of the ventral postcleithrum (or the postcleithrum, if only one is present). The fins are subthoracic if they are inserted at or slightly behind the tip of the ventral postcleithrum.

The Dorsal and Anal Fins

(See Weitzman, 1962, pp. 72-73, Figs. 16-17)

The anterior elements of the dorsal and anal fins are usually true spines. The spinous portion of the dorsal fin may be separated from the soft portion (composed of rays). The spines may exhibit a variety of specializations. The internal (supporting) skeleton of the dorsal and anal fins consists of a series of elements termed pterygiophores. Each pterygiophore is typically composed of three discrete elements--a proximal, middle and distal radial. Incomplete pterygiophores are those which do not consist of three separate parts. The anterior pterygiophores of the fins are usually incomplete, and their radials usually modified, due to the fact that they are often involved with the support of the fin spines. The proximal end of a pterygiophore is that which lies closest to the vertebral column. The proximal ends of the proximal radials of the dorsal and anal fins interdigitate with the tips of the neural and hemal spines.

The proximal radials provide a site for the fleshy origin of the muscles of the fins. They often bear distinct crests or ridges which bisect their lateral surfaces. The middle radials lie between and articulate with the proximal and distal radials. The distal radials are "clasped" by the bases of the lepidotrichia (i.e., the bases of the two halves of each lepidotrichium articulate with the lateral surfaces of a distal radial). Fin stays (vestigial radials) may be present behind the last pterygiophore of the dorsal and anal fins.

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[1] The number of spines and rays in the dorsal and anal fins is expressed in a similar type of formula.

A variable number of predorsals and supraneurals may be present. The predorsals resemble the proximal radials of the dorsal fin, with which they are serially homologous. The supraneurals represent detached neural spines.

The Caudal Skeleton and Fin (Fig. 57)

The caudal skeleton is complex and exhibits a wide variety of specializations. Nybelin (1963, p. 487) has demonstrated that it is useful to recognize two regions in the caudal skeleton of teleosts--a preural region and a ural region. The parhypural (see below) marks the junction between these regions. The vertebrae of the caudal skeleton are therefore designated as preural or ural vertebrae. From anterior to posterior, the vertebrae of the caudal skeleton in beryciforms are as follows: third preural vertebra (PU3), second preural vertebra (PU2), first preural vertebra (PU1), first ural vertebra (U1) and second ural vertebra (U2). The caudal skeleton is considered to begin at the level of PU3 because the elements of this segment are usually the first to exhibit modifications for the support of the caudal fin. The fourth preural vertebra (PU4) is included in the illustrations of the caudal skeleton merely for comparison.

PU3 and PU2 are never fused to each other. PU1 and U1 are always fused (PU1 + U1). The last vertebra (U2) may be autogenous or fused with respect to PU1 + U1.

The neural arch of PU3 is always fused to its centrum, but the neural arch of PU2 may be autogenous or fused. The neural spine of PU2 varies in its degree of development.

The stegural is an element which is expanded and plate-like proximally. Distally it is drawn out into a long, slender process which projects posterodorsally. The proximal portion of the stegural may be autogenous or fused with respect to the underlying compound vertebra.

There are almost always three epurals (rarely two). They lie just above the proximal portion of the stegural and between the neural spine of PU3 (or PU2, if it bears a complete spine) anteriorly and the spinous process of the stegural posteriorly.

There is usually a single pair of uroneurals. The uroneurals are the only paired elements of the caudal skeleton [although the stegural, which represents a modified uroneural (Patterson, 1968, p. 50), may show traces of its bilateral origin]. The uroneurals are usually long and blade-like (tapered at both ends). They partially overlie the lateral surfaces of the spinous process of the stegural.

The hemal arches of PU2 and PU3 are usually autogenous. The hemal arch and spine of PU1 constitute an element which is given a special name--the parhypural. The parhypural is always autogenous (proximally, it articulates with PU1 + U1). The parhypural is the last structure to be perforated by the caudal artery and vein, and it bears the hypurapophysis (Patterson, 1968, p. 50). The hypurapophysis is a process which projects outward from the proximal portion of the parhypural. It serves as the anterolateral portion of the proximal attachment of the hypochordal longitudinal muscle (Nursall, 1963, p. 459). The size and shape of the hypurapophysis vary.

The stegural, epurals and uroneurals lie dorsal to the vertebral axis. Lying below this axis is a series of plate-like elements termed the hypurals. The proximal ends of the hypurals articulate with the terminal vertebrae. The distal portions of the hypurals support the principal rays

of the caudal fin. The number of hypural bones varies from two to six. Two factors are responsible for this variation: (1) loss of elements and (2) fusion between adjacent elements.

The caudal fin contains either 18 (9 + 9 = 18) or 19 (10 + 9 = 19) principal rays. The first number in the formula indicates the number of rays in the upper lobe of the fin, while the second represents the number in the lower lobe. The outermost principal ray in the upper and lower lobe is never branched distally. Lying anterior to the principal rays is a series of procurrent elements. The foremost members of the series are always spinous. Posterior to the procurrent spines is a variable number of procurrent rays. Procurrent rays are never branched distally.

Fulcral scales and urodermals are not present in the caudal skeleton.

CHAPTER IV

THE OSTEOLOGY OF THE BERYCIFORMES

(DETAILED DESCRIPTIONS)

The osteology of one species representative of each of the beryciform families (except the Stephanoberycidae, Gibberichthyidae and Melamphaeidae) is described in detail on the following pages. Bones which do not present any noteworthy features other than those discussed in the preceding chapter are not described. Following each major section of the description is a paragraph entitled "Remarks." Only the important morphological similarities and differences seen in the other members of the family are stressed here.[1] In general, important similarities and differences are those which involve characters that have been selected for analysis in this investigation.

Family Polymixiidae

Osteology of *Polymixia lowei* Günther

The neurocranium (Fig. 6)

The skull roof

The nasals are small, delicate bones. The upper edge of the nasal is reflected to form a partial canal for the lateral line.

The frontals are moderate sized. Anteriorly, the frontal articulates with the mesethmoid and lateral ethmoid (but not the nasal). Medially, the frontal meets its fellow (straight suture). Posteriorly, the frontal articulates with the supraoccipital, parietal, pterotic and both sphenotics (from medial to lateral). The orbital lamina of the frontal is poorly developed and only slightly overlaps the pterosphenoid. The frontal bears a low, smooth, bony canal which encloses the lateral line. There are no crests or ridges separating

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[1] The comments in the sections entitled "Remarks" apply only to the beryciform species listed in table 8 unless the names of additional species are specifically mentioned.

large mucous cavities, as in many other beryciforms.

The parietals meet the frontals anteriorly, the epiotics posteriorly, the supraoccipital medially and the pterotics posterolaterally. The parietal is unornamented except for a small, thin crest which projects dorsally from its lateral portion.

The epiotic meets the parietal anteriorly, the supraoccipital medially and the exoccipital posteroventrally.

The supraoccipital is large and extends anteriorly for a considerable distance. The anterior end of the supraoccipital partially overlies the frontals. The dorsal surface of the supraoccipital bears a very long, but rather low, crest. Although the supraoccipital crest is rather thin and delicate, the lateral surface of its posterior portion is reinforced by a thickened ridge.

The supratemporal fossa is extensive, extending anteriorly to a level well-ahead of the middle of the orbit. The supraoccipital forms most of the floor of the fossa. The posteromedial portion of the frontal, the parietal and the dorsal surface of the epiotic also contribute to the floor. The parietal crest forms a partial lateral boundary for the fossa.

The posttemporal fossa is quite small. The dorsal surface of the pterotic forms its entire floor. Projecting up from the dorsal surface of the pterotic is a thin, but well-developed, flange. This flange contacts the crest of the parietal anteriorly, and forms the lateral wall of the fossa. The lateral surface of the epiotic forms most of the medial wall.

The ethmoid region

The mesethmoid is relatively large. In this specimen it is completely surrounded by ethmoid cartilage. The mesethmoid bears a pair of anterolaterally-directed flanges for support of the nasals.

The lateral ethmoids are rather square-shaped. The medial portion of the lateral ethmoid is obliquely pierced by a round foramen for I.

The vomer bears an elongate patch of short, conical teeth. These teeth are not confined to the head of the vomer, as in most beryciforms, but rather extend back onto the anterior portion of the vomerine tail.

The orbital region

The parasphenoid is straight. It extends all the way back to the posterior end of the basioccipital (unlike the condition in most beryciforms). The shaft of the parasphenoid bears a pair of flanges for articulation with the endopterygoids. The ascending process is pierced by a small, round foramen for the internal carotid artery.

The orbitosphenoid is reduced in size. It is Y-shaped in cross section due to the development of a small plate or keel which projects ventrally into the interorbital septum.

The pterosphenoids are widely separated. The pterosphenoid articulates with the orbitosphenoid anteriorly, the frontal dorsally and the autosphenotic and prootic posteriorly. The pterosphenoid forms most of the lateral margin of the optic fenestra (the prootic contributes to the lateral margin more posteriorly). The ventral edge of the pterosphenoid is weakly notched for IV.

The basisphenoid is small. The arms of the basisphenoid articulate with the prootics. The pedicel is a slender rod whose upper portion is somewhat constricted. In another specimen of Polymixia which was examined, most of the basisphenoid pedicel was absent (replaced by strong ligamentous fibers).

The otic region

The prootic meets the pterosphenoid anterodorsally, the ascending process of the parasphenoid anteroventrally, the exoccipital posteriorly, the autosphenotic and pterotic dorsally, and the arm of the basisphenoid medially. The pars jugularis has three external openings which are separated by two struts of bone. The anterior strut is rather thick, but the posterior one is very slender. The lateral opening is very large. IX issues through a foramen situated close to the posterior opening of the pars jugularis.

The autosphenotic bears a poorly developed postorbital process. The autosphenotic and prootic form a concave facet for the anterior head of the hyomandibula.

The pterotic meets the frontal, parietal and both sphenotics anteriorly, the exoccipital posteriorly and the prootic ventrally. The pterotic does not bear a distinct facet for articulation with the posterior head of the hyomandibula. The dorsal surface of the pterotic is grooved for the main cephalic lateral line. This groove lies between the vertical flange of the pterotic (lateral wall of the posttemporal fossa) medially and the outer edge of the pterotic laterally. The outer (lateral) edge of the pterotic is slightly reflected upward. The preopercular lateral line branches off from the main cephalic lateral line just posterior to this reflected edge.

The intercalar presents no noteworthy features.

The auditory bulla is quite large. The wall of the bulla is formed by the prootic anterodorsally, the exoccipital posterodorsally and the basioccipital posteroventrally. In this specimen (83 mm SL) there is also a large area of cartilage in the wall of the bulla which separates the prootic and basioccipital. However, in a larger specimen of P. lowei (98 mm SL), as well as in the specimen of P. japonica figured by Starks (1904, p. 614, fig. 9), the cartilaginous area referred to above is absent (extensive prootic-basioccipital contact).

The occipital region

The exoccipital articulates with the pterotic and prootic anteriorly, the epiotic anterodorsally, the supraoccipital dorsally and the basioccipital ventrally. The vagal foramen is rather large. The exoccipital does not appear to be pierced by the occipital nerves. Apparently the latter issue through the foramen magnum.

Baudelot's ligament does not attach to the basioccipital. Rather, it is inserted onto the first vertebra.

The circumorbital bones (Fig. 7)

The antorbital is a small, delicate, crescent-shaped bone which lies just above the anterior end of the lacrimal and lateral to the nasal. Like the nasal,

the antorbital "floats freely" in the surrounding soft tissues (i.e., it does not make a firm articulation with any of the adjacent bones).

The lacrimal is shallow and elongate. The posterior four-fifths of the lacrimal extends back below the first infraorbital. The anterodorsal corner of the lacrimal bears a concave facet for articulation with the ventral end of the lateral ethmoid. The anterior part of the upper edge of the lacrimal is reflected to form a flange which overhangs the lateral line. The ventral border of the lacrimal is weakly serrated.

All of the infraorbitals are shallow. They decrease in size from the first to the fourth. The first infraorbital articulates with the lacrimal anteriorly and ventrally, while the fourth meets the dermosphenotic dorsally. The infraorbitals are poorly ornamented. The upper edges of all four are reflected outward for the lateral line, but only that of the first is serrated (weakly). The lower borders of all of the infraorbitals are irregular in outline, and are only feebly serrated. However, in some specimens the ventral edges of the third and fourth infraorbitals are more strongly ornamented.

A subocular shelf is developed on the posterior portion of the first infraorbital and the entire margins of the other three infraorbitals.

The dermosphenotic is a small, thin bone. The edge of the dermosphenotic is reflected in relation to the dorsal portion of the infraorbital lateral line. This reflected edge is smooth and is continuous with the orbital margin of the frontal.

The hyopalatine bones (Fig. 7)

The head of the hyomandibula is double. The anteroventral corner of the dorsal portion of the hyomandibula is prolonged into a distinct spike of bone which just barely touches the dorsal part of the metapterygoid. The symplectic process of the hyomandibula articulates with the posterior border of the metapterygoid. A short opercular process projects posteriorly.

The metapterygoid, quadrate and symplectic do not present any noteworthy features.

The oval-shaped endopterygoid meets the dorsal edge of the palatine anteriorly, the metapterygoid posteriorly and the dorsal limb of the ectopterygoid laterally. The medial edges of the endopterygoids articulate with the flanges on the shaft of the parasphenoid. The entire surface of the endopterygoid is covered with small, conical teeth.

The ectopterygoid is a gently curved, blade-like element. The ventral limb is very short, but the dorsal limb is long and tapered. The ectopterygoid bears small, conical teeth.

The palatine articulates with the ecto- and endopterygoids posterodorsally. There is some cartilage on the dorsal portion of the palatine in the region of articulation with the endopterygoid. Anterodorsally, the palatine bears a distinct facet for articulation with the ventral end of the lateral ethmoid. The anterior one-half of the long maxillary process is cartilaginous. The entire length of the palatine bears teeth.

The dermal upper jaw (Fig. 7)

The ascending process of the premaxilla is short. It is about one-quarter of the length of the alveolar process. The alveolar process tapers to a sharp

point distally. The entire length of the alveolar process is covered with closely set, conical teeth which decrease somewhat in size near its tip. The postmaxillary process is rather weakly developed. It is a shallow, gently convex flange (i.e., its posterior border is weakly convex) which arises from nearly the entire length of the alveolar process.

The distal portion of the maxillary shaft is strongly expanded into a thin, flat plate behind the tip of the alveolar process of the premaxilla. The lower edge of this plate is feebly serrated.

There are two supramaxillae. Both are thin, flat bones, and are devoid of ornamentation. The posterior supramaxilla is about three times larger than the anterior. In contrast to all of the other beryciform species examined, the posterior supramaxilla is truncated anteriorly.

The lower jaw (Fig. 7)

The dentary curves somewhat medially to meet its fellow in the mandibular symphysis. The upper border of the long ascending process bears short conical teeth along its entire length. Near the symphysis, the teeth are slightly expanded onto the lateral surface. Like the other bones of the lower jaw, the dentary is unornamented.

The angulo-articular bears a well-developed retroarticular process which projects posterodorsally. The jaw articulation is located slightly behind the posterior border of the orbit. The ascending process of the angulo-articular is not prominent, and together with that of the dentary, forms a low coronoid process.

The retroarticular presents no noteworthy features.

The mandibular lateral line is largely closed. It communicates with the surface via six pores. The largest opening lies within the angulo-articular at the point where it receives the lateral line from the preopercle. Another pore lies at the junction of the angulo-articular and dentary. The remaining pores lie entirely within the dentary.

The opercular bones (Fig. 7)

The opercle is diamond-shaped. The middle of its posterior border is weakly notched, resulting in the formation of two short and rather blunt projections. The opercle is otherwise devoid of ornamentation (the lateral surface is smooth, unlike the condition in many beryciforms where it bears serrated crests or ridges). The facet for the opercular process of the hyomandibula is reinforced by a thickened ridge.

The subopercle is elongate and somewhat rectangular.

The dorsal portion of the interopercle is more strongly ossified than the remainder of the bone. The lower edge of the interopercle is weakly serrated.

The preopercle consists of a long dorsal limb and a very short ventral limb. The anterior border of the preopercle is reflected to form a flange which protects the lateral line, and is bound to the suspensorium (mainly the hyomandibula) by connective tissue. The angle of the preopercle is feebly serrated.

The hyoid arch and branchiostegal rays (Figs. 8-9)

The interhyal presents no noteworthy features.

The epihyal is separated from the ceratohyal by a narrow strip of cartilage. The lateral surfaces of the epihyal and ceratohyal are distinctly grooved for the hyoidean artery.

The dorsal border of the ceratohyal is straight, but its ventral border bears several shallow indentations. The dorsal portion of the ceratohyal is perforated by an elongate (slit-like) foramen, which lies just above the groove for the hyoidean artery. [Two other specimens of Polymixia showed a similar condition with respect to the ceratohyal foramen. These observations do not agree with Patterson's statement (1964, p. 302) that the ceratohyal of Polymixia is imperforate]. Anteriorly, the groove for the hyoidean artery leads into a canal between the dorsal and ventral hypohyals. The canal then passes forward, and opens onto the medial surface of the hyoid arch between the hypohyals.

A narrow band of cartilage separates the hypohyals. The dorsal hypohyal is rather elongate. Its posterior portion is cartilaginous. The ventral hypohyal is slightly deeper than the dorsal hypohyal. The broad urohyal-hypohyal ligament attaches to the medial surfaces of both hypohyals.

The basihyal is broad anteriorly but tapered posteriorly. The anterior two-thirds of the basihyal is cartilaginous. Embedded within the epithelium over the dorsal surface of the basihyal is a large, oval tooth plate.

The urohyal is relatively shallow. It is very thin and pliable. The dorsal border is weakly concave; the ventral border weakly convex. The posterodorsal corner is drawn out into a moderately long, pointed process, but the posteroventral corner is only slightly attenuated. The anterodorsal corner of the urohyal bears an ill-defined process for the attachment of a ligament from the tips of the third hypobranchials. The anterior border of the urohyal is distinctly grooved. The urohyal-hypohyal ligaments attach to the lips of this groove.

The epithelium overlying the dorsal surface of the dorsal hypohyal may have small tooth patches embedded in it (two of three specimens).

There are seven branchiostegal rays. The first three rays articulate with the ventral border of the ceratohyal, the fourth, fifth and sixth with the lateral surface of the ceratohyal, and the seventh with the lateral surface of the epihyal. The first three rays are shorter than the others, and are modified to support the hyoid barbel (note: there are two barbels--one on each side). The first two rays are identical morphologically. They are sinuous or "twisted." They lie close together, and run parallel to each other. The third ray is broad and flat (leaf-like). The distal ends of the first three rays clasp the proximal portion of the barbel, thereby providing support for it. The presence of branchiostegal rays modified for the support of a barbel was not seen in any of the other beryciform species examined.

The branchial arches (Fig. 9)

BB1 is square-shaped. It is ossified superficially but cartilaginous internally. BB2 is rather rod-like. Its ends are capped with cartilage. BB2

has a very large, elongate tooth plate fused to its dorsal surface. This plate also extends anteriorly over BB1 and posteriorly over BB3, but it is not fused to these elements. BB3 is the longest basibranchial. Its posterior tip is cartilaginous and is bent downward. The anterior end of BB3 is slightly expanded for support of the tooth plate described above. BB4 is a small cartilaginous block.

The hypobranchials and epibranchials present no noteworthy features.

CB5 differs from the other ceratobranchials in that a large, triangular tooth plate is fused to its dorsal surface. The teeth are short and conical. The proximal end of CB5 is tied to the posteroventral aspect of BB4 by a short ligament.

There are four pharyngobranchials. PB2 and PB3 have tooth patches fused to them. The tooth plate of PB4 is moderate sized.

The vertebral column and ribs

The vertebral formula is 12 + 17 = 29. The neural arch of the first vertebra is autogenous. The first hemal spine is shorter and slightly more robust than the others. Prezygapophyses begin to become distinct on the anterior caudal vertebrae. Postzygapophyses are present on the second through the twenty-sixth vertebrae.

The centra of the third through the twelfth vertebrae bear basapophyses. The basapophyses of the third, fourth and fifth vertebrae project more laterally than the others. The basapophyses of the third through the ninth vertebrae are not fused together in the midline. The remaining basapophyses are partially fused, thus forming a canal for the dorsal aorta.

Pleural ribs are present on all except the first two abdominal vertebrae. The first three pleurals articulate more or less directly with the centra, adjacent to the basapophyses. The other pleurals articulate with their basapophyses.

Epipleural and epineural ribs are also present. The epipleurals articulate with the last four pleural ribs (as their name suggests) and with the lateral surfaces of the first seven hemal spines. Epineurals are borne by all of the abdominal and the first seven caudal vertebrae. Only the anterior and posterior members of the series of epineurals articulate with neural arches or spines, as their name suggests. P. lowei is the only beryciform species examined which possesses epineurals.

The pectoral girdle and fin (Fig. 10)

The extrascapular is rather small, thin and irregular in shape. It lies in the skin over the posttemporal fossa, but does not articulate directly with any other bone. The extrascapular is unornamented except for a delicate crest formed by the reflection of its anteroventral edge. This crest forms a partial canal for the lateral line.

The posttemporal consists of a flat, blade-like dorsal limb and a long, slender ventral limb. The posttemporal overlies the upper portion of the supracleithrum, but there is no distinct facet on its medial surface for articulation with the dorsal end of that bone. The posttemporal bears a thin crest which partially protects the lateral line. The posterodorsal edge of

the posttemporal is weakly serrated.

The supracleithrum is blade-like. Its anterior edge and dorsal end are thickened.

The cleithrum has a moderately short dorsal limb and a long ventral limb. The dorsal limb is spike-like above. A thin but distinct posterior lamina is present.

There are two postcleithra. The dorsal postcleithrum is thin and plate-like, and is rather elongate. Its anterior edge is somewhat thickened. The ventral postcleithrum is very long and slender except dorsally, where it is weakly expanded.

The center of the scapula is pierced by a large, round foramen.

The coracoid process is of moderate length, but is not particularly slender (gracile) The posteroventral border of the coracoid is slightly reflected.

The first actinost is short and stout, and is hourglass-shaped. The other three are more elongate and rod-like in appearance. The first two actinosts articulate with the scapula, the third with the scapula and the cartilage between the scapula and coracoid, and the fourth entirely with this cartilage. In another specimen the third actinost articulated solely with the scapula.

There are three distal radials. They are small, partially ossified nodules related to the bases of the second, seventh and ninth fin rays.

The pectoral fin contains 17 rays. All except the first are segmented, and all except the first, second, fifteenth, sixteenth and seventeenth are branched distally.

The pelvic girdle and fin (Fig. 11)

The pelvic bones are relatively elongate and are not firmly united in the midline. The rachis divides the dorsolateral surface of the pelvic bone into a small ventral and a large, plate-like dorsal portion. The anterior portion of the rachis is cylindrical, but it becomes thin and crest-like posteriorly. The anterior tip of the rachis closely approaches its fellow. The posterior end of the rachis is considerably thickened, and forms a substantial portion of the articular surface for the radial of the outermost fin rays. The ventral surface of the pelvic bone bears a very short, low crest which rapidly becomes thickened posteriorly. This crest and thickening are confined to the posterior part of the ventral surface, and correspond in position to the posterior part of the crest and thickened end of the rachis on the dorsal surface.

The posteromedial portion of the pelvic bone bears two processes. There is a strong, moderately long medial process which overlaps its fellow. There is also a much longer, but equally well-ossified, posterior process. The posterior processes of the pelvic bones run parallel but do not lie very close together. The posterior process is slightly expanded in its middle portion, but it tapers to a point distally. Anterior and lateral processes of the pelvic bone are absent.

The pelvic fin formula is 0,7. The outermost ray is heavier (more spinous) than the others. All of the rays are segmented, and all except the first are branched distally. The pelvic fins are subthoracic.

There are three radials. The first two are completely ossified, but the third is cartilaginous internally. The first radial is a large, wedge-shaped

element, with two shallow, concave facets for articulation with the bases of the first two fin rays. The second radial is related to the bases of the third and fourth rays, and the third radial to the fifth and sixth rays. The seventh ray articulates directly with the pelvic bone, at a point just lateral to the base of the posterior process.

The dorsal fin

The dorsal fin formula is IV,32. The spines increase in length from front to rear. The first spine is quite small, but the fourth is very long. All of the rays are segmented, and all except the first are branched distally.

There are 35 pterygiophores. The first eight are incomplete. The first two spines are related to the first pterygiophore; behind this level there is a 1:1 relationship between pterygiophores and spines or rays. The first 13 proximal radials are broad and plate-like. The remaining proximals are slender, rod-like elements. The first proximal is inserted between the fourth and fifth neural spines. The middle radials (especially the posterior ones) are weakly ossified superficially. The distal radials of the first four pterygiophores are modified for articulation with the fin spines. The distals of the other pterygiophores are more typical in form, being cartilaginous nodules which are ossified on their dorsolateral surfaces. There is one dorsal fin stay. It is small and weakly ossified (cartilaginous internally).

The three predorsals resemble the proximal radials of the dorsal fin, except that they lack prominent ridges on their lateral surfaces. The first predorsal is inserted between the skull and the first neural spine, the second between the first and second neural spines, and the third between the third and fourth neural spines.

Supraneurals are absent.

The anal fin

The anal fin formula is IV,16. The spines increase in length from front to rear. The first spine is very small but the fourth is very long. All of the rays are segmented and branched distally.

There are 18 pterygiophores, the first six of which are incomplete. The first three spines are related to the first pterygiophore. The first proximal radial is highly modified. It is much larger than the others. The tapered upper end of the first proximal projects far dorsally, and lies within a groove on the anterior aspect of the first hemal spine. The lower portion of the first proximal is greatly expanded, and bears a well-developed spinous process which projects anteriorly. The lateral surface of this expanded portion provides a site for the attachment of a muscle which inserts, by tendinous slips, onto the bases of the first two spines. The spinous process is for the tendinous origin of the retractor ischii muscle. In addition to the modifications already noted, the anterior surface of the first proximal is deeply excavated for reception of the posterior end of the swim bladder. The lower portions of the succeeding seven proximals are also somewhat expanded, and bear distinct ridges on their lateral surfaces. The ninth proximal is transitional in nature, while the remaining elements are slender and rod-like, without ridges on their surfaces.

The middle radials are similar in morphology to those of the dorsal fin. The first two distal radials are modified, like those of the dorsal fin, for articulation with the fin spines. The other distals are cartilaginous nodules which are ossified on their superficial surfaces. The anal fin stay is identical to that of the dorsal fin.

The caudal skeleton and fin (Fig. 12)

U2 is autogenous with respect to PU1 + U1. U2 is rather large and a faint line on its surface suggests that it may be compound (i.e., represent two fused vertebrae).

The neural spines of PU3 and PU2 are longer than that of PU4. The presence of a complete neural spine on PU2 is unique to P. lowei among the beryciform species examined. The base of the neural spine of PU3 is slightly expanded and that of PU2 considerably expanded in the sagittal plane. The hemal spines of PU3, PU2 and the parhypural are also longer and more expanded than that of PU4. There is an elongate piece of cartilage which articulates with the anterior aspect of the distal portion of the hemal spine of PU3. The parhypural bears a long, spike-like hypurapophysis which projects posterolaterally. The neural arch of PU2 is fused to its centrum. The hemal arches of PU2 and PU3 are autogenous.

The stegural is autogenous. Its proximal portion overlies the dorsolateral aspects of PU1 + U1. There is a single pair of blade-like uroneurals.

The three epurals are long, slender, rod-like elements. They decrease slightly in length from the first to the third. The epurals are closely packed together. Ventrally, the epurals articulate with small facets on the dorsal edge of the stegural.

There are six hypurals (H1-H6), all of which are autogenous. Proximally, the first and second hypurals articulate with PU1 + U1 (the second also articulates slightly with U2). The third, fourth and fifth hypurals articulate with U2. The sixth hypural is wedged in between the fifth hypural below and the uroneurals above. It fails to contact U2. The proximal ends of the fifth and sixth hypurals are forked; in the case of the fifth hypural, the halves of the forked base lie on either side of U2. The first, third and fourth hypurals are large. The posterior edge of the third hypural is irregular in outline, and is not as distinctly notched as in the specimen of P. nobilis figured by Patterson (1968, p. 56, fig. 6). The second hypural is moderate in size, while the fifth and sixth are rather small, slender elements.

The caudal fin formula is 9 + 9 = 18. There are six procurrents above and five below. The first four above and the first three below are spinous. The bases of the procurrent spines are forked. The first procurrent above is supported by the tip of the neural spine of PU3. The first procurrent below is supported by the tip of the hemal spine of PU3 and the piece of cartilage described above.

The squamation

Ventral ridge scales are absent.

Family Anoplogasteridae

Osteology of *Anoplogaster cornuta* (Valenciennes)

The neurocranium (Figs. 13-14)

The skull roof

The nasals are large, well-ornamented bones which are firmly bound to one another in the midline. The medial and lateral edges of the nasal are reflected upward, forming a trough for the lateral line. Anteriorly, a bridge of bone joins the edges of the nasal, thus forming a roof over the lateral line. The edges of the nasal and the bridge of bone referred to above bear small serrations.

The frontals are large and form most of the dorsal surface of the skull. They extend back a considerable distance beyond the posterior border of the orbit. Anteriorly, the frontal is broad and is slightly overlain by the nasal. The anterior end of the frontal overlaps the dorsal aspects of the mesethmoid and lateral ethmoid. Medially, the frontal meets its fellow in a straight suture. Posteriorly, the frontal articulates with the supraoccipital, parietal, pterotic and both sphenotics (from medial to lateral). The frontal contacts the pterosphenoid and autosphenotic in the orbit. The portion of the frontal overlying the orbital region is fenestrated with tiny pores, some of which transmit branches of the superficial ophthalmic nerves.

The frontal bears a series of serrated crests which separate rather deep mucous cavities. The crests are arranged in a $\rtimes$ pattern. There is an anteromedial crest which meets its fellow in the midline anteriorly, and which is continuous with the medial crest (edge) of the nasal. A low, broad, anterolateral crest runs out to the portion of the frontal which overlies the lateral ethmoid. It is continuous with the lateral crest (edge) of the nasal. Posteriorly, there are three diverging crests--posteromedial, posterolateral and posterointermediate. In some specimens, the posteromedial and posterointermediate crests are not sharply differentiated. The posteromedial crest is separated from its fellow in the midline by a small gap. The posterolateral crest is short but distinct. The posterointermediate crest runs straight back and closely approaches a longitudinal crest on the parietal.

The parietals are large. The parietal meets the frontal anteriorly, the epiotic ventrally, the supraoccipital medially and the pterotic laterally. The parietal extends back to overlie the entire dorsal surface of the epiotic. Thus the parietal, not the epiotic, forms the posterodorsal corner of the neurocranium. The dorsal surface of the parietal bears two serrated crests. The more lateral crest is much more prominent, and runs longitudinally for most of the length of the bone.

The epiotic meets the parietal dorsally, the pterotic and exoccipital ventrally, and the supraoccipital medially. The epiotic is visible only in posterior view, where it forms a vertical plate on the occipital surface of the skull.

The supraoccipital bears a very small, rather triangular-shaped crest.

The supraoccipital crest projects posteriorly from the occipital surface of the skull. The tip of the crest is prolonged into a tiny spine. The lateral surface of the crest is reinforced by many fine trabeculae.

Supratemporal and posttemporal fossae are absent. The epaxial musculature inserts on the occipital surface of the skull (including the supraoccipital crest). The epiotic and exoccipital form most of this surface.

The ethmoid region

The mesethmoid is rather small (although not as reduced as in some beryciforms). Dorsally the mesethmoid is overlain by the anterior ends of the frontals and the posterior ends of the nasals.

The lateral ethmoids are large, and are cartilaginous internally. The lateral ethmoid meets the frontal dorsally, the orbitosphenoid and mesethmoid medially, and the vomer and shaft of the parasphenoid ventrally. Ventrolaterally, the lateral ethmoid bears facets for articulation with the lacrimal and palatine. The center of the lateral ethmoid is pierced by a large, round foramen for I.

The vomer is short and broad. It bears large, smooth facets for articulation with the heads of the maxillae. The vomer is toothless.

The orbital region

The parasphenoid is straight. Posteriorly, it overlies the anterior one-half of the ventral aspect of the basioccipital. The parasphenoid shaft is flattened dorsoventrally. The shaft sends up a pair of flanges or thin sheets of bone which meets the "leaves" of the basisphenoid pedicel and the orbitosphenoid keel (see below). The ascending processes are weakly developed. The ascending process articulates with the anteroventral part of the prootic, but an oval space exists between the edges of the bones for the internal carotid artery.

The orbitosphenoid is large. Ventrally, it is expanded into a large plate or keel which, along with the basisphenoid pedicel (also expanded) and the flanges of the parasphenoid, forms an ossified interorbital septum. The orbitosphenoid keel and basisphenoid pedicel each consist of two thin sheets (leaves) of bone. The interorbital septum is therefore double-walled. Just anterior to the keel, the orbitosphenoid bears a round foramen in the midline for I.

The pterosphenoids are rather large, but fail to meet one another. The pterosphenoid meets the orbitosphenoid anteriorly, the autosphenotic and prootic posteriorly, the frontal dorsally, and the arm of the basisphenoid ventrally. There is a small foramen for IV in the ventral portion of the pterosphenoid, slightly above its articulation with the basisphenoid.

The arms of the basisphenoid are broad, and articulate with the orbitosphenoid, pterosphenoids and prootics. The optic fenestra is small and is bounded <u>entirely</u> by the arms of the basisphenoid (arms exclude both the prootics and pterosphenoids from entering into the margin of the fenestra--an unusual condition among beryciforms). The pedicel of the basisphenoid is strongly compressed, and meets the orbitosphenoid keel anteriorly and the flanges of the parasphenoid ventrally. The myodome is very small.

The otic region

The prootic meets the pterosphenoid anteriorly, the parasphenoid anteroventrally, the exoccipital posteriorly, the autosphenotic and pterotic dorsally, and the basisphenoid medially. The pars jugularis has only two external openings. Just medial to the anterior opening, the orbital face of the prootic bears a large, round foramen for the superficial ophthalmic nerves and the infraorbital trunk. III emerges through an elongate foramen between the edges of the prootic and basisphenoid, while IX leaves through a small foramen located just anterior to the suture with the exoccipital.

The autosphenotic does not possess a distinct postorbital process, although its lateral edge does provide a site for the tendinous origin of the levator arcus palatini. The anterior one-third of the facet for the head of the hyomandibula is formed within the cartilage between the autosphenotic and prootic.

The pterotic meets the frontal and both sphenotics anteriorly, the exoccipital posteriorly, the parietal and epiotic dorsally, and the prootic ventrally. The posterior two-thirds of the elongate facet for the head of the hyomandibula is formed within the pterotic. The posterolateral corner of the pterotic is prolonged into a small, delicate process. The lateral edge of the pterotic forms a weakly serrated crest. The main cephalic lateral line passes forward on the pterotic just medial to this crest. The preopercular branch passes ventrally onto the dorsal limb of the preopercle between the delicate process of the posterolateral corner of the pterotic and the posterior end of the pterotic crest.

The intercalar presents no noteworthy features.

The auditory bulla is oval-shaped and is greatly inflated. The wall of the bulla is formed by the prootic anterodorsally, the exoccipital posterodorsally and the basioccipital posteroventrally. The parasphenoid also makes a slight contribution to the medial portion of the anteroventral part of the bullar wall. A large portion of the bulla is formed by cartilage.

The occipital region

The exoccipital meets the prootic and pterotic anteriorly, the epiotic and supraoccipital dorsally, and the basioccipital ventrally. The exoccipital is very thin anteroventrally, where it contributes to the wall of the auditory bulla. X issues through a moderately large, round foramen.

The basioccipital presents no noteworthy features, except that Baudelot's ligament is absent.

The circumorbital bones (Fig. 15)

The antorbital is absent.

The lacrimal is a deep, square-shaped bone which meets the first infraorbital posteriorly. Anterodorsally the lacrimal bears a concave facet for articulation with the ventral portion of the lateral ethmoid--this articulation is strengthened by ligamentous fibers. Three narrow struts of bone roof over the lateral line. The lacrimal, infraorbitals, and all of the other dermal elements of the jaws, opercular apparatus and hyopalatine series are fenestrated with innumerable tiny pores, which give the bones a "lacy" appearance.

All four infraorbitals are very deep. The first infraorbital is rectangular. The second is deeply notched on its ventral border, resulting in the

formation of two long processes. The third and fourth infraorbitals are similar in shape--the ventral portion of each is prolonged into a single, long process. The more posterior process of the second infraorbital, as well as those of the third and fourth infraorbitals, extends back to make a firm articulation with the dorsal limb of the preopercle. The anterior process of the second and the ventral edge of the first infraorbital slightly overlap the maxillary shaft (the necessity of a mobile maxilla precludes a firm articulation with the infraorbitals). Narrow struts of bone roof over the lateral line. There are two struts on each of the first two infraorbitals, but only a single strut on infraorbitals three and four.

There is a weakly developed subocular shelf along the entire length of the second infraorbital (note: the eyes in Anoplogaster are very small). The subocular shelf was examined in three specimens, and in all it was of the same peculiar form--quite different from that seen in other beryciforms. The upper portion of the second infraorbital is split into medial and lateral laminae. It is the medial lamina, which projects upward (mainly) and slightly medially, which constitutes the shelf. My observations do not agree with those of Woods and Sonoda (1973, p. 386), who report that a subocular shelf is absent in Anoplogaster.

The dermosphenotic is a small, thin bone. It bears a delicate, weakly serrated crest which roofs over the lateral line as it passes ventrally onto the fourth infraorbital.

The hyopalatine bones (Fig. 15)

The hyomandibula is obliquely oriented, sloping backward at a rather large angle. The hyomandibula bears a single head. The opercular process is well-developed and slopes posteroventrally. The anterior edge of the dorsal portion of the hyomandibula is prolonged into a short, spinous process which fails to contact the metapterygoid. The anterior edge of the symplectic process of the hyomandibula articulates with the posterior border of the metapterygoid.

The metapterygoid does not present any noteworthy features.

The quadrate is deep.

The symplectic is very long and slopes forward from the tip of the symplectic process of the hyomandibula, making an angle of 140° with the latter.

The endopterygoid is irregular-shaped. It meets the palatine anteroventrally, the metapterygoid posteriorly and the dorsal limb of the ectopterygoid laterally. The endopterygoid is toothless.

The ectopterygoid possesses dorsal and ventral limbs which are long and tapered. The angle between the limbs is not sharp. At the junction of the two limbs, the ectopterygoid is overlapped by the metapterygoid. The ectopterygoid is toothless.

Posterodorsally, the palatine articulates with the dorsal limb of the ectopterygoid and the anterior part of the endopterygoid. Anterodorsally, the palatine bears a facet for articulation with the ventral portion of the lateral ethmoid. The palatine bears a short maxillary process which is not capped with cartilage. The palatine is feebly toothed (in this specimen, there are two tiny teeth on one side and four on the other).

The dermal upper jaw (Fig. 15)

The ascending process of the premaxilla is only one-fourth of the length

of the alveolar process. The dorsal portion of the rostral cartilage is superficially ossified. The alveolar process is very long, and bears three fang-like teeth. The first (most anterior) fang is the largest, and tapers to a sharp point. The other two fangs are somewhat shorter and are approximately equal in length. The tips of these two fangs are weakly expanded (bulbous). The fangs are set within sockets in the alveolar process, and interdigitate with those of the lower jaw. Between the fangs there are a few very small, conical teeth. Posterior to the third fang, the alveolar process also bears a series of small teeth which extend nearly to its tip. In contrast to the other beryciform species examined, a postmaxillary process is not present.

The head of the maxilla is grooved anteriorly for reception of the articular process of the premaxilla. Although areas corresponding to the two condyles of other forms are recognizable, distinct dorsal and anteromedial condyles are not present. The maxillary shaft is very long and cylindrical. It is poorly ossified. The distal portion of the shaft is not expanded behind the tip of the alveolar process.

There is a single supramaxilla. It is plate-like posteriorly, but its anterior end tapers to a short, spinous process. The supramaxilla is unornamented except for a few feeble serrations along its ventral edge.

The lower jaw (Fig. 15)

The dentary is slightly deepened at the symphysis. The ascending processes of the dentary and angulo-articular meet one another (there is no gap, spanned by membrane, as in many other forms). Together, the ascending processes form a low, rounded coronoid process. The dentary bears three fangs. As in the upper jaw, the anterior fang is tapered distally, while the other two bear bulbous cusps. A row of very small conical teeth is present posterior to the third fang. A pocket within the epithelium of the palate forms a sheath for the anterior fang of the lower jaw when the mandible is adducted. The dentary, like the other bones of the lower jaw, is unornamented.

The facet which the angulo-articular bears for the quadrate condyle is located well-behind the posterior border of the orbit. Unlike the other beryciforms examined, the facet is not "notched out" of the upper edge of the angulo-articular, but rather is located on the medial aspect of the bone. This is due to the fact that the angulo-articular sends back a prominent flange just lateral to the facet, thereby forming a bony lateral wall for the jaw joint. There is no retroarticular process.

The retroarticular presents no noteworthy features.

The mandibular lateral line is largely open. In the anterior part of the dentary, however, there are two bridges of bone which roof over the lateral line, resulting in the formation of two pores. The posterior bridge is narrow but the anterior one is much wider. The pore just ahead of the posterior bridge is of moderate size and is oval in shape. The anterior pore is a small, round opening located close to the symphysis. Posteriorly, the angulo-articular also bears a rather wide bridge of bone which protects the lateral line.

The opercular bones (Fig. 15)

The opercle is small due to the fact that it is very narrow anteroposteriorly. The facet for the opercular process of the hyomandibula is

reinforced by a short ridge. The posterior edge of the opercle is scalloped, resulting in the formation of three distinct spines. The entire lateral surface of the opercle bears low, delicate ridges which are weakly serrated along their edges. The ridges radiate outward to the edge of the opercle.

The subopercle is small. Its posterior portion is membranous.

The interopercle is long and narrow. It tapers to a point at both ends.

The preopercle consists of a very long dorsal limb and a short ventral limb. The angle between the limbs is not sharp (about 145°). The dorsal limb lies against a ridge on the lateral surface of the hyomandibula. The lateral line lies in an open groove except near the angle, where a wide bridge of bone roofs over it. This bridge bears a short spine on its edge. The lower border of the ventral limb also bears several distinct spines, the posteriormost of which is the largest.

The hyoid arch and branchiostegal rays (Fig. 16)

The interhyal presents no noteworthy features.

The epihyal meets the ceratohyal in a straight suture. The lateral surfaces of the epihyal and the posterior one-half of the ceratohyal are distinctly grooved for the hyoidean artery.

The ventral margin of the ceratohyal is deeply indented. Anteriorly, the ceratohyal articulates directly with the dorsal and ventral hypohyals, although connective tissue strengthens the junction between these elements. In this specimen, the center of the ceratohyal bears a small, oval foramen (in another specimen the ceratohyal was imperforate). Anterior to the level of the foramen, the hyoidean artery lies in a very shallow, indistinct groove. This contrasts with the condition seen in many other beryciforms, in which there is a deep groove (or canal) within the anterior portion of the ceratohyal. From the anterior end of the ceratohyal, the hyoidean artery passes into a canal within the dorsal hypohyal. The artery finally emerges onto the medial surface of the dorsal hypohyal.

The hypohyals meet in a straight suture. The dorsal hypohyal is both deeper and longer than the ventral hypohyal, and its posterior edge is cartilaginous. The medial aspect of the ventral hypohyal is the site of attachment of the urohyal-hypohyal ligament.

The basihyal is absent.

The urohyal is greatly reduced. It is about one-half of the size of the ventral hypohyal. The urohyal is roughly triangular in lateral view. The anterior edge of the bone is flattened into a broad surface for attachment of the urohyal-hypohyal ligaments.

There are eight branchiostegal rays (although in another specimen there were eight rays on one side and nine on the other). The rays increase in length from front to rear. The first four rays articulate with the ventral edge of the ceratohyal, the fifth with the lateral surface of the ceratohyal, and the last three with the lateral surface of the epihyal.

The branchial arches

BB1 and BB2 are ossified on their dorsal and lateral surfaces, but are cartilaginous internally. The anterior end of BB3 is also cartilaginous, but

posteriorly it is well-ossified. BB4 is a large block of cartilage; not a small, nodular element, as in many other forms. The basibranchials are toothless.

The hypobranchials show no unusual features except that the proximal end of HB2 has a moderate sized patch of needle-like teeth fused to it.

All of the ceratobranchials are slender, rod-like bones. The proximal end of CB5 articulates directly with the posteroventral portion of BB4 (not indirectly via a ligament). A direct articulation between CB5 and BB4 occurs only in Anoplogaster and Gibberichthys among the beryciforms examined. CB5 has a row of seven needle-like teeth fused to it.

The epibranchials present no unusual features except that a considerable portion of the proximal end of EB4 is cartilaginous, and that EB3 does not have any teeth fused to it.

There are three pharyngobranchials. PB2 has two or three needle-like teeth fused to it. PB3 is a large element whose proximal portion has a patch of needle-like teeth (several of which are quite formidable) fused to it. PB4 is absent but its tooth plate persists. The plate is triangular and is tightly articulated to the proximal end of PB3, but is mainly supported by the expanded distal end of EB4. The teeth on this plate resemble those on the other pharyngobranchials.

The vertebral column and ribs

The vertebral formula is 13 + 15 = 28. The vertebrae are weakly ossified (fenestrated with pores). The neural arch of the first vertebra is fused to its centrum. The pedicels of the neural arches are pierced by foramina for the spinal nerves. The neural spines of the first 12 vertebrae slope very strongly backward. The spines of the thirteenth and fourteenth vertebrae are transitional--the remaining spines project posterodorsally in typical fashion. The abdominal vertebrae bear distinct pre- and postzygapophyses. The anterior caudal vertebrae bear only prezygapophyses.

The ventrolateral portions of the centra of the seventh through the thirteenth vertebrae bear basapophyses. The basapophyses of the seventh and eighth vertebrae are poorly developed, but beginning with the ninth vertebra they meet in the midline, thus forming a bony canal. The size of the basapophyses and the amount of fusion between them increases from front to rear, thus producing successively longer spines (similar to the hemal spines). The proximal ends of the posterior pleural ribs closely approach (but do not articulate with) the tips of these spines.

Pleural ribs are present on the third through the thirteenth vertebrae. They are slender, delicate bones. Epineural and epipleural ribs are absent.

The pectoral girdle and fin (Fig. 17)

The extrascapular is a very small, delicate, oval-shaped bone. Its anterior edge is reflected outward to form a thin crest for the lateral line. The supratemporal lateral line passes above the crest, while the main cephalic lateral line passes below it. The edge of the crest bears a few feeble serrations.

The posttemporal bears a moderately long dorsal limb and a short ventral limb. The dorsal limb articulates with the posterior aspect of the parietal

(not with the epiotic, as in many other forms). A broad flange extends back from the dorsal limb. The edge of this flange is weakly scalloped, resulting in the formation of several short spines.

The supracleithrum is blade-like.

The dorsal and ventral limbs of the cleithrum are exceedingly long. The dorsal limb projects anterodorsally and makes a sharp angle (about 95°) with the ventral limb. The posterior lamina is very poorly developed. The cleithrum is unornamented, but like the other dermal bones of the pectoral girdle (except the postcleithrum), it is fenestrated with numerous tiny pores.

There is a single postcleithrum. It is a long, slender, curved rod, and is cylindrical for its entire length.

The circular scapular foramen is very large, and is located in the center of the bone.

The coracoid is relatively deep. The coracoid process is long, but is not particularly gracile. A large coraco-cleithral fenestra is present. The posteroventral portion of the coracoid is prolonged into a short, blunt process.

The first actinost is a short, stubby element, but the other three are laterally compressed. The first two actinosts articulate with the scapula, the third with the scapula and the cartilage between the scapula and coracoid, and the fourth with the cartilage covering the posterodorsal part of the coracoid.

Cartilaginous distal radials are present, but their number could not be determined.

The pectoral fin contains 15 rays. All of the rays except the first are segmented, and all except the first, second and fifteenth are branched distally.

The pelvic girdle and fin (Fig. 18)

The pelvic bone is very slender. The rachis is cylindrical distally. It projects well-beyond the margin of the pelvic bone. The tip of the rachis is bound to its fellow by connective tissue (the pelvic bones are otherwise separated from one another). More proximally, the rachis becomes ridge-like, and divides the lateral surface of the pelvic bone into anteroventral and posterodorsal portions. The posterolateral edge of the pelvic bone is convex. The posteromedial portion of the pelvic bone bears a long, tapered posterior process. Anterior, medial and lateral processes are absent.

The pelvic fin formula is 0,7. All of the rays are segmented, and all except the first are branched distally. The pelvic fins are thoracic.

Pelvic radials are absent.

The dorsal fin

The dorsal fin formula is 0,17. It was not possible to determine which rays of the dorsal and anal fins were segmented and branched distally in any of the specimens examined (ends broken off).

There are 16 pterygiophores. The first two rays are associated with the first pterygiophore. The first four pterygiophores, as well as the last, are

incomplete. The proximal radials are slender, delicate rods which expand abruptly at their distal ends. The proximals lack crests on their lateral surfaces. The proximals do not interdigitate with the neural spines below, due to the strong inclination of the latter elements. The first proximal lies above the fourth neural spine. The middle radials are blocks of cartilage which are ossified only on their lateral surfaces. The distal radials are cartilaginous nodules which are ossified on their dorsolateral surfaces. There is one dorsal fin stay. It represents a vestigial proximal radial. The stay is indistinguishably fused with the proximal ahead of it for a portion of its length.

Predorsals are absent.

There is one supraneural. It is a slender, sigmoid element. The proximal end of the supraneural lies above the tip of the second neural spine.

The anal fin

The anal fin formula is 0,8.

There are seven pterygiophores, all of which are incomplete. The first two rays are related to the first pterygiophore. The proximal and distal radials are similar to those of the dorsal fin. The proximals of the first three pterygiophores have very long, slender, rod-like portions, the tips of which lie just anterior to the first hemal spine.

There is no anal fin stay.

The caudal skeleton and fin (Fig. 19)

U2 is autogenous with respect to PU1 + U1. U2 is very small (see below).

PU3 bears long, sloping neural and hemal spines (considerably longer than those of PU4). The neural spine of PU2 is reduced to a low crest which varies between one-fourth to one-third of the length of the neural spine of PU3. This crest is fused to its centrum. The hemal arches of PU2 and PU3 are autogenous. The hypurapophysis of the parhypural is a well-developed flange which is tapered distally.

The stegural is fused to PU1 + U1. The spinous process of the stegural is short. There are no uroneurals. The absence of uroneurals in Anoplogaster is unique among the beryciform species examined (although the uroneurals are strongly reduced in the Melamphaeidae).

The three epurals decrease in length from the first to the third. The proximal ends of the epurals are flattened. The distal portions of the first and second epurals are cylindrical, while that of the third epural is expanded. The proximal end of the first epural is supported by the neural crest of PU2 while those of the second and third epurals are supported by the dorsal edge of the stegural.

Five or six hypural bones may be present. In two of the three specimens examined, the third and fourth hypurals are partially fused into a large plate (H1,H2,H3+4,H5,H6). In the other specimen there are six separate hypurals (H1-H6). In the specimens with only five hypurals, the proximal portion of the large plate (H3+H4) is fused to U2. The fusion is so complete, and U2 so small, that the latter almost appears as if it is merely the basal portion

of the hypural plate. In the specimen with six hypurals, only the proximal end of the fourth hypural is fused to U2. All of the other hypurals (in all three specimens) are autogenous. Fusion of the proximal ends of the hypurals with the terminal vertebrae is rare among the beryciforms examined.

The caudal fin formula is 10 + 9 = 19. There are seven procurrents above and below. The first six (above and below) are spinous. The basal portions of the procurrent spines are forked. The foremost procurrents are supported by the tips of the neural and hemal spines of PU3.

The squamation

Ventral ridge scales are absent. In contrast to many other beryciforms, the lateral line in Anoplogaster lies in an open channel (i.e., does not pierce the scales). Scales bound the lateral line above and below, and are joined to one another at regular intervals beneath it, thus forming a bony floor (see Woods and Sonoda, 1973, p. 390, fig. 64).

Family Diretmidae

Osteology of Diretmus argenteus Johnson

The neurocranium (Figs. 20-22)

The skull roof

The nasals are rather large and meet in the midline for part of their length. The nasal broadens posteriorly, where it overlaps and is firmly bound to the anterior end of the frontal. The medial and lateral edges of the nasal are reflected upward to form a trough for the lateral line. These edges are serrated along most of their length. A narrow bridge of bone roofs over the lateral line in the middle portion of the nasal.

The frontals are moderately large, but are somewhat constricted in the orbital region due to the enormous size of the eyes. Anteriorly, the frontal meets the nasal, mesethmoid and lateral ethmoid. Posteriorly, it meets the supraoccipital, parietal, pterotic and sphenotic. Medially, it meets its fellow in a straight suture. In the orbit the frontal contacts the pterosphenoid. The frontals bear high, thin crests which are serrated along their edges. These crests separate deep mucous cavities. The crests are arranged in a < pattern, and extend for most of the length of the bone. Anteriorly, the crests meet the posterior ends of the medial and lateral crests (edges) of the nasal. The more medial crest of the frontal also meets its fellow anteriorly. Posteriorly, the crests converge. The posterior portion of the frontal also bears a small, delicate crest, well-separated from the other two. The orbital margin of the frontal is weakly serrated.

The parietal meets the frontal anteriorly, the epiotic posteriorly and the supraoccipital medially. The dorsal surface of the parietal bears a high crest which is serrated on its edge.

The epiotic meets the exoccipital posteroventrally, the supraoccipital medially, the pterotic laterally and the parietal dorsally.

The supraoccipital bears a very large, triangular crest which begins slightly behind the middle of the orbit. Two ridges strengthen the lateral surface of the crest.

The supratemporal fossa is large, and extends anteriorly to the middle of the orbit. The floor of the fossa is formed by the supraoccipital medially and the parietal and dorsal surface of the epiotic laterally. The posterior portion of the frontal and the parietal form a partial anterolateral wall for the fossa.

The posttemporal fossa is very small. The floor of the fossa is formed by the pterotic, the medial wall by the epiotic, and the lateral wall by a poorly developed flange on the dorsal surface of the pterotic.

The ethmoid region

The mesethmoid is a small, ^-shaped bone. The limbs of the ^ are flanges which project ventrolaterally. The dorsal surfaces of these flanges are overlain by the frontals.

The lateral ethmoid is somewhat deeper than it is wide. Its lateral edge is slightly concave; its medial edge slightly convex. The center of the lateral ethmoid is pierced by a moderate sized, round foramen for I.

In this specimen, the vomer bears a tiny, slightly curved, conical tooth. The vomer in Diretmus is usually toothless (Woods and Sonoda, 1973, p. 290).

The orbital region

The posteriormost portion of the parasphenoid is bent upward, and overlies the anterior one-fourth of the ventral surface of the basioccipital. The shaft of the parasphenoid is cylindrical. The ascending processes are small, and are pierced by oval foramina for the internal carotid arteries.

The orbitosphenoid is moderate sized. It bears an oval foramen for the exit of I.

The pterosphenoids are rather large. Anteriorly, the lower edges of the pterosphenoids meet in the midline, closing off the optic fenestra as they do so. The lateral margins of the optic fenestra are formed by the pterosphenoids (anteriorly) and the prootics (posteriorly). The prootics also close off the fenestra posteriorly. The center of the pterosphenoid bears a small foramen for IV. The pterosphenoid meets the orbitosphenoid anteriorly, the sphenotic and prootic posteriorly and the frontal dorsally.

The basisphenoid is absent. The myodome is very shallow.

The otic region

The prootic meets the pterosphenoid anterodorsally, the parasphenoid anteroventrally, the exoccipital posteriorly and the sphenotic and pterotic dorsally. The pars jugularis has three external openings, separated by two narrow struts of bone. The prootic bears a small foramen for IX.

The dermosphenotic is fused to the autosphenotic (also fused in D. pauciradiatus). The dermal part of the sphenotic bears a small, delicate crest or process which is serrated along its edge. This crest lies

next to a similar crest on the pterotic. The infraorbital lateral line passes ventrally just anterior to the crest on the dermal part of the sphenotic. The sphenotic possesses a distinct postorbital process. The facet for the anterior portion of the head of the hyomandibula is formed entirely within the sphenotic.

The pterotic articulates with the sphenotic and frontal anteriorly, the exoccipital posteriorly, the epiotic medially and the prootic ventrally. The posterior portion of the head of the hyomandibula articulates with an elongate facet on the pterotic. The pterotic bears a vertical flange which forms the lateral wall of the posttemporal fossa. The posterior end of this flange is reflected outward. Just lateral to the flange is a groove for the main cephalic lateral line. The preopercular lateral line branches off from the main lateral line and passes ventrally between the reflected end of the pterotic flange (posteriorly) and a small, delicate crest on the pterotic (anteriorly).

The intercalar does not present any noteworthy features.

The auditory bulla is prominent. The posterior aspect of the bulla is depressed. The prootic forms the entire anterior wall (except for a very small contribution from the parasphenoid) and most of the lateral wall. The exoccipital forms the posteriormost part of the lateral wall. The posterior wall is formed by the basioccipital and by an area of membrane which widely separates this element from the prootic.

The occipital region

The exoccipital meets the pterotic anteriorly, the epiotic anterodorsally, the prootic anteroventrally, the supraoccipital dorsally and the basioccipital ventrally. The vagal foramen is round and moderate sized.

The basioccipital lies in a plane which makes a 45° angle with the parasphenoid shaft. The posterior portion of the basicranium is therefore bent strongly upward.

The circumorbital bones

The antorbital is absent.

The lacrimal bears a concave facet anterodorsally for articulation with the lateral ethmoid. Posteriorly the lacrimal meets the first infraorbital. The upper edge of the lacrimal, which is reflected for protection of the lateral line, is weakly serrated. The lateral surface of the lacrimal bears several thin, serrated crests.

The infraorbitals are rather shallow, and are approximately equal in size. The reflected edges of all of the infraorbitals bear serrations, although those on the fourth are not very distinct. The first three infraorbitals also bear very delicate, serrated crests or ridges on their lateral surfaces.

A subocular shelf is developed on the entire margins of the first two infraorbitals, and all but the posteriormost portion of the third (in D. pauciradiatus, the shelf is present only on the first two infraorbitals).

The dermal portion of the compound sphenotic is described above.

The hyopalatine bones (Fig. 23)

The hyomandibula is long (deep) and narrow. Its dorsal portion is not

broad and plate-like, as in many other forms. The lateral surface bears a prominent ridge for articulation with the dorsal limb of the preopercle. The opercular process is short and curved. The head of the hyomandibula is single. The anterior edge of the symplectic process articulates with the posterior border of the metapterygoid. At the point where the symplectic process begins, the hyomandibula sends down a short, jagged process which meets a spike-like process from the dorsal edge of the metapterygoid.

The metapterygoid and symplectic do not present any noteworthy features.

The quadrate is very deep (in the shape of an isoceles triangle).

The endopterygoid articulates anteriorly with a cone-shaped piece of cartilage which overlies the posterodorsal part of the palatine. Posteriorly, the endopterygoid is slightly overlapped by the metapterygoid. The medial edge of the endopterygoid is separated from the shaft of the parasphenoid by connective tissue, while the lateral edge articulates with the dorsal limb of the ectopterygoid. The endopterygoid is toothless.

The ectopterygoid is composed of slender dorsal and ventral limbs which are tapered distally. At the junction of the two limbs there is a small, thin process which projects dorsally. This process is overlain by the metapterygoid. The ectopterygoid is toothless.

Attached to the dorsal aspect of the palatine is a cone-shaped piece of cartilage. The endopterygoid and dorsal limb of the ectopterygoid articulate with the apex of this cone. The base of the cone is excavated, producing a concave facet for articulation with the cartilaginous condyle on the ventral end of the lateral ethmoid. The maxillary process of the palatine is long and slender, and is capped with cartilage distally. The palatine is toothless.

The dermal upper jaw (Fig. 23)

The ascending process of the premaxilla is about one-fourth of the length of the alveolar process. The alveolar process is very long and slender, and bears small conical teeth along its entire length. The postmaxillary process is weakly developed along most of the length of the alveolar process. Near the proximal end of the alveolar process, however, the postmaxillary process is drawn out into a distinct, rather hook-like flange.

The maxillary shaft is quite long and is somewhat compressed. Its distal end is not expanded behind the tip of the alveolar process of the premaxilla.

The supramaxilla is a very large, triangular bone. Its anterior end is prolonged into a slender process. The lateral surface of the supramaxilla is highly ornamented with thin crests which run parallel to one another.

The lower jaw (Fig. 23)

The ascending process of the dentary bears small conical teeth along most of its length. Distally, the ascending process slightly overlaps that of the angulo-articular. The dentary is slightly deepened at the symphysis. The lateral surface of the dentary bears thin, serrated crests which run parallel to one another.

The angulo-articular bears a distinct ascending process. A short ligament from the tip of the ventral limb of the preopercle attaches to the lateral surface of the retroarticular process. The facet for the quadrate condyle lies

approximately at the level of the posterior border of the orbit. The angulo-articular is ornamented like the dentary.

The retroarticular presents no noteworthy features.

The mandibular lateral line is open except near the symphysis, where two small flanges form a roof over it.

The opercular bones (Fig. 23)

The opercle is rather small, and is narrow anteroposteriorly. The facet for the opercular process of the hyomandibula is reinforced by a very small ridge. The opercle is highly ornamented. Its lateral surface bears numerous thin crests which are finely serrated along their edges. These crests radiate outward to the edge of the bone. The posterodorsal border of the opercle is scalloped, resulting in the formation of about five indistinct spines.

The subopercle is long and narrow. Its posterior portion is membranous, and is deeply cleft, resulting in the formation of seven finger-like processes. The lateral surface of the anterior portion of the subopercle bears several crests, similar to those on the opercle.

The interopercle is irregular-shaped. Its posteroventral portion is prolonged into a distinct spine. The lateral surface of the anterior portion of the interopercle bears low ridges which run to the ventral edge of the bone, where they end in serrations.

The preopercle is large, and consists of a very long dorsal limb and a short ventral limb. The angle is not produced into a spine, but it is expanded into a triangular plate. The edges of the dorsal and ventral limbs are reflected for protection of the lateral line. The reflected edge of the dorsal limb contacts the lateral surface of the bone, so that a complete canal is formed. The lowest portion of the posterior edge of the dorsal limb, and the entire length of the ventral edge of the ventral limb, bear serrations. The lateral surface of the preopercle is also highly ornamented with thin, serrated crests.

The hyoid arch and branchiostegal rays (Fig. 24)

The interhyal presents no unusual features.

The epihyal meets the ceratohyal in a straight suture. The epihyal and posterior one-half of the ceratohyal are not distinctly grooved for the hyoidean artery.

The ceratohyal meets the ventral hypohyal anteriorly but is separated from the dorsal hypohyal by some connective tissue. The dorsal border of the ceratohyal is straight, while the ventral border is concave. The center of the ceratohyal is perforated by a small, oval foramen. Anterior to the foramen, the ceratohyal bears a deep groove for the hyoidean artery. This groove leads into a canal between the hypohyals. The canal continues anteriorly, and opens onto the medial surface of the hyoid arch.

The hypohyals meet in a straight suture. The posterior part of the dorsal hypohyal is cartilaginous. The urohyal-hypohyal ligament attaches to the medial surface of the anteroventral corner of the ventral hypohyal.

The basihyal is absent.

The urohyal is a thin plate with a straight dorsal border and a weakly

convex posterior border. Part of the anteroventral border is grooved. The anterodorsal corner of the urohyal bears a rather indistinct process which projects anterodorsally. The urohyal-hypohyal ligaments attach to the anterior edge of this process and to the lips of the groove along the anteroventral border.

There are eight branchiostegal rays. They increase in size from front to rear. The first four rays articulate with the ventral edge of the ceratohyal, the fifth with the lateral surface of the ceratohyal, the sixth with the lateral surface of the cerato-epihyal junction, and the seventh and eighth with the lateral surface of the epihyal.

The branchial arches (Fig. 25)

BB1 is square-shaped and is ossified only superficially. BB2 and BB3 are rod-like. BB2 is quite stout, and is completely ossified. BB3 is more slender. The posterior one-third of BB3 is cartilaginous and is bent downward. BB4 is a very small, cartilaginous nodule. The basibranchials are toothless.

The hypobranchials do not present any unusual features.

The proximal tip of CB5 is cartilaginous, and is tied to BB4 by a short ligament CB5 has numerous sharp, conical teeth fused to it.

The epibranchials present no unusual features, except that EB3 does not have a tooth patch fused to it.

There are three pharyngobranchials. PB2 is toothless. PB3 is covered with moderately long, sharp, conical teeth (teeth fused to PB3). PB4 is absent but its tooth plate persists. The plate is slightly less than one-half of the size of PB3. The teeth on this plate resemble those on PB3.

The vertebral column and ribs

The vertebral formula is 14 + 18 = 32. The neural arch of the first vertebra is fused to its centrum. The neural arches and spines of the first five vertebrae are more robust than the others. The anterior surface of the first hemal spine is grooved for the upper ends of the first four proximal radials of the anal fin. Distinct pre- and postzygapophyses are present only on the first five vertebrae.

Basapophyses are present on the fifth through the fourteenth vertebrae. The basapophyses of the fifth vertebra are paired, ventrolateral projections. Those of the sixth through the tenth vertebrae are partially fused in the midline. The basapophyses of the eleventh through the fourteenth vertebrae are completely fused into spinous projections which resemble the hemal spines except that they are shorter, less tapered, and bear pleural ribs.

Pleural ribs are present on the third through the fourteenth vertebrae. They are slender and delicate. The pleurals on the third and fourth vertebrae articulate with the centra; the others articulate with the basapophyses. Epipleurals are present only on the first two vertebrae. There are no epineurals.

The pectoral girdle and fin (Fig. 26)

The extrascapular is a delicate bone of irregular shape. Its lateral

surface bears several thin crests.

The posttemporal is rather triradiate, although its posterior portion is not drawn out into a distinct limb. The dorsal limb of the posttemporal is long but the ventral limb is much shorter. The anterior edge of the posttemporal is reflected to form a partial canal for the lateral line. The posterodorsal edge is weakly serrated.

The supracleithrum is blade-like, although its dorsal end is somewhat rounded where it articulates with the posttemporal. The leading edge of the supracleithrum is thickened. The dorsal end of the supracleithrum does not bear a canal for the lateral line.

The cleithrum bears a very long, spike-like dorsal limb which is equal in length to the ventral limb. The angle between the limbs is about 150°. The lateral surface of the posterior lamina bears several ridges.

There is only one postcleithrum. The upper portion is thin and plate-like; the lower portion rod-like.

The center of the scapula is pierced by a round, moderate sized foramen.

The coracoid is large and deep. The coracoid process is strongly developed. The posteroventral portion of the coracoid is prolonged into a broad, flat process.

The first actinost is a very small, block-like element. The actinosts are weakly compressed. The first two actinosts articulate with the scapula, the third with the scapula and the cartilage between the scapula and coracoid, and the fourth with the cartilage covering the upper part of the posterior border of the coracoid.

All of the distal radials, except that associated with the second fin ray, are completely cartilaginous. The distal of the second ray is ossified superficially.

The pectoral fin contains 18 rays. All of the rays are segmented, and all except the first, second and eighteenth are branched distally.

The pelvic girdle and fin (Fig. 27)

The pelvic bones are rather loosely connected to one another. The pelvic bone is triangular in lateral view. The rachis is very long and slender, and extends well-beyond the margin of the main part of the pelvic bone. The rachis projects almost directly dorsally (slightly anteriorly). The proximal part of the rachis is in the form of a low ridge which divides the lateral surface of the pelvic bone into a large anterior and a somewhat smaller posterior portion. The pelvic bone is concave in ventral view. There are no crests or ridges on the ventral surface. The posteromedial portion of the pelvic bone bears two processes. There is a moderately long posterior process which lies parallel to its fellow. It tapers to a blunt point. There is also a very short, slender, anterior process. There are no medial or lateral processes.

The pelvic fin formula is I,6. The spine is strongly developed. All of the rays are segmented and branched distally. The pelvic fins are thoracic.

There is only one radial. It is a small, partly cartilaginous nodule, and is related to the bases of the fin spine and outermost ray.

The dorsal fin

The dorsal fin formula is 0,27. All except the first few rays are

weakly segmented. None of the rays is branched distally. The anteriormost rays are larger and stronger (more spinous) than the others. The first eight rays bear serrations along their lateral edges (hence the popular name, spinyfins).

There are 27 pterygiophores, all of which are complete. The proximal radials are elongate elements which are somewhat expanded above and tapered below. The first 15 bear ridges on their lateral surfaces. The first proximal is inserted between the second and third neural spines. The middle radials are short, cylindrical blocks. All are ossified superficially except the first, which is entirely cartilaginous. The distal radials are small nodules of cartilage which are ossified on their dorsolateral surfaces. There is one dorsal fin stay. It is small and is cartilaginous internally.

There are two predorsals. They are slender, rod-like elements which lack ridges on their lateral surfaces. The first predorsal is inserted between the skull and the first neural spine; the second between the first and second neural spines.

Supraneurals are absent.

The anal fin

The anal fin formula is 0,21. All except the first three rays are weakly segmented. None of the rays is branched distally. The first three rays are serrated along their lateral edges. Furthermore, the basal portions of all of the rays (except the last) bear spinous projections.

There are 19 pterygiophores, the first two of which are incomplete. The first three rays are related to the first pterygiophore. The proximal, middle and distal radials are essentially similar to those of the dorsal fin. Only the following points need to be mentioned. The first proximal is much larger than the others. It may represent two (or more) proximals which have fused together [a view also expressed by Abe (1975, p. 33)]. The distal portion of this proximal is plate-like. Anteriorly, this plate-like portion tapers to a blunt point. The first three distal radials are completely ossified. There is one anal fin stay, similar to that of the dorsal fin.

The caudal skeleton and fin (Fig. 28)

U2 is rather small, and is autogenous with respect to PU1 + U1.

The neural and hemal spines of PU3 are much longer than those of PU4. In another specimen the hemal spine of PU3 was doubled. The neural spine of PU2 is reduced to a low crest which is only one-fifth of the length of the spine of PU3. The neural arch of PU2 is fused. The hemal arches of PU2 and PU3 are autogenous. The parhypural does not possess a distinct hypurapophysis.

The stegural is fused to PU1 + U1. The spinous process of the stegural is paired. The proximal portion of the stegural is probably also paired. There is a single pair of uroneurals which lie wedged in between the spinous process of the stegural and the uppermost hypural.

There are three epurals. The third is shorter than the others. The distal one-third of the third epural is forked. The proximal end of the first epural is supported by the posterior part of the edge of the neural crest of PU2 and the anterior part of the edge(s) of the stegural. The second and third epurals are supported by the posterior part of the edge(s) of

the stegural.

There are four hypural bones (H1 + H2, H3, H4, H5, --). The first and second hypurals are indistinguishably fused into a large plate. This plate supports the principal rays of the lower lobe of the caudal fin. The sixth hypural is absent. All of the hypurals are autogenous. The first hypural bone articulates with PU1 + U1. The second and third hypural bones articulate broadly with U2. The fourth hypural bone barely contacts U2. The proximal portion of the fourth hypural bone is slightly forked.

The caudal fin formula is 10 + 9 = 19. There are five procurrents above and below. The first three (above and below) are spinous. The procurrents are ornamented with serrations (small spines). The bases of the procurrent spines are forked. A small piece of cartilage lies just anterior to the tips of the neural and hemal spines of PU3. The foremost procurrents are supported by the tips of the neural and hemal spines of PU3, as well as by these pieces of cartilage.

The squamation

Ventral ridge scales are present. In Diretmus (both D. argenteus and D. pauciradiatus) they lie both anterior and posterior to the anus. The ridge scales in the other beryciforms examined are preanal, except in Paratrachichthys, where they are postanal (note: the anus in Paratrachichthys has migrated anteriorly). The lateral line is absent on the trunk in Diretmus.

Family Berycidae

Osteology of Centroberyx affinis (Günther)

The neurocranium (Fig. 29)

The skull roof

The nasals are moderate sized bones which fail to meet in the midline. The anterior edge of the nasal is weakly convex. Laterally, it is prolonged into a short, blunt process. Posteriorly, the nasal is tapered. The nasals are well-ornamented. The anterior border of the nasal bears a series of seven or eight short spines which project anteroventrally. A broad flange covered with small tubercles roofs over the lateral line.

The frontal meets the mesethmoid and lateral ethmoid anteriorly and the supraoccipital, parietal, pterotic and both sphenotics posteriorly (from medial to lateral). Medially, the frontal meets its fellow in a slightly wavy suture. The orbital lamina of the frontal articulates with both the orbito- and pterosphenoids. The orbital surface of the frontal is perforated by small foramina for the superficial ophthalmic nerves. The frontals bear high, thin crests which separate large, deep mucous cavities. The edges of the crests are rather sharp and are feebly serrated (the orbital margin of the frontal is also weakly serrated). Patterson (1964, p. 339, fig. 65) has

accurately figured the pattern of the frontal crests in Centroberyx. The ⋋ pattern seen in some beryciforms is not present. However, based on the position and relationships of the crests in Centroberyx, it seems possible to establish homologies with the crests in those forms in which the ⋋ pattern is present.

In Centroberyx, the "main" frontal crest is obliquely oriented (anteromedial to posterolateral). Anteriorly, this crest closely approaches its fellow (in the specimen figured by Patterson, they appear to make contact). This crest may be homologous with the anteromedial crest of other forms. At about the middle of the bone, the main crest divides into three diverging crests (perhaps homologous with the posteromedial, posterolateral and posterointermediate crests of other forms). The "posteromedial" crest is continuous with a flange of bone which meets its fellow in the midline. This flange forms the posterior boundary of the large median mucous cavity of the skull roof and the anterior boundary of the supratemporal fossa. The "posterolateral" and "posterointermediate" crests run back to closely approach the anterior ends of the ventral and dorsal limbs (respectively) of the crest on the extrascapular (see below). Also, the lateral part of the parietal is reflected upward, and is pressed against the posterior portion of the medial aspect of the "posterointermediate" crest. In addition to the crests described above, the frontal bears a thin, horizontally oriented flange which braces the "anteromedial" crest and which roofs over the supraorbital lateral line. A bony strut on the anterior end of the frontal covers the lateral line as it passes onto the nasal.

The parietal is a thin bone which meets the frontal anterolaterally, the epiotic posteriorly, the supraoccipital medially and the pterotic laterally. The articulation with the pterotic is in the lateral wall of the posttemporal fossa.

The epiotic is strut-like posteroventrally, where it articulates with a similar strut of the exoccipital.

The supraoccipital is large. The supraoccipital crest is a very large, triangular plate which projects well-above the dorsal surface of the skull. The crest is well-ossified and its lateral surface is reinforced by two ridges. The anterior edge of the crest is thin and sharp.

The supratemporal fossa is extensive. It is long but rather narrow. The fossa extends anteriorly to a level well-ahead of the middle of the orbit. The floor of the fossa is formed by the supraoccipital (medially), the parietal and epiotic (laterally) and the posterior end of the frontal (anteriorly). Anteriorly, there is a well-developed lateral wall formed by the "posterointermediate" crest of the frontal reinforced by the reflected edge of the parietal. The anterior wall of the supratemporal fossa is described above.

The posttemporal fossa is also large. It is quite broad, due to the fact that the lateral surface of the epiotic (which forms most of its medial wall) is deeply excavated. The exoccipital makes a slight contribution to the medial wall of the fossa. The floor of the fossa is formed by the dorsal surface of the pterotic, as well as by an irregular-shaped area of cartilage between the pterotic, epiotic, exoccipital and autosphenotic. A distinct anterior wall is present, and is formed by the slightly excavated posterior surface of the autosphenotic. The lateral wall of the posttemporal fossa is formed by a low ridge on the dorsal surface of the pterotic (and slightly by the portion of the parietal which articulates with it).

Remarks: The skull roof of Beryx shows a number of similarities to that of Centroberyx. The most important of these include (1) shape of the nasals

(2) large size of the supratemporal fossa (with the posterior portion of the frontal contributing substantially to its floor) (3) morphology of the supraoccipital crest (nearly identical in the two genera-- even in such details as the position of the ridges which reinforce its lateral surface) and (4) pattern of the frontal crests (including the fact that the lateral portion of the parietal is reflected upward and is pressed against the "postero-intermediate" crest in Beryx, just as in Centroberyx). Several minor differences in the pattern of the frontal crests do occur, however. As in Centroberyx, the crests separate deep mucous cavities.

The ethmoid region

The mesethmoid is a large, well-ossified bone. It extends ventrally all of the way to the vomer. The mesethmoid bears a pair of anterolaterally-directed processes which support the posterior portions of the nasals.

The lateral ethmoid is broad. The medial portion of the lateral ethmoid is pierced obliquely by a circular foramen for I.

The vomer possesses well-developed wings which make firm articulations with the ventral portions of the lateral ethmoids. The vomer bears a D-shaped patch of small, conical teeth.

Remarks: The bones of the ethmoid region of Beryx show no important differences from those of Centroberyx.

The orbital region

The parasphenoid shows a slight amount of postorbital curvature. The parasphenoid overlies the anterior one-half of the ventral surface of the basioccipital. The parasphenoid shaft gradually broadens as it passes anteriorly from the level of the ascending processes. The shaft is rather triangular in cross section, although there is a shallow groove on its ventral aspect. The ascending processes are very well-developed. The foramen for the internal carotid artery lies between the prootic and the posterior edge of the ascending process.

The orbitosphenoid bears a foramen in the ventral midline for I.

The pterosphenoids are large bones which just fail to contact one another. The posteroventral portion of the orbitosphenoid is drawn out into a pointed process which slightly intervenes between the pterosphenoids and which closes off the optic fenestra anteriorly. The lateral margins of the optic fenestra are formed by the pterosphenoids (anteriorly) and the arms of the basisphenoid (posteriorly). The anteroventral portion of the pterosphenoid is pierced by a tiny foramen for IV. The pterosphenoid meets the orbitosphenoid anteriorly, the autosphenotic and prootic posteriorly, the frontal dorsally and the basisphenoid ventrally.

The arms of the basisphenoid articulate with the prootics and pterosphenoids. The basisphenoid pedicel is long and is somewhat laterally compressed. It gradually broadens as it passes ventrally.

Remarks: The postorbital curvature of the parasphenoid is more pronounced in Beryx than in Centroberyx. In B. splendens, the pterosphenoids meet in the midline for a short distance (B. decadactylus shows a condition similar to that seen in Centroberyx).

The otic region

The prootic meets the pterosphenoid anterodorsally, the ascending process of the parasphenoid anteroventrally, the exoccipital posteriorly, the basioccipital posteroventrally, the autosphenotic and pterotic dorsally, and the basisphenoid medially. The prootic is also partially overlain by the intercalar. The pars jugularis has three external openings. Posteroventral to the lateral opening is a projecting flange which is somewhat tapered distally. This flange appears to "lead" the hyomandibular trunk of VII to the foramen on the medial surface of the hyomandibula. The prootic bears a small foramen for IX at the point of its articulation with the intercalar.

The autosphenotic bears a stout postorbital process. The dilatator fossa is an excavation in the autosphenotic and adjacent part of the pterotic. The dermosphenotic forms the roof of the dilatator fossa. The socket for the anterior head of the hyomandibula is located entirely within the autosphenotic.

The pterotic meets the frontal, parietal, and both sphenotics anteriorly, the exoccipital posteriorly, and the prootic ventrally. The posterior head of the hyomandibula fits into a shallow, elongate facet on the ventral surface of the pterotic. Delicate crests developed on the lateral edge of the pterotic bound the preopercular lateral line in front and behind as it passes ventrally onto the preopercle.

The intercalar does not present any noteworthy features.

The auditory bulla is inflated, and rather globular in appearance. The wall of the bulla is almost entirely bony. It is formed by the prootic anteriorly, the exoccipital posterodorsally and the basioccipital posteroventrally. A narrow strip of cartilage separates the prootic and basioccipital for a small portion of their length.

Remarks: The bones of the otic region of Beryx show no important differences from those of Centroberyx.

The occipital region

The exoccipital meets the prootic and pterotic anteriorly, the epiotic and supraoccipital anterodorsally, and the basioccipital ventrally. The tripartite facet for the first vertebra is very deep. An elongate, ventrally-directed foramen transmits X.

The basioccipital presents no noteworthy features.

Remarks: The glossopharyngeal foramen is located within the exoccipital in Beryx.

The circumorbital bones

The antorbital is absent.

The lacrimal is large and elongate. The medial aspect of the anterodorsal portion of the lacrimal bears a concave facet for articulation with the lateral ethmoid. Posteriorly, the lacrimal extends back below the first infraorbital to articulate with the second infraorbital. Near the anterior end of the bone, the reflected upper border of the lacrimal meets the lateral surface, thus forming a complete canal for the lateral line. The lower border of the lacrimal is feebly serrated.

The first two infraorbitals are irregular in shape. The third and fourth are rather rectangular. The second infraorbital is about twice as large as the others. The surfaces of the reflected borders of the infraorbitals are weakly ornamented with small tubercles. The lower portion of each infraorbital (except the first) bears a weakly ornamented crest which projects toward the reflected upper border.

A subocular shelf is developed along the entire margins of the second, third and fourth infraorbitals. The portion of the shelf on the second infraorbital is deeper than that on the third and fourth. The edge of the shelf on the second infraorbital is rounded, and is bound to the endopterygoid by connective tissue. There is a low thickening on the dorsal surface of the endopterygoid for the attachment of this tissue.

The dermosphenotic is moderate sized and rather elongate. Its outer and inner edges are reflected for partial protection of the lateral line The outer edge bears small spines.

Remarks: Of particular significance is the fact that as in Centroberyx, the lacrimal of Beryx extends posteriorly below the first infraorbital to articulate with the second. A noteworhty difference between the two genera is the presence of a strong spine on the lateral surface of the anterior end of the lacrimal in Beryx.

The subocular shelf of Centroberyx is more extensive than in Beryx In B. splendens, the shelf is confined to the second infraorbital (although developed along its entire margin). In B. decadactylus, the shelf arises from the entire margins of the first and second infraorbitals. The portion on the first infraorbital is very poorly developed, however.

The hyopalatine bones

The hyomandibula is double-headed. The opercular process is well-developed. The foramen for the hyomandibular trunk of VII is located well-above the level of the opercular process. The lateral surface of the hyomandibula bears a crest against which lies the dorsal limb of the preopercle. The anteroventral corner of the broad, dorsal portion of the hyomandibula contacts a thin flange which projects up from the dorsal part of the metaptervgoid The symplectic process articulates with the posterior border of the metapterygoid.

The metapterygoid does not present any noteworthy features.

The quadrate is slightly deepened.

The symplectic is long and lies at a 45° angle to the symplectic process of the hyomandibula.

The oval-shaped endopterygoid articulates with the palatine anteriorly, the metapterygoid posteriorly and the dorsal limb of the ectopterygoid laterally. A small amount of cartilage is present in the region of the endopterygoid-palatine articulation. Numerous small, irregular-shaped tooth patches lie scattered in the epithelium overlying the endopterygoid (mainly), palatine, vomer and parasphenoid. These patches are not fused to the bones A similar condition was seen in two other specimens.

The ectopterygoid is composed of a long, slender ventral limb and a broad dorsal limb. The ectopterygoid is toothless.

The palatine meets the endo- and ectopterygoids posteriorly. Anterodorsally, the palatine bears an elongate, concave facet for articulation with the lateral ethmoid. The tip of the maxillary process is capped with cartilage The palatine bears a strip of very small, conical teeth

Remarks: In Beryx, the head of the hyomandibula is single. The dorsal portion of the hyomandibula is narrow (not broad or expanded as in Centroberyx). The epithelium overlying the endopterygoid and adjacent bones does not contain tooth patches in Beryx.

The dermal upper jaw

The ascending process of the premaxilla is one-third of the length of the alveolar process. The anterodorsal portion of the rostral cartilage is weakly ossified. The alveolar process bears a strip of small, blunt teeth. The teeth on the proximal portion of the process are somewhat larger and more conical, however. The postmaxillary process is a shallow, gently convex flange which arises from the entire length of the alveolar process.

The maxilla has a strong, cylindrical shaft. The distal portion of the shaft is expanded, however, and lies behind the tip of the alveolar process of the premaxilla.

Two supramaxillae are present. The anterior supramaxilla is a small, oval bone. The posterior supramaxilla is large. It is rather elongate, and gradually deepens as it passes anteriorly. The anterodorsal corner of the posterior supramaxilla bears a long, spike-like process which overlies the anterior supramaxilla. Both supramaxillae are weakly ornamented with low ridges and small spines.

Remarks: The upper jaw of Beryx shows no important differences from that of Centroberyx.

The lower jaw

The dentary forms the anterior two-thirds of the lower margin of the mandible. The upper edge of the ascending process is sinuous. The entire oral border of the dentary (except the tip of the ascending process) bears teeth. Anteriorly, the teeth are small and conical. More posteriorly, the strip of teeth broadens and the teeth become more blunt. These latter teeth are primarily located on the medial aspect of the ascending process. The lower one-half of the lateral surface of the dentary bears low, serrated ridges.

Anterior to the facet for the quadrate, the angulo-articular rises abruptly into a triangular ascending process. The jaw articulation is located at the level of the posterior border of the orbit and is strengthened by a prominent retroarticular process. A small slip of bone, lying just dorsal to the posterior end of Meckel's cartilage, is tightly articulated to the medial surface of the angulo-articular. The ornamentation on the angulo-articular is similar to, but somewhat less extensive than, that on the dentary.

The retroarticular does not present any noteworthy features.

The mandibular lateral line is nearly completely enclosed. It communicates with the surface through numerous but tiny pores in the dentary and anterior portion of the angulo-articular. In the posterior one-half of the angulo-articular, however, the lateral line lies in a wide groove which is covered only by membrane.

Remarks: In Beryx, the mandibular lateral line is not as enclosed as it is in Centroberyx.

The opercular bones

The opercle is a rather large, deep bone. The dorsal border is rounded. Ventrally, the opercle tapers to a point. The posterior border of the opercle is drawn out into two prominent spines. The upper spine is slightly larger. The lateral surface of the opercle is smooth except for a series of very low, fine ridges along the posterior border. These ridges run out to the posterior border and end in tiny serrations.

The ventral border of the subopercle is deeply notched.

The interopercle is large. It is rather oval in shape, although its posteroventral portion is distinctly notched. The lateral surface of the ventral part of the interopercle is weakly ornamented with low ridges similar to those on the opercle.

The dorsal limb of the preopercle is deep. The leading edge of the preopercle is reflected outward to form a partial canal for the lateral line, and is weakly ornamented with fine serrations. The lowest portion of the dorsal limb and the entire length of the ventral limb bear fine serrations along their outer edges. Low ridges lead out to these serrations, as in the other opercular bones. In the region of the angle of the preopercle the ridges and serrations are more pronounced.

Remarks: The opercular bones of Beryx show no important differences from those of Centroberyx.

The hyoid arch and branchiostegal rays (Figs. 30-31)

The interhyal is a well-ossified rod of bone, although its ends are covered with cartilage. Ventrally, the interhyal thickens, and is rather triangular in cross section.

The epihyal is short and deep. Dorsally, its lateral surface is deeply grooved for the hyoidean artery, as is the lateral surface of the posterior one-third of the ceratohyal. The suture between the epihyal and ceratohyal is obscured in medial view by the development of short, finger-like processes on the ceratohyal. These digitations cross the line of suture and are pressed against the medial face of the epihyal.

The ceratohyal is rather rectangular although its posterior portion is somewhat deepened. The ceratohyal meets the ventral hypohyal anteriorly. A small gap, filled with connective tissue, separates the ceratohyal from the dorsal hypohyal. Slightly above the center of the bone, the ceratohyal is pierced by a moderate sized, oval foramen. The anterior portion of the ceratohyal bears a canal for the hyoidean artery which is continuous anteriorly with a canal in the dorsal hypohyal. The artery emerges on the medial surface of the hyoid arch through an oval foramen which lies directly on the suture between the hypohyals. Lying scattered in the epithelium over the dorsal one-half of the medial surface of the ceratohyal are numerous tiny tooth patches.

The suture between the hypohyals is interdigitated along part of its length. The dorsal hypohyal is rectangular in lateral view. The ventral hypohyal is square-shaped, and is somewhat larger than the dorsal hypohyal. The anteroventral corner of the ventral hypohyal is slightly deepened for the attachment of the broad urohyal-hypohyal ligament.

The basihyal is a rather small, rod-like element. The anterior end of the basihyal is capped with cartilage. The basihyal is toothless.

The urohyal is large and gradually increases in depth posteriorly. Its posteroventral corner is prolonged into a prominent spike-like process; the posterodorsal corner is prolonged into a much shorter (blunter) process. The anterodorsal corner of the urohyal bears a small but distinct dorsally-directed process for the attachment of ligaments from the tips of the third hypobranchials. The anteroventral corner of the urohyal bears a pair of stout, slightly diverging processes for the attachment of the urohyal-hypohyal ligaments.

There are eight branchiostegal rays which increase in size from front to rear. The anterior borders of the third and fourth rays are finely serrated. The first four rays articulate with the ventral border of the ceratohyal, the fifth with the lateral surface of the ceratohyal, the sixth with the lateral surface of the cerato-epihyal junction, and the seventh and eighth with the lateral surface of the epihyal.

Remarks: In Beryx, the epihyal-ceratohyal suture is not as strongly interdigitated as in Centroberyx. The ceratohyal foramen in B. splendens (but not B. decadactylus) is smaller than in Centroberyx. Tooth patches are not present in the epithelium over the ceratohyal in Beryx, and the branchiostegals are not ornamented.

The branchial arches

BB1 is a deep, square-shaped element. BB2 is a curved rod with laterally-directed flanges. BB3 is somewhat similar to BB2, except that its posterior end is capped with a finger-like piece of cartilage which lies ventral to the plane of the other basibranchials. BB4 is a small cartilaginous block. Tooth patches lie embedded in the epithelium over BB1-BB3. Those over BB1 are tiny; the others are moderate sized. The patches over BB2 are confined to its lateral edges (flange-like portions).

The hypobranchials and epibranchials do not present any noteworthy features.

The proximal end of CB4 is spatulate and has a tooth patch fused to it. CB5 is attached to BB4 by a ligament. CB5 has a triangular patch of small, conical teeth fused to it. In addition, the epithelium over the posterior part of CB5 has several tooth patches embedded in it.

There are three pharyngobranchials. PB2 and PB3 have teeth fused to them. PB4 is absent but its tooth plate (which is round) persists.

Remarks: The branchial arches of Beryx show no important differences from those of Centroberyx. As in Centroberyx, CB4 has a patch of teeth fused to it. The basibranchial dentition of berycids is illustrated by Nelson (1969a, p. 498, figs. 10A and 10B).

The vertebral column and ribs

The vertebral formula is 10 + 14 = 24. The neural arch of the first vertebra is autogenous. The first five neural spines are stronger than the others. The first few hemal spines are also more robust than those succeeding them. The anterior face of the first hemal spine is grooved for the upper end of the first proximal radial of the anal fin. The first 11 vertebrae bear distinct prezygapophyses; the first five bear distinct postzygapophyses.

Basapophyses are present on the sixth through the tenth vertebrae. Those on the sixth vertebra are rudimentary, but the others are well-developed and meet one another in the midline.

Pleural ribs are present on the third through the tenth vertebrae. They are long, well-ossified bones. The pleurals on the tenth vertebra are expanded and blade-like. The first three pairs of pleurals articulate with the dorsolateral portions of their centra; the others with their basapophyses.

Epipleural ribs are present on all of the abdominal and the first two caudal vertebrae. The first two or three pairs of epipleurals are relatively strong, but the others are slender and delicate. Epineural ribs are absent.

Remarks: The vertebral column of Beryx resembles that of Centroberyx in most respects. As in Centroberyx, there are only 24 vertebrae. Pleural ribs are present on the third through the ninth vertebrae in Beryx. The absence of pleurals on the last abdominal vertebra (which nevertheless bears a pair of distinct basapophyses) is very unusual. Another peculiar feature concerns the hemal spine of the first caudal vertebra in Beryx. This spine is enormous, and its lower portion curves anteriorly, not posteriorly (i.e., the spine is recurved). The first hemal spine is also recurved in B. decadactylus.

The pectoral girdle and fin

The extrascapular is a large, irregular-shaped bone. It is rather elongate. Anteriorly, the lateral surface bears a <-shaped crest; the dorsal limb of the crest is longer and is finely serrated along its edge. The limbs of the crest "lead" the lateral line onto the parietal and pterotic. Posteriorly, the lateral surface of the extrascapular bears two other crests; the more dorsal crest is weakly serrated along its edge. The lateral line from the posttemporal passes onto the extrascapular between these two crests.

The posttemporal bears long dorsal and ventral limbs. The dorsal limb is spatulate; the ventral rod-like. Posteriorly, the posttemporal is prolonged into a short but distinct spine. The posterodorsal edge of the bone is finely serrated. A crest on the lateral surface of the posttemporal "leads" the lateral line toward the extrascapular.

The supracleithrum is rather broad. Its dorsal end is not pierced by a canal for the lateral line. Rather, the lateral line passes from the anteriormost lateral line scale past the thin, flange-like dorsal end of the supracleithrum, and onto the posttemporal. The posterodorsal edge of the supracleithrum is weakly serrated.

The cleithrum has a short, spike-like dorsal limb and a very long ventral limb. The posterior lamina is large.

There are two postcleithra. The dorsal postcleithrum is large and scale-like. The ventral postcleithrum is scale-like dorsally, but its ventral portion is rod-like and tapered distally.

The scapular foramen is very large and is centrally placed.

The coracoid is a large, plate-like bone. The coracoid process is long and deep. Posteroventrally, the coracoid is prolonged into a short, blunt process. The lower border of the coracoid is reflected outward.

The first actinost is short and stubby; the other three are more rod-like. The first three actinosts articulate with the scapula and the fourth with the cartilage between the scapula and coracoid.

There is an ossified distal radial related to the base of the second fin ray. Cartilaginous distal radials are also present, but their number could not be determined.

The pectoral fin is composed of 13 rays. The first two rays are not branched distally. All of the rays are segmented.

Remarks: The pectoral girdle of Beryx resembles that of Centroberyx in

a number of respects. An important similarity is the absence of a canal in the supracleithrum for the lateral line. The coracoid of Beryx is even deeper than that of Centroberyx, and as in that form the lower border is reflected outward. Correlated with the greater expansion of the coracoid is the fact that the actinosts are strongly compressed in Beryx.

The pelvic girdle and fin (Fig. 32)

The pelvic bones are firmly bound to one another. The pelvic bones are prolonged into long pointed processes which project anterodorsally, and which are bound to the ventral limbs of the cleithra by ligamentous fibers. The lateral surface of the pelvic bone is divided into anteroventral and posterodorsal portions by a low ridge (rachis). The posteromedial part of the pelvic bone bears three processes: (1) a medial process which partially overlaps its fellow (2) a long and slender anterior process which originates from the tip of the medial process and (3) a moderately long posterior process which is weakly expanded in its middle portion but tapered distally. A well-developed lateral process is also present. Ligamentous fibers from the ventral postcleithrum attach to this process, and the tendon of the muscle which extends the fin spine passes medial to it.

The pelvic fin formula is I,7. The spine is strong and its surface is weakly striated. All of the rays are segmented and branched distally. The pelvic fins are thoracic.

There are three radials, all of which are ossified. The first is irregular-shaped and is related to the base of the fin spine. It articulates with a thickening on the pelvic bone; this thickening is merely the lower end of the rachis. The second radial is a small, U-shaped element. It is associated with the first ray, and fits into a notch on the posterior edge of the pelvic bone. The third radial is related to the fourth and fifth rays.

Remarks: The overall shape of the pelvic bones of Beryx is very similar to that of Centroberyx. As in Centroberyx, anterior and posterior processes are present (the anterior processes are exceedingly long; the posterior processes are not expanded). Medial and lateral processes are absent in Beryx. The pelvic fin of Beryx is unusual in that it contains a large number of rays (usually 11, rarely 10) in addition to a spine.

The dorsal fin

The dorsal fin formula is VII,12. The spines are strong, and increase in length from front to rear. All of the rays are segmented and branched distally.

There are 18 pterygiophores. The first seven are incomplete. The first two spines are related to the first pterygiophore. The proximal radials have crests which bisect their lateral surfaces. The most posterior proximals are obliquely oriented, slanting backward (posterodorsally) from their points of insertion. The first proximal is inserted between the third and fourth neural spines. The middle radials are short, well-ossified rods. The distal radials associated with the soft portion of the dorsal fin are also well-ossified. Each distal is divided into two bilateral parts. There is one dorsal fin stay. It is a small, irregular-shaped piece of bone.

There are three predorsals. They are slender, laterally compressed rods, and are weakly expanded at their distal ends. The first predorsal is inserted between the skull and the first neural spine, the second between the first and second neural spines, and the third between the second and third neural spines.

Supraneurals are absent.

The anal fin

The anal fin formula is IV,12. The spines gradually increase in size from front to rear. The first spine is very short. All of the rays are segmented and branched distally.

There are 14 pterygiophores. The first four are incomplete. The first three spines are associated with the first pterygiophore. The upper portions of the first two proximal radials are fused together (a faint line of fusion is discernible). The lower portion of the first proximal is moderately expanded. The anal fin stay is similar to that of the dorsal fin.

Remarks: There are two dorsal and anal fin stays in Beryx. The lower portion of the first proximal radial of the anal fin is greatly expanded, providing a surface for the origin of musculature which inserts, by strong tendons, onto the bases of the first two spines. As in Centroberyx, there are three predorsals.

The caudal skeleton and fin (Fig. 33)

U2 is fused to the preceding compound vertebra (PU1 + U1 + U2).

The neural and hemal spines of PU3 are very long (twice the length of those of PU4). The neural spine of PU2 is reduced to a broad crest which is one-fourth of the length of the spine of PU3. The crest articulates with the anterior edge of the stegural posteriorly. The hemal spine of PU2 bears a well-developed flange which projects from its anterior edge. The hypurapophysis is exceedingly well-developed. It projects posterolaterally from the parhypural. The neural arch of PU2 is fused. The hemal arches of PU2 and PU3 are autogenous.

The stegural is fused to PU1 + U1 + U2. There is a single pair of blade-like uroneurals.

The proximal ends of all three epurals are expanded. The first epural is supported by the edge of the neural crest of PU2 and the anterior portion of the dorsal edge of the stegural. The other epurals are supported by the posterior part of the edge of the stegural.

There are four hypural bones (H1, H2, H3 + H4, H5, --). The third and fourth hypurals are fused into a large, fan-shaped plate. The sixth hypural is absent. All of the hypural bones are autogenous.

The caudal fin formula is 10 + 9 = 19. There are five procurrents above and below. The first four procurrents above and below are spinous. The procurrent spines are forked basally, where they receive their support. The foremost procurrents are supported by the tips of the neural and hemal spines of PU3.

Remarks: The caudal skeleton and fin of Beryx are very similar to those of Centroberyx, although a few noteworthy differences do occur. In Beryx, there are only three hypural bones (H1 + H2, H3 + H4, H5, --). A line of fusion is visible within both the upper and lower hypural plates. In

B. splendens (but not B. decadactylus), the upper hypural plate (H3 + H4) is fused proximally to the PU1 + U1 + U2 + stegural complex. Finally, the foremost procurrent spine above is supported by the distal end of the first epural (not the neural spine of PU3).

The squamation

Ventral ridge scales are present in Centroberyx but are absent in Beryx.

Family Anomalopidae

Osteology of Photoblepharon palpebratus (Boddaert)

The neurocranium (Fig. 34)

The skull roof

The nasals are large, well-ornamented bones which meet in the midline. Posteriorly, the nasals are firmly bound to the anterior ends of the frontals. The anterolateral portion of the nasal is prolonged into a distinct process, the distal end of which makes a firm articulation with the ventrolateral corner of the lateral ethmoid. The nasals curve downward from their articulations with the frontals, giving the snout a characteristic blunt, rounded appearance. The nasal is trough-like posteriorly, with its medial and lateral edges raised into spinous crests for protection of the lateral line. Anteriorly this trough is roofed over by a rather broad flange which is also ornamented with small spines.

The frontals are largely confined to the orbital region of the skull. They are very broad posteriorly. The frontal meets the nasal, mesethmoid and lateral ethmoid anteriorly. Medially, it articulates with its fellow in a sinuous suture. Posteriorly, the frontal meets the supraoccipital, parietal, pterotic and both sphenotics (from medial to lateral). The orbital lamina of the frontal meets the orbito- and pterosphenoids. The frontals bear a series of low, broad crests which separate mucous cavities of moderate depth. The crests are arranged in a $\gtrless$ pattern. There are anteromedial and anterolateral crests which meet the posterior ends of the medial and lateral crests (edges) of the nasal. The anteromedial crest is slightly separated from its fellow in the midline. The posteromedial crest runs back to contact its fellow while the posterolateral crest meets the anterior end of the ventral limb of the extrascapular crest. Between the posteromedial and posterolateral crests is a posterointermediate crest. It runs back to meet the anterior end of the parietal crest. The surfaces of all of these crests bear numerous fine, spinous ridges.

The parietal articulates with the frontal anteriorly, the epiotic posteriorly, the supraoccipital medially and the pterotic ventrolaterally. The dorsal surface of the parietal bears a low spinous crest.

The epiotic meets the parietal anteriorly, the exoccipital posteroventrally and the supraoccipital medially. The epiotic is prolonged into a

small flange which partially "overhangs" the posttemporal fossa. The dorsal limb of the posttemporal rests upon this flange.

The supraoccipital bears a triangular crest which projects only slightly above the rest of the dorsicranium. The upper edge of the crest is thin (sharp)

The supratemporal fossa is moderately well-developed, extending anteriorly to a level slightly ahead of the posterior border of the orbit. The floor of the fossa is formed by the supraoccipital medially, the parietal and epiotic laterally, and the posterior end of the frontal anteriorly (slightly). An indistinct ridge on the parietal forms a partial lateral boundary for the fossa, while a low ridge on the posterior part of the frontal marks its anterior extent.

The posttemporal fossa is moderately developed. Its floor is formed by the pterotic and its medial wall by the epiotic. The lateral wall is in the form of a low, thick flange on the dorsal surface of the pterotic.

Remarks: The skull roof of Anomalops shows several important similarities to that of Photoblepharon. These include (1) the presence of an articulation between the anterolateral portion of the nasal and the lateral ethmoid (2) the marked curvature of the nasals (blunt snout) and (3) the morphology and pattern of the frontal crests.

The ethmoid region

The mesethmoid is small and confined to a position between the dorsomedial portions of the lateral ethmoids.

The lateral ethmoid is a stout, square-shaped element. Its medial border is deeply notched for I.

The vomer bears a pair of well-developed wings which articulate with the ventromedial portions of the lateral ethmoids. The vomer is toothless.

Remarks: The mesethmoid in Anomalops is slightly larger than in Photoblepharon.

The orbital region

The parasphenoid is straight. Posteriorly, it overlies the anterior one-half of the ventral surface of the basioccipital. The parasphenoid shaft is T-shaped in cross section. The cross bar of the T is represented by a pair of laterally-directed flanges. The ascending processes are rather poorly developed, and are pierced by foramina for the passage of the internal carotid arteries into the myodome.

The orbitosphenoid is a large, Y-shaped bone. The keel of the orbitosphenoid is a well-developed plate which projects anteroventrally in the orbital midline. I issues through a foramen located just anterior to the keel

The pterosphenoids are widely separated. The pterosphenoid meets the orbitosphenoid anteriorly, the autosphenotic and prootic posteriorly, and the frontal dorsally. The lateral margins of the optic fenestra are formed by the pterosphenoids (anteriorly) and the prootics (posteriorly). The foramen for IV could not be identified.

The arms of the basisphenoid articulate with the prootics. The pedicel is laterally compressed. It gradually broadens as it passes ventrally.

Remarks: The parasphenoid shaft in Anomalops bears a pair of ventrolaterally-directed flanges for articulation with the medial edges of the

endopterygoids. In Anomalops, the trochlear foramen is located within the pterosphenoid, close to the margin of the optic fenestra.

The otic region

The prootic meets the pterosphenoid anterodorsally, the ascending process of the parasphenoid anteroventrally, the exoccipital posteriorly, the autosphenotic and pterotic dorsally, and the arm of the basisphenoid medially. The pars jugularis has three external openings separated by two struts of bone of approximately equal size. A foramen near the point of articulation with the basisphenoid probably transmits III.

The autosphenotic bears a blunt postorbital process. This process forms the anterior wall of the dilatator fossa. The floor of the fossa is formed by the autosphenotic (anteriorly) and the pterotic (posteriorly). The socket for the anterior portion of the head of the hyomandibula is formed equally by the autosphenotic and prootic.

The pterotic meets the parietal, frontal, and both sphenotics anteriorly, the exoccipital posteriorly, and the prootic ventrally. The pterotic is narrowly separated from the epiotic in the posttemporal fossa. The ventral surface of the pterotic bears a groove for the posterior portion of the head of the hyomandibula. Just above this groove, and separated from it by a low, sharp ridge is the posterior part of the dilatator fossa. The lateral edge of the pterotic is weakly serrated. Just medial to this edge is a channel for the main cephalic lateral line.

It was not possible to determine if the intercalar is present.

The auditory bulla is round to oval in shape, and is only slightly inflated. Its wall is formed by the prootic anterodorsally, the exoccipital posterodorsally and the basioccipital ventrally. A narrow space spanned by membrane separates the prootic and basioccipital and completes the wall.

Remarks: In Anomalops, the pars jugularis possesses four external openings. In addition to the three openings present in Photoblepharon, there is another opening in the prootic for the entrance of the orbital artery. The intercalar is present in Anomalops.

The occipital region

The exoccipital meets the prootic and pterotic anteriorly, the epiotic anterodorsally, the supraoccipital dorsally and the basioccipital ventrally. A small, anteriorly-directed foramen located close to the suture with the prootic transmits IX. A large, oval, ventrally-directed foramen transmits X.

The basioccipital presents no noteworthy features.

Remarks: The occipital region of the neurocranium was poorly preserved in the specimen of Anomalops which was examined.

The circumorbital bones

The antorbital is absent.

The lacrimal is a shallow, slightly elongate, tubular bone. It has three or four pores for the lateral line. The lacrimal-lateral ethmoid articulation is very peculiar. Projecting from the medial aspect of the

anterior end of the lacrimal is a ⊂-shaped process. The lower limb of the ⊂ runs medially and articulates with the dorsal aspect of the maxillary process of the palatine. The process then bends upward and back upon itself, thus forming the upper limb of the ⊂. The upper limb runs laterally. It tapers to a point distally. The dorsal surface of the upper limb is flat, and articulates with nearly the entire ventral end of the lateral ethmoid. Thus, the lacrimal intervenes between the palatine and lateral ethmoid (i.e., it prevents the two bones from articulating with each other). Posteriorly, the lacrimal meets the first infraorbital.

All of the infraorbitals are shallow. The third and fourth are tubular. Two bridges of bone, separating three pores, roof over the lateral line on each of the first two infraorbitals. The third and fourth infraorbitals each bear a single bridge which separates two pores. The anterior pore of one infraorbital is confluent with the posterior pore of the infraorbital just ahead of it. The lateral surfaces of the infraorbitals bear tiny spines.

A subocular shelf is developed along the entire margins of the first and second infraorbitals. The portions of the shelf on the anterior part of the first infraorbital and the posterior part of the second infraorbital are deep, while the intervening portion is very poorly developed (shallow). The shelf therefore appears to be "discontinuous." The subocular shelf and a portion of the endopterygoid form the floor of the "fossa" which houses the subocular light organ.

The dermosphenotic is relatively large. It bears a spinous crest which roofs over the infraorbital lateral line. The orbital margin of the dermosphenotic also bears tiny spines.

Remarks: The circumorbitals of Anomalops resemble those of Photoblepharon. The most important similarities include (1) the presence of a ⊂-shaped process on the lacrimal for articulation with the lateral ethmoid and (2) the presence of a "discontinuous" subocular shelf on the first and second infraorbitals.

The hyopalatine bones (Figs. 35-36)

The hyomandibula bears a single head. The opercular process is short. The lateral surface of the hyomandibula bears a crest for articulation with the dorsal limb of the preopercle. The symplectic process is short and meets the posterior border of the metapterygoid anteriorly.

The metapterygoid and quadrate do not present any noteworthy features.

The symplectic is long.

The endopterygoid is oval-shaped. It articulates with the palatine anteriorly, the metapterygoid posteriorly and the dorsal limb of the ectopterygoid laterally. The endopterygoid is toothless.

The dorsal and ventral limbs of the ectopterygoid are short and stout. The ectopterygoid is toothless.

The palatine articulates with the anterior portions of the endo- and ectopterygoids posteriorly. The maxillary process is capped with cartilage distally. The palatine bears a strip of tiny, conical teeth.

Remarks: The hyopalatine bones of Anomalops show no important differences from those of Photoblepharon.

The dermal upper jaw (Figs. 35-36)

The premaxilla possesses a long, slender ascending process which is two-thirds of the length of the alveolar process. The alveolar process

bears a band of short, conical teeth which extends for its entire length. The postmaxillary process is a gently convex flange which arises from most of the length of the alveolar process. The postmaxillary process is deepest at the midpoint of the alveolar process.

The shaft of the maxilla is irregular in cross section except at its distal end, where it broadens into a plate. This plate bears a small patch of spines which extends somewhat beyond its margin. The maxilla is not expanded behind the tip of the alveolar process of the premaxilla.

There are two supramaxillae. The anterior supramaxilla is small and triangular. The posterior supramaxilla is much larger. Projecting from its anterodorsal corner is a slender, spike-like process which overlies the anterior supramaxilla. The lateral surfaces of the lower one-half of the posterior supramaxilla and all of the anterior supramaxilla are covered with small spines.

Remarks: In Anomalops, the maxilla is unornamented and there is only one supramaxilla. The anterior end of the supramaxilla bears a long, slender process.

The lower jaw (Figs. 35-36)

The oral border of the dentary bears small, conical teeth which end slightly ahead of the tip of the ascending process. Near the symphysis the teeth become somewhat stouter, and are greatly expanded onto its lateral surface.

The facet which the angulo-articular bears for the quadrate condyle is located somewhat ahead of the middle of the orbit. Anterior to this facet the angulo-articular rises sharply into the ascending process. The ascending processes of the angulo-articular and dentary combine to form a large, rounded coronoid process.

The retroarticular does not present any noteworthy features.

The mandibular lateral line is largely closed. The portion in the dentary communicates with the surface via five pores. The most anterior pore is a tiny opening located directly on the mandibular symphysis. The most posterior pore is confluent with a pore in the angulo-articular; together they form a single, oval-shaped opening. A wide bridge of bone roofs over the lateral line in the angulo-articular. Posterior to this bridge is an opening where the angulo-articular receives the lateral line from the preopercle. The lateral surfaces of the lower portions of the dentary and angulo-articular (including the bridges of bone which cover the lateral line) bear low, spinous crests.

Remarks: The lower jaw of Anomalops shows no important differences from that of Photoblepharon.

The opercular bones (Figs. 35-36)

Most of the lateral surface of the opercle is covered with a series of fine, radiating crests which are weakly serrated along their edges. The facet for the opercular process of the hyomandibula is braced by a short strut of bone.

The subopercle is elongate. The posterior portion is membranous and is deeply cleft, resulting in the formation of numerous finger-like processes.

The lateral surface of the anterior part of the subopercle bears low, sinuous ridges and tiny spines.

The interopercle is large. The portion of the lateral surface of the interopercle which is not overlain by the preopercle is covered with tiny spines.

The preopercle is composed of distinct dorsal and ventral limbs. The ventral limb is about two-thirds of the length of the dorsal limb. The lateral line is completely enclosed within a tube in the dorsal limb, but is open in the ventral limb. A bridge of bone roofs over the sensory canal at the angle of the preopercle. The lateral surface of the preopercle is well-ornamented with tiny spines. There are several small patches of spines along the lower border of the ventral limb.

Remarks: The opercular bones of Anomalops show no important differences from those of Photoblepharon.

The hyoid arch and branchiostegal rays (Fig. 37)

The interhyal does not present any noteworthy features.

The epihyal meets the ceratohyal in a straight suture. In this specimen, the lateral surfaces of the epihyal and posterior portion of the ceratohyal are distinctly grooved for the hyoidean artery (in another specimen this groove is absent).

The ceratohyal is rather rectangular. Its posterior portion is slightly deepened. Anteriorly, the ceratohyal makes a direct articulation with the dorsal and ventral hypohyals. The ceratohyal is perforated by a large, oblong foramen (the foramen is somewhat smaller in another specimen). Anterior to the foramen, the hyoidean artery runs within a groove in the ceratohyal before passing into a canal within the dorsal hypohyal. The artery finally emerges through a foramen on the medial face of the dorsal hypohyal.

The hypohyals are square-shaped elements of about equal size. The urohyal-hypohyal ligament attaches to the medial surface of the ventral hypohyal.

The basihyal is absent.

The urohyal is large and diamond-shaped. Its anterodorsal and anteroventral borders are thicker than the rest of the bone, which is nevertheless well-ossified. A distinct process for the attachment of ligamentous fibers from the tips of the third hypobranchials is not present. However, the antero- and posterodorsal borders of the urohyal do meet in a blunt apex, which serves as a site for the attachment of these fibers. Projecting from the anterior end of the urohyal is a pair of stout processes for the attachment of the band-like urohyal-hypohyal ligaments.

There are eight branchiostegal rays. They increase in size from front to rear. The second, third, fourth and fifth rays bear tiny spines along their anterior borders. The first four rays articulate with the ventral border of the ceratohyal, the fifth and sixth with the lateral surface of the ceratohyal, and the seventh and eighth with the lateral surface of the epihyal.

Remarks: In Anomalops, the epihyal and posterior part of the ceratohyal are distinctly grooved for the hyoidean artery. The ceratohyal foramen is large. The urohyal is not shaped as in Photoblepharon. An indistinct process on the dorsal border of the urohyal serves for the attachment of ligamentous fibers from the third hypobranchials. Nine branchiostegal rays are present in Anomalops. The rays are unornamented.

The branchial arches

The basibranchials are toothless.

The hypobranchials and epibranchials do not present any noteworthy features.

CB5 is attached to BB4 by a short ligament. CB5 has a large tooth plate fused to it. The teeth are small and conical.

There are three pharyngobranchials. PB2 and PB3 have small, conical teeth fused to them. Both PB4 and its tooth plate are absent.

Remarks: The branchial arches of Anomalops show no important differences from those of Photoblepharon.

The vertebral column and ribs

The vertebral formula is 13 + 17 = 30. The neural arch of the first vertebra is fused to its centrum.

Basapophyses are present on the fifth through the thirteenth vertebrae. Beginning with the eighth vertebra, the basapophyses meet in the midline, thus enclosing a canal. The degree of fusion between the basapophyses gradually increases due to the fact that the peritoneal cavity becomes progressively narrower.

Long, slender pleural ribs are present on all except the first two abdominal vertebrae. The pleurals of the third and fourth vertebrae articulate with their centra; the others with their basapophyses.

Epipleural ribs are present, but their extent could not be determined with certainty. They are probably present on the first 14 vertebrae. Epineural ribs are absent.

Remarks: The vertebral formula in Anomalops is 14 + 16 = 30. Epipleural ribs are present on the first 12 abdominal vertebrae.

The pectoral girdle and fin (Fig. 38)

The extrascapular is moderate sized and rather irregular-shaped. It bears a <-shaped crest for the lateral line. The surface of this crest is well-ornamented with tiny spines.

The posttemporal has a long, spatulate dorsal limb and a short, robust ventral limb. The posttemporal is highly ornamented with spinous crests. The most prominent crest protects the lateral line. Several other small, delicate crests lie along the posterodorsal border of the bone.

The supracleithrum is rather blade-like. Its anterior border and dorsal end are thickened. The lateral surface of the supracleithrum is weakly ornamented with low ridges.

The cleithrum possesses well-developed dorsal and ventral limbs. The dorsal limb is spike-like above. The posterior lamina is very distinct and is ornamented like the supracleithrum.

There is only one postcleithrum. It is scale-like dorsally and rod-like ventrally. The leading edge of the dorsal portion of the postcleithrum is thickened.

The center of the scapula is pierced by a rather large, round foramen.

The coracoid is somewhat deepened. The coracoid process is rather long

and slender. The posteroventral portion of the coracoid is prolonged into a short, spinous process.

The actinosts are rod-like. The first three articulate with the scapula and the fourth with the cartilage between the scapula and coracoid.

There is an ossified distal radial related to the base of the second fin ray. Most of the other rays have cartilaginous distal radials.

The pectoral fin contains 16 rays. All of the rays are segmented, and all except the first, second and sixteenth are branched distally.

Remarks: The pectoral girdle of Anomalops shows no important differences from that of Photoblepharon.

The pelvic girdle and fin (Fig. 39)

The pelvic bones are not firmly united in the midline. Only their distal portions make contact. The tips of the pelvic bones are bound to the ventral limbs of the cleithra. The pelvic bone is a thin, triangular plate. The rachis is cylindrical distally but crest-like proximally. It divides the surface of the bone into anteroventral and posterodorsal portions. The rachis extends only slightly beyond the margin of the pelvic bone. The posteromedial portion of the pelvic bone bears three processes: (1) a well-developed medial process, which slightly overlaps its fellow (2) a short, blunt anterior process, which arises from the tip of the medial process and (3) an indistinct posterior process. The posterior process is short and blunt (i.e., truncated distally). Posterolaterally, the pelvic bone bears a rather well-developed lateral process.

The pelvic fin formula is 0,7. In another specimen, there are only six rays. All of the rays are segmented and all except the first are branched distally. The pelvic fins are thoracic.

There are two ossified radials. One radial is related to the second ray; the other to the third, fourth and fifth rays.

Remarks: The pelvic fin formula of Anomalops is 0,6. The anterior and posterior processes of the pelvic bone are much better developed than in Photoblepharon. The anterior process of the left pelvic bone largely overlies that from the right. A short process (the "lateral spur" of Woods and Sonoda, 1973, p. 265; fig. 1C, p. 266) projects laterally from the basal portion of the posterior process.

The dorsal fin

The dorsal fin formula is II,19. The first spine is quite short; the second is twice as long. All of the rays are segmented, and all except the first five are branched distally.

There are 20 pterygiophores. All except the first are complete. The first pterygiophore supports the two spines. The proximal radials are tapered below, where they interdigitate with the tips of the neural spines. Distinct crests bisect their lateral surfaces. The first proximal is inserted between the third and fourth neural spines. The middle radials are cylindrical elements which are only superficially ossified. The distal radials are small, well-ossified nodules. Each distal is divided into two bilateral parts. There is a small, completely cartilaginous dorsal fin stay.

There are two predorsals. They are compressed, rod-like elements. The first is slightly curved; the second is straight. Both are weakly expanded distally. The first predorsal is inserted between the skull and the

first neural spine; the second between the first and second neural spines.

Supraneurals are absent.

The anal fin

The anal fin formula is II,13. All of the rays are segmented, and all except the first two are branched distally.

There are 13 pterygiophores. The first six are incomplete. The two spines and the first ray are related to the first pterygiophore. The radials are similar to those of the dorsal fin. There is one anal fin stay. It is largely cartilaginous.

Remarks: The dorsal fin formula in Anomalops is VI,14. In contrast to Photoblepharon, the spinous and soft portions of the fin are partially separated externally. The first five spines decrease in length from front to rear (spinous portion). The "soft" portion of the fin is composed of one spine (the sixth) and 14 rays. The sixth spine is much longer than the fifth. The first proximal radial is inserted between the second and third neural spines in Anomalops.

The anal fin of Anomalops shows no important differences from that of Photoblepharon.

The caudal skeleton and fin (Fig. 40)

U2 is autogenous with respect to PU1 + U1.

The neural and hemal spines of PU4 are slightly longer than those of the preceding vertebra; the spines of PU3 are in turn somewhat longer (and stronger) than those of PU4. The hemal spine of PU3 shows some indication of duplication (distally, there is a shallow notch separating the two parts of the spine). The neural spine of PU2 is reduced to a low crest which is slightly greater than one-fourth of the length of the spine of PU3. The parhypural bears a very well-developed hypurapophysis. The hypurapophysis is broad (not spike-like), although it does taper to a point distally. The neural arch of PU2 and the hemal arches of PU2 and PU3 are autogenous.

The stegural is autogenous with respect to PU1 + U1. There is a single pair of blade-like uroneurals.

The epurals are rod-like elements which are weakly expanded proximally. The first epural is supported by the neural crest of PU2; the second and third by the edge of the stegural.

There are six hypurals (H1-H6). All are autogenous. The first two hypurals articulate with PU1 + U1 (the second also makes a slight contact with U2). The third, fourth and fifth hypurals articulate with U2 (the proximal end of the fifth just touches the tip of U2). The sixth hypural fails to articulate with U2. It lies wedged between the fifth hypural below and the spinous process of the stegural above. The first and fourth hypurals are large, plate-like bones. The second and third hypurals are the next largest (the third is slightly larger). The fifth and sixth hypurals are narrow, rod-like elements.

The caudal fin formula is 10 + 9 = 19. There are 11 procurrents above and 10 below. The first 10 above and the first nine below are spinous. The bases of the spines are forked. The foremost procurrents are supported by the tips of the neural and hemal spines of PU4 (not PU3, as in many other forms).

Remarks: The caudal skeleton of Anomalops is very similar to that of Photoblepharon.

The squamation

Ventral ridge scales are absent in Photoblepharon but are present in Anomalops.

Family Monocentridae

Osteology of Monocentris japonicus (Houttuyn)

The neurocranium (Figs. 41-42)

The skull roof

The nasals are very large, highly ornamented bones which meet in the midline along their entire length. Posteriorly, the nasals overlap and are firmly bound to the anterior ends of the frontals. The medial and lateral edges of the nasal are reflected upward to form prominent crests which bear small spines. Anteriorly, the crests are joined by a bridge of bone which forms a roof over the lateral line.

The frontals are very broad. Anteriorly, the frontal meets the nasal, mesethmoid and lateral ethmoid. In the midline, it meets its fellow in a wavy suture. Posteriorly, the frontal meets the supraoccipital, parietal, pterotic and both sphenotics (from medial to lateral). The frontal also articulates with an enlarged scale posteromedially (see below, under supraoccipital). The orbital lamina of the frontal meets the pterosphenoid (in a larger specimen, the orbital lamina also contacts the orbitosphenoid). The frontals are well-ornamented with a series of high, thin crests which are spinous along their edges. The crests separate deep mucous cavities, and are arranged in a ✕ pattern. There is an anteromedial crest which meets its fellow as well as the posterior end of the medial crest (edge) of the nasal. The anterolateral crest runs out toward the orbital margin of the frontal, and closely approaches the posterior end of the lateral crest (edge) of the nasal. The posteromedial crest runs back to contact its fellow. The posterolateral crest meets the anterior end of a crest on the extrascapular. The posterointermediate crest, which courses directly posteriorly, meets the anterior end of a crest on the parietal. In addition to the crests described above, the frontal is ornamented along its orbital margin with numerous small spines.

The parietal is moderate sized and articulates with the frontal anteriorly and the supraoccipital (and an enlarged scale) medially. Posteriorly, the parietal overlies the anterior portion of the epiotic; laterally it contacts a vertical flange on the dorsal surface of the pterotic. The parietal bears a large spinous crest which runs longitudinally for most of its length.

The epiotic articulates with the parietal anteriorly, the exoccipital posteriorly, the supraoccipital medially and the pterotic laterally.

The anterior portion of the supraoccipital is overlapped by an enlarged, highly ornamented scale. This scale is tightly articulated (but not fused)

to the supraoccipital. Starks (1904, p. 617, fig. 10) incorrectly labelled this element as being part of the supraoccipital. The supraoccipital crest is a small, triangular plate. The anterior edge of the crest is thickened, and is reflected laterally as a low ridge. This ridge forms the anterolateral boundary of the supratemporal fossa. The lateral surface of the supraoccipital crest is weakly reinforced by a small strut of bone.

The supratemporal fossa is poorly developed, ending well-behind the posterior border of the orbit. The floor of the fossa is formed by the supraoccipital medially and the epiotic laterally (the parietal does not contribute to the floor, as in many other forms).

The posttemporal fossa is a very small, shallow excavation in the posterolateral portion of the neurocranium. The floor of the fossa is formed by the pterotic, the medial wall by the epiotic, and the lateral wall by a low flange on the dorsal surface of the pterotic.

Remarks: The dorsicranium of Cleidopus is very similar to that of Monocentris. The frontal crests are arranged in a $\times$ pattern and separate deep mucous cavities. In Cleidopus, however, the edges of these crests are broad (not thin and sharp, as in Monocentris) and are more highly ornamented. An enlarged, highly ornamented scale overlying part of the supraoccipital is present in Cleidopus, just as in Monocentris.

The ethmoid region

The mesethmoid is small and confined to a position between the dorsomedial portions of the lateral ethmoids.

The lateral ethmoid is squat, being about as broad as it is deep. The medial edge of the lateral ethmoid is deeply notched for I.

The vomer is short and broad. In this specimen, the vomerine wings are separated from the lateral ethmoids by portions of the ethmoid cartilage, but in a larger specimen there is a slight amount of contact. The vomer is toothless.

Remarks: In Cleidopus, the mesethmoid forms the medial margin of the olfactory foramen (i.e., it converts the notch in the medial border of the lateral ethmoid for I into a foramen). Dorsolaterally, near its articulation with the frontal, the lateral ethmoid bears a patch of spinous ornamentation. Ornamentation on this bone is quite unusual.

The orbital region

The parasphenoid is straight. Posteriorly, it overlaps the anterior two-thirds of the ventral surface of the basioccipital. The shaft of the parasphenoid is strong and is dorsoventrally compressed. The shaft gradually increases in width as it passes anteriorly. The ascending process of the parasphenoid is pierced by a foramen for the internal carotid artery.

The orbitosphenoid is of moderate size. The orbitosphenoid is basically a V-shaped element, although a small, posteroventrally-directed process projects from the fused edges of the laminae. Anteriorly, in the midline, there is a rather large, oval foramen for I.

The pterosphenoids are moderate sized and are widely separated. The pterosphenoid meets the orbitosphenoid anteriorly, the autosphenotic and prootic posteriorly, and the frontal dorsally. The lateral margins of the large optic fenestra are formed by the pterosphenoids (anteriorly) and the prootics

(posteriorly). Posterodorsally, the edge of the pterosphenoid is notched by a foramen which transmits a twig of the superficial ophthalmic nerves. Close to the margin of the optic fenestra, the pterosphenoid bears a small foramen for IV.

The arms of the basisphenoid articulate with the prootics. The pedicel increases slightly in width as it passes ventrally. Its tip just fails to contact the parasphenoid shaft. The myodome is rather small and shallow.

Remarks: The bones of the orbital region of Cleidopus show no important differences from those of Monocentris.

The otic region

The prootic meets the pterosphenoid anterodorsally, the ascending process of the parasphenoid anteroventrally, the exoccipital posteriorly, the autosphenotic and pterotic dorsally, and the arm of the basisphenoid medially. The pars jugularis has only two external openings, separated by a thick strut of bone.

The autosphenotic bears a blunt (but distinct) postorbital process. Just posterior to this process is an oval fossa (dilatator fossa) for the origin of the dilatator operculi muscle. The dilatator fossa is also located in the ventral surface of the adjacent part of the pterotic. The autosphenotic and prootic contribute equally to the formation of the socket for the anterior portion of the head of the hyomandibula.

The pterotic meets the frontal, parietal, and both sphenotics anteriorly, the epiotic medially, and the prootic and exoccipital ventrally. The pterotic bears a facet for the posterior one-half of the head of the hyomandibula. A distinct ridge of bone on the ventral surface of the pterotic separates this facet from the more laterally situated dilatator fossa. The pterotic bears a well-developed spinous crest which forms a complete roof over the lateral line as it passes ventrally onto the preopercle.

The intercalar does not possess any noteworthy features.

The auditory bulla is moderate in size. Its wall is composed of the prootic anterodorsally, the exoccipital posterodorsally and the basioccipital posteroventrally. The prootic and basioccipital are widely separated by an area of membrane.

Remarks: In Cleidopus, the pterotic bears a crest for protection of the preopercular lateral line which is strikingly similar to that of Monocentris. There is no membranous area in the wall of the auditory bulla of Cleidopus.

The occipital region

The exoccipital articulates with the prootic and pterotic anteriorly, the epiotic anterodorsally, the supraoccipital dorsally and the basioccipital ventrally. The glossopharyngeal foramen is small, and is located close to the suture with the prootic. The foramen for X is round and is moderate in size.

The basioccipital presents no noteworthy features. Although Baudelot's ligament could not be found in this specimen, Woods and Sonoda (1973, p. 280) list "[b]audelot's ligament attached to basioccipital" as a feature of their Suborder Berycoidei (which includes the Monocentridae).

Remarks: The bones of the occipital region of Cleidopus show no important differences from those of Monocentris.

The circumorbital bones (Fig. 43)

The antorbital is absent.

The lacrimal is deep and square-shaped. Anterodorsally, the lacrimal bears a blunt, medially-directed flange. The upper surface of this flange is somewhat concave, and articulates with the ventral end of the lateral ethmoid. Posteriorly, the lacrimal articulates with the first infraorbital. Anteriorly, a bridge of bone connects the reflected upper border of the lacrimal with its lateral surface, thus forming a complete canal for the lateral line. The surface of this reflected border is covered with small spines. The lower border of the lacrimal is weakly serrated.

All of the infraorbitals (but especially the first and second) are deep. The upper borders of all of the infraorbitals are reflected outward for protection of the lateral line, but only those of the second and fourth meet the lateral surfaces (forming complete canals). The surfaces of these reflected borders bear small spines. The lower borders of the first two infraorbitals are weakly serrated.

A subocular shelf is developed along only part of the length of the second infraorbital. The shelf is in the form of a narrow, rather finger-like flange which is curved or hooked anteriorly. A stout ligament runs from the tip of the shelf to the dorsal surface of the lateral part of the endopterygoid.

The dermosphenotic bears a well-developed crest which forms a complete roof over the lateral line as it passes ventrally onto the fourth infraorbital. The surface of this crest, as well as the orbital margin of the dermosphenotic, bears small spines.

Remarks: The posterior portion of the lacrimal in Cleidopus is strongly reduced. It consists of a chain of about five small ossicles which lie embedded in a ligament that runs from the lacrimal "proper" to the first infraorbital. The reduction of the lacrimal is due to the fact that the maxillary shaft is bowed or curved dorsally. As a result, the shaft has "encroached upon" and "eaten away" the posterior part of the lacrimal (in Monocentris the maxillary shaft is straight and is largely overlain by the lacrimal).

The subocular shelf is identical to that of Monocentris (including the ligamentous attachment to the endopterygoid).

The hyopalatine bones (Figs. 43-44)

The hyomandibula bears a single head. The opercular process is not sharply set off from the remainder of the bone. The anteroventral corner of the dorsal portion of the hyomandibula is prolonged into a spinous process which just fails to contact a similar process on the dorsal border of the metapterygoid. The symplectic process is stout. Anteriorly, it meets the posterior border of the metapterygoid.

The metapterygoid and quadrate do not possess any noteworthy features.

The symplectic is long.

The endopterygoid is oval-shaped. Anteriorly, the endopterygoid meets the palatine. Posteriorly, it is slightly overlapped by the metapterygoid. The lateral edge of the endopterygoid articulates with the dorsal limb of the ectopterygoid. In this specimen, the endopterygoid bears two tiny patches of small, conical teeth on one side, but is toothless on the other side. In eight other specimens of M. japonicus which were examined, the endopterygoid is

toothless in six. It is also toothless in the specimen of M. reedi which was examined.

The ectopterygoid consists of dorsal and ventral limbs which are tapered distally. The ectopterygoid is usually toothless (seven of nine specimens of M. japonicus; also toothless in one specimen of M. reedi).

The palatine bears a facet for articulation with the lateral ethmoid anterodorsally. Posteriorly, the palatine articulates with the anterior ends of the endo- and ectopterygoids. The maxillary process is completely ossified. The palatine bears a strip of closely set, small, conical teeth. On one side, there are a few tiny tooth patches embedded in the epithelium over the palatine, in addition to this strip of teeth.

Remarks: The hyopalatine bones of Cleidopus show no important differences from those of Monocentris except that the endo- and ectopterygoids are toothed (large patch of teeth on the endopterygoid; small to moderate sized tooth patch on the ectopterygoid). Two specimens of Cleidopus were examined.

The dermal upper jaw (Figs. 43-44)

The premaxilla possesses a very well-developed ascending process (slightly greater than one-half the length of the alveolar process). The rostral cartilage is rather small. The entire length of the alveolar process bears numerous small, conical teeth. The postmaxillary process originates from the entire length of the alveolar process. Near the midpoint of the latter, it rises into a distinct, rather triangular plate.

The maxillary shaft is straight. Above, the lateral aspect of the shaft is overlain by the ventral portion of the lacrimal. The maxilla is not expanded behind the tip of the alveolar process of the premaxilla.

The supramaxilla is large. Anteriorly, it tapers to a long, spike-like process. The supramaxilla is weakly ornamented with small spines along its ventral and posterior edges.

Remarks: In Cleidopus, the alveolar process of the premaxilla is bowed dorsally, paralleling the maxillary shaft. The postmaxillary process has a somewhat more restricted origin from the alveolar process, and is rather rectangular. The lateral aspect of the maxillary shaft bears patches of rugose, spinous ornamentation.

The lower jaw (Figs. 43-44)

The dentary is slightly deepened at the symphysis. Just behind the symphysis, the lower border of the dentary is distinctly notched. The upper border of the dentary is curved. This is due to the fact that the ascending process is set at a slight angle to the rest of the dorsal border. Small conical teeth are present along the edge of the dentary except near the tip of the ascending process. At the symphysis, the teeth are greatly expanded onto the lateral surface.

The facet which the angulo-articular bears for the quadrate condyle is located slightly ahead of the posterior border of the orbit and is reinforced by a well-developed retroarticular process. Immediately anterior to the facet, the angulo-articular rises steeply into the ascending process, which, along with that of the dentary, forms a large, high coronoid process. A tiny, plate-like piece of bone, tightly articulated to the medial surface of

the posterior part of the angulo-articular, probably represents an ossification of Meckel's cartilage.

The retroarticular is weakly ornamented with tiny spines.

The mandibular lateral line is nearly completely open. Two slender struts of bone roof over the lateral line in the dentary. A somewhat larger strut protects the lateral line in the angulo-articular. The edges of the groove for the lateral line, as well as the surface of the strut of bone on the angulo-articular, bear small spines.

Remarks: Meckel's cartilage is more complete in Cleidopus. Its posterior portion is weakly ossified in several places. The most posterior of these ossifications appears to correspond with the tiny element present in Monocentris. The ornamentation on the lower jaw in Cleidopus is much more extensive than in Monocentris. Particularly important is the fact that the lower border of the dentary is distinctly notched, just as in Monocentris.

The opercular bones (Figs. 43-44)

The opercle is rather small. The facet for the opercular process of the hyomandibula is reinforced by a ridge which runs back for one-half of the anteroposterior length of the bone. The posterodorsal border of the opercle is excavated (wide, moderately deep notch). The lateral surface of the opercle is highly ornamented with a series of radiating ridges which bear small spines. One of these ridges (corresponding in position to the ridge on the medial surface described above) is much thicker than the others.

The subopercle is rather elongate. Its posterior portion is thin but not membranous. The lateral surface and lower edge of the subopercle are weakly ornamented with small spines.

The interopercle is rather blade-like. Its lower border is feebly serrated.

The preopercle consists of distinct dorsal and ventral limbs. The angle between the limbs is about 140°. The lateral line is completely open except near the angle, where two bridges of bone roof over it. Small spines ornament the surfaces of these bridges, as well as the edges of the dorsal and ventral limbs.

Remarks: The opercular bones are more highly ornamented in Cleidopus than in Monocentris.

The hyoid arch and branchiostegal rays (Fig. 45)

The interhyal presents no noteworthy features.

The epihyal meets the ceratohyal in a straight suture. The lateral surfaces of the epihyal and posterior two-thirds of the ceratohyal are not distinctly grooved for the hyoidean artery.

The ceratohyal is rather short and deep. A moderate amount of connective tissue fills in the gap between the ceratohyal and dorsal hypohyal. The center of the ceratohyal is perforated by a small, slender foramen. Anterior to the foramen, the ceratohyal bears a deep groove for the hyoidean artery. This groove leads into a canal between the dorsal and ventral hypohyals. The canal passes anteromedially to emerge on the medial surface of the hyoid arch between the hypohyals.

A small amount of connective tissue separates the hypohyals. The ventral hypohyal is slightly deeper than the dorsal hypohyal. The urohyal-hypohyal

ligament is broad, and attaches to the medial surface of the ventral hypohyal for its entire depth.

The basihyal is absent.

The urohyal is short and deep. It is well-ossified. The anterior border of the urohyal is flattened into a surface which is perpendicular to the main portion of the bone. The urohyal-hypohyal ligaments attach to the edges of this border. The posterior border of the urohyal is irregular in outline. Projecting from the anterodorsal corner of the urohyal is a rather distinct process, to which the tips of the third hypobranchials are bound by tough connective tissue.

There are eight branchiostegal rays. They increase in size from front to rear. In this specimen the rays are not ornamented, but in a number of others (including M. reedi) the rays are serrated along their anterior borders. The first four rays articulate with the ventral border of the ceratohyal, the fifth and sixth with the lateral surface of the ceratohyal, the seventh with the lateral surface of the cerato-epihyal junction, and the eighth with the lateral surface of the epihyal.

Remarks: In Cleidopus, the suture between the epihyal and ceratohyal is obscured in medial view by the development of short, finger-like processes on the epihyal. These digitations cross the line of suture and are pressed against the medial face of the ceratohyal. The lateral surfaces of the epihyal and posterior portion of the ceratohyal are distinctly grooved for the hyoidean artery in Cleidopus.

The ceratohyal is pierced by a moderate sized, oblong foramen. All of the branchiostegals except the first are ornamented with spines. The urohyal of Cleidopus is very similar to that of Monocentris.

The branchial arches

BB1 and BB2 are short and deep. They are shells of bone which were probably filled with cartilage. BB3 is more elongate and is more strongly ossified. It tapers to a point posteriorly. BB4 is a small block of cartilage. The epithelium overlying BB1, BB2 and BB3 contains tooth patches. The patches over BB1 and BB2 are small, but BB3 supports a rather large, oval-shaped plate.

The hypobranchials and epibranchials do not present any noteworthy features.

CB5 does not articulate directly with BB4. A large tooth plate is fused to CB5. The teeth are short and conical.

There are three pharyngobranchials. PB2 and PB3 have teeth fused to them. Both PB4 and its tooth plate are absent.

Remarks: The branchial arches of Cleidopus show no important differences from those of Monocentris. Nelson (1969a, pp. 497 and 499, figs. 8B and 8C) has described and illustrated the basibranchial dentition of both of these genera. Nelson noted that in Cleidopus there is a large, median tooth patch fused to BB3 (a similar element is present in the specimen examined for this report, but it was not possible to determine whether it was fused to BB3). In Monocentris, Nelson found that the basibranchial dentition comprised a random arrangement of irregular plates, with no two specimens having the same pattern. He suggested that the tooth patch of BB3 in Cleidopus arose by the consolidation of patches such as those of Monocentris. This suggestion is supported by the observation that in the specimen of Monocentris described

above, BB3 is, in fact, closely associated (but not quite fused) with a large, oval tooth patch.

The vertebral column and ribs

The vertebral formula is 12 + 15 = 27. The neural arch of the first vertebra is fused to its centrum. Distinct zygapophyses are present only on the abdominal vertebrae.

Basapophyses are present on the sixth through the twelfth vertebrae. Those on the sixth vertebra are very rudimentary. The basapophyses on the other vertebrae are well-developed and are completely fused in the midline, thus producing unpaired spinous projections. These projections gradually increase in length; those on the posterior abdominal vertebrae closely resemble the hemal spines.

Pleural ribs are present on the sixth through the twelfth abdominal vertebrae. The pleurals are rather slender. The first and last members of the series are shorter than the others. The pleurals of the sixth through the ninth vertebrae are bound to their basapophyses by ligaments which become progressively shorter as one passes posteriorly. The remaining pleurals articulate directly with their basapophyses.

Delicate epipleural ribs are borne by the seventh through the eleventh abdominal vertebrae. Epineural ribs are absent.

Remarks: The vertebral formula of Cleidopus is 13 + 14 = 27. Pleural ribs begin on the seventh abdominal vertebra. Epipleural ribs are absent.

The pectoral girdle and fin (Fig. 46)

The extrascapular is moderately large and irregular-shaped. It bears a broad crest which roofs over the lateral line. The surface of this crest bears small spines.

The posttemporal has a well-developed dorsal limb and a short, stout ventral limb. The posterodorsal edge of the bone is serrated. The posttemporal bears a short canal for the lateral line. The roof of this canal bears small spines.

The supracleithrum is of a very peculiar shape. It is not at all blade-like (long and tapered). Rather, it is short (dorsoventrally) and broad (anteroposteriorly) (i.e., it is squat). The lower border of the supracleithrum is distinctly notched. The posterodorsal edge of the supracleithrum is serrated, and its lateral surface bears several low, serrated ridges.

The cleithrum is a strong, stout bone. The dorsal and ventral limbs are rather well-developed; the angle between them is about 120°. The posterior lamina is large and its surface bears low, serrated ridges.

There is only one postcleithrum. The dorsal end is expanded; the ventral portion is long and rod-like.

The center of the scapula bears a large, oval foramen.

The coracoid is relatively deep. The coracoid process is rather long but is not slender. The posteroventral portion of the coracoid is prolonged into a blunt process.

The first actinost is short and stubby. The other three are more elongate and are rather hourglass-shaped in profile. The first two actinosts articulate with the scapula, the third with the scapula and the connective tissue between the scapula and coracoid and the fourth entirely with this connective tissue.

There are two distal radials. They are ossified nodules which are related

to the bases of the second and fourth fin rays.

The pectoral fin contains 14 rays. All of the rays except the first are segmented, and all except the first, second and fourteenth are branched distally.

Remarks: The pectoral girdle of Cleidopus shows no important differences from that of Monocentris except that the ornamentation on the dermal bones is more prominent. Of particular importance is the fact that the supracleithrum is shaped exactly as in Monocentris.

The pelvic girdle and fin (Fig. 47)

The pelvic bones are firmly united to each other. They are strong, well-ossified elements. The pelvic bone is rather triangular in lateral view. The rachis does not project beyond the margin of the pelvic bone. Distally, the rachis is in the form of a thickened ridge. Proximally, it becomes more crest-like, and blends into a large process which extends out laterally, just above the base of the pelvic fin spine. The outer edge of this laterally-directed process fuses with the lower part of the main portion of the pelvic bone, and in doing so encloses a rather large opening. The posteromedial portion of the pelvic bone is expanded into a broad, semicircular plate. The medial edges of the two plates (one from each pelvic bone) interdigitate in the midline. The homology of this plate with the processes of the pelvic bone seen in the other beryciforms examined is not certain. However, it seems probable that the plate corresponds to both the medial and posterior processes of those forms. Anterior and lateral processes of the pelvic bone are absent.

The pelvic fin formula is I,3. The spine is extremely large. Its surface is distinctly grooved. The base of the spine and the portion of the pelvic bone with which it articulates are modified in a fashion such that when the spine is fully extended, it becomes "locked" into place. The fin rays are rudimentary. They are segmented, but are not branched distally. The pelvic fins are thoracic.

There is only one radial. It is a tiny sliver of bone related to the base of the first fin ray.

Remarks: The pelvic girdle and fin of Cleidopus are very similar to those of Monocentris. In Cleidopus, there are two rudimentary rays on one side and three on the other (two specimens examined).

The dorsal fin

The dorsal fin formula is VI,11. The spinous and soft portions of the fin are separate. The second and third spines are very large (the second is the largest). The first and fourth spines are short but stout. The last two spines are scale-like. The dorsal fin is very peculiar in that when it is erected, the spines project strongly in alternate directions (to the right and left). All of the rays of the dorsal fin are segmented, and all except the first two are branched distally.

There are 17 pterygiophores. The first six and last four are incomplete. The proximal radials are plate-like above and tapered below. All of the proximals bear crests which bisect their lateral surfaces. The first proximal is inserted between the neural spines of the second and third vertebrae. The posteriormost members of the series of middle radials are very small and are poorly ossified. The distal radials are small, nodular elements. There

is one dorsal fin stay. It is small and weakly ossified.

There are two predorsals. They are elongate, flattened elements. The first predorsal is inserted between the skull and the first neural spine; the second between the first and second neural spines.

Supraneurals are absent.

The anal fin

The anal fin formula is 0,10. All of the rays are segmented, and all except the first are branched distally.

There are nine pterygiophores, all of which are incomplete. The proximal and distal radials are similar to those of the dorsal fin. There is one anal fin stay which resembles that of the dorsal fin except that it is somewhat smaller.

Remarks: As in Monocentris, the spines of the dorsal fin of Cleidopus project strongly in alternate directions when erected. Spines are not present in the anal fin of Cleidopus (also as in Monocentris).

The caudal skeleton and fin (Fig. 48)

U2 is a moderate sized element which is autogenous with respect to PU1 + U1.

The neural and hemal spines of PU3 are expanded (fan-shaped), and quite unlike those of the preceding vertebra. The neural spine of PU2 is reduced to a low crest which is one-third of the length of the neural spine of PU3. Dorsally, this crest is prolonged into a very short process which projects up between the proximal ends of the first two epurals. The parhypural bears a rather well-developed hypurapophysis. The neural arch of PU2 and the hemal arches of PU2 and PU3 are autogenous.

The base of the stegural overlies and is tightly articulated to PU1 + U1. There is a single pair of blade-like uroneurals.

There are three epurals. They decrease in length from the first to the third. The proximal portions of the epurals are flattened and weakly expanded. The first epural is supported below by the dorsal edge of the neural crest of PU2, while the second and third epurals are supported by the dorsal edge of the stegural.

All six hypurals (H1-H6) are autogenous. The first two hypurals articulate with PU1 + U1 (the second hypural also makes a slight articulation with U2). The third, fourth and fifth hypurals articulate with U2. The sixth hypural fails to meet U2; it lies between the fifth hypural below and the spinous process of the stegural above. The first and fourth hypurals are large, plate-like bones (the first is slightly larger). The second and third hypurals are somewhat narrower, and are approximately equal in size. The fifth and sixth hypurals are rod-like. The sixth hypural is the smallest.

The caudal fin formula is 10 + 9 = 19. There are five procurrents above and four below. The first four above and the first three below are spinous. The bases of the spines are forked. The procurrents increase in length from front to rear. The foremost procurrents are supported by the neural and hemal spines of PU3.

Remarks: The caudal skeleton of Cleidopus is very similar to that of

Monocentris (including the presence of fan-shaped neural and hemal spines on PU3). In Cleidopus, however, the caudal fin formula is 9 + 9 = 18, and the first procurrent above is supported by the distal tip of the first epural.

The squamation

The scales on the body are very large and thick, so that the fish is completely covered with a heavy armor (hence the popular name--pinecone fish). A series of midventral scales bearing well-developed ridges or keels is present (the keel is especially prominent in M. reedi). These scales seem to correspond to the ventral ridge scales of various other forms. It should be noted, however, that all of the body scales bear ridges on their surfaces.

Remarks: As in Monocentris, the scales of Cleidopus form a heavy armor. Ventral ridge scales similar to those of Monocentris are also present.

Family Trachichthyidae

Osteology of Paratrachichthys sp.[1]

The neurocranium (Figs. 49-50)

The skull roof

The nasals are quite large but fail to meet in the midline. Posteriorly, the nasals overlie the anterior ends of the frontals. The medial and lateral edges of the nasal are reflected upward to form crests which protect the lateral line. These crests, as well as a slender bar of bone which roofs over the lateral line anteriorly, bear small serrations.

The frontals are rather short and broad, and do not extend beyond the posterior border of the orbit. The frontal meets the mesethmoid, lateral ethmoid and nasal anteriorly. Posteriorly, the frontal articulates with the supraoccipital, parietal, pterotic and both sphenotics (from medial to lateral). In the midline, the frontals meet in a sinuous suture (the frontals overlap one another). The orbital lamina of the frontal contacts the orbito- and pterosphenoids. Small foramina perforate the orbital surface of the frontal and serve to transmit twigs of the superficial ophthalmic nerves which innervate the supraorbital lateral line.

The frontals are highly ornamented with a series of spinous crests which separate rather deep mucous cavities. The crests are arranged in a ✕ pattern (although a couple of much smaller crests on the posterior part of the frontal partially obscure this pattern). The anteromedial and anterolateral crests run forward to meet the medial and lateral crests (edges) of the nasal.

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[1]The specimen which is described in this section is a representative of a new and undescribed species of Paratrachichthys (Woods, personal communication). It is referred to in this investigation as either Paratrachichthys or Paratrachichthys sp. (in those cases where comparisons with other species of Paratrachichthys are made).

The anteromedial crest just fails to contact its fellow. The posteromedial crest is separated from its fellow by a somewhat larger gap. The posterolateral crest runs back toward the ventral limb of the crest on the extrascapular, but is separated from it by a rather wide interval. The posterointermediate crest runs posteriorly to become continuous with a longitudinal crest on the dorsal surface of the parietal. In addition to the crests described above, the orbital margin of the frontal bears numerous tiny spines.

The parietals are moderate sized and partially overlie the supraoccipital (medially) and the epiotics (posteriorly). The parietal meets the frontal anteriorly and the anterior end of a low ridge (the lateral wall of the posttemporal fossa) on the dorsal surface of the pterotic laterally. The contact with the pterotic is very slight. The parietal is ornamented with a spinous crest.

The epiotic articulates with the parietal anteriorly, the exoccipital posteroventrally, the supraoccipital medially and the pterotic laterally.

The supraoccipital possesses a moderately well-developed crest for the insertion of the epaxial musculature. Although the crest is thin it is rather strong, due to the presence of two ridges which reinforce its lateral surface. The leading edge of the supraoccipital crest is sharp.

The supratemporal fossa extends anteriorly to a level slightly ahead of the posterior border of the orbit. The fossa is floored by the supraoccipital, parietal, epiotic and a very small portion of the posterior end of the frontal. The parietal crest forms a partial lateral boundary for the fossa.

The posttemporal fossa is rather large. The pterotic forms most of its floor (posteriorly, the exoccipital makes a small contribution). The medial wall of the fossa is formed by the epiotic and the lateral wall by a low ridge on the pterotic (the lateral wall is poorly developed). The posttemporal fossa also has a distinct anterior wall formed by the autosphenotic and a small area of cartilage.

Remarks: The nasals are large and meet in the midline in other trachichthyids. In Gephyroberyx and Hoplostethus the nasals bear a pair of short spines which project anteriorly (one spine on each nasal). These spines are absent in Trachichthys and all species of Paratrachichthys which were examined (Paratrachichthys sp., P. fernandezianus, P. prosthemius) except P. argyrophanus (see Woods and Sonoda, 1973, fig. 25).

The frontals in all trachichthyids bear crests which separate deep mucous cavities and which are arranged in a $\times$ pattern. The relationships of these crests to one another, as well as to the crests on the nasals, parietals and extrascapulars are similar in all forms (although minor differences do occur). The upper edges of the crests are broad in Trachichthys, not thin (sharp) as in the other genera.

The ethmoid region

The mesethmoid is a small, $\wedge$-shaped bone. It is confined to a position between the dorsomedial portions of the lateral ethmoids.

The lateral ethmoids are squat, being nearly as broad as they are deep. The medial portion of the lateral ethmoid is pierced obliquely by a moderate

sized, oval foramen for I. The lower portion of the lateral edge of the lateral ethmoid is serrated.

The vomerine wings barely contact the lateral ethmoids. Five or six very small teeth are present on the head of the vomer.

Remarks: The lateral border of the lateral ethmoid is not serrated in other trachichthyids. The vomer is toothed in all trachichthyids except Hoplostethus (although in one specimen, two tiny teeth were present).

The orbital region

The parasphenoid is straight. Posteriorly, it overlies the anterior one-third of the ventral surface of the basioccipital. The parasphenoid shaft is cylindrical. The ascending processes flare up to articulate with both the anteroventral portions of the prootics and the arms of the basisphenoid (slightly). The ascending processes form the entire lateral walls of the myodome, in contrast to many other forms in which the prootics also make a contribution. The internal carotid artery enters the myodome through the space between the ascending process and the adjacent portion of the prootic.

The orbitosphenoid is large and irregular in shape. A plate-like keel projects ventrally from its lower border, as does another (but much less distinct) process further anteriorly. Just ahead of this latter process is a large, oval foramen for I.

The pterosphenoids do not meet in the midline. The pterosphenoid meets the orbitosphenoid anteroventrally, the autosphenotic and prootic posteriorly, the frontal dorsally, and the basisphenoid ventrally. The margins of the large, oval-shaped optic fenestra are formed by the orbitosphenoid (anteriorly) and the basisphenoid (posteriorly) (the posteroventral portion of the orbitosphenoid is attenuated, and excludes the pterosphenoid from entering into the margin of the fenestra). The trochlear foramen could not be identified.

The arms of the basisphenoid articulate with the prootics, pterosphenoids, orbitosphenoid and ascending processes of the parasphenoid. The pedicel is constricted above. The tip of the pedicel is separated from the parasphenoid by a small piece of cartilage.

Remarks: In contrast to other trachichthyids, the parasphenoid in Trachichthys exhibits postorbital curvature. The foramen for the internal carotid artery pierces the ascending process of the parasphenoid in Gephyroberyx and Hoplostethus (unlike Trachichthys and Paratrachichthys).

The lower border of the orbitosphenoid in Trachichthys is not prolonged into a keel as in other forms. As in Paratrachichthys, the orbitosphenoid in Trachichthys extends back below the pterosphenoid, but in the latter genus it only partially excludes the pterosphenoid from the margin of the optic fenestra. In Gephyroberyx and Hoplostethus, the full length of the pterosphenoid enters into the margin of the fenestra. The trochlear foramen pierces the center of the pterosphenoid in Trachichthys and the lower portion of the bone in Hoplostethus.

The otic region

The prootic meets the pterosphenoid anterodorsally, the parasphenoid anteroventrally, the exoccipital posteriorly, the autosphenotic and pterotic dorsally, and the basisphenoid medially. Two struts of bone separate the

three external openings of the pars jugularis. In the region of the posterior strut, the prootic sends up a thin sheet of bone which overlies the prootic-pterotic suture. The foramen for IX could not be identified in this specimen, but in P. fernandezianus it is located in the prootic, close to the suture with the exoccipital.

The autosphenotic bears a short, blunt postorbital process. The facet for the anterior part of the head of the hyomandibula is formed by the autosphenotic (upper three-fourths) and prootic.

The pterotic meets the parietal, frontal, and both sphenotics anteriorly, the exoccipital posteriorly, the epiotic medially, and the prootic ventrally. The ventral surface of the pterotic bears a shallow, elongate facet for the posterior part of the head of the hyomandibula. The lateral edge of the pterotic is raised into a serrated crest, the posterior end of which is bent downward. The preopercular lateral line passes ventrally just behind this crest, while the main cephalic lateral line passes anteriorly just medial to it.

The intercalar presents no noteworthy features.

The auditory bulla is moderately large and is oval in shape. Its wall is formed by the prootic anteriorly, the exoccipital posterodorsally and the basioccipital posteroventrally. A large area of cartilage between the prootic and basioccipital completes the wall.

Remarks: The glossopharyngeal foramen is located in the prootic in Gephyroberyx, the intercalar in Hoplostethus and the exoccipital in Trachichthys.

The occipital region

The exoccipital meets the prootic and pterotic anteriorly, the epiotic anterodorsally, the supraoccipital dorsally and the basioccipital ventrally. A large, oval foramen transmits X.

The basioccipital presents no noteworthy features.

Remarks: The bones of the occipital region of other trachichthyids do not show any important differences from those of Paratrachichthys.

The circumorbital bones (Fig. 51)

The antorbital is absent.

The lacrimal is shallow and rather elongate. Anterodorsally, the lacrimal bears a concave facet for articulation with the lateral ethmoid. Posteriorly it meets the first infraorbital. The reflected upper borders of the lacrimal and infraorbitals form a partial canal for the lateral line and bear tiny spines. Near the anterior end of the lacrimal, however, a small flange roofs over the lateral line completely.

All of the infraorbitals (but especially the first and second) are deep. The lower border of the second infraorbital is deeply notched. The lateral surfaces of the infraorbitals bear delicate crests which are serrated along their edges.

A subocular shelf is developed along a limited portion of the margin of the second infraorbital. The shelf consists of a narrow, blunt flange which does not show any trace of curving anteriorly.

The dermosphenotic is small and delicate. Its outer border is reflected upward to form a serrated crest for protection of the lateral line. The dermosphenotic also bears a small, delicate process which just contacts the anterior end of the crest on the lateral edge of the pterotic.

Remarks: In all trachichthyids, the subocular shelf is developed on only a portion of the second infraorbital. In contrast to Paratrachichthys sp., the shelf in all of the other trachichthyid species examined (including P. fernandezianus) shows a slight trace of curving or hooking anteriorly (reminiscent of the condition present in the Monocentridae).

The hyopalatine bones (Fig. 51)

The head of the hyomandibula is single. The opercular process is short but distinct. The lateral surface of the dorsal portion of the hyomandibula bears a ridge for articulation with the dorsal limb of the preopercle. The anteroventral corner of the dorsal part of the hyomandibula meets a large, stout process from the upper border of the metapterygoid in an interdigitating suture. The symplectic process articulates with the posterior border of the metapterygoid.

The metapterygoid and quadrate present no noteworthy features.

The symplectic is long.

The endopterygoid is roughly oval in shape. It meets the palatine anteriorly, the metapterygoid posteriorly and the dorsal limb of the ectopterygoid laterally. The endopterygoid is toothless.

The ectopterygoid consists of long, tapered dorsal and ventral limbs. At the junction of the limbs, the ectopterygoid is slightly overlapped by the metapterygoid. The ectopterygoid bears an elongate patch of small, conical teeth. Anteriorly, these teeth are continuous with those on the palatine.

Anterodorsally, the palatine bears a facet for articulation with the ventral end of the lateral ethmoid. Posteriorly, the palatine meets the endo- and ectopterygoids. The maxillary process is completely ossified. The palatine bears a strip of small, conical teeth.

Remarks: The anteroventral corner of the dorsal part of the hyomandibula articulates with a process from the upper border of the metapterygoid in Trachichthys (as in Paratrachichthys). The ectopterygoid is toothless in Trachichthys, Gephyroberyx and Hoplostethus.

The dermal upper jaw (Fig. 51)

The ascending process of the premaxilla is one-fourth of the length of the alveolar process. The alveolar process is very long and slender. It bears numerous short, conical teeth which are set closely together. Most of the postmaxillary process is in the form of a shallow, gently convex flange which arises from the greater portion of the length of the alveolar process. About one-third of the way down the length of the alveolar process, however, the postmaxillary process is prolonged into a distinct, hook-like flange.

The shaft of the maxilla is long and cylindrical except distally, where it broadens somewhat into a flat, plate-like portion. The maxilla is not expanded behind the tip of the alveolar process of the premaxilla. The lateral surface of the maxillary shaft bears several low, spinous ridges.

The supramaxilla is large. It is plate-like posteriorly but spike-like anteriorly. The lateral surface of the supramaxilla is covered with low, spinous ridges.

Remarks: The alveolar process of the premaxilla in all trachichthyids is very long. The shape of the postmaxillary process varies. In Gephyroberyx

the process resembles that of Paratrachichthys (hook-like). In Hoplostethus and Trachichthys the postmaxillary process rises into a rather broad, plate-like flange.

The lower jaw (Fig. 51)

The dentary is slightly deepened at the symphysis. The oral border of the dentary bears small conical teeth which extend nearly to the tip of the ascending process. Near the symphysis the teeth expand onto the lateral surface of the bone, almost reaching its ventral edge. The lower portion of the lateral surface of the dentary bears serrated crests.

The facet which the angulo-articular bears for the quadrate condyle is located slightly ahead of the posterior border of the orbit. The ascending process of the angulo-articular is rounded, and forms a low coronoid process along with that of the dentary. The ornamentation on the angulo-articular resembles that on the dentary.

The retroarticular presents no noteworthy features.

The mandibular lateral line is largely open. Three slender struts of bone roof over the sensory canal in the anterior one-half of the dentary, however. The lateral line in the posterior part of the angulo-articular is also enclosed.

Remarks: In all trachichthyids, the teeth on the dentary are greatly expanded onto the lateral surface of the symphysis. The mandibular lateral line is more enclosed in Gephyroberyx than in other trachichthyids.

The opercular bones (Fig. 51)

The opercle is roughly semicircular in shape. The facet for the opercular process of the hyomandibula is rather deep, and is reinforced by a ridge which runs back for one-half of the width of the bone. The lateral surface of the opercle bears numerous low, spinous ridges which radiate out to the posterior border of the bone, where they end in small serrations. One of these ridges is more prominent than the others. It corresponds in position to the ridge on the medial face of the opercle described above.

The subopercle is weakly ossified posteriorly. Its posterior end is deeply cleft, resulting in the formation of numerous finger-like processes. The lower border of the subopercle is distinctly notched (broad indentation). The lateral surface of the bone is covered with tiny spines.

The interopercle is ornamented like the opercle.

The preopercle consists of a long (deep) dorsal limb and a well-developed ventral limb. The angle between the limbs is almost 90°. The reflected border of the preopercle forms a partial canal for the lateral line; near the angle a strut of bone roofs over the lateral line completely. The posterior, ventral and reflected borders of the preopercle are finely serrated. In addition, the angle of the preopercle is prolonged into a prominent spine.

Remarks: The opercular bones in all trachichthyids are similar in several respects, including (1) the presence of serrated crests or ridges on the lateral surface of the opercle (2) the deep vertical limb of the preopercle and (3) the presence of a prominent spine at the angle of the preopercle.

The hyoid arch and branchiostegal rays (Fig. 52)

The interhyal presents no noteworthy features.

The epihyal meets the ceratohyal in a straight suture. The lateral surfaces of the epihyal and posterior one-third of the ceratohyal are not distinctly grooved for the hyoidean artery.

The ceratohyal is elongate. Anteriorly it meets the ventral hypohyal (connective tissue fills in the gap between the ceratohyal and dorsal hypohyal). The center of the ceratohyal is pierced by a large, oval foramen. A deep groove on the lateral surface of the anterior one-third of the ceratohyal leads the hyoidean artery to a canal between the hypohyals. The artery finally emerges onto the medial face of the hyoid arch between the hypohyals.

The ventral hypohyal is larger than the dorsal hypohyal. Anteriorly, the suture between the hypohyals is interdigitated. The medial surface of the anteroventral corner of the ventral hypohyal is the site of attachment of the urohyal-hypohyal ligament.

The basihyal is absent.

The urohyal is a thin, shallow plate. It is strengthened by a low ridge on the anterior one-half of its lateral surface. The posterior border of the urohyal is concave, and the posterodorsal corner is prolonged into a pointed process. Connective tissue binds the tips of the third hypobranchials to the dorsal border of the urohyal (the urohyal does not bear any distinct process for the attachment of this tissue, however). A pair of short, ventrolaterally-directed processes at the anterior end of the urohyal serve for the attachment of the urohyal-hypohyal ligaments.

There are eight branchiostegal rays. They increase in size from front to rear. The anterior borders of rays two through five are weakly serrated. The first four rays articulate with the ventral border of the ceratohyal, the fifth with the lateral surface of the ceratohyal, the sixth with the lateral surface of the cerato-epihyal junction, and the seventh and eighth with the lateral surface of the epihyal.

Remarks: The hyoid arch and branchiostegal rays of Trachichthys differ from those of other trachichthyids in the following ways: (1) the epihyal and posterior part of the ceratohyal are distinctly grooved for the hyoidean artery (2) the ceratohyal foramen is only moderate in size (3) the ventral border of the ceratohyal is deeply notched for the branchiostegal rays (4) the ornamentation on the rays is more prominent and (5) the anterodorsal corner of the urohyal bears a well-developed process for the attachment of ligaments from the third hypobranchials (a tiny, ill-defined process is present in Gephyroberyx). The suture between the hypohyals is interdigitated in all trachichthyids (but only weakly in Trachichthys and Hoplostethus).

The urohyal is not shallow in other trachichthyids (unlike Paratrachichthys). In Gephyroberx and Hoplostethus, both the posterodorsal and posteroventral corners of the urohyal are drawn out into processes, while in Trachichthys and Paratrachichthys only the posterodorsal corner is attenuated. In Trachichthys, there are ventrolaterally-directed processes (similar to those in Paratrachichthys) for the attachment of the urohyal-hypohyal ligaments.

The branchial arches (Fig. 53)

BB1 is rather deep and is completely ossified. BB2 and BB3 are more elongate. The posterior tip of BB3 is cartilaginous and is bent slightly

downward. BB4 is a small, diamond-shaped block of cartilage. The basibranchials are toothless.

The hypobranchials and epibranchials present no noteworthy features.

CB5 is tied to the ventral surface of BB4 by a short ligament. CB5 is covered with sharp, conical teeth (teeth fused to CB5).

There are three pharyngobranchials. PB2 and PB3 have conical teeth fused to them. Both PB4 and its tooth plate are absent.

Remarks: In Paratrachichthys fernandezianus there is a small patch of teeth fused to BB3. In Trachichthys, small tooth patches lie embedded in the epithelium over BB2 and BB3. The basibranchials are toothless in other trachichthyids.

The vertebral column and ribs (Fig. 54)

The vertebral formula is 13 + 14 = 27. The neural arch of the first vertebra is fused to its centrum. The first six vertebrae bear distinct pre- and postzygapophyses.

Basapophyses are present on the fourth through the thirteenth vertebrae. Those on the fourth and fifth vertebrae are poorly developed. Beginning with the seventh vertebra, the basapophyses meet in the midline (partial fusion). The last four pairs of basapophyses are completely fused into unpaired spines which resemble the hemal spines more posteriorly.

Pleural ribs are present on the third through the thirteenth vertebrae. All of the pleurals are long and slender except the first, which is slightly expanded, and the last, which is considerably shorter than the others. The pleurals of the third vertebra articulate with the centrum; the others with the tips of the basapophyses. Epineural ribs are absent.

A large, plate-like element, termed the "tympanic plate" or "anterior rib plate" (Woods and Sonoda, 1973, p. 325, fig. 27) is present in Paratrachichthys. This plate is well-ossified and is rather oval in shape. Its medial surface is concave; its lateral surface weakly convex. Projecting from the medial surface of its anterodorsal portion is a spherical condyle which articulates with a socket on the lateral aspect of the pedicel of the first neural arch. In addition to this direct articulation with the first vertebra, the dorsal border of the plate is bound to the lateral aspects of the second and third neural arches by short, ligamentous fibers. A small flange on the dorsal edge of the plate provides a site for the attachment of these fibers.

Remarks: The vertebral formulae in other trachichthyids are as follows: Paratrachichthys fernandezianus -- 12 + 16 = 28; Trachichthys -- 12 + 15 = 27; Gephyroberyx -- 12 + 15 = 27; Hoplostethus -- 11 + 16 = 27.

The "tympanic plate" and various associated structures (levator epipleuralis muscle, occipito-spinal nerve, Baudelot's ligament and swim bladder) in Paratrachichthys trailli, P. prosthemius, Trachichthys australis and Optivus elongatus have recently been described in an excellent paper by Shimizu (1977). Shimizu (1977, p. 193, fig. 1) illustrated the "tympanic plate" of all of these species; in addition, the plate of Paratrachichthys argyrophanus was figured by Woods and Sonoda (1973, p. 325, fig. 27), and that of Paratrachichthys sp. is included in this report (fig. 54). Shimizu (1977, p. 196) provided evidence that the "tympanic plate" represents a modified (expanded) first epipleural rib (or perhaps in some forms, an expanded first epipleural which has incorporated the second epipleural), a conclusion with which I concur. One difference between Shimizu's findings and my own which is

perhaps worth noting concerns the second epipleural in Trachichthys. Whereas Shimizu (1977, p. 194) did not find a second epipleural in Trachichthys (thereby indicating that it has been lost or become fused into the "tympanic plate"), a small, slender second epipleural, similar to that seen in females of Paratrachichthys trailli and in Optivus elongatus (Shimizu, 1977, p. 193, figs. 1B and 1E), was present in the specimen which I examined. Whether this difference indicates intraspecific variation, or is simply the result of size differences between the specimens examined, seems uncertain.

Shimizu (1977, pp. 195-196) presented evidence that the special muscle which attaches to the lateral surface of the "tympanic plate", termed the levator epipleuralis, is a derivative of the anteriormost portion of the epaxialis. Shimizu also demonstrated that the size and shape of the "tympanic plate" and levator epipleuralis show obvious sexual dimorphism in Paratrachichthys trailli and P. prosthemius, and that in both of these species (as well as in Optivus elongatus and Trachichthys australis) the anterior part of the swim bladder extends laterally to attach to the medial surface of the "tympanic plate". Shimizu (1977, p. 197) concluded that the specialized morphological complex present in the four species noted above probably serves in sound production, and that the sounds produced by the males and females of P. trailli and P. prosthemius are probably different because of the sexual dimorphism seen in this complex.

In Hoplostethus mediterraneus and Gephyroberyx japonicus a "tympanic plate" (and associated specialized structures) is not present, there being instead two normal (slender) epipleural ribs on the first two vertebrae (Shimizu, 1977, p. 195). Normal epipleurals are also present on the first two vertebrae in G. darwini (personal observation).

The pectoral girdle and fin (Fig. 55)

The extrascapular is triradiate. Its lateral surface bears a <-shaped, spinous crest for the lateral line. The posterodorsal border of the extrascapular is weakly serrated.

The posttemporal is also triradiate. In addition to well-developed dorsal and ventral limbs there is a short, spine-like posterior limb. The lateral surface of the posttemporal bears a serrated crest for the lateral line. Tiny spines lie along the posterodorsal border of the bone.

The supracleithrum is blade-like.

The cleithrum possesses well-developed dorsal and ventral limbs which lie at an angle of 140° to one another. The posterior lamina is very distinct and bears several low ridges on its lateral surface.

There is only one postcleithrum. It is scale-like dorsally and rod-like ventrally.

The scapula is pierced by two foramina. There is a small, oval foramen in the center of the bone which is homologous with the single foramen seen in various other forms. There is also a tiny, round foramen, located close to the concave facet for the base of the first lepidotrichium. As usual, the "main" foramen transmits the nerve which supplies the pectoral fin musculature. It was not possible to determine the function of the other foramen.

The coracoid is prolonged anteroventrally into a long and slender (gracile) process. The tip of the coracoid process meets the ventral limb of the cleithrum somewhat above the lowest portion of the symphysis. Posteroventrally, the coracoid is drawn out into a short, blunt process.

The actinosts are rod-like. The first three articulate with the scapula;

the fourth with the cartilage between the scapula and coracoid.

There is one distal radial. It is a moderate sized nodule of bone related to the second fin ray.

The pectoral fin contains 13 rays. All of the rays are segmented, and all except the first, second and thirteenth are branched distally.

Remarks: The dermal bones of the pectoral girdle are more strongly ornamented in Trachichthys than in the other genera (e.g., the posttemporal spine is very prominent, and the postcleithrum bears a small patch of tiny spines on its surface). The coracoid and its anteroventral process are rather deep in Trachichthys, in contrast to other trachichthyids. The scapula bears two foramina in Hoplostethus, as in Paratrachichthys.

The pelvic girdle and fin (Fig. 56)

Due to the forward migration of the anus the pelvic bones are widely separated from one another. Only their anterodorsal tips make contact. The pelvic bones are roughly triangular in lateral view. The rachis is cylindrical distally but is thin and crest-like proximally. It divides the surface of the pelvic bone into anteroventral and posterodorsal portions. The rachis does not project beyond the margin of the pelvic bone. The posteromedial portion of the pelvic bone bears two processes: (1) a long and slender (but well-ossified) anterior process and (2) an even longer posterior process, which tapers to a point distally. The anterior processes converge as they pass forward, but their tips are separated by a small gap. The posterior processes are widely separated and run parallel to one another. The medial process seen in some other forms is absent. The posterolateral part of the pelvic bone bears a strongly developed lateral process.

The pelvic fin formula is I,6. All of the rays are segmented and branched distally. The pelvic fins are thoracic.

There are two radials. The first is small and crescent-shaped. It is related to the base of the spine and the outermost ray. The other is a small, flat piece of bone associated with the bases of the third and fourth rays.

Remarks: The pelvic girdle and fin of all trachichthyids are similar in the following respects: (1) presence of a well-developed lateral process (2) presence of a long, tapered posterior process and (3) presence of one spine and six rays in the fin. Medial processes, which partially overlap in the midline, are present in all genera except Paratrachichthys (note: the anus does not separate the pelvic bones in other trachichthyids). A long, slender anterior process, originating from the tip of the medial process, is present in Hoplostethus. Anterior processes are absent in Gephyroberyx and Trachichthys.

The dorsal fin

The dorsal fin formula is V,13. The spines increase in length from front to rear. All of the rays are segmented and all except the first are branched distally.

There are 17 pterygiophores. The first two are incomplete. The first two spines are related to the first pterygiophore. All of the proximal radials bear crests on their lateral surfaces. The first proximal is inserted between the second and third neural spines. The middle radials are completely

ossified. The first six middles bear wing-like flanges which project laterally; the others are short, cylindrical rods. All except the first two distal radials consist of shells of bone which were presumably filled with cartilage. A dorsal fin stay is present. It is a moderate sized, triangular plate of bone, and probably represents a vestigial proximal radial.

Two predorsals are present. They are slender, rod-like bones. The first is inserted between the skull and the first neural spine; the second between the first and second neural spines.

Supraneurals are absent.

The anal fin

The anal fin formula is III,8. The spines increase in length from front to rear. All of the rays are segmented and branched distally.

There are nine pterygiophores. The first three are incomplete. All three spines are associated with the first pterygiophore. The radials and anal fin stay resemble those in the dorsal fin (except that the middle radials do not bear wing-like flanges).

Remarks: The dorsal and anal fins of other trachichthyids do not show any important differences from those of Paratrachichthys.

The caudal skeleton and fin (Fig. 57)

U2 is autogenous with respect to PU1 + U1. Although U2 appears to be rather small, its posterior end is tapered and is largely concealed by the stegural.

The neural and hemal spines of PU3 are considerably longer than those of PU4. The neural spine of PU2 is reduced to a crest which is one-fourth of the length of that of PU3. The parhypural bears a moderately long hypurapophysis which is tapered distally. The neural arch of PU2 and the hemal arches of PU2 and PU3 are autogenous.

The stegural is autogenous with respect to PU1 + U1. The distal portion of its spinous process is paired. There is a single pair of slender, blade-like uroneurals.

There are three epurals. The proximal portions of the epurals are expanded. The distal portions are rod-like. The distal end of the third epural shows a slight indication of being paired. The proximal end of the first epural is supported by the dorsal edge of the neural crest of PU2 and the anterior part of the dorsal edge of the stegural. The proximal ends of the second and third epurals are supported only by the edge of the stegural.

There are six autogenous hypurals (H1 - H6). The first and second hypurals articulate with PU1 + U1 (the second also articulates slightly with U2). The third, fourth and fifth hypurals articulate with U2 (the proximal end of the fifth just contacts the posterior end of U2). The sixth hypural is short, and fails to contact U2. The first and fourth hypurals are large and plate-like. The second and third hypurals are the next largest. The fifth and sixth hypurals are slender, rod-like bones.

The caudal fin formula is 10 + 9 = 19. There are seven procurrents above and six below. The first six above and the first five below are spinous. The bases of the spines are forked. The foremost procurrent above is supported

by a pair of small, thin, triangular ossifications which lie just anterior to the distal portion of the neural spine of PU3. The foremost procurrent below is supported by the distal portion of the hemal spine of PU3.

Remarks: The caudal skeletons of other trachichthyids are very similar to that of Paratrachichthys. Intraspecific variation was observed in several characters, however. Thus, in Hoplostethus the hemal arch of PU4 is occasionally autogenous (one of three specimens) and the neural arch of PU2 occasionally fused (one of four specimens; note: the neural arch of PU2 is also autogenous in the individual of Hoplostethus figured by Patterson, 1968, p. 67, fig. 13). In Trachichthys, the third and fourth hypurals were partially fused in one specimen (93 mm SL), but x-ray examination of three other individuals (70, 90, 97 mm SL) revealed the presence of six separate hypurals, as in other trachichthyids.

The spinous process of the stegural in Trachichthys is paired, as in Paratrachichthys. The pair of small ossifications lying anterior to the neural spine of PU3 in Paratrachichthys was not seen in the other genera.

The squamation

Ventral ridge scales are present in all trachichthyids.

Family Holocentridae

Osteology of Ostichthys trachypoma Günther

The neurocranium (Fig. 58)

The skull roof

The nasals are rather small, rectangular bones which are well-separated from one another. The medial and lateral edges of the nasal are reflected upward to form a trough for the lateral line. Anteriorly, a broad flange roofs over the trough. The reflected edges of the nasal are serrated, and the surface of the flange bears tiny spines.

The frontals form a large portion of the skull roof. They are narrow in the orbital region but are very broad posteriorly. Anteriorly, the frontal meets the mesethmoid and lateral ethmoid. In the midline the frontal meets its fellow (there is a slight amount of overlap posteriorly). Posteriorly, the frontal articulates with the supraoccipital, parietal, pterotic and both sphenotics (from medial to lateral). The orbital lamina of the frontal meets the orbito- and pterosphenoids. The frontals bear a series of weakly serrated crests and ridges. These are not arranged in a $\times$ pattern, as in some other beryciforms. The crests separate mucous cavities which are shallow to moderate in depth. Nearly the entire length of the supraorbital margin of the frontal bears weak serrations (these serrations are continuous with those on the anterior border of the dermosphenotic).

The parietal is rather small. It overlies a small portion of the supraoccipital (medially) and epiotic (posteriorly). Anteriorly, it is partially overlain by the frontal. Laterally, the parietal articulates with a flange on the dorsal surface of the pterotic. The dorsal surface of the parietal bears

a small, thin crest which is weakly serrated along its edge. This crest protects the terminal portion of the supratemporal lateral line.

The epiotic meets the supraoccipital medially, the pterotic laterally and the exoccipital posteroventrally. Its dorsal surface is partially overlapped by the parietal. The lateral surface of the epiotic is excavated (concave).

The supraoccipital bears a small, triangular crest which projects back mainly from the occipital surface of the skull. The leading edge of the crest is thickened basally, and a ridge on its lateral surface provides further support. In addition to the supraoccipital crest, the dorsal surface of the supraoccipital bears a transversely oriented crest (actually slightly V-shaped, with the apex pointing posteriorly). This transverse crest runs across the base of the supraoccipital crest, and forms the anterior boundary of the supratemporal fossa. The edge of the transverse crest is serrated.

The supratemporal fossa is very small, ending well-behind the posterior border of the orbit. The floor of the fossa is formed by the dorsal surface of the epiotic, along with small contributions from the supraoccipital and parietal. The anterior boundary of the fossa is described above. There is no distinct lateral boundary (the angle between the dorsal and lateral surfaces of the epiotic marks the lateral limit of the fossa).

The posttemporal fossa is large. Since the fossa extends anteriorly for a considerable distance, the autosphenotic contributes to its floor and medial wall (in addition to the pterotic and epiotic). The lateral wall of the fossa is formed by a prominent flange on the dorsal surface of the pterotic. The posttemporal fossa is also partially roofed by the parietal and pterotic, which make contact in its lateral wall (see above, under parietal).

Remarks: The ornamentation on the frontals in Plectrypops is rather similar to that in Ostichthys, although the crests and ridges are more strongly serrated in the former. The mucous cavities on the skull roof in Ostichthys and Plectrypops are somewhat deeper than in the other genera examined. In Myripristis, Holocentrus and Adioryx, the frontals are ornamented with low, smooth, radiating ridges. The ornamentation in the latter two genera is strikingly similar.

An important feature shared by all holocentrids is the presence of a transverse crest on the dorsal surface of the supraoccipital. The morphology and relationships of this crest in other forms are identical to those described for Ostichthys.

The supratemporal fossa in Myripristis is better developed than in other holocentrids. In Myripristis, the fossa extends to the posterior border of the orbit. The posttemporal fossa is partially roofed in all holocentrids.

The ethmoid region

The mesethmoid is large. It is separated from the vomer by only a small amount of ethmoid cartilage.

The lateral ethmoid is irregular-shaped. Its lateral border is smooth and convex. The medial portion of the lateral ethmoid is obliquely pierced by a round foramen for I.

The vomer bears a pair of well-developed wings which articulate with the lateral ethmoids. The head of the vomer bears a triangular patch of small, conical teeth.

Remarks: The bones of the ethmoid region of other holocentrids do not show any important differences from those of Ostichthys.

The orbital region

The parasphenoid is straight. Posteriorly, it overlies the anterior one-half of the ventral surface of the basioccipital. The parasphenoid shaft bears a distinct pair of flanges for articulation with the endopterygoids. The ascending processes are spike-like flanges which rise steeply to meet the prootics. The foramen for the internal carotid artery lies behind the posterior edge of the ascending process.

The orbitosphenoid is small. Anteriorly, in the midline, the laminae are not fused together, with the result that there is an elongate space or foramen for I. The ventral edge of the orbitosphenoid is rounded (not sharp).

The pterosphenoid meets the orbitosphenoid anteriorly, the autosphenotic and prootic posteriorly, the frontal dorsally and the basisphenoid ventrally. The pterosphenoid also makes a slight contact with its fellow, thus closing off the optic fenestra anteriorly. The lateral margins of the fenestra are formed by the pterosphenoids (anteriorly) and the arms of the basisphenoid (posteriorly). The trochlear foramen could not be identified.

The arms of the basisphenoid articulate with the pterosphenoids and prootics. The pedicel is long and slender and is somewhat laterally compressed. It curves slightly forward as it passes ventrally. The tip of the pedicel is separated from the parasphenoid by a small gap. The myodome is rather small.

Remarks: The parasphenoid is straight in Plectrypops (as in Ostichthys). In Myripristis, Holocentrus and Adioryx the parasphenoid exhibits postorbital curvature. In all holocentrids, the parasphenoid bears flanges for articulation with the endopterygoids, the pterosphenoids meet in the midline for a short distance, and the foramen for the internal carotid artery lies between the ascending process of the parasphenoid and the prootic.

In Plectrypops, the arms of the basisphenoid form the entire margin of the optic fenestra, unlike the condition seen in other holocentrids.

In Myripristis and Holocentrus the trochlear foramen lies within the pterosphenoid.

The otic region

The prootic meets the pterosphenoid anterodorsally, the parasphenoid anteroventrally, the exoccipital posteriorly, the autosphenotic and pterotic dorsally, and the basisphenoid medially. The pars jugularis has three external openings separated by two bony struts, the anterior of which is thicker. A rather short, blunt process projects posterolaterally from below the lateral opening. It appears to "lead" the hyomandibular trunk of VII to the foramen on the medial face of the hyomandibula. A large foramen near the prootic-basisphenoid suture transmits III (and perhaps other fibers as well). IX issues through a small foramen which lies close to the posterior opening of the pars jugularis.

The autosphenotic bears a blunt postorbital process. The autosphenotic forms the anterior two-thirds of the floor of the dilatator fossa (the pterotic forms the posterior one-third). The dermosphenotic forms the roof of the fossa. The autosphenotic and prootic contribute equally to the formation of the socket for the anterior head of the hyomandibula.

The pterotic meets the frontal, parietal, and both sphenotics anteriorly, the exoccipital posteriorly, the epiotic medially, and the prootic ventrally.

The ventral surface of the pterotic bears a shallow facet for the posterior head of the hyomandibula. A low ridge separates this facet from the dilatator fossa. The lateral edge of the pterotic is reflected upward to form a thin crest. The main cephalic lateral line passes anteriorly between this crest (laterally) and a flange on the dorsal surface of the pterotic (medially). The preopercular lateral line passes ventrally in a groove just posterior to the crest.

The intercalar presents no noteworthy features.

The auditory bulla is strongly inflated. It is spherical (globular) in shape. The prootic, exoccipital and basioccipital flare out into thin plates which form the anterodorsal, posterodorsal and posteroventral parts (respectively) of the wall. The parasphenoid also contributes slightly to the bullar wall (anteroventrally). A large space, spanned by membrane, lies in the lateral wall and widely separates the prootic and basioccipital. The anterior end of the swim bladder rests against this membranous area.

Remarks: In Adioryx, the pars jugularis has four external openings (not three as in other holocentrids). A bony process, projecting laterally from beneath the lateral opening of the pars jugularis, is present in Myripristis and Plectrypops (as in Ostichthys). A similar process was seen in the specimens of Holotrachys lima and Flammeo sammara which were examined. This process is not present in Holocentrus and Adioryx. In Myripristis and Plectrypops, the glossopharyngeal foramen is located in the prootic (as in Ostichthys), while in Holocentrus and Adioryx the foramen is in the exoccipital (although close to its suture with the prootic).

The autosphenotic and prootic form the socket for the anterior head of the hyomandibula in all holocentrids except Myripristis. In Myripristis, the facet for the anterior portion of the head of the hyomandibula (which is single) lies entirely within the autosphenotic.

Nelson (1955) has shown that three distinct types of relationship exist between the swim bladder and auditory bulla in the Holocentridae. (1) In Adioryx, there is a membranous area in the lateral wall of the bulla which partially (but not completely) separates the prootic and basioccipital. The swim bladder in this form fails to contact the wall of the bulla. (2) In Holocentrus (H. rufus and H. ascensionis), the membranous area of the bulla faces posteriorly and is in contact with the anterior end of the swim bladder. In these two species, the posteroventral portion of the prootic is greatly prolonged posteriorly, with the result that the bulla is elongate or tubular in shape (see Nelson, 1955, plate 2, fig. 3--H. ascensionis). The prootic and basioccipital make a large contact with one another anterior to this membranous area. (3) In the remaining holocentrids (Myripristis, Ostichthys, Plectrypops, Holotrachys and Corniger), the anterior end of the swim bladder meets a large membranous area in the lateral wall of the bulla. In the specimens of Ostichthys and Plectrypops which were examined, this membranous area completely separates the prootic and basioccipital. In Myripristis, however, there is a slight amount of contact between these bones in the anteroventral part of the bullar wall.

The occipital region

The exoccipital meets the prootic and pterotic anteriorly, the epiotic anterodorsally, the supraoccipital dorsally and the basioccipital ventrally. The exoccipital bears a large, oval foramen for X and several small foramina

for the occipital nerves. Near the margin of the foramen magnum, the lateral surface of the exoccipital bears a crescent-shaped opening or "fenestra" of unknown function. This fenestra is completely spanned by a tough membrane. Two other specimens of Ostichthys showed a similar condition.

The ventral surface of the posterior end of the basioccipital bears a pair of small, thick, ventrolaterally-directed flanges. These flanges are related to the fibrous wall of the anterior end of the swim bladder. It was not possible to ascertain whether the swim bladder was actually attached to these flanges.

Remarks: The occipital region of Myripristis shows two very important similarities with that of Ostichthys: (1) the presence of a crescent-shaped exoccipital "fenestra" and (2) the presence of ventrolateral flanges on the ventral surface of the posterior end of the basioccipital. The fenestra and flanges are absent in Plectrypops, Holocentrus and Adioryx.

The circumorbital bones (Fig. 59)

The antorbital is small and crescent-shaped. Its anterior and posterior ends closely approach the edge of the nasal, and are bound to it by short ligamentous fibers. Posteriorly, the edge of the antorbital is feebly serrated.

The lacrimal is rather shallow and elongate. Anterodorsally, it bears a medially-directed flange. The upper surface of this flange is concave and articulates with the lateral ethmoid. Posteriorly, the lacrimal meets the first infraorbital. The lateral line is completely open except near the anterior end of the lacrimal, where it is roofed by a bridge of bone ornamented with small spines. The reflected upper borders of the lacrimal and infraorbitals are distinctly serrated. The posterior one-half of the lower border of the lacrimal is also serrated. More anteriorly, the lower border bears a single, strong serration.

The infraorbitals are moderately deep. The nature of the ornamentation along the lower borders of the infraorbitals is noteworthy. The serrations along the first and anterior part of the second infraorbital form a continuous series, and are not unusual. However, on the posterior part of the second and the middle parts of the third and fourth infraorbitals, the serrations stand out as distinct "patches" of ornamentation.

A subocular shelf is developed along the entire margins of all four infraorbitals.

The dermosphenotic is small. Its anterior border is reflected outward to form a groove for the lateral line as it passes ventrally onto the fourth infraorbital. Both the anterior and posterior borders are serrated.

Remarks: The circumorbitals of other holocentrids resemble those of Ostichthys in the presence of an antorbital and a subocular shelf on all four infraorbitals. The infraorbitals in other holocentrids (except Plectrypops) are shallow. The lower borders of the infraorbitals are strongly serrated in all holocentrids, but only in Ostichthys do the serrations stand out as "patches" of ornamentation, as described above. In Plectrypops retrospinis the serrations (spines) on the first infraorbital are recurved.

The hyopalatine bones (Figs. 59-60)

The hyomandibula is double-headed. The opercular process is short. The

lateral surface of the broad, dorsal part of the hyomandibula bears a crest for articulation with the dorsal limb of the preopercle. The anteroventral corner of the dorsal part of the hyomandibula just fails to contact a well-developed process from the upper border of the metapterygoid. The symplectic process of the hyomandibula meets the posterior border of the metapterygoid.

The metapterygoid, quadrate and symplectic present no noteworthy features.

The endopterygoid is rather oval-shaped. Its medial edge articulates with a flange on the parasphenoid shaft. The endopterygoid meets the palatine anteriorly, the metapterygoid posteriorly and the dorsal limb of the ectopterygoid laterally. The endopterygoid is toothless.

The ectopterygoid consists of a very short ventral limb and a very long dorsal limb. The anterior one-half of the dorsal limb is greatly attenuated. At the junction of the two limbs, the ectopterygoid sends back a short, blunt process which just fails to meet the metapterygoid. The ectopterygoid is toothless.

The anterodorsal portion of the palatine bears a small process for articulation with the lateral ethmoid. The palatine meets the endo- and ectopterygoids posteriorly. The tip of the well-developed maxillary process is covered with cartilage. Projecting dorsally from the base of the maxillary process is a broad flange for the attachment of the palatopalatine ligament. The palatine bears a narrow strip of very small, conical teeth.

Remarks: As in Ostichthys, the head of the hyomandibula is double in Plectrypops, Holocentrus and Adioryx. In Adioryx, however, the head is not as distinctly divided as in the other three genera. In Myripristis, the head of the hyomandibula is single and is short anteroposteriorly (not elongate, as in most forms with a single-headed hyomandibula). The ectopterygoid in Plectrypops and Myripristis is toothless (as in Ostichthys). The ectopterygoid is toothed in Holocentrus and Adioryx.

The dermal upper jaw (Figs. 59-60)

The ascending process of the premaxilla is about one-third of the length of the alveolar process. The rostral cartilage is thick. The alveolar process bears a strip of small conical teeth which extends to its tip. The postmaxillary process is a very distinct, triangular flange which arises from most of the length of the alveolar process.

The maxilla possesses a strong, cylindrical shaft. Distally, the shaft expands into a plate which enters into the gape behind the tip of the alveolar process of the premaxilla. The lateral surface of the maxillary shaft bears weakly serrated crests.

There are two supramaxillae. The anterior supramaxilla is very small and rather triangular in shape. The posterior supramaxilla is shallow and elongate. Projecting from its anterior end is a long, spike-like process which overlies the anterior supramaxilla. The anterior supramaxilla bears a single crest on its lateral surface (this crest is not serrated). The posterior supramaxilla is highly ornamented with serrated crests and tiny spines.

Remarks: A distinct postmaxillary process is present in all holocentrids. The postmaxillary process in Myripristis and Plectrypops is very similar to that in Ostichthys. In Holocentrus and Adioryx the process is also rather triangular, but it has a more restricted origin from the alveolar process than in the other genera.

Myripristis is the only living beryciform in which the maxilla bears

teeth. Maxillary teeth were present in the specimens of M. argyromus, M. murdjan and M. parvidens which were examined. M. jacobus shows intraspecific variation in this character. In some individuals the maxilla is well-toothed while in others teeth are absent. M. jacobus is also peculiar in that it possesses only one supramaxilla (two supramaxillae were present in all of the other holocentrid species examined). The supramaxilla in M. jacobus represents the posterior supramaxilla of other forms since its anterior end bears a slender process.

The lower jaw (Figs. 59-60)

The oral border of the dentary is weakly sinuous and bears a band of small, conical teeth which extends almost to the tip of the ascending process. At the symphysis, the band of teeth broadens and is slightly expanded onto its lateral surface. The lateral surface of the lower one-half of the dentary is highly ornamented with serrated crests which run parallel to one another. A small portion of the ventral border of the dentary is also serrated.

Anterior to the facet for the quadrate condyle, which is located at the posterior border of the orbit, the angulo-articular rises sharply into the ascending process. The jaw articulation is strengthened posteriorly by a well-developed retroarticular process. A tiny nodule of bone lies against the medial surface of the angulo-articular. The angulo-articular is ornamented like the dentary.

The lateral surface of the lower portion of the retroarticular bears a few serrated crests.

The mandibular lateral line is largely closed. The portion of the lateral line in the dentary and anterior one-half of the angulo-articular communicates with the surface via numerous but tiny pores (two round, moderate sized pores lie near the symphysis). The lateral line in the posterior one-half of the angulo-articular is covered with membrane.

Remarks: In Myripristis and Plectrypops, the teeth on the dentary are slightly expanded onto the lateral surface of the symphysis, as in Ostichthys. In Holocentrus and Adioryx the teeth are confined to the oral border of the dentary. The jaw articulation in Ostichthys, Myripristis and Plectrypops is located at the level of the posterior border of the orbit. In Holocentrus and Adioryx, the jaw joint is located more anteriorly (middle of the orbit in Adioryx; about one-half of the way between the middle and anterior border of the orbit in Holocentrus).

The opercular bones (Figs. 59-60)

The opercle is rather triangular. The facet for the opercular process of the hyomandibula is reinforced by a short, thick strut of bone. At the level of this facet, the lateral surface of the opercle bears a low ridge which runs posteriorly to end in a large spine. Just above this spine, the posterior border of the opercle is notched. A large portion of the lateral surface of the opercle is ornamented with needle-like spines which project posteriorly.

The subopercle is elongate. The anterior and posterior parts of its ventral border are distinctly serrated. The lateral surface of the subopercle bears a few small spines similar to those on the opercle.

The interopercle is rather large. Low ridges on its lateral surface radiate out to the ventral border, where they end in distinct serrations. The lateral surface of the anterior part of the interopercle bears small spines like the other opercular bones.

The preopercle possesses distinct dorsal and ventral limbs which are set at an angle of 125° to one another. The dorsal limb slopes slightly backward. The leading edge of the preopercle is reflected outward to form a flange which partially protects the lateral line. The edges of this flange, as well as the outer edges of the dorsal and ventral limbs, are distinctly serrated. Near the angle of the preopercle the serrations increase in size, but a prominent spine is not present.

Remarks: As in Ostichthys, the angle of the preopercle in Myripristis and Plectrypops lacks a distinct spine (the serrations at the angle of the bone are slightly larger than the others, however). In Holocentrus and Adioryx the angle of the preopercle bears a very prominent, posteriorly-directed spine.

The hyoid arch and branchiostegal rays (Fig. 61)

The interhyal presents no noteworthy features.

The epihyal meets the ceratohyal in a straight suture. The lateral surfaces of the epihyal and posterior one-third of the ceratohyal are distinctly grooved for the hyoidean artery.

The ceratohyal is rather deep and rectangular. It meets both the dorsal and ventral hypohyals anteriorly (the anteroventral portion of the ceratohyal is prolonged into a stout, cylindrical process which articulates with the ventral hypohyal). The ventral border of the ceratohyal is strongly notched for reception of the heads of the second, third and fourth branchiostegal rays. The upper portion of the ceratohyal is pierced by a small, slit-like foramen. Anterior to the foramen is a canal, continuous with a canal in the dorsal hypohyal, for the hyoidean artery. After passing anteriorly for a short distance, the artery emerges through a foramen on the medial face of the dorsal hypohyal.

The dorsal hypohyal is shallow and elongate. Its posterior edge is cartilaginous. The ventral hypohyal is square-shaped. The urohyal-hypohyal ligament attaches to the medial surface of the anteroventral portion of the ventral hypohyal.

The basihyal is slightly tapered posteriorly. The anterior one-third of the basihyal is cartilaginous. The basihyal is toothless.

The urohyal is a large, thin plate. Its posterior border is concave. Its anterodorsal corner bears a small but distinct process for the attachment of ligamentous fibers from the tips of the third hypobranchials. The anteroventral border of the urohyal is grooved; the urohyal-hypohyal ligaments attach to the lips of this groove.

There are eight branchiostegal rays. They gradually increase in length from front to rear. The anterior borders of the second, third and fourth rays are serrated. The first four rays articulate with the ventral border of the ceratohyal, the fifth and sixth with the lateral surface of the ceratohyal, and the seventh and eighth with the lateral surface of the epihyal.

Remarks: The hyoid arch in other holocentrids shows several similarities to that of Ostichthys. These include (1) presence of distinct notches on the ventral border of the ceratohyal for the heads of the second,

third and fourth branchiostegal rays (2) presence of a distinct process at the anterodorsal corner of the urohyal and (3) presence of a basihyal. Furthermore, the ceratohyal foramen in holocentrids is either very small and slit-like (Ostichthys, Plectrypops) or completely absent (Myripristis, Holocentrus, Adioryx). The basihyal was toothless in all specimens examined except for one individual of Adioryx (in which there was a small patch of teeth fused to the basihyal). The branchiostegals in Plectrypops are serrated, as in Ostichthys. The rays in the other genera are unornamented.

The branchial arches

BB1 - BB3 are well-ossified. BB4 is a small, cartilaginous block. The basibranchials are toothless.

The hypobranchials and epibranchials present no noteworthy features.

CB5 is tied to the posteroventral aspect of BB4 by a short, slender ligament. CB5 has a large, triangular tooth plate fused to it. The teeth are small and conical.

There are three pharyngobranchials. PB2 and PB3 have teeth fused to them. PB4 is absent but its tooth plate persists. The tooth plate of PB4 is a moderate sized element which articulates with the proximal end of PB3 but is mainly supported by the distal end of EB4.

Remarks: In Myripristis, Holocentrus and Adioryx, the epithelium over the lateral portions of BB2 (as well as the adjacent portions of the second hypobranchials) contains a pair of tooth patches. In Plectrypops the basibranchials are toothless (as in Ostichthys).

The vertebral column and ribs

The vertebral formula is 11 + 16 = 27. The neural arch of the first vertebra is autogenous. The neural arches and spines of the first eight vertebrae are more robust than the others. The distal portions of the first two hemal spines are bent back at a rather sharp angle. The first 20 vertebrae bear distinct pre- and postzygapophyses.

Basapophyses are present on the seventh through the eleventh vertebrae. Beginning with the eighth vertebra, the basapophyses meet in the midline, thus forming a canal for the dorsal aorta.

Pleural ribs are present on the third through the eleventh vertebrae. They are strong, well-ossified bones. The last pair of pleurals is shorter than the others. The first three pleurals articulate with their neural arches, the fourth with its centrum, and the remainder with the tips of their basapophyses.

Epipleural ribs are present on all of the abdominal and the first caudal vertebrae. They are slender, delicate bones. Epineural ribs are absent.

Remarks: In Myripristis, the vertebral formula is 11 + 15 = 26 (11 + 16 = 27 in other holocentrids, including Ostichthys). However, the vertebral counts in Ostichthys and Holocentrus were made on specimens in which U2 (the twenty-seventh vertebra) was autogenous. In larger specimens of Ostichthys and Holocentrus, U2 is fused to the preceding compound vertebra (PU1 + U1). In these larger specimens, there were presumably only 26 vertebrae (11 + 15 = 26).

The pectoral girdle and fin (Fig. 62)

The extrascapular is rather triangular. A serrated crest on its lateral surface roofs over the lateral line. The posterodorsal edge of the extrascapular is also serrated.

The posttemporal has a blade-like dorsal limb and a rod-like ventral limb. A lamina projects back from the dorsal limb; its edge is distinctly serrated. The lateral line is partially protected by a weakly serrated crest on the lateral surface of the posttemporal.

The supracleithrum is rather broad anteroposteriorly. Its anterior border is thickened, but the rest of the bone is thin and plate-like. The upper part of the posterior border of the supracleithrum is serrated.

The cleithrum consists of a short dorsal limb and a ventral limb of moderate length. The angle between the limbs is about 135°. The posterior lamina is well-developed. Its lateral surface bears several low, smooth ridges which end in small serrations along its posterior border.

There are two postcleithra. The dorsal postcleithrum is scale-like. It is elongate dorsoventrally. The ventral postcleithrum is scale-like dorsally but rod-like ventrally.

The center of the scapula bears a large, oval foramen.

The coracoid bears a moderately long and slender process, the tip of which meets the ventral limb of the cleithrum well-above the lowest part of the symphysis. Posteroventrally, the coracoid is prolonged into a short, blunt flange.

The actinosts are hourglass-shaped. The first three articulate with the scapula, while the fourth articulates with the cartilage between the scapula and coracoid.

There are nine distal radials. They are ossified nodules which decrease in size from the first to the ninth. The first distal is associated with the base of the second fin ray.

The pectoral fin contains 15 rays. All of the rays are segmented, and all except the first, second and fifteenth are branched distally.

Remarks: The pectoral girdle in other holocentrids shows no important differences from that of Ostichthys.

The pelvic girdle and fin (Figs. 63-64)

The pelvic bones are firmly united in the midline. Anterodorsally, they are bound to the ventral limbs of the cleithra by ligaments. In lateral view, the anterior border of the pelvic bone is distinctly concave. The rachis does not extend beyond the margin of the bone. The posteromedial portion of the pelvic bone bears two processes: (1) a long and slender (but well-ossified) anterior process and (2) a well-developed posterior process which lies close to its fellow. The distal portion of the posterior process flares out into a flat plate. The medial process of some other forms is absent. The posterolateral portion of the pelvic bone bears an exceedingly well-developed lateral process.

The pelvic fin formula is I,7. The spine is strong, and its surface is distinctly striated. All of the rays are segmented and branched distally. The pelvic fins are thoracic.

There are four radials, all of which are ossified. The first radial is the largest. It is irregular in shape and bears a peculiar, hook-like process which projects into the base of the fin spine. The other three radials are nodular elements related to the bases of the fin rays.

Remarks: The pelvic girdle and fin of other holocentrids are very similar to those of Ostichthys. Two very important features shared by all holocentrids are (1) the expansion of the distal portion of the posterior process of the pelvic bone into a distinct flange or plate and (2) the presence of a hook-like process on the first pelvic radial which projects into the base of the fin spine (Gosline, 1961, p. 18, fig. 5D illustrates the first radial and the base of the spine in Myripristis). With respect to the first feature, it is important to note that the shape of the expansion of the posterior process varies among the different genera. In Holocentrus and Adioryx, the posterior process flares out into an elongate and rather narrow flange. Although some differences in the shape of the expansion do occur in Ostichthys, Myripristis and Plectrypops, as noted by Woods and Sonoda (1973, p. 266), it is rather broad and plate-like in all three genera.

The dorsal fin

The dorsal fin formula is XII, 13. The spines increase in length from the first to the third (the third and fourth spines are of equal length), and then decrease in length to the eleventh. The twelfth spine is slightly longer than the eleventh. All of the rays are segmented, and all except the first are branched distally.

There are 24 pterygiophores. The first 11 are incomplete. The first two spines are associated with the first pterygiophore. The spines of the dorsal fin are "locked" into place due to the development of an intricate "chain-link" mechanism. The detailed morphology of the radial elements which are involved in this mechanism is accurately described and illustrated by Bridge (1896, pp. 560-562; plate 22, figs. 21-22) for Holocentrus spinifer. The condition present in Ostichthys is identical. The proximal radials of the spinous part of the fin are more robust than the others, and the crests on their lateral surfaces are more prominent. The first proximal is inserted between the second and third neural spines. The middle radials of the soft part of the fin are short and cylindrical; the distals are small, bony nodules. There is one dorsal fin stay. It is a small, flat piece of bone.

There are two predorsals. They are slender, laterally compressed rods. The first is inserted between the skull and the first neural spine; the second between the first and second neural spines.

Supraneurals are absent.

The anal fin

The anal fin formula is IV, 11. The first spine is very small. The third spine (penultimate) is the largest. It is both longer and thicker (more robust) than the fourth. All of the rays are segmented and branched distally.

There are 13 pterygiophores, the first three of which are incomplete. The first three spines are related to the first pterygiophore. The first two proximal radials are much larger than the others, and are tightly

articulated to one another. The middle and distal radials, as well as the anal fin stay, resemble those of the dorsal fin.

Remarks: In all holocentrids, the spinous portion of the dorsal fin is very long (11 or 12 spines), and the radial elements are modified to form a "chain-link" mechanism. The anal fin always contains four spines, the third of which is greatly enlarged. Although the penultimate anal spine is always thicker than the fourth, it is not always longer. An examination of a series of Myripristis parvidens revealed that in this species the relative length of the penultimate spine changes with an increase in size. Thus, in small individuals (42 mm SL), the penultimate spine is slightly longer than the fourth, whereas in large specimens (127 mm SL) it is considerably shorter. In Ostichthys trachypoma, however, the penultimate spine is both thicker and longer in specimens ranging in size from 23 mm SL to 119 mm SL.

In Myripristis and Plectrypops, the first proximal radial of the dorsal fin is inserted between the second and third neural spines (as in Ostichthys). In Holocentrus and Adioryx, the first proximal is inserted between the first and second neural spines (as is the second predorsal). The condition in which both the first proximal radial and the last predorsal are inserted between the same two neural spines is unique to Holocentrus and Adioryx among the beryciform species examined.

In all holocentrids, the first two proximal radials of the anal fin are enlarged and are tightly articulated to one another.

The caudal skeleton and fin (Fig. 65)

In this specimen and in another of the same size (64-65 mm SL), U2 is autogenous with respect to PU1 + U1. In two larger specimens (the smallest of which was 120 mm SL) U2 was fused to PU1 + U1.

The distal portions of the neural and hemal spines of PU4 and PU5 are expanded. The neural and hemal spines of PU3 are much longer than those of PU4 and are tapered distally. The neural spine of PU2 is reduced to a crest which is one-third of the length of that of PU3. The parhypural bears a long, slender hypurapophysis which projects posterolaterally. The neural arch of PU2 is fused. The hemal arches of PU2 and PU3 are autogenous.

The situation with respect to the stegural is similar to that described above for U2. In the two smaller specimens, the stegural is autogenous (with respect to PU1 + U1); in the others it is fused (to PU1 + U1 + U2). There is a single pair of blade-like uroneurals.

There are three epurals. The lower ends of the first (especially) and second epurals are compressed. The epurals are supported proximally by the upper edges of the neural crest of PU2 (first epural) and the stegural (all epurals).

There are five autogenous hypurals (H1-H5,--). The sixth hypural of various other forms is absent. The first and second hypurals articulate with PU1 + U1 (the second also contacts U2). The third and fourth hypurals articulate with U2. The fifth hypural just fails to contact the posterior tip of U2. The proximal end of the fifth hypural is bifid. The first and fourth hypurals are large and plate-like. The second and third are moderate sized. The fifth hypural is a small, rod-like bone.

The caudal fin formula is 10 + 9 = 19. There are five procurrents above and four below. The first four above and the first three below are spinous.

The bases of the spines are forked. The foremost procurrents are supported by the tips of the neural and hemal spines of PU3.

Remarks: The caudal skeletons of other holocentrids (including Holotrachys lima and Flammeo sammara) are very similar to that of Ostichthys. An important similarity shared by all holocentrids is the morphology of the neural and hemal spines of PU4 and PU5 (tips expanded). U2 was autogenous in one specimen of Holocentrus rufus (74 mm SL) but fused to PU1 + U1 in a larger specimen (exact SL unknown). In all other holocentrids (except occasionally in Ostichthys -- see above) U2 is fused. Ostichthys was the only form examined in which the stegural was occasionally autogenous (fused to PU1 + U1 + U2 in other holocentrids).

The squamation

Ventral ridge scales are absent in all holocentrids.

CHAPTER V

SELECTION OF CHARACTERS FOR ANALYSIS

It is evident from the preceding descriptions that there exists a vast amount of comparative osteological data from which to select characters. In this investigation, some potentially useful characters were not considered because they were relatively inaccessible. For example, the morphology of the otoliths is sometimes used in ichthyological systematics. The use of otolith and other internal characters of the neurocranium would have required partial or complete disarticulation of the skull. For a number of reasons, this was not practical in this investigation.

The following criteria were applied in selecting characters for analysis.

1. Characters were selected so that nearly all portions of the skeletal system were represented. Of the 70 characters which are utilized in this investigation (tables 10-79), 16 involve the neurocranium, three the circumorbital bones, four the hyopalatine bones, two the dermal upper jaw, two the lower jaw, one the opercular bones, four the hyoid arch and branchiostegal rays, four the branchial arches, six the vertebral column and ribs, six the pectoral girdle and fin, six the pelvic girdle and fin, five the dorsal and anal fins, nine the caudal skeleton and fin, and two the squamation.
2. Characters were selected that have been traditionally used in ichthyology and that have been shown to contain useful phylogenetic information in other groups. Examples include the presence or absence of fin spines, the number of rays in the pelvic fin, and several of the characters of the caudal skeleton.
3. Characters were selected that have not been traditionally used in ichthyology (i.e., new characters were selected). This was done with the hope that additional characters would be discovered that have some phylogenetic significance, and to provide other investigators with an indication as to what characters might be useful in their studies. A number of the characters of the pelvic girdle, as well as several characters of the neurocranium (presence/absence of parasphenoid flanges, position of foramen for internal carotid artery, etc.) fall into this category.

By applying these criteria, a list of 105 characters was compiled. Thirty-five of these characters were subsequently eliminated. The elimination process consisted of a series of steps. The reasons for eliminating characters were as follows:

1. Computational. The computer program (Combinatorial Method) which was used cannot always handle extremely large data sets. The number of combinations implied by large data sets may be too great for the computer's storage capacity.
2. Homology. It was not possible to determine the homology of certain structures in some of the species which were examined. Thus, there was

a risk of assigning the wrong character states to these taxa. The presence or absence of a medial process of the pelvic girdle is an example of a character which was eliminated for this reason.

3. Intraspecific variation. Characters that frequently exhibited intraspecific variation (e.g., ornamentation of the branchiostegal rays) were eliminated. Simpson (1961, p. 101) and Mayr (1969, p. 222) state that highly variable characters are unreliable, that is, are poor indicators of phylogenetic relationship. Some characters which showed intraspecific variation were retained, however. The problem which intraspecific variation presents when differentiating character states is discussed in chapter 6.
4. Differentiation of character states. In some instances, it was not possible to objectively differentiate character states. For example, the distinctness of the groove (for the hyoidean artery) on the epihyal and posterior part of the ceratohyal was one character under consideration. Since there was no practical way to measure the distinctness of this groove, the character was eliminated.
5. Construction of character state trees. Characters in which the primitive state or the sequence of change among the derived states could not be determined were eliminated. For example, one of the characters of the caudal skeleton (number of hypurals, see table 82) was eliminated because its tree is partially circular (i.e., two equally probable sequences of change occur).
6. Distribution of character states. Characters in which (1) all members of the group (Beryciformes) share the same derived state (e.g., fusion of PU1 and U1 in the caudal skeleton) and (2) only one member of the group possesses the derived state (e.g., presence of fang-like teeth in Anoplogaster) were eliminated. Such characters are of no value for ascertaining intragroup relationships.

Character Correlation

After eliminating characters from the initial list for the reasons discussed above, 70 characters remained. The correlation between these characters was then measured. There were two reasons for doing this:

1. To provide a basis for further elimination of characters (see below).
2. Knowledge of character correlation can be helpful when using the Combinatorial Method for ascertaining phylogenetic relationships (chapter 9).

There are several methods for measuring the correlation between characters. Chi-square (X^2) is one measure of character association, but its usefulness is limited in an investigation of this sort (see Voris, 1971, pp. 444-445 for a discussion of the limitations of the use of the chi-square test for measuring character correlation). In this investigation, character correlation was measured by calculating a value c, a normal deviate, for each of the pairwise combinations of characters.[1] Since there are 70 characters,

[1] A computer program written by Harold Voris and Joseph Felsenstein was used to calculate the normal deviate values.

there are $\frac{70 \times 69}{2} = 2415$ combinations and corresponding c values. The c values were computed by utilizing the following formula, taken from Voris (1971, p. 445):

$$c = \sqrt{\frac{9d}{2}} \left[\frac{3X^2}{d} - 1 + \frac{2}{9d} \right]$$

where X^2 represents the chi-square value for the two characters and d represents the number of degrees of freedom.[1]

For 2415 tests, a c value > 4.10 is significant at the 5% level (i.e., the probability that the two characters are correlated due to chance alone is less than 5%) (Voris, 1971, p. 445). Of the 2415 pairs of characters, 49 pairs (involving 37 different characters) were found to be significantly correlated at the 5% level (the c values range from 4.11 to 5.39). The next step was to determine the cause of these correlations.

Characters (or more properly, the states of characters) may be correlated for many different reasons (Simpson, 1953, p. 64 and p. 275; Mayr, 1969, p. 221 and p. 225; Voris, 1969, pp. 145-148). Voris, for example, in his study of the sea snakes, recognizes the following possibilities as potential causes of character correlation (these categories are not always mutually exclusive).

1. Correlation due to redundancy.
   (a) Redundancy due to physical factors of measurement. In the Beryciformes, for example, the total number of elements in the dorsal fin is equivalent to the number of spines plus the number of rays in the fin. These two characters are redundant because they describe the same feature.
   (b) Redundancy due to character repetitions. This type of redundancy occurs when two or more characters describe the same type of feature. In the Beryciformes, recognition of the presence/absence of a notch on the ventral border of the ceratohyal for branchiostegal ray 2, ray 3, and ray 4 as separate characters would introduce redundancy into the data set because these characters are repetitious.
   (c) Redundancy due to pleiotropy. Two or more characters may be correlated because they are controlled by a single gene. However, character associations of less than 100% cannot be due to pleiotropy under usual circumstances (Voris, 1969, p. 146). Since detailed genetic studies on most organisms have not been performed, it is usually possible to state only that pleiotropy could be the cause in cases of 100% correlation (Voris, 1969, p. 147).

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[1] Chi-square was computed by utilizing the following formula:

$$X^2 = \sum \frac{(O - E)^2}{E}$$

where O represents the observed and E represents the expected cell frequency for each cell of the contingency table. A computer program written by Harold Voris was used to calculate the chi-square values.

(d) Redundancy due to mechanical relationships. This refers to situations in which characters are correlated by physical necessity. Two characters used in this study which are partially correlated due to mechanical relationship are characters 55 and 56. Character 55 has two states: I - dorsal fin spines absent; II - dorsal fin spine(s) present. Character 56 also has two states: I - dorsal fin spines do not project strongly in opposite directions; II - dorsal fin spines do project strongly in opposite directions. State I of character 55 is necessarily correlated with state I of 56, but state II of 55 may occur with either state I or II of 56.

2. Correlation due to adaptation.
Characters are often correlated because they represent adaptations to the same aspect of the environment. These characters constitute what Mayr (1969, p. 225) terms a functional character complex. Mayr (1969, p. 221) states that characters that are functionally correlated are of low weight and do not deserve to be treated as separate characters because, being members of a single functional complex, they are redundant. Bigelow (1958, p. 54) and Voris (1969, p. 148), however, point out that adaptively correlated characters may have historical components.

Bigelow (1958, p. 54) states:

> Actually, most of the best taxonomic characters known are adaptive. Practically every truly distinctive characteristic of birds is an adaptation for flight. Mammalian hair is adaptive. The amnion is adaptive. The sucking mouthparts of bugs are adaptive; as are the biting mouthparts of beetles. The four limbs of tetrapods are adaptive, and so on. It is not adaptive characters, but convergent characters, that should be avoided. To avoid adaptive characters summarily involves passing over most of the best possible taxonomic characters.

Thus, adaptively correlated characters may reflect convergence or common history (phylogenetic relationship). Adaptive character suites cannot therefore be logically rejected from a study on an *a priori* basis (before a tentative phylogeny is formed) (Voris, 1969, p. 148). However, Voris does state that in order to insure that an adaptive suite of characters does not constitute the majority of all characters, it is necessary to include a broad sample of types of characters. It is for this reason that characters from all parts of the skeleton were selected for analysis.

3. Correlation due to common ancestry.
The joint possession of characters by two or more species may be the result of common descent. Such characters are said to be phyletically correlated (Mayr, 1969, p. 221). Phyletically correlated characters, of course, are those which systematists wish to identify and to use in their investigations concerning the evolutionary relationships among groups of organisms.

Using Voris' list as a basis, the cause of the correlation for each pair

of characters (where $\underline{c} > 4.10$) was determined. It is evident from the preceding discussion that characters which are correlated because of redundancy (1a - 1d) should be eliminated. None of the 70 characters, however, is correlated for reasons 1a, 1b or 1d. Twelve characters (10 pairs) are 100% correlated [e.g., character 3 (presence/absence of a transverse crest on the supra-occipital) and character 51 (presence/absence of a distinct flange or plate on the distal portion of the posterior process of the pelvic bone)]. However, in the absence of positive evidence of pleiotropy, these characters were retained. Five characters (three pairs) are adaptively correlated [e.g., character 56 (presence/absence of a strong inclination of the dorsal fin spines) and character 69 (presence/absence of body armor)]. Five other characters (four pairs) may also be correlated for functional reasons. Since adaptively correlated characters may reflect phylogenetic relationship, they too were retained.

In summary, an analysis of the bases of the observed correlations of the 49 pairs of characters revealed that neither redundancy nor adaptation (reflecting convergence) is definitely responsible. All 70 characters were therefore included in the data set.

CHAPTER VI

DIFFERENTIATION OF CHARACTER STATES

General Remarks

One very important procedure involved in this investigation was the differentiation of character states. In each character, it was necessary to recognize the phenetic variation which occurred with regard to all of the beryciform species examined, and to assign numerical character states to represent the categories of variation.[1]

Characters are of two types--quantitative and qualitative. The method which was used to differentiate states in each type of character will be discussed separately.

Quantitative Characters

Quantitative characters include meristic and proportional characters. Only seven of the characters used in this investigation are meristic. Intraspecific variation was not adequately sampled to permit treatment of meristic characters as continuous variables, and to use measures of variability [such as span, used by Marx and Rabb (1970, 1972)] to segment these characters into classes (character states). Meristic characters were, therefore, treated as discontinuous variables. Each class or category of phenetic expression was recognized as a separate state [e.g., in character 32, number of branchiostegal rays, each of the four classes of variation (nine, eight, seven, six rays) was recognized as a separate state].

Qualitative Characters

Qualitative characters have states that differ in form or shape, in the presence or absence of features, in position, articulation, etc. (Marx and Rabb, 1970, p. 530). States in qualitative characters were assigned to represent classes of phenetic expression which were separated from other such classes by gaps or discontinuities. For many of the qualitative characters, these discontinuities were easily recognized (sharply defined). Characters in which the classes of phenetic expression were of a presence or absence nature therefore presented no difficulties. In other cases, however, sharp

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[1]The phenetic variation present in fossil beryciforms was also taken into consideration when designating character states. The data for the fossil species were taken from the literature. Six of the characters used in this investigation have states which are unique to fossil taxa.

gaps or discontinuities were not present. Consider, for example, character 18 (lacrimal-lateral ethmoid articulation). Three states are recognized: state I - lacrimal bears a concave facet or flange (for articulation with the lateral ethmoid); state II - lacrimal bears a C-shaped process; state III - lacrimal bears a splint-like ascending process. States II and III are sharply separated from each other and from state I. Furthermore, no variation in the morphology of the C -shaped process or the ascending process occurs. State I, however, is a "catch-all" state because it represents more than one kind of variation. For example, slight differences in the depth of the lacrimal facet and in the degree of development of the flange upon which the facet may be borne are present in some species. In cases such as this, it was not possible to objectively designate character states to represent all of the subtle phenotypic variation. It should be emphasized that character states were always carefully defined so that any "catch-all" states were exclusive of the other states which were recognized.

The use of "catch-all" states has both an advantage and a disadvantage in this investigation. The advantage is readily apparent when the method used to determine phylogenetic relationships is taken into consideration. The Combinatorial Method joins taxa together (forms combinations) on the basis of the total number of shared derived character states. Information pertaining to the sequence of change in character states is also utilized. Thus, a taxon is considered to bear not only the derived state which it actually possesses, but all derived states which are phylogenetically antecedent to that state. For example, in a character with three states which are related in a linear fashion (i.e., $a \rightarrow a' \rightarrow a''$), a taxon bearing state a" is considered to possess not only a", but also a', since a" arose phylogenetically from a'. Since the main criterion for selecting combinations is parsimony (i.e., combinations sharing more states are selected in favor of those with fewer states), the more states that a character contains (which are related in a linear fashion), the more weight it will have in determining the phylogenetic relationships of the taxa. Recognition of "catch-all" states is, therefore, desirable, because it provides a means for reducing the number of character states and for partially eliminating the problem of character weighting. Character weighting (in the sense described above) would be completely avoided by utilizing only two-state characters, because the total number of derived states shared by the taxa of a combination would then be equal to the total number of "derived characters" held in common (i.e., characters in which the taxa of the combination share derived states).

The disadvantage in combining different classes of phenetic expression into a single state is that some useful phylogenetic information is lost. Failure to discriminate between all of the classes of variation present in characters must, to at least some degree, affect the final results concerning phylogenetic relationships.

For some characters, a consideration of other factors was helpful in deciding whether to form "catch-all" states. For example, no attempt was made to segment the total range of variation in the number of teeth on the palatine bone into numerous classes (character states). Only two states (palatine toothed/toothless) were recognized. Previous studies have shown that reduction or loss of the palatal dentition has occurred independently in many phyletic lineages within the Teleostei (e.g., Greenwood et al., 1966). It seemed unwise, therefore, to recognize a large number of states in this character. This would have resulted in weighting a character which is known

to be quite susceptible to parallelism or convergence, and hence not strongly indicative of phylogenetic relationship. Mayr (1969, pp. 222-223) also states that regressive characters (such as reduction of palatine teeth) often occur repeatedly in independent phyletic lineages, and are, therefore, usually of low taxonomic weight.

Intraspecific Variation

Finally, the manner in which intraspecific variation was treated needs to be considered. Intraspecific variation was observed in 13 of the characters used in this investigation (table 80). For these characters, it was necessary to decide whether or not to recognize the variation as a separate state [the Combinatorial Method does not allow an OTU (operational taxonomic unit) to possess more than one state]. In this investigation, intraspecific variation was not recognized as a separate state. There were two reasons for this. First, recognition of an additional state to incorporate intraspecific variation (e.g., $a \rightarrow a, a' \rightarrow a'$) results in character weighting (above). Second, the sample sizes were too small (for most species, only one specimen was examined) to draw reliable conclusions concerning intraspecific variation. In cases where different individuals of a single species showed different states, the most frequently occurring state was designated to represent the species. When equal numbers of individuals showed different states, the most derived state was chosen to represent the species.

CHAPTER VII

DETERMINATION OF DERIVATIVENESS OF CHARACTER STATES

General Remarks

Hennig (1966) has shown that it is essential to utilize only the derived states of characters when attempting to ascertain phylogenetic affinities. The problem which must now be resolved is the selection of a method for determining the primitive and derived states of characters. Hennig (1966, pp. 95-96) discusses four criteria for determining the derivativeness (and sequence of change) of character states. For both theoretical and practical reasons, these criteria were not utilized in this investigation. For example, Hennig's third criterion, ontogenetic character precedence (i.e., the transformation of a character during ontogeny "recapitulates" the phylogenetic transformation of this character), has restricted validity (as Hennig admits). Furthermore, embryonic and larval material was not available for examination in this investigation.

The method which was used to determine derivativeness of character states involved making "out-group" comparisons. The members of the Order Beryciformes compose the "in-group" while all other teleosts constitute the "out-group". By examining a wide variety of the members of the "out-group" both below (more primitive than) and above (more advanced than) the Beryciformes in terms of their level of structural organization, it was usually possible to decide which state represented the primitive beryciform condition.

In this investigation, species belonging to five of the eight superorders of teleosts recognized by Greenwood et al. (1966) were initially selected to represent the "out-group". The species which were chosen are listed below.

1. Elopomorpha - Elops saurus, Albula vulpes
2. Clupeomorpha - Etrumeus micropus
3. Osteoglossomorpha - Hiodon tergisus
4. Protacanthopterygii - Salvelinus fontinalis, Osmerus mordax
5. Acanthopterygii - Mycteroperca venosa, Morone americanus, Girella nigricans, Cichla ocellaris

There is general agreement among ichthyologists that fishes belonging to the first four groups listed above are more primitive than the Acanthopterygii (which includes the Order Beryciformes) in their overall level of structural organization (e.g., Greenwood et al., 1966; Greenwood, 1973; Forey, 1973a; Radovčić, 1975b). All of the species belonging to the fifth group (the Acanthopterygii) are members of the Suborder Percoidei, the basal group of the Order Perciformes (Gosline, 1968, pp. 4-12). The Order Perciformes is the central acanthopterygian group, and is generally recognized as being derived from the Order Beryciformes (e.g., Jordan, 1905; Patterson, 1964; Greenwood et al., 1966; Gosline, 1968; McAllister, 1968). It seems clear, therefore,

that an examination of the character states which are present in the species listed above should provide a sound basis for determining the derivativeness of the states present in the "in-group" (the Beryciformes).

Although it should be possible in most cases to correctly interpret the derivativeness of character states in the Beryciformes by examining only the taxa already included in the "out-group," faulty conclusions will be reached in certain instances. The reason for this is that the terms primitive and derived are relative (see p. 47). Thus, the primitive teleost condition (determined through examination of the primitive members of the "out-group" -- i.e., Elops, etc.) does not necessarily represent the primitive beryciform condition.

Figure 1 depicts the three different situations which could occur in terms of the changes in character states between primitive teleosts and members of the Beryciformes. In this figure, the primitive beryciform condition denotes the condition (state) present in the actual ancestor of the Beryciformes. Note that in characters II and III, the primitive beryciform condition is not identical to the primitive teleost condition--rather, the former is derived relative to the latter.

Character	Primitive teleost condition	Primitive beryciform condition	Conditions present in the Beryciformes	
I	a (e.g., 5 rays)	→ a (5 rays)	→ a (5 rays)	→ a' (6 rays)
II	b (e.g., 50 vertebrae)	→ b' (40 vertebrae)	→ b' (40 vertebrae)	→ b'' (30 vertebrae)
III	c (e.g., 0 spines)	→ c' (10 spines)	→ c' (10 spines)	→ c (0 spines)

Fig. 1.--Changes in character states between primitive teleosts and members of the Beryciformes. See text for further explanation.

Figure 1 indicates that in certain cases the primitive beryciform condition would be incorrectly identified if only the distribution of character states in the primitive members of the "out-group" was taken into consideration. In character I, no change has occurred between the primitive teleost and primitive beryciform conditions. In this case, state a would be designated as primitive and state a' as derived for the Beryciformes (since state a is widely distributed in teleosts which are structurally more primitive than the Beryciformes). This would be the correct interpretation. In character II, the primitive beryciform condition (b') is intermediate between the primitive teleost condition (b) and that seen in some members of the Beryciformes (b''). In this case, state b' would probably be designated as primitive and b'' as derived for the Beryciformes, since b' is phenetically more similar to the primitive teleost condition. This would also be the correct interpretation. In character III, state c would be designated as primitive and c' as derived for the Beryciformes (for the same reason as in character I). This interpretation would be incorrect, however, since a reversal in the change of character states has occurred (0 spines → 10 spines → 0 spines). Thus, faulty

conclusions will be reached regarding the derivativeness of states in the Beryciformes for all of the characters which have evolved according to the pattern outlined for character III.

In order to avoid the danger of incorrectly interpreting the derivativeness of character states is those cases where reversals have occurred, an investigation was undertaken to identify the actual ancestor (or the forms close to the ancestry) of the Beryciformes. Since the Beryciformes are structurally the most primitive acanthopterygians and the first to appear in time (base of the Upper Cretaceous), the origin of the Acanthopterygii as a whole is to be found in the ancestry of the Beryciformes (Patterson, 1964, p. 459).

The Origin of the Acanthopterygii

Introduction

Two groups have been proposed as containing the ancestor of the Acanthopterygii: the Suborder Myctophoidei and the Order Ctenothrissiformes. Both of these groups are placed in the Superorder Protacanthopterygii by Greenwood et al. (1966, p. 395). Woodward (1901, pp. viii-ix; 1912, p. 253), Boulenger (1904, p. 605) and Gosline (1961, p. 36) have suggested that the Myctophoidei are ancestral to the Acanthopterygii. On the other hand, Regan (1907, p. 642), Gregory (1933, p. 237), Bertin and Arambourg (1958, p. 2207), Patterson (1964, p. 466) and Romer (1966, p. 64) favor a ctenothrissiform ancestry for acanthopterygians. Greenwood et al. (1966, p. 371) and Goody (1969, p. 232) also believe that the Ctenothrissiformes are ancestral to the Acanthopterygii [based on the evidence presented by Patterson (1964)].

The Myctophoidei appear in the Upper Cretaceous and today represent a moderately successful group of marine fishes. Sardinioides and Nematonotus are two well-known fossil myctophoids. The Order Ctenothrissiformes is confined to the Upper Cretaceous.[1] This group has undergone a number of systematic changes since it was first established by Patterson (1964) to include the genera Ctenothrissa, Aulolepis and Pateroperca. Thus, Pattersonichthys was described and added to the Ctenothrissiformes by Goody (1969), only to be removed and made the type of a new order, the Pattersonichthyiformes, by Gaudant (1976). Pateroperca was also removed from the Ctenothrissiformes by

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[1] Marshall (1961) presented evidence that Macristium chavesi (Family Macristiidae), known only by two post-larval specimens, is related to the Ctenothrissidae. Marshall noted a number of superficial similarities in the fin pattern between Macristium and the Ctenothrissidae. In 1967, Berry and Robins described a second macristiid, Macristiella perlucens. Still later, Rosen (1971) described an additional Macristium-like larva. In this paper, Rosen presented strong evidence that all of these forms are larval or juvenile myctophoids (probably belonging to the families Bathysauridae and Ipnopidae). The Order Ctenothrissiformes therefore appears to be represented only by fossil taxa.

Gaudant (1978a), being placed incertae sedis in the group Ctenosquamata of Rosen (1973). Finally, in Gaudant's most recent study of the Ctenothrissiformes (1978b), a new genus, Heterothrissa, was added to the remaining forms (Ctenothrissa and Aulolepis), thus bringing the total number of genera in the group to three.

Patterson's treatment (1964, pp. 448-466) of the problem of the origin of the Acanthopterygii is the most rigorous. Because of the importance of determining the ancestor of the Acanthopterygii (Beryciformes) for interpreting the derivativeness of character states, it is essential to critically evaluate Patterson's argument for a ctenothrissiform ancestry.

Patterson's Argument

Patterson's argument for a ctenothrissiform ancestry of the Acanthopterygii began by comparing the osteology of Elops (the most primitive living teleost) and Serranus (a generalized perciform acanthopterygian). He was able to compile a long list of disparate skeletal character states by which acanthopterygians may be differentiated from primitive teleosts (Patterson, 1964, pp. 449-451). Patterson then proceeded to show how most of these acanthopterygian character states were correlated with one of three major functional trends which have occurred in acanthopterygian evolution: (1) trend toward increased maneuverability, involving changes in the position of the paired fins and in the shape of the body, modifications of the neurocranium, etc. (2) trend toward a reduction of buccal dentition and an increase in pharyngeal dentition, followed by the development of a protrusile mouth and (3) trend to develop defense mechanisms, such as fin spines, ctenoid scales and ornamentation on the dermatocranial bones.

Patterson then compared the Cretaceous myctophoids (Sardinioides) with the ctenothrissiforms (mainly Aulolepis) in terms of these acanthopterygian character states (trends). He pointed out that the presence of many of these character states in Aulolepis was indicative of a ctenothrissiform ancestry for the Acanthopterygii.

Patterson also discussed the distribution in time and the anatomical specializations of the myctophoids and ctenothrissiforms when evaluating their merits as acanthopterygian ancestors. He noted that although no known myctophoid or ctenothrissiform could have been directly ancestral to the Acanthopterygii (because the earliest myctophoids, ctenothrissiforms and beryciforms are contemporary), the distribution in time of the Ctenothrissiformes as a group supports the idea that they gave rise to the acanthopterygians. Thus, the

> Ctenothrissiformes became extinct at the base of the Turonian . . . , and Aulolepis and Pateroperca, the more generalized members, are rare even in the Cenomanian, where the Beryciformes [Acanthopterygii] first appear. The extinction of the group soon after the first appearance of the Beryciformes is what one would expect if the Ctenothrissiformes had given rise to the latter (Patterson, 1964, p. 465).

On the other hand, the distribution in time of the myctophoids is against their having given rise to the Beryciformes.

> The myctophoids are rare in the Cenomanian . . . , become very common in the Senonian, and persist throughout the

> Tertiary to the present day. This is not the distribution we should expect of a group which had given rise to the highly successful acanthopterygians, . . . but suggests rather that the myctophoids are a group evolving to some extent parallel with, but separate from, the acanthopterygians (Patterson, 1964, p. 462).

Patterson also stated that all myctophoids and ctenothrissiforms are excluded from the direct ancestry of the Acanthopterygii because they are too specialized in certain anatomical features. For example, Sardinioides (Myctophoidei) possesses the following morphological specializations (Patterson, 1964, p. 462): (1) toothless maxilla (2) reduced ventral postcleithrum and (3) expanded subopercle. Similarly, Ctenothrissa (Ctenothrissiformes) cannot have been directly ancestral to the Acanthopterygii because it exhibits such specializations as (1) the strong postorbital curvature of the parasphenoid (2) the almost edentulous condition of the palate (3) the peculiar structure of the maxilla and (4) the absence of a roof over the posttemporal fossa (Patterson, 1964, pp. 463-465).

In summary, Patterson concluded that a consideration of all of the evidence indicates that, while no known ctenothrissiform could be directly ancestral to the Acanthopterygii (Beryciformes), the Ctenothrissiformes "approach the Beryciformes more closely than any other Cretaceous forms" and "the Beryciformes arose from Albian or Aptian fishes which would be placed in or near the Ctenothrissiformes" (Patterson, 1964, p. 463 and p. 466, resp.).

Evaluation of Patterson's Argument

Patterson is certainly correct in stating that none of the Cretaceous myctophoids or ctenothrissiforms could have been a direct ancestor of the acanthopterygians. According to Hennig (1966), an ancestral (mother) species "ceases to exist" after giving rise to a descendant (daughter) species (i.e., the ancestral and descendant species cannot coexist). As mentioned above, the earliest known myctophoids, ctenothrissiforms and beryciforms are contemporary (Cenomanian). Furthermore, the presence of various anatomical specializations in the myctophoids and ctenothrissiforms would necessitate the assumption that reversals have occurred (if directly ancestral). In at least some cases, such as Sardinioides and Ctenothrissa, which possess a relatively large number of specializations, this possibility seems most improbable [note: Gaudant's (1978b) description of three new ctenothrissiforms--Ctenothrissa protodorsalis, C. enigmatica and Heterothrissa signeuxae-- does not affect this situation, for all occur in Cenomanian deposits and all exhibit morphological specializations which preclude them from being direct ancestors]. However, it is still necessary to evaluate Patterson's proposal that the Ctenothrissiformes lie closer to the ancestry of the Acanthopterygii than the Myctophoidei.

The possible relationship of the Myctophoidei or Ctenothrissiformes to the Acanthopterygii is expressed in figure 2. Patterson's statement that the Ctenothrissiformes, although not directly ancestral, are phylogenetically closer to the Acanthopterygii than any other group means that the Ctenothrissiformes represent the sister group of the Acanthopterygii. If this is true, it should be possible to find derived character states which are present only in ctenothrissiforms and acanthopterygians. On the other hand, if the myctophoids represent the sister group of the acanthopterygians, it should be

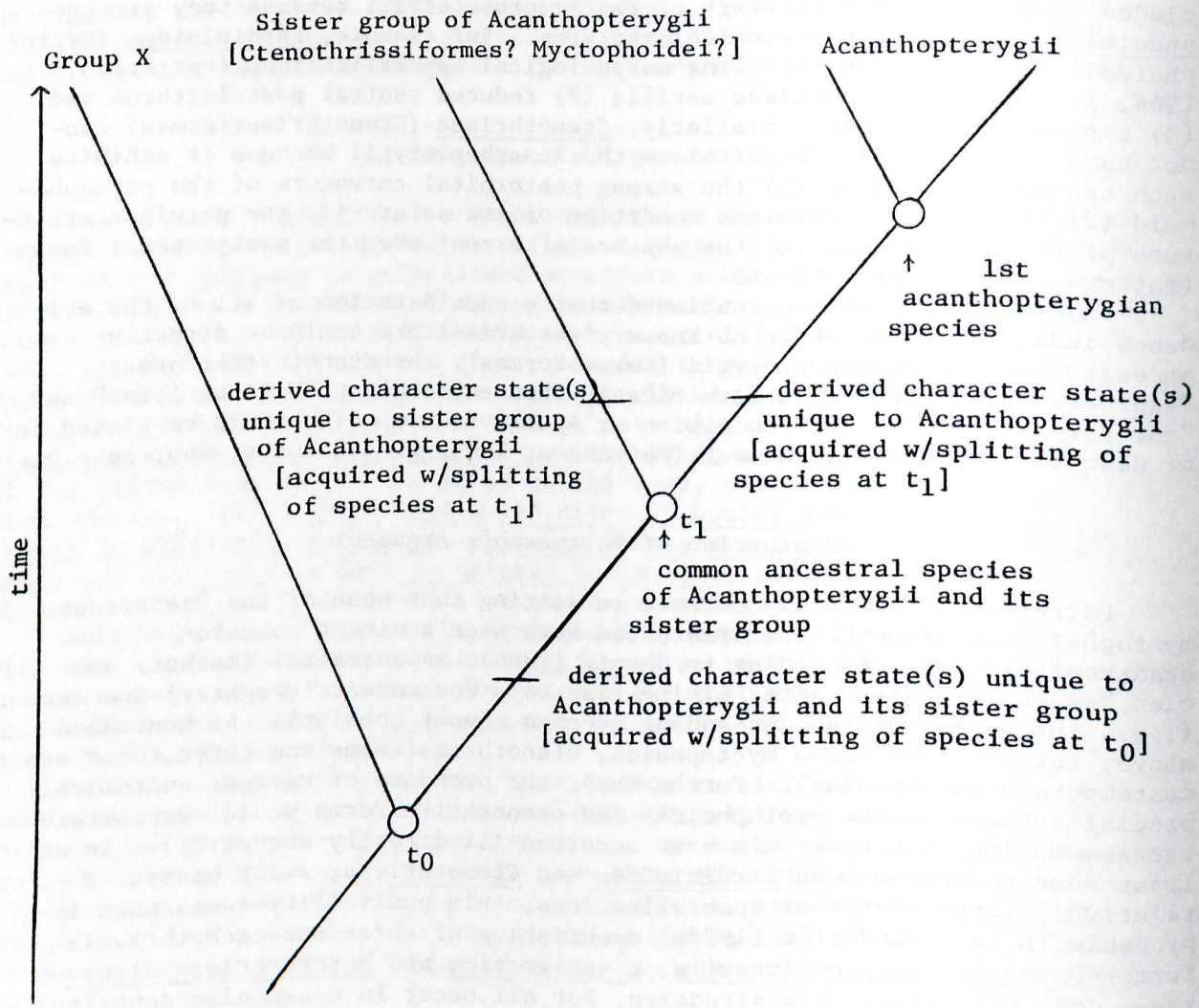


Fig. 2.--Diagram showing sister group relationship between Ctenothrissiformes or Myctophoidei and Acanthopterygii.

possible to identify derived character states which are unique to the group Myctophoidei + Acanthopterygii. In either case, the derived character states (or state) in question would have arisen during the splitting (at time t_o in fig. 2) of the species which represents the common ancestor of the Acanthopterygii + its sister group and "Group X." Furthermore, if the situation is as depicted in figure 2, one should be able to demonstrate the presence of derived character states unique to each of the sister groups (i.e., Acanthopterygii and Myctophoidei or Ctenothrissiformes). These character states would have been acquired at time t_1, with the splitting of the species which represents the common ancestor of the Acanthopterygii and its sister group.

Patterson's argument may be criticized on two counts. First, he worked under the assumption that the Ctenothrissiformes are monophyletic, and that certain of the acanthopterygian features seen in some forms are also present in others (even though direct fossil evidence was not available). Thus, he states that

> Pateroperca is very similar to Aulolepis, and since the latter is better known, the morphological discussion [concerning advancements toward the acanthopterygian level of organization] will be confined to it, and it may be assumed that the points mentioned also apply to Pateroperca (Patterson, 1964, p. 464).

However, the resemblances between Pateroperca and Aulolepis which Patterson (1964, p. 371) cites as evidence of relationship are as follows: (1) shape of the neurocranium (long and low) (2) lack of ornamentation on the bones of the head (3) depth of the mandible (4) subthoracic pelvic fins (5) cycloid scales and (6) rather shallow trunk. The significance of the third feature is not known; Patterson (1964, p. 370) merely states that the mandible of Pateroperca is about as deep as it is in Aulolepis. However, all of the other features (except 4) are primitive [Patterson himself (1964, p. 248) states that the presence of a long, low neurocranium is a primitive feature] and are therefore not indicative of phylogenetic relationship. Furthermore, the recent discovery of new material of Pateroperca has enabled Gaudant (1978a, pp. 202-203) to demonstrate that there are, in fact, many differences between Pateroperca and Aulolepis, and that the former should not be included in the Ctenothrissiformes.

Although removal of Pateroperca from the Ctenothrissiformes seems justified, there is still a possibility that this order (as understood by Gaudant, 1978b) is not monophyletic. Thus, the diagnosis of the order given by Gaudant (1978b, p. 13) largely follows that of Patterson (1964, p. 218), in which most of the character states listed are primitive and none of the derived states is unique to ctenothrissiforms. The changes which Gaudant makes in Patterson's diagnosis do not rectify the situation, for they include: 1) suppressing one derived state (body moderately deep and compressed) 2) adding one primitive state (presence of supraorbital) and 3) adding two derived states (presence of lacrimal - lateral ethmoid articulation, presence of eight pelvic fin rays), neither of which, however, is unique to ctenothrissiforms.

The monophyly of the Suborder Myctophoidei is also questionable. Greenwood et al. (1966, p. 366) state that they were unable to find any features that are unique to the myctophoids.

> If one reviews the structural details of the salmonoids, argentinoids, galaxioids, esocoids, and stomiatoids [other suborders of the Order Salmoniformes], it is evident that the main characteristics of the myctophoids are merely the "advanced" features of the first five groups collected together.

Since the monophyly of the Myctophoidei and Ctenothrissiformes has not been satisfactorily demonstrated, it seems best to consider separately the merits of each form as a relative of the actual ancestor of the Acanthopterygii.

The second, most serious weakness of Patterson's argument is that he has assumed that the osteological character states present in the generalized percoid Serranus are present in all acanthopterygians. However, many of the advanced features of Serranus (and higher acanthopterygians) listed by Patterson are not present among members of the Beryciformes, generally recognized as the most primitive of the Acanthopterygii. In other words, there are exceptions to many of these supposed acanthopterygian character states if the Beryciformes are taken into consideration. Thus, some of the similarities between ctenothrissiforms and acanthopterygians cited by Patterson are not evidence of a close relationship since not all acanthopterygians possess these character states.

An Alternate Approach to the Problem of the Origin of the Acanthopterygii

The solution to the problem of whether any of the ctenothrissiforms or myctophoids under consideration lie particularly close to the ancestry of the Acanthopterygii will be obtained only by answering the following questions.

(1) What derived character states are present in all acanthopterygians?
(2) How many of these character states are unique to acanthopterygians?
(3) How many of these character states are unique to acanthopterygians and any of the ctenothrissiforms?
(4) How many of these character states are unique to acanthopterygians and any of the myctophoids?

A fifth question which should perhaps be asked in connection with the present discussion of the origin of the Acanthopterygii concerns the Order Pattersonichthyiformes, a group containing three monotypic genera (Pattersonichthys, Phoenicolepis, Humilichthys) recently described in detail by Gaudant (1978b). Although the Pattersonichthyiformes have not been proposed as being ancestral to the Acanthopterygii [in fact, their distribution in time (Cenomanian) and morphological specializations (absence of an orbitosphenoid) (Gaudant, 1978b) preclude them from being directly ancestral], Gaudant's (1977, 1978b) anatomical studies of pattersonichthyiforms have shown that they are relatively advanced fishes which share many features (a number of them derived) with myctophoids such as Sardinioides. It therefore seems reasonable to consider the possibility that pattersonichthyiforms are fishes close to the ancestry of the Acanthopterygii. Thus, it is necessary to add to the questions listed above:

(5) How many of the derived character states present in all acanthopterygians are unique to acanthopterygians and any of the pattersonichthyiforms?

The analysis was begun by determining which of the character states on Patterson's list are present in all acanthopterygians. Due to the tremendous size of this group, it was obviously not possible to examine all of the species. It was therefore necessary to "compromise" somewhat by making certain assumptions. Since the Beryciformes are generally recognized as the most primitive acanthopterygians, there is good reason to assume that any exceptions to the acanthopterygian character states listed by Patterson which occur among the Beryciformes represent truly primitive conditions (i.e., not secondarily primitive conditions or reversals). For example, one of the character states listed is the absence of the orbitosphenoid. Nearly all beryciforms possess an orbitosphenoid [it is absent only in stephanoberyciforms and in the fossil Sphenocephalus (Rosen and Patterson, 1969, p. 401)]. Because the orbitosphenoid is present in some members of the Beryciformes, structurally the most primitive acanthopterygians, its occurrence probably represents a retention of the primitive teleost condition (and not a reversal which has occurred within the Acanthopterygii). Furthermore, the possibility of a reversal in this character state (and in other cases in which exceptions among the Beryciformes are widespread) is highly improbable, since it would necessitate the assumption that the bone has been reacquired in numerous beryciform lineages. Character states in which exceptions occurred among members of the Beryciformes were therefore eliminated from further consideration.[1]

A logical extension of the first assumption discussed above is that any exceptions to the character states listed by Patterson which occur only in higher, non-beryciform acanthopterygians represent reversals. For example, the number of vertebrae exceeds 45 in some members of the Family Blenniidae of the Order Perciformes (Springer, 1968, p. 53). However, since the vertebral number does not exceed 32 in the Beryciformes (the basal stock from which the Perciformes are believed to have been derived), the assumption that the

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[1]There were three character states, however, which were not eliminated for this reason--character states #7, 32 and 36 in table 2. In the latter two cases only a single exception occurred and comparative morphological evidence provided a basis for believing that the exceptional conditions were secondary. Thus, the contact between the extrascapulars (which cover the entire dorsal aspects of the epiotics, parietals and much of the supraoccipital) in Gibberichthys is probably secondary for the relationships of the extrascapulars in the primitive members of the "out-group" are not the same. The presence of 10-11 pelvic rays in Beryx is also considered secondary, for a comparison with the primitive members of the "out-group" reveals that only Elops (with 13-14 rays) has a larger number. Exceptions to character state #7 (parasphenoid toothless) involve certain species of Polymixia. Patterson (1975, p. 529) noted the "sporadic occurrence" of parasphenoid teeth in P. lowei (small tooth patch in three of six specimens; note: both specimens of P. lowei examined in this investigation lacked parasphenoid teeth) and P. nobilis (small tooth patch in one of four specimens). Patterson did not find parasphenoid teeth in any of the three individuals of P. japonica examined. In accordance with the manner in which intraspecific variation was treated for other characters used in this study, the most frequently occurring state (parasphenoid toothless) was assigned to represent P. lowei and P. nobilis.

high number of vertebrae in some blenniids represents a secondary condition is well-founded. Character states in which exceptions were known to occur only in non-beryciform acanthopterygians were therefore retained.

It is evident from the preceding discussion that, in view of the practical limitations involved, selection of the Beryciformes (not the Perciformes) as a group to represent the Acanthopterygii when attempting to determine features characteristic of the entire superorder is the most reasonable. If derived character states are present in all members of the Beryciformes it is reasonable to assume that they are also present in more advanced acanthopterygians, and in those cases where exceptions are known to exist in more advanced acanthopterygians, a strong argument for assuming that reversals have occurred can be presented.

Table 2 is a list of the character states (with a few modifications) which Patterson (1964) claims are typical of all acanthopterygians. Members of the Beryciformes which do not possess these character states are also listed. For many of the character states, not all of the exceptions which are known to occur have been recorded. In preparing this list, every fossil beryciform species described by Patterson (1964, 1967, 1968), Gaudant (1969) and Radovčić (1975a)[1], as well as all of the living species which I examined, were taken into consideration. I found that only 20 of the 42 character states listed by Patterson can be considered to be typical of all acanthopterygians.

The answers to questions 2, 3, 4 and 5 (no. of derived character states unique to acnthptrygns., acnthptrygns./ctnthrssfrms., acnthptrygns./myctphds., acnthptrygns./pttrsnchthyfrms.) on page 160 can be obtained by considering the data presented in tables 3-5. In table 3, the 20 acanthopterygian character states are listed on the left. On top are listed the myctophoids (species 7-10), ctenothrissiforms (species 11-12) and pattersonichthyiforms (species 13) which are being compared in terms of the number of these states which they possess (the species represented are those for which the most complete data were available). Unless otherwise indicated, the data for the fossils have been taken from the following sources: Aulolepis and Ctenothrissa (Patterson, 1964, 1968); Sardinioides (Goody, 1969); Nematonotus (Rosen and Patterson, 1969); Pattersonichthys (Gaudant, 1978b). In addition to the two Cretaceous myctophoids (Nematonotus and Sardinioides), two living members of this group (Aulopus and Chlorophthalmus) have been included. Both of the latter forms are very generalized myctophoids (Parr, 1929, p. 3). Finally, the primitive teleosts (species 1 - 6) and the advanced teleosts (species 14 - 17) of the "out-group" have been included for comparison. Recall that species 14 - 17 are members of the Percoidei, the basal suborder of the Perciformes. An important point is that all of the percoids possess all 20 of the acanthopterygian character states (except Cichla, which does not possess state 22--≤32 vertebrae). This adds considerable strength to the argument that any exceptional condition which occurs in a non-beryciform acanthopterygian is probably secondary.

Table 4 lists the rank of the genera examined in terms of the total number of acanthopterygian character states possessed. The list indicates that, to a very slight extent, the ctenothrissiforms compare most favorably as forms near the ancestry of the Acanthopterygii. However, the myctophoids and pattersonichthyiforms are not too distantly removed from the ctenothrissiforms--there are no sharp breaks between the three groups with respect to the number

(text continues on page 166)

[1]The three fossil species which Radovčić (1975a) assigned to the Order Polymixiiformes were also taken into consideration.

TABLE 2

LIST OF BERYCIFORMS SHOWING EXCEPTIONS TO "ACANTHOPTERYGIAN" CHARACTER STATES
(+ denotes fossil taxon)

the neurocranium

1. supraoccipital completely separates parietals
   exceptions: NONE
2. posttemporal fossa loses bony roof
   exceptions: Ostichthys, Myripristis, Holocentrus, Adioryx, Plectrypops, +Hoplopteryx, +Trachichthyoides, +Lissoberyx, etc.
3. development of supratemporal fossa
   exceptions: Anoplogaster, Gibberichthys, Stephanoberyx, Melamphaes, Scopelogadus
4. development of exoccipital condyles (tripartite occipital condyle), along with development of specialized atlas vertebra to fit tripartite condyle
   exceptions: NONE
5. orbitosphenoid lost
   exceptions: all beryciforms (except stephanoberyciforms and possibly +Sphenocephalus)
6. pars jugularis of trigemino-facialis chamber simplified by confluence of foramina for orbital artery, jugular vein, and hyomandibular trunk of VII (i.e., two openings)
   exceptions: most beryciforms
7. parasphenoid toothless
   exceptions: NONE

the circumorbital bones

8. supraorbital lost
   exceptions: NONE
9. antorbital lost
   exceptions: Polymixia, Myripristis, Ostichthys, Holocentrus, Plectrypops, Adioryx, +Hoplopteryx, +Sphenocephalus, +Stichopteryx (?)
10. lacrimal has strong articulation with lateral ethmoid
    exceptions: NONE
11. subocular shelf present
    exceptions: stephanoberyciforms, +Sphenocephalus

the jaws

12. maxilla toothless
    exceptions: Myripristis, +Hoplopteryx macracanthus (only this species), +Gnathoberyx

TABLE 2--cont.

13. premaxilla enlarged by development of ascending and articular processes
exceptions: NONE

14. premaxilla enlarged by great increase in length of toothed alveolar process (alveolar process forms more than one-third margin of upper jaw)
exceptions: NONE

15. the two supramaxillae lost
exceptions: nearly all beryciforms

16. endopterygoid toothless
exceptions: Monocentris, Cleidopus, Polymixia, +Berycopsis, +Homonotichthys, +Omosoma, etc.

the hyoid arch

17. number of branchiostegal rays reduced to nine (or fewer)
exceptions: NONE

the branchial arches

18. basibranchials toothless
exceptions: Polymixia, Trachichthys, Centroberyx, Beryx, Adioryx, Monocentris, Cleidopus

19. upper pharyngeals (PB2, PB3, PB4) and lower pharyngeals (CB5) have increased in size and developed a strong dentition
exceptions: Anoplogaster (PB2, CB5 limited dentition)
Scopelogadus unispinus (CB5 limited dentition)
Gibberichthys (" " ")
Melamphaes eulepis (" " ")
Melamphaes macrocephalus (PB3, CB5 limited dentition)

20. on all of the branchial arches except the first, the gill-rakers have been transformed into loosely attached tooth plates
exceptions: Photoblepharon, Anomalops, Polymixia, Plectrypops, etc.

the superficial bones of the head

21. superficial head bones develop ornament and spines (opercle, preopercle, lacrimal typically spiny)
exceptions: Polymixia, +Lissoberyx dayi (only this species), +Berycopsis, +Homonotichthys, etc.

the vertebral column

22. number of vertebrae reduced to 32 (or fewer)
exceptions: NONE

23. no more than one (the first) autogenous neural arch (anterior to PU2)
exceptions: NONE

TABLE 2--cont.

24. development of prominent pre- and postzygapophyses
exceptions: Photoblepharon, +Berycopsis, +Homonotichthys

25. loss of all epineural ribs
exceptions: Polymixia, +Berycopsis, +Homonotichthys, +Omosoma, etc.

26. loss of epipleural ribs on caudal vertebrae
exceptions: Myripristis, Adioryx, Plectrypops, Ostichthys, Centroberyx, +Berycopsis, +Homonotichthys, +Omosoma, etc.

the caudal skeleton

27. reduction in number of hypurals to six (or fewer)
exceptions: NONE

28. first preural and first ural vertebrae fused (PU1 + U1)
exceptions: NONE

29. urodermal lost
exceptions: NONE

30. reduction in number of uroneurals to two (or fewer), with the first uroneural fusing with the first ural and preural neural arches to produce a stegural
exceptions: NONE

31. loss of caudal scute (fulcral scale) above and below caudal skeleton
exceptions: NONE

the pectoral girdle

32. dorsal limb of extrascapular (supratemporal) reduced, failing to meet its fellow in midline
exceptions: NONE (contact between extrascapulars in Gibberichthys secondary)

33. mesocoracoid arch lost
exceptions: NONE

34. pectoral fin inserted vertically on flank (not horizontally on ventral border of trunk)
exceptions: NONE

the pelvic girdle and fin

35. pelvic fins subthoracic (or thoracic) in position
exceptions: NONE

36. number of pelvic fin rays reduced to eight (or fewer)
exceptions: NONE (10-11 rays in Beryx secondary)

37. outer pelvic ray is spinous (i.e., presence of pelvic fin spine)
exceptions: Anoplogaster, Anomalops, Photoblepharon, Polymixia, +Berycopsis, +Homonotichthys, +Omosoma, etc.

TABLE 2--cont.

the median fins
38. anterior rays of dorsal and anal fins spinous exceptions: Anoplogaster, Diretmus lack dorsal and anal fin spines Monocentris, Cleidopus lack anal fin spines
39. dorsal fin divided, partially or completely, into an anterior spinous fin and a posterior soft fin exceptions: Polymixia, Beryx, Centroberyx, Hoplostethus, Paratrachichthys, Photoblepharon, +Lissoberyx, +Gnathoberyx, +Stichocentrus, etc.
40. number of principal rays in caudal fin reduced to 17, with 15 branched exceptions: all beryciforms
the squamation
41. scales ctenoid exceptions: Anoplogaster, stephanoberyciforms, +Pycnosteroides, +Pharmacichthys, +Acrogaster, +Aipichthys (?)
42. scales cover opercle exceptions: many extant beryciforms, +Pharmacichthys (?), +Erugocentrus (?)

of character states they possess. Note also that the myctophoid Nematonotus is the only member of the three groups which does not possess more than half of the acanthopterygian character states.

The data in table 5 provide direct answers to questions 2-5 (no. of derived character states unique to acnthptrygns., acnthptrygns./ctnthrssfrms., acnthptrygns./myctphds., acnthptrygns./pttrsnchthyfrms.) posed on page 160. The important points to be noted are: (1) none of the character states is unique to acanthopterygians (2) none of the character states is unique to any of the ctenothrissiforms and acanthopterygians (3) only one character state (#23) is unique to one of the myctophoids (Chlorophthalmus) and acanthopterygians (4) none of the character states is unique to pattersonichthyiforms and acanthopterygians and (5) seven of the character states are restricted to ctenothrissiforms, myctophoids, pattersonichthyiforms and acanthopterygians.

These facts can be interpreted as follows.

1. The absence of derived character states unique to members of the Acanthopterygii indicates that there is a possibility that this group is not monophyletic. (text continues on page 172)

TABLE 3

A COMPARISON OF MYCTOPHOIDS, CTENOTHRISSIFORMS, PATTERSONICHTHYIFORMS AND MEMBERS OF THE "OUT-GROUP," IN TERMS OF 20 ACANTHOPTERYGIAN CHARACTER STATES

+ indicates presence of acanthopterygian condition - indicates absence of acanthopterygian condition blank indicates no information (fossil taxa) Character state	1. Elops saurus	2. Albula vulpes	3. Etrumeus micropus	4. Hiodon tergisus	5. Salvelinus fontinalis	6. Osmerus mordax	7. Nematonotus longispinus	8. Sardinioides minimus	9. Aulopus japonicus	10. Chlorophthalmus agassizi	11. Ctenothrissa radians	12. Aulolepis typus	13. Pattersonichthys delicatus	14. Mozone americanus	15. Giralia nigricans	16. Mycteroperca venosa	17. Cichla ocellaris
1. supraoccipital separates parietals	-	-	+	-	+	+	-	-	-	-	-	-	-	+	+	+	+
4. exoccipital (tripartite) condyles/atlas	-	+	-	+	+	-			+	+	+	+		+	+	+	+
7. parasphenoid toothless	-	-	+	-	+	+		+	+	+	+	+	+[7]	+	+	+	+
8. supraorbital lost	-	-	-	+	+	-	-	+	-	-	-[3]	-[3]	+	+	+	+	+
10. lacrimal/lateral ethmoid articulation	-	-	-	-	-	-			-	+	+	+		+	+	+	+
13. premaxilla enlarged--ascend., artic. proc.	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+
14. premaxilla enlarged--toothed alveolar proc. (>1/3 margin upper jaw)	- (1/3)	+ (1/2)	- (1/5)	+ (5/12)	- (1/5)	+ (2/5)	+ (3/4)	+ (all)	+ (17/19)	+ (all)	- (1/4)	- (1/3)	+ (1/2)	+ (2/3)	+ (6/7)	+ (3/4)	+ (5/6)
17. ≤9 branchiostegal rays	- (30)	- (11-13)	- (15)	+ (9)	- (13)	+ (7)	- (10)	+ (8 or 9)	- (14)	+ (8)	+ (9)	+ (9)	- (10)	+ (7)	+ (6)	+ (7)	+ (5)
22. ≤32 vertebrae	- (77)	- (71)	- (54)	- (59)	- (58)	- (63)	+(?) (32)	+ (32)	- (43)	- (48)	+[4] (33-35)	- (34-36)	+ (30-31)	+ (25)	+ (28)	+ (24)	- (35)
23. ≤1 autogenous neural arch	- (all)	- (all)	-(1^{st}27)	-(1^{st}30)	-(1^{st}28)	-(1^{st}28)		- (>1)	-(1^{st}10)	+(1st)	-(1^{st}5)	-(1^{st}5)	-[7](1^{st}13)	+(1st)	+(1st)	+ (≤1)	+ *(none)*

TABLE 3--cont.

27. ≤6 hypurals	- (7)	+ (6)	+ (6)	- (7)	+ (6)	+ (6)	+ (6)	+ (6)	+ (6)	+ (6)	+ (6)	+ (6)	+ (6)	+ (5)	+ (5)	+ (5)	+ (5)
28. PU1/U1 fused	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+
29. urodermal lost	-	+	+	+	+	-	-	-	-	+			-	+	+	+	+
30. ≤2 uroneurals (1st → stegural)	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+
31. caudal scutes (fulcral scales) lost	-	-	+	+	+	+	-	-	-	-	-	-	-	+	+	+	+
32. extrascapular dorsal limb reduction → midline gap	-	-	+	+	-	+	+		+	+	-	+		+	+	+	+
33. mesocoracoid arch lost	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+
34. pectoral fin inserted vertically on flank	-	-	-	+	-	-	+	+	+	+	+	+	+	+	+	+	+
35. pelvic fins (sub)thoracic	- a[1]	- a	- a	- a	- a	- a	- a	- a	+ s	- a	+ t	+ s	+ s	+ t	+ t	+ t	+ t
36. ≤8 pelvic fin rays	- (13-14)	- (10)	+ (8)	+ (7)	+ (8)	+ (8)	- (9)	+[2] (8)	- (9)	- (9)	+[5] (8)	+[6] (8)	+ (8)	+ (5)	+ (5)	+ (5)	+ (5)
TOTAL	0	4	7	9	8	9	9	12	11	14	13	13	12	20	20	20	19

[1] a - abdominal; s - subthoracic; t - thoracic.

[2] Gaudant (1978b, p. 120).

[3] Gaudant (1978b, p. 18).

[4] Presence of 33-35 vertebrae in C. radians is probably secondary (see Patterson, 1964, p. 240).

[5] Gaudant (pers. comm.).

[6] Gaudant (1978a, p. 202).

[7] Goody (1969).

TABLE 4

RANK OF GENERA EXAMINED IN TERMS OF NUMBER OF ACANTHOPTERYGIAN CHARACTER STATES POSSESSED

Elops	0 of 20
Albula	4 of 20
Etrumeus	7 of 20
Salvelinus	8 of 20
Hiodon	9 of 20
Osmerus	9 of 20
*Nematonotus	9 of 20
*Aulopus	11 of 20
*Sardinioides	12 of 20
**Pattersonichthys	12 of 20
***Ctenothrissa	13 of 20
***Aulolepis	13 of 20
*Chlorophthalmus	14 of 20
Cichla	19 of 20
Morone	20 of 20
Girella	20 of 20
Mycteroperca	20 of 20

* - myctophoid

** - pattersonichthyiform

*** - ctenothrissiform

TABLE 5

CHARACTER STATES UNIQUE TO SELECTED GROUPS

	Character states unique to myctophoids, ctenothrissiforms, pattersonichthyiforms and acanthopterygians	Character states unique to pattersonichthyiforms and acanthopterygians	Character states unique to myctophoids and acanthopterygians	Character states unique to ctenothrissiforms and acanthopterygians	Character states unique to acanthopterygians
	10,13,22,23,30,33,35		23		
TOTAL	7	0	1	0	0

2. The fact that there are no derived character states unique to any of the Ctenothrissiformes and the Acanthopterygii means that there is no sound evidence that any of the members of the former group are particularly closely related to the Acanthopterygii.

3. There is no strong evidence that any of the myctophoids are particularly closely related to the Acanthopterygii. Although Chlorophthalmus does share one character state (no more than one autogenous neural arch) with the Acanthopterygii that is not present in any of the other forms, the amount of significance which should be attributed to this similarity is questionable. Both of the ctenothrissiforms (Ctenothrissa, Aulolepis) are also quite advanced in this character (i.e., the percentage of autogenous neural arches is low).

4. The fact that there are no derived character states unique to Pattersonichthys (Pattersonichthyiformes) and the Acanthopterygii means that there is no sound evidence that this form is particularly closely related to acanthopterygians.

5. The data do indicate that the myctophoids, ctenothrissiforms and pattersonichthyiforms are relatively advanced fishes, which are approaching the acanthopterygian level of organization. Thus, all ctenothrissiforms, pattersonichthyiforms and myctophoids (but none of the primitive teleosts) have an advanced upper jaw in which the premaxilla bears articular and ascending processes. Similarly, in all ctenothrissiforms, pattersonichthyiforms and myctophoids (but in none of the primitive teleosts) the number of uroneurals in the caudal skeleton has been reduced to two and the first uroneural has been modified into a stegural, as in beryciforms and higher acanthopterygians. Also, the mesocoracoid arch of the pectoral girdle is absent in all ctenothrissiforms, pattersonichthyiforms and myctophoids but is present in all of the primitive teleosts examined. The other four (of the seven) character states which are restricted to ctenothrissiforms, pattersonichthyiforms, myctophoids and acanthopterygians have a more limited distribution. These character states are as follows: (1) presence of a strong articulation between the lacrimal and lateral ethmoid (2) presence of subthoracic or thoracic pelvic fins (3) vertebrae reduced to 32 or fewer and (4) no more than one autogenous neural arch. Although not all myctophoids, ctenothrissiforms and pattersonichthyiforms have attained the acanthopterygian level with regard to the latter two character states, it is evident that they have all (with the possible exception of Nematonotus and Sardinioides, for which there is insufficient information concerning the number of autogenous neural arches) progressed further toward this level than any of the primitive teleosts under consideration. Thus, the number of vertebrae in myctophoids, ctenothrissiforms and pattersonichthyiforms ranges from 30-31 (Pattersonichthys) to 48 (Chlorophthalmus), compared with 54 (Etrumeus) to 77 (Elops) in the primitive teleosts. Similarly, the percentage of autogenous neural arches in myctophoids, ctenothrissiforms and pattersonichthyiforms varies from 2% (Chlorophthalmus) to 42% (Pattersonichthys), compared with 44% (Osmerus) to 100% (Elops and Albula) in the primitive teleosts. Finally, there are two derived character states (fusion of the first preural and first ural vertebrae in the caudal skeleton, and the high, vertical insertion of the pectoral fin) which are present in all ctenothrissiforms, pattersonichthyiforms, myctophoids and acanthopterygians, but which occur only rarely in primitive teleosts (Osmerus and Hiodon, resp.).

In summary, the evidence presented above indicates quite clearly that,

while there is no sound basis for stating that any one of the three groups under consideration (myctophoids, ctenothrissiforms, pattersonichthyiforms) lies closer to the ancestry of the Acanthopterygii than the other two, all three groups are closer to this ancestry than any of the other teleosts which have been examined[1].

Other Remarks Concerning "Out-Group" Comparisons and Their Application in This Investigation

The significance of the results of the previous analysis to this investigation may now be considered. First, since the possibility exists that the Beryciformes (Acanthopterygii) are polyphyletic, it would be dangerous to rely too heavily on the phenotypic variation in any one group to represent the ancestral character state pool when interpreting the derivativeness of character states in the Beryciformes [a similar view is expressed by Marx and Rabb (1970, p. 530) in their study on advanced snakes]. Second, since there is sound evidence that the Myctophoidei, Ctenothrissiformes and Pattersonichthyiformes are relatively advanced (compared to the non-perciform teleosts of the "out-group") toward the level of structural organization expected in the actual ancestor (or ancestors) of the Beryciformes, most emphasis was placed on the distribution of states in myctophoids, ctenothrissiforms and pattersonichthyiforms when interpreting derivativeness of character states [i.e., the group Myctophoidei + Ctenothrissiformes + Pattersonichthyiformes was designated as phenetically representing the actual ancestor(s) of the Beryciformes].

The use of "out-group" comparisons for character analysis in phylogenetic investigations can be summarized in two criteria (Marx and Rabb, 1970, pp. 530-531).

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[1]As noted on page 162, the ctenothrissiform and pattersonichthyiform species which appear in table 3 are those for which the most complete data were available. However, even if all of the known species of the Ctenothrissiformes (Ctenothrissa radians, C. microcephala, C. vexillifer, C. signifer, C. protodorsalis, C. enigmatica, Aulolepis typus, Heterothrissa signeuxae) and Pattersonichthyiformes (Pattersonichthys delicatus, Phoenicolepis arcuatus, Humilichthys orientalis) had been included in table 3 and taken into consideration during the analysis discussed above, the results obtained would have been identical to those already described--i.e., one would discover that: (1) none of the character states is unique to acanthopterygians (2) none of the character states is unique to any of the ctenothrissiforms and acanthopterygians (3) only one character state (#23) is unique to one of the myctophoids (Chlorophthalmus) and acanthopterygians (4) none of the character states is unique to any of the pattersonichthyiforms and acanthopterygians and (5) seven of the character states (#10, 13, 22, 23, 30, 33, 35) are restricted to myctophoids, ctenothrissiforms, pattersonichthyiforms and acanthopterygians. Furthermore, it should be noted that even if all of the ctenothrissiforms and pattersonichthyiforms had been included in the "out-group", the character state trees for the 70 characters analyzed in this investigation (tables 10-79) would have been the same.

1. Uniqueness. The group which represents the ancestral phenetics unequivocally determines the direction of change in any character having a state unique to the descendant group. Such a state is derived.
2. Relative abundance. This criterion is a probabilistic extension of the uniqueness criterion and concerns the relative frequencies of states. Thus, a character state which is widely distributed in the ancestral group is primitive for the descendant group because such a state has a greater probability of having had its genotype transferred to the descendant group than does a rare state.

The fact that the group Myctophoidei + Ctenothrissiformes + Pattersonichthyiformes was designated to phenetically represent the actual ancestor(s) of the Beryciformes does not mean that the distribution of states in the other members of the "out-group" was of no use in the character analyses. On the contrary, a consideration of the distribution of the states in these forms was helpful for two reasons. (1) Since all of the ctenothrissiforms, pattersonichthyiforms and myctophoids (except Aulopus and Chlorophthalmus) are fossils, there were incomplete data for many of the characters which were analyzed. In these cases, it was necessary to rely more heavily on the nature of the character states present in the other members of the "out-group" in order to determine derivativeness. (2) Examination of the distribution of character states in the other members of the "out-group" often provided additional support to my conclusions concerning the primitive beryciform condition. A discussion of two of the characters of the caudal skeleton analyzed in this investigation will clarify this point.

- In character 60 (second ural centrum), two states are present in the Beryciformes:

  state I - U2 autogenous (with respect to PU1 + U1)
  state II - U2 fused (to PU1 + U1)

  - Since state I is present in all myctophoids, ctenothrissiforms and pattersonichthyiforms it is designated to represent the primitive beryciform condition.
  - Examination of the more primitive members of the "out-group" (Elops, etc.) reveals that state I is also the primitive teleost condition. On the other hand, in all of the more advanced members of the "out-group" (members of the Order Perciformes), state II is present.

- In character 66 (number of uroneurals), three states are present in the Beryciformes:

  state I - single pair of uroneurals present; not reduced
  state II - single pair of uroneurals present; strongly reduced
  state III - uroneurals absent

  - Since state I is present in all myctophoids, ctenothrissiforms and pattersonichthyiforms it is designated to represent the primitive beryciform condition.
  - Examination of the more primitive members of the "out-group" indicates that the presence of 2 or 3 pairs of unreduced uroneurals is the primitive teleost condition. On the other hand, state III is the most prevalent condition in the Perciformes.

For both of these characters, I am confident that state I represents the primitive beryciform condition. There are two reasons for this: (1) state I is widely distributed in the "ancestral group" (myctophoids + ctenothrissiforms + pattersonichthyiforms) and (2) when the phyletics of

these two characters in a much larger group of teleosts is taken into consideration, the designation of state I as the primitive beryciform condition is the most evolutionarily sound (in the sense that it is not necessary to assume reversals in character states). Designation of state II (character 60) or state II or III (character 66) as the primitive beryciform condition would imply a reversal in the change of character states (see fig. 3).

There are several characters, however, in which an examination of the distribution of states in the other members of the "out-group" does not reinforce my conclusions regarding the primitive beryciform conditions. For example, in character 8 (flanges on the shaft of the parasphenoid), two states are recognized in the Beryciformes--presence/absence of flanges. Since all of the ctenothrissiforms, pattersonichthyiforms and myctophoids (except Nematonotus and Sardinioides, for which there is no information) possess parasphenoid flanges, there is good reason to believe that their presence in beryciforms is primitive. However, in all of the other members of the "out-group," parasphenoid flanges are absent. In this case, it is necessary to conclude that a reversal in character states has occurred [i.e., flanges absent (primitive teleost condition) → flanges present (primitive beryciform condition) → flanges absent (condition present in some beryciforms and in perciforms)].

The method in which "out-group" comparisons are made in order to determine derivativeness of character states has been used by a number of other investigators (e.g., Voris, 1969; S. Liem, 1970; Liem et al., 1971; Marx and Rabb, 1970, 1972). This investigation differs from those cited above, however, in that the "out-group" includes forms in addition to those designated as phenetically representing the ancestral group.

Character	Primitive teleost condition	Primitive beryciform condition	Conditions present in the Beryciformes	Condition(s) present in the Perciformes
60 (2nd ural centrum)	I →	I →	I → II	→ II

Designation of state I as primitive beryciform condition implies no reversals in phyletics of this character.

state I - U2 autog.
state II - U2 fused

I	→	II	→ II (R I)	→ II

Designation of state II as primitive beryciform condition does imply reversal (R) in phyletics of this character.

0	→	I	→ I → II → III	→ III
				→ I

Designation of state I as primitive beryciform condition implies no reversals in phyletics of this character.

66 (no. uroneurals)

state 0 - 2 or 3 prs. urnrls., not rdcd.
state I - 1 pr. urnrls., not rdcd.
state II- 1 pr. urnrls., strngly. rdcd.
state III-urnrls. absent

0	→	II	→ II → III	→ III
			R → I	→ I

Designation of state II as primitive beryciform condition does imply reversal (R) in phyletics of this character.

0	→	III	→ III → I	→ I
			R → II	→ III

Designation of state III as primitive beryciform condition does imply reversal (R) in phyletics of this character.

Fig. 3.--Two examples which show that knowledge of the states present in primitive teleosts and perciforms may be useful for determining the primitive beryciform condition.

CHAPTER VIII

DETERMINATION OF SEQUENCE OF CHANGE IN CHARACTER STATES

Use of the Combinatorial Method requires the construction of character state trees. Construction of a character state tree involves (1) determination of the primitive state and (2) determination of the correct sequence of change among the remaining (derived) states.

For two-state characters, the sequence of change in states is established with the determination of the primitive state (i.e., primitive → derived). The trees of multiple state characters, however, may be unidirectional (linear), multidirectional (branched) or circular. Circular trees are those in which the characters evolve their states in one or more directions, but show some convergence to a single character state (Marx and Rabb, 1972, p. 9). Circular character state trees are not permitted when using the Combinatorial Method. Only one character (number of hypurals) analyzed in this investigation has a circular tree (table 82). It was, therefore, not included in the group of characters used when making the computer run.

For multiple state characters, the sequence of change in states was determined by ordering the states such that the least complex evolutionary pathway was assumed (criterion b of S. Liem, 1970, p. 9). In other words, the character states were arranged in a logical numerical or phenetic sequence after the primitive state was determined.

Two characters will serve as examples of how the sequence of change in multiple state characters was determined. In character 14 (number of external openings in the pars jugularis of the trigemino-facialis chamber), three states are present in the Beryciformes: state I - four openings; state II - three openings; state III - two openings. State I was designated as primitive. The logical numerical sequence is, therefore, I → II → III. The other possible sequences, I → III → II and $I \nearrow^{II}_{III}$, represent more complex evolutionary pathways (a reversal is assumed to have occurred in the first case and parallelism in the second).

In character 63 (length of the neural spine of the second preural vertebra), three states are present in the Beryciformes: state I - neural spine of PU2 = 1/2 length of spine of PU3; state II - neural spine of PU2 crest-like ($\leq$1/3 length of spine of PU3); state III - neural spine of PU2 complete (= length of spine of PU3). State I was designated as primitive. The logical phenetic sequence is, therefore, $I \nearrow^{II}_{III}$. Character 63 also illustrates the manner in which intraspecific variation can be utilized to determine the sequence of change in character states. The fossil beryciform Aipichthys minor

exhibits variation between states I and III (Patterson, 1968, p. 63). Intraspecific variation between two states suggests that one of the states has been modified from the other (Marx and Rabb, 1972, p. 7). The presence of intraspecific variation between states I and III in A. minor therefore makes one of the two other possible sequences (I → II → III) even more improbable.

Table 81 is a summary of the different kinds of character states trees which were encountered in this investigation. Fifty-two of the 70 characters have only two states. The advantage in utilizing two-state characters in the Combinatorial Method is discussed on p. 151.

Tables of the 70 characters analyzed in this investigation are included in appendix I (tables 10-79). Each table includes the following information: (1) character states present in the Beryciformes (2) distribution of character states in the members of the "out-group" (i.e., the evidence upon which determination of primitiveness and derivativeness of character states is based) and (3) character state tree showing the direction and sequence of change in character states in the Beryciformes.

CHAPTER IX

DISCUSSION

The Combinatorial Method

Before discussing the actual results, it is necessary to describe some of the features of the computer program, the Combinatorial Method, which was used to achieve these results. It should be emphasized that the Combinatorial Method is only a tool which can be used to investigate phylogenetic relationships. The program was written by Glenn Sharrock and run on the IBM 370 computer at the University of Chicago.

For n OTUs (operational taxonomic units) considered one or more at a time, there are 2^n-1 different combinations. The Combinatorial Method prints out a list of only a certain type of these combinations--namely, all of the nonredundant, monothetic combinations. A nonredundant, monothetic combination is the largest combination of OTUs sharing a given set of derived character states (primitive states are deleted because they are not useful for ascertaining phylogenetic relationships). For each nonredundant, monothetic combination, the following information is given: (1) the number of the combination (2) the number of OTUs in the combination (3) the number of character states shared by the OTUs in the combination and (4) a list of the actual character states possessed by the OTUs in the combination. The combinations in the list are ordered according to the total number of character states which their OTUs possess, beginning at the highest level. For convenience, the OTUs of each combination are listed in numerical order, and an index at the end of the report lists the numbers of the first 20 combinations in which each OTU appears.

The most fundamental assumption which I have made in utilizing the Combinatorial Method is that the degree of phylogenetic relationship among OTUs is proportional to the number of derived character states which they share.

The procedures which are followed when using the report to construct a dendrogram (phylogenetic tree) will now be described. One begins by examining the combinations at the top of the list (highest level of shared character states). The first combinations which appear in the list are individual OTUs. Individual OTUs are plotted on graph paper at the appropriate level (according to the number of states which they possess). One proceeds down the list until a combination of two or more OTUs is encountered. If the OTUs in this combination do not appear in other combinations at the same level of shared character states, then this combination is selected [although each of the OTUs in this combination may appear with different OTUs in combinations at lower levels, the latter combinations need not be considered since they are less parsimonious (involve fewer character states)]. After a combination is selected, its OTUs are joined by a horizontal line at the appropriate

level. Once OTUs are joined together, they are never separated. Thus, a previously formed group of OTUs can not be joined with another OTU unless all of the OTUs of the group are present in the combination.

Two OTUs (or two groups of OTUs) may be joined together if they appear in the same combination, even though other OTUs are also present. However, these other OTUs must have already joined at a higher level with OTUs which are not present in the combination.

A problem arises when an OTU appears in two (or more) combinations at the same level of shared character states, and both of the combinations are possible. In this case, parsimony does not permit selection of either combination. Additional criteria must be applied in order to make a choice.

In this investigation, selections between combinations sharing the same number of character states were made as follows. First, the list of character states present in each combination was examined. Only the states which differed between the combinations were recorded. The combinations were then compared with respect to the following criteria.

1. Number of different characters involved. Although two combinations may be equivalent in terms of the total number of character states which their OTUs possess, the states in one combination may be distributed among more different characters than in the other [in the Combinatorial Method, an OTU is considered to possess all of the derived states of a character which are phylogenetically antecedent to the state which it actually bears (see p. 151)]. Combinations with more different characters were preferred because the similarity among their OTUs involved a greater portion of the phenotype.
2. Correlation of characters. Characters which differed between combinations were examined to determine their degree of correlation with other characters. The number of pairs of significantly correlated characters ($c > 4.10$) was recorded for each combination. Each pair of correlated characters was then examined to determine whether the correlation was "direct" (i.e., primitive state with primitive state, derived state with derived state) or "inverse" (primitive state with derived state, derived state with primitive state). If the correlation was direct, all of the OTUs in the combination were checked to insure that each possessed the derived state of both characters in question. Since the presence of derived states in directly correlated characters among a group of species may be the result of inheritance from a common ancestor, combinations with more pairs of correlated characters were preferred over those with fewer pairs.
3. Character state weighting. In a few cases, a particular character state in one of the combinations was considered to be "more important" than those in the other combination. Morphologically complex character states and character states which were unique to the OTUs of a particular combination (or which occurred only rarely in other OTUs) were assigned high weight. The probability that species which are only distantly related would become similar in highly complex structures by convergence is extremely low (Mayr, 1969, p. 220). The presence of derived character states which are unique to a group of two or more species is strong evidence that the group is monophyletic (Hennig, 1966, pp. 90-91).
4. Additional morphological evidence. Consideration of characters which were not included in the original data set was often helpful in choosing between combinations.

No attempt was made to rank these four criteria in terms of their significance. In certain cases, some of the criteria were not applicable. After a comparison between two combinations was completed, the combination favored by the most criteria was selected.

Dendrogram #1

By following the procedures discussed above, a dendrogram (#1) showing the phylogenetic relationships (relative branching sequence) of the species examined was constructed (fig. 4).

The total number of derived states present in a species or shared by a group of species is indicated on the left of the dendrogram. In the Combinatorial Method, each of the derived character states is assigned a number. A total of 94 derived states was used in this investigation.[1] The derived states which are present in each of the lineages have been included. A character state which appears at the base of a major lineage is not represented again in its sublineages. A check (✓) beside a character state indicates that it appears only once in the dendrogram (i.e., that it is unique to a particular lineage[2]). Table 6 lists the names of each of the 94 derived character states.

The dashed lines in dendrogram #1 indicate the points at which it was necessary to choose between two combinations. Discussions of what combinations were involved and the reasons for selecting the particular combinations shown in the dendrogram are presented below.

The groups in dendrogram #1 may be described as being either contested or uncontested. A contested group is one which is denoted by a dashed line, indicating that the OTUs of one of its two subgroups appeared with different OTUs in another combination at the same level of shared states, or one which is denoted by a solid line, but which would not have formed had a different combination (or set of combinations) been selected at a higher level in the dendrogram. For example, OTUs 9-16 (which are joined together by a solid line at a level of 14 states) form a contested group--this group would not have formed had the combination consisting of OTUs 9, 7 and 8 been selected instead of the combination 9, 10 and 11 at a level of 23 states. All of the groups which form at a level of less than 26 states in dendrogram #1 are contested. In fact, depending on the particular set of combinations which is chosen (beginning at a level of 23 states), it is possible to construct any one of 10 different dendrograms (dendrogram #1 represents only one of these). All of the groups which form at a level of 26 or more states (except OTU groups 3-4, 5-6 and 12-13) are uncontested. Uncontested groups are those

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[1] Actually, there are 96 derived states present in the 70 characters selected for analysis (table 81). However, since two of these states [III - character 18 (table 27); IV - character 32 (table 41)] occur only in fossil taxa and represent terminal states within their character state trees, they do not appear in the dendrogram.

[2] The word unique as used here and in the remaining discussion pertaining to dendrogram #1 applies only to the 26 species which appear in the dendrogram.

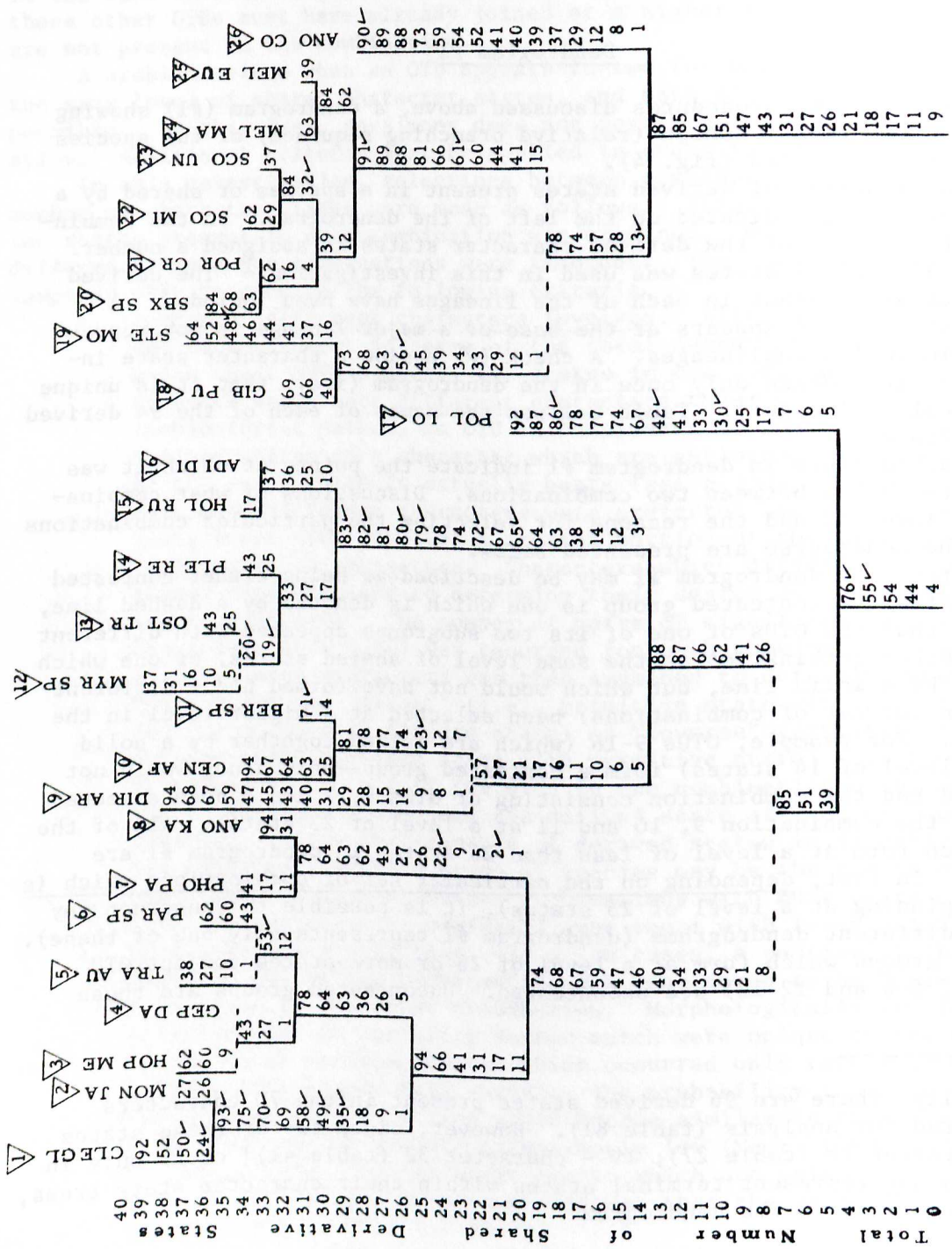


Fig. 4.--Dendrogram #1. For full names of species denoted by numbers 1-26, see table 7.

whose OTUs always join together, regardless of any choices which may have been made at a higher level in the dendrogram.

The phylogenetic relationships represented in dendrogram #1 will now be discussed. A summary of the evidence for the monophyletic nature of each of the families will be presented first. Following this will be a consideration of intrafamilial relationships. Finally, the relationships between the families of the Order Beryciformes will be discussed.

Evidence for the Monophyletic Nature of the Families of the Order Beryciformes

Perhaps the most important finding of this investigation is that all of the Recent families of the Beryciformes represent uncontested groups. The strongest evidence that a group is monophyletic is the presence of derived character states which are unique to its members (autapomorphous character states of Hennig, 1966). Each of the beryciform families except the Trachichthyidae possesses at least one derived state which is unique to it (all trachichthyids bear a prominent spine at the angle of the preopercle, however--this feature occurs elsewhere only in the holocentrids Adioryx and Holocentrus). The derived character states which are unique to each of the families of the Beryciformes are listed below.

Family Monocentridae (species 1-2):

(1) presence of a distinct notch on the ventral border of the dentary
(2) pleural ribs which begin on the sixth (Monocentris) or seventh (Cleidopus) abdominal vertebra
(3) presence of a distinct notch on the ventral border of the supracleithrum
(4) presence of three (or fewer) pelvic fin rays
(5) presence of dorsal fin spines which are strongly inclined to the right and left
(6) presence of large, thick scales on the body (armor).

Family Trachichthyidae (species 3-6):

No derived character states could be found which are unique to trachichthyids (above).

Family Anomalopidae (species 7-8):

(1) anterolateral portion of the nasal prolonged into a distinct process which articulates with the lateral ethmoid
(2) presence of a ⊂ -shaped process on the lacrimal for articulation with the lateral ethmoid.

Other derived character states which are unique to anomalopids, but which were not included in the original data set are:

(3) downward curvature of the nasal bones, producing a blunt snout
(4) presence of a subocular light organ
(5) presence of a "discontinuous" subocular shelf.

Note: The subocular shelf assumes a wide variety of forms among the members of the Beryciformes. It is questionable which of these conditions represents the primitive state. Smith and Bailey (1962, p. 3) state that a well-developed shelf (on infraorbitals 1-4) seems to represent the primitive beryciform condition (this view is supported by the

fact that the shelf is well-developed in primitive forms such as Polymixia and holocentrids). However, regardless of which condition is primitive, there is little doubt that the peculiar structure of the shelf in the Anomalopidae (as well as its structure in the Monocentridae and Trachichthyidae) represents a derived state.

Family Diretmidae (species 9):

Not one of the 94 derived states of the original data set is unique to Diretmus. However, two derived states which are unique to Diretmus are:

(1) presence of a compound sphenotic bone, formed by fusion of the dermo- and autosphenotic
(2) presence of both pre- and postanal ventral ridge scales.

Family Berycidae (species 10-11):

(1) lacrimal extended posteriorly below infraorbital 1 to articulate with infraorbital 2.

Although only one derived state is unique to the Berycidae, certain other features of the family provide strong evidence of phylogenetic relationship. These include the presence of an exceedingly well-developed supratemporal fossa, three predorsals, and a vertebral formula of 10 + 14 = 24. The first two features occur elsewhere only in Polymixia, and Scopelogadus unispinis was the only species examined in which there are fewer than 24 vertebrae.

Family Holocentridae (species 12-16):

(1) presence of a transverse crest on the dorsal surface of the supraoccipital
(2) distal portion of the posterior process of the pelvic bone expanded into a distinct flange or plate
(3) presence of a hook-like process on the outermost radial of the pelvic fin
(4) presence of an enlarged penultimate anal fin spine
(5) distal portions of the neural and hemal spines of PU4 and PU5 expanded.

Family Polymixiidae (species 17):

(1) posterior supramaxilla truncated, without a slender process overlying the anterior supramaxilla
(2) presence of only seven branchiostegal rays
(3) presence of a complete neural spine on PU2.

Other derived character states which are unique to Polymixia, but which were not included in the original data set are:

(4) anterior branchiostegal rays modified for the support of a hyoid barbel
(5) anterior aspect of the first proximal radial of the anal fin deeply excavated for reception of the swim bladder.

Family Gibberichthyidae (species 18):

Not one of the 94 derived states of the original data set is unique to Gibberichthys. However, one derived character state which is unique to Gibberichthys is:

(1) presence of fusion between the anterior spines of the dorsal and

anal fins and the underlying radial elements (these spines are also partially fused to each other).

Family Stephanoberycidae (species 19):

(1) pleural ribs which begin on the second abdominal vertebra.

Another derived character state which is unique to Stephanoberyx, but which was not included in the original data set is:

(2) absence of teeth on CB5.

Family Melamphaeidae (species 20-25):

(1) presence of an enlarged fourth actinost which shows evidence of fusion with another actinost

(2) parhypural fused to the first hypural (which in turn is fused to the second hypural, thus forming a large plate for the lower lobe of the caudal fin).

Another derived character state which is unique to melamphaeids, but which was not included in the original data set is:

(3) presence of high, thin (membranous) crests on the frontal bones which are arranged in a pattern unlike that of other beryciforms.

Family Anoplogasteridae (species 26):

(1) absence of uroneurals in the caudal skeleton.

Other derived character states which are unique to Anoplogaster, but which were not included in the original data set are:

(2) strong reduction in the size of the urohyal

(3) presence of fang-like teeth on the premaxilla and dentary

(4) strong backward inclination of the neural spines of the abdominal vertebrae

(5) facet for the quadrate condyle located on the medial aspect of the angulo-articular bone.

Intrafamilial Relationships

Relationships within the families Anoplogasteridae (monotypic), Gibberichthyidae, Anomalopidae, Berycidae, Diretmidae, Monocentridae, Polymixiidae and Stephanoberycidae will not be discussed since only one or two species in each was examined.

Six species (20-25) of the Family Melamphaeidae were examined. Although all of the groups within this family are uncontested, only one of them (the two species of Scopelogadus) is characterized by the presence of a unique, derived state (32 - absence of supramaxillae). It is perhaps worth noting that one character state (84 - fusion of the hemal arch of PU3) suggests that Scopeloberyx is more closely related to Scopelogadus and Melamphaes than to Poromitra. State 84 is unique to the first three genera mentioned above. The relationships shown in dendrogram #1 imply that state 84 has either arisen independently in three lineages or that it has been secondarily lost in Poromitra.

Both of the groups within the Family Trachichthyidae (species 3-6) are contested. Since the same number of derived character states was involved, it was necessary to choose between the combinations Hoplostethus/Gephyroberyx

and Hoplostethus/Paratrachichthys. In this case, only one of the criteria (4) discussed above was applicable. Consideration of other morphological characters indicates that Hoplostethus is more closely related to Gephyroberyx than to Paratrachichthys. The nasal bones in Hoplostethus and Gephyroberyx bear small (but distinct) spinous projections. This is a derived character state which is not present in any species of Paratrachichthys except P. trailli (Woods and Sonoda, 1973, p. 322) and P. argyrophanus. The shape of the urohyal in Hoplostethus and Gephyroberyx is also similar in that the posterodorsal and posteroventral corners are drawn out into distinct processes. A relationship between Hoplostethus and Gephyroberyx has also been suggested by Woods and Sonoda (1973, p. 299).

It was also necessary to choose between the combinations Trachichthys/Hoplostethus + Gephyroberyx and Trachichthys/Paratrachichthys. Both of the criteria (3,4) which were applicable indicated that the latter combination was correct. State 53, presence of a tympanic plate, is unique to Trachichthys and Paratrachichthys (criterion 3) among the species examined. Furthermore, this structure is morphologically quite complex. It seems highly unlikely that the striking similarity between these two genera with respect to this character state is the result of parallelism. Shimizu (1977, p. 197) also concluded that the presence of a tympanic plate in Trachichthys, Paratrachichthys and Optivus (a form not examined in this study) indicates that they form a distinct phyletic line within the Trachichthyidae.

Additional morphological evidence (criterion 4) can also be adduced for a relationship between Trachichthys and Paratrachichthys. In both of these forms, the urohyal bears a pair of ventrolaterally-directed processes for the attachment of the urohyal-hypohyal ligaments (these processes are absent in Gephyroberyx and Hoplostethus). The orbitosphenoid in Trachichthys and Paratrachichthys is also similar in that it is attenuated posteroventrally, partially or completely excluding the pterosphenoid from the margin of the optic fenestra.

The Family Holocentridae (species 12-16) is clearly divisible into two groups [(1) Myripristis, Ostichthys and Plectrypops and (2) Holocentrus and Adioryx]. The first group is characterized by the absence of teeth on the ectopterygoid (state 27) and by the presence of teeth on the lateral surface of the dentary (state 33). The members of the second group possess a large spine at the angle of the preopercle (state 36). Although none of these character states is unique to either group, the presence of a connection between the swim bladder and the lateral wall of the auditory bulla in Myripristis, Ostichthys and Plectrypops indicates that these three genera constitute a monophyletic assemblage. Other characters which serve to distinguish the two groups and which may be of phylogenetic significance include the following:

(1) morphology of the postmaxillary process of the premaxilla (triangular-shaped in all, but with a more extensive origin from the alveolar process in Myripristis, Ostichthys and Plectrypops)

(2) morphology of the posterior process of the pelvic bone (distal portion of the posterior process expanded into a broad plate in Myripristis, Ostichthys and Plectrypops; expanded into a narrow and elongate flange in Holocentrus and Adioryx)

(3) bony process projecting from beneath the lateral opening of the pars jugularis (present in Myripristis, Ostichthys and Plectrypops; absent in Holocentrus and Adioryx)

(4) position of the foramen for IX (within the prootic in Myripristis, Ostichthys and Plectrypops; within the exoccipital in Holocentrus and Adioryx)
(5) position of the quadrate-mandibular articulation (posterior border of the orbit in Myripristis, Ostichthys and Plectrypops; more anterior in Holocentrus and Adioryx)
(6) insertion of the second predorsal and the first proximal radial of the dorsal fin (between different neural spines in Myripristis, Ostichthys and Plectrypops; between the same two neural spines in Holocentrus and Adioryx).

The evidence presented above supports the views of other investigators that the Family Holocentridae consists of two distinct subfamilies--the Myripristinae and the Holocentrinae (E. Nelson, 1955, p. 126; Greenfield, 1966, pp. 170-171; Woods and Sonoda, 1973, p. 331; J. Nelson, 1976, pp. 189-190).

The relationships within the Myripristinae will now be discussed. Since the same number of derived character states was involved, it was necessary to choose between the combinations Ostichthys/Myripristis and Ostichthys/Plectrypops. Two of the criteria (2,3) favored the former combination, while only one criterion (4) favored the latter. The presence of an exoccipital fenestra (state 19) and ventrolateral flanges on the basioccipital (state 20) in Ostichthys and Myripristis are derived character states which are not only significantly correlated with each other (criterion 2), but which are unique to these two genera (criterion 3).

Interfamilial Relationships

Most of the interfamilial relationships shown in dendrogram #1 are contested. The only interfamilial relationships which are uncontested are those between the families Monocentridae (species 1-2) and Trachichthyidae (species 3-6) and between the families Gibberichthyidae (species 18) and Stephanoberycidae (species 19).

Monocentrids and trachichthyids share 26 of the 94 derived states, but none of these is unique to them. Two additional characters, however, provide strong evidence that the Monocentridae + Trachichthyidae constitutes a monophyletic group. One character is the morphology and pattern of the frontal crests. Although the $\gtrless$ pattern of the frontal crests in monocentrids and trachichthyids is also present in anomalopids and Anoplogaster, the morphology of the crests is most similar in the first two groups. The other character is the structure of the subocular shelf. In all monocentrids and trachichthyids, the subocular shelf is developed along only a portion of the margin of the second infraorbital, and in all except Paratrachichthys sp. it is curved anteriorly (hook-like) (note: the shelf is hook-like in Paratrachichthys fernandezianus, however). Lamber (1963, p. 73) also concluded, on the basis of the morphology of the otoliths (sagittae), that the Monocentridae and Trachichthyidae are closely related phylogenetically.

Monocentrids, trachichthyids and anomalopids (species 1-8) probably represent a monophyletic group, although there are no derived character states which are unique to them. The strongest evidence for a relationship

between these groups is the absence of the dermal tooth plate of the fourth pharyngobranchial (PB4). Stephanoberyx is the only other beryciform in which the tooth plate of PB4 is absent. However, since there is strong evidence that Stephanoberyx is related to Gibberichthys, the absence of the tooth plate in the former is probably the result of parallelism.

The families Diretmidae (species 9) and Berycidae (species 10-11) share 23 derived states, none of which is unique to them. Diretmus also shares 23 states with the Anomalopidae. In addition to the fact that anomalopids appear to be related to monocentrids and trachichthyids, all three of the criteria (1,2,4) which were applicable in this case favored the combination Diretmus/Berycidae. Consideration of additional morphological evidence (criterion 4) was particularly convincing. This evidence is as follows:

(1) presence of a large, triangular-shaped supraoccipital crest
(2) first proximal radial of the anal fin expanded distally
(3) absence of the sixth hypural in the caudal skeleton.

Other similarities between Diretmus and the Berycidae which have been noted by previous investigators include:

(4) presence of an obliquely striated pelvic fin spine (Regan, 1911, p. 5)
(5) presence of expanded coracoids (Regan, 1911, p. 5)
(6) similar morphology of the otoliths (sagittae) (Lamber, 1963, p. 47 and p. 73)
(7) presence of small, bell- or shield-shaped scales (Woods and Sonoda, 1973, p. 281 and p. 290).

The relationship between the Diretmidae + Berycidae (species 9-11) and the Holocentridae (species 12-16), as well as the relationship between both of these groups and the Monocentridae + Trachichthyidae + Anomalopidae (species 1-8), is highly questionable. In neither case are the derived character states unique to the groups--in fact, they are all widely distributed among other groups [e.g., state 26 (toothless endopterygoid) of the group Diretmidae + Berycidae + Holocentridae occurs in all of the other species in the dendrogram except Cleidopus gloriae-maris and Polymixia lowei].

The relationship between Polymixia (species 17) and the Monocentridae + Trachichthyidae + Anomalopidae + Diretmidae + Berycidae + Holocentridae (species 1-16) is also questionable, even though there are two derived states (55 - absence of supraneurals; 76 - presence of two predorsals) which are unique to the entire assemblage. Consideration of other characters (below) indicates that Polymixia is not closely related to other beryciforms.

The relationship between Gibberichthys (species 18) of the Family Gibberichthyidae and Stephanoberyx (species 19) of the Family Stephanoberycidae is based on sound evidence. Gibberichthys and Stephanoberyx possess two derived character states which are not present in other beryciforms. One of these involves the morphology of the extrascapular bone of the pectoral girdle (state 56). In both of these forms, the extrascapular is expanded into a large, plate-like element which covers the entire dorsal aspects of the epiotic and parietal, as well as most of the supraoccipital. The second feature concerns the pattern of the crests on the frontal bones. These crests are arranged in a —< pattern. In addition to short anteromedial and anterolateral crests, there is a longitudinal crest which runs posteriorly to meet a crest on the extrascapular. As in many other beryciforms, the frontal crests in Gibberichthys and Stephanoberyx separate deep

mucous cavities.

Another interesting feature of Gibberichthys and Stephanoberyx is the presence of only three infraorbitals. All other beryciforms possess four infraorbitals. The size, relationships, and presence of a fissure on the ventral border of one of the elements indicate that the reduced number of infraorbitals in Gibberichthys and Stephanoberyx is the result of fusion. However, in Gibberichthys the fusion is between the first and second infraorbitals, while in Stephanoberyx it is between the second and third infraorbitals.

Gibberichthys and Stephanoberyx (species 18-19) share 19 derived states with both the Melamphaeidae (species 20-25) and Anoplogaster (species 26). Two of the three criteria (2,3,4) which were applicable indicated that Gibberichthys and Stephanoberyx are more closely related to the Melamphaeidae than to Anoplogaster. The absence of an orbitosphenoid (state 13) in Gibberichthys, Stephanoberyx and melamphaeids, and the absence of pelvic fin radials (state 73) in Gibberichthys, Stephanoberyx and Anoplogaster, are derived character states which are unique to these groups (selection of a combination on the basis of these two character states was therefore not possible). However, the absence of palatine teeth (state 28) and the absence of a canal in the supracleithrum (state 57) are derived character states which are present in Gibberichthys, Stephanoberyx and melamphaeids, but which occur only rarely in other beryciforms. These character states were therefore assigned high weight (criterion 3). Additional morphological evidence (criterion 4) also suggests a relationship between Gibberichthys, Stephanoberyx and melamphaeids. This evidence is summarized below:

(1) presence of a postmaxillary process on the premaxilla [the postmaxillary process is in the form of a gently convex flange which arises from the entire length (or most of the length) of the alveolar process]

(2) absence of a subocular shelf [although the absence of a subocular shelf may be primitive for beryciforms, it is possible that it has been secondarily lost in Gibberichthys, Stephanoberyx and melamphaeids as a result of their adaptation to the deep-sea environment (Ebeling and Weed, 1973, p. 398)]

(3) supramaxilla reduced or absent (Ebeling and Weed, 1973, p. 398).

The families Gibberichthyidae, Stephanoberycidae and Melamphaeidae are sometimes collectively referred to as the Stephanoberyciformes.

Anoplogaster (species 26) is the only member of the Family Anoplogasteridae. It is a highly specialized form and its phylogenetic affinities have been disputed. A number of previous investigators [Regan (1911), Jordan (1923), Norman (unpublished manuscript), Lamber (1963), Rosen (1973)] have placed Anoplogaster in a group with some (or all) of the stephanoberyciform families. In some instances [Regan (1911), Jordan (1923), Lamber (1963)], the group so formed was considered to constitute a distinct order, separate from the more typical beryciform families (Order Beryciformes). Although the relationships shown in dendrogram #1 support these views, careful consideration of the evidence suggests that they may be incorrect. Thus, none of the 14 derived states which Anoplogaster shares with the stephanoberyciforms is unique to them. As with some of the other groups discussed above, most of these states are widely distributed among other taxa. An exception is character state 18 (two external openings in the pars jugularis). This state occurs elsewhere only in the Monocentridae. However, since such closely related forms as Photoblepharon and Anomalops differ in the number

of openings which are present in the pars jugularis, the significance of this character is questionable. It should also be noted that some of the resemblances between Anoplogaster and stephanoberyciforms may simply represent parallel adaptations to the deep-sea environment (Ebeling and Weed, 1973, p. 400).

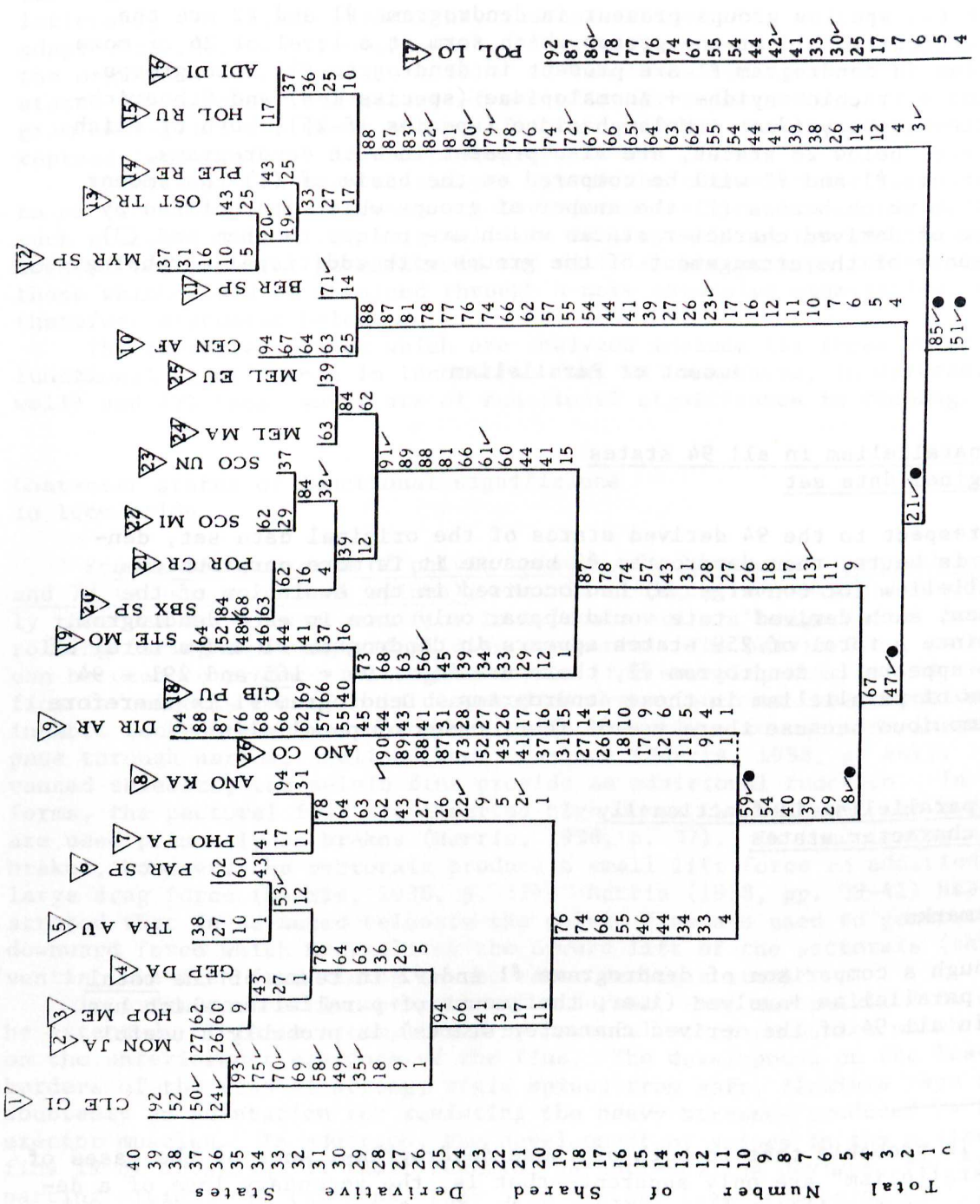
Consideration of additional morphological data indicates that Anoplogaster is most closely related to certain non-stephanoberyciform families. This evidence will be discussed below.

Dendrogram #2

Figure 5 is another dendrogram (#2) showing the phylogenetic relationships among the Beryciformes. The reason for presenting it as an alternative to dendrogram #1 is that in certain respects it is a better representation of the phylogenetic relationships of the 26 species examined. Dendrogram #2 is not one of the 10 different dendrograms which can be constructed by following the procedures described above. Rather, dendrogram #2 was constructed on the belief that by rearranging certain groups in dendrogram #1, a phylogeny could be produced in which 1) more of the groups would be defined by the presence of unique, derived character states (even though such a rearrangement might be less parsimonious in terms of the amount of parallelism required) and 2) the new arrangement of groups would be more consistent with certain additional morphological characters (i.e., characters not included in the original data set).[1] There were two reasons why these additional characters were not included in the original data set: 1) the Combinatorial Method cannot always handle extremely large data sets and 2) in some cases it was not possible to construct complete character state trees as required by the Combinatorial Method. For example, the presence/absence of maxillary teeth is a character that was not included in the original data set so as to keep it within a reasonable size. The pattern of ornamentation on the frontal bones, in contrast, is an example of a character that was not included in the original data set for the second reason stated above. In this character it was not possible to determine the sequence of change between some of the derived states. Nevertheless, it was felt that this character contained a significant amount of phylogenetic information (since distinct patterns of frontal ornamentation were found to characterize many groups of species) and that it should therefore be used as much as possible to determine relationships.

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[1]Although dendrogram #2 is based on a consideration of characters in addition to those of the original data set, only the 94 derived states of the original data set are represented in order to facilitate comparison with dendrogram #1. Since a list of derived states is given for each OTU or combination of OTUs in the computer report, it was an easy task to identify the groups of dendrogram #2 in the report and then go back and "fill in" the character states possessed by each of them. A check (✓) beside a character state in dendrogram #2 indicates that it is unique to a particular lineage. The word unique as used here and in the remaining discussion pertaining to dendrogram #2 applies only to the 26 species which appear in the dendrogram.



A dot (•) beside a checked (✓) state indicates that the state is not unique to any group in dendrogram #1.

Fig. 5.--Dendrogram #2. For full names of species denoted by numbers 1-26, see table 7.

Comparison of Dendrogram #1 and Dendrogram #2

General Remarks

Many of the species groups present in dendrograms #1 and #2 are the same. In particular, all of the groups which form at a level of 26 or more derived states in dendrogram #1 are present in dendrogram #2. The groups Monocentridae + Trachichthyidae + Anomalopidae (species 1-8) and Gibberichthyidae + Stephanoberycidae + Melamphaeidae (species 18-25), both of which form at a level below 26 states, are also present in both dendrograms.

Dendrograms #1 and #2 will be compared on the basis of (1) the amount of parallelism which occurs (2) the number of groups which are defined by the presence of derived character states which are unique to them and (3) the consistency of the arrangement of the groups with additional morphological data.

Amount of Parallelism

Amount of parallelism in all 94 states of the original data set

With respect to the 94 derived states of the original data set, dendrogram #1 is better than dendrogram #2 because it is more parsimonious. If no parallelism (or convergence) had occurred in the evolution of the Beryciformes, each derived state would appear only once in each dendrogram. However, since a total of 259 states appears in dendrogram #1 and a total of 291 states appears in dendrogram #2, there are 259 - 94 = 165 and 291 - 94 = 197 cases of parallelism in these dendrograms. Dendrogram #1 is therefore more parsimonious because there are 32 fewer cases of parallelism.[1]

Amount of parallelism in functionally important character states

General remarks

Although a comparison of dendrograms #1 and #2 in terms of the total amount of parallelism involved (i.e., the amount of parallelism which has occurred in all 94 of the derived character states) is probably a useful

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[1] It is probable that in both of these dendrograms, some of the cases of "parallelism" are only apparent--that is, the secondary loss of a derived state (reversal) in one or more species has led to the appearance that parallelism has occurred. Two examples in which it seems probable that reversal rather than parallelism has occurred are discussed on the following pages.

means for assessing the degree to which they represent the true phylogenetic relationships of the species, perhaps a more meaningful approach is to determine the amount of parallelism which has occurred in character states that are of obvious functional significance. Functionally important character states might be considered to be better indicators of phylogenetic relationship than others, since they indicate the ways in which organisms are adapted to their environment--i.e., they reflect more of the biology of the organisms (see Bigelow, 1958). If functionally important character states are stronger indicators of evolutionary relationship, then the dendrogram exhibiting the least amount of parallelism in these states is the best representation of the actual phylogeny.

No attempt was made to analyze all of the character states believed to be of functional significance. However, the results obtained by analyzing 15 such states (13 from the original data set, as well as two additional states, loss of teeth on the parasphenoid and maxilla) are perhaps indicative of those which would be obtained through a more extensive examination, and are therefore discussed below.

The character states which are analyzed include (1) those which are of functional significance in locomotion (and in some cases, in defense, as well) and (2) those which are of functional significance in feeding.

Character states of functional significance in locomotion

States 66 (presence of pelvic spines), 74 (presence of dorsal spines) and 78 (presence of anal spines).--Harris (1938, p. 43) has shown experimentally that the dorsal and anal fins in teleosts act as "bilge keels" to prevent rolling during swimming and gliding movements. The pelvic fins, in contrast, can be used to produce rolling movements [for example, this use of the pelvic fins is commonly met with in deep-bodied forms, such as chaetodontids, which inhabit rocky areas, and which must tilt themselves to one side in order to pass through narrow, inclined rock crevices (Harris, 1938, p. 44)]. In advanced teleosts, the pelvic fins provide an additional function. In these forms, the pectoral fins are inserted high up on the sides of the body and are used primarily as brakes (Harris, 1938, p. 37). In functioning as brakes, however, the pectorals produce a small lift force in addition to the large drag force (Harris, 1938, p. 37). Harris (1938, pp. 39-41) has demonstrated that in advanced teleosts the pelvic fins are used to generate a downward force which neutralizes the upward lift of the pectorals (thus preventing the fish from rising in the water during a stop).

In order to function properly, the dorsal, anal and pelvic fins must be extended. This is accomplished by powerful erector muscles which insert on the anteriormost elements of the fins. The development on the leading borders of the fins of strong, rigid spines from soft, flexible rays is undoubtedly an adaptation for resisting the heavy stresses produced by the erector muscles. In addition, the development of spines in the median fins is of advantage in their function as anti-rolling devices, for by imparting rigidity to the fins, they help prevent them from being distorted by lateral pressure of the water; this is perhaps especially important when the fish is turning (Patterson, 1964, p. 454).

Although the fins in fishes are primarily concerned with locomotion, they serve other purposes as well. One that is common to many advanced teleosts is to provide a measure of defense in the form of strong, sharp, strategically located fin spines (Gosline, 1971, p. 43). Gosline (1971, p. 44) notes that in terms of defensive effectiveness, there seem to be three main requirements of fin spines:

> First, they must be strong and firm . . . Second, they must be so placed that they expand the perimeter of the fish to the maximum possible extent. Whether one fish will fit into another fish's mouth depends upon its maximum diameter, and fin spines that add to that diameter may make the difference between fitting and not fitting. [For example], if the fish is deep bodied, then spines protruding beyond the top and bottom surfaces at the point of maximum depth will be most effective . . . The third requirement of fin spines for defensive efficiency is that they be firmly based. A firm spine on a flabby base would be of little use.

With respect to the third requirement mentioned by Gosline, the need for a firm basal articulation, it may be noted that both the development of large, well-ossified proximal radials and the loss of middle and distal radials in the spine-bearing pterygiophores of the median fins are of adaptive value (Patterson, 1964, p. 457).

The fin spines of beryciforms generally fulfill these three requirements. Some of the more striking examples include the presence of exceedingly strong spines in the dorsal and pelvic fins of the Monocentridae, the strategic location of the spines in deep-bodied forms such as the Berycidae, Monocentridae and most Trachichthyidae, and the fusion of the dorsal and anal spines with the underlying radials in the Gibberichthyidae. The peculiar structure of the dorsal fin in the Monocentridae (with the spines alternately inclined to the right and left), and the presence of numerous dorsal spines in the Holocentridae (more numerous than the mechanical function would require; see Patterson, 1964, p. 457) also indicate that fin spines in beryciforms may play an important role in defense.

Comparison of dendrograms #1 and #2 reveals that state 74 (presence of dorsal spines) appears five times in each. This means that there are four cases of parallelism in each dendrogram (the appearance of a character state x times in a dendrogram denotes $x - 1$ cases of parallelism). Similarly, state 78 (presence of anal spines) appears an equal number of times (six) in the two dendrograms. Thus, neither dendrogram is more parsimonious in terms of the amount of parallelism involved in these two functionally important character states.

It is possible that the absence of dorsal and anal spines in Diretmus (species 9) and Anoplogaster (species 26), as well as the absence of anal spines in Cleidopus (species 1) and Monocentris (species 2), represent secondary losses (and not primitive conditions) (note: all other beryciforms possess dorsal and anal spines). Reversal in these two characters does not seem improbable. For example, Patterson (1964, p. 443) has presented evidence that in the Cretaceous beryciform Aipichthys, fin spines developed from segmented but unbranched lepidotrichia, either by loss of the segments during ontogeny or by fusion of the segments with the basal segment. A simple failure to lose segments or to fuse segments during ontogeny could therefore result in a secondary condition.

With respect to the defensive role of fin spines, it is perhaps worth noting that in Cleidopus and Monocentris, the absence of anal spines may be of little or no consequence. The enormous pelvic spines in these forms may provide adequate protection to the abdominal area. Thus, a possible explanation for the secondary loss of anal spines in monocentrids is that the great increase in the size of the pelvic spines rendered the anal spines superfluous. However, this explanation is not entirely satisfactory, for although it accounts for the secondary loss of the anal spines, it raises the problem of the reason for the increase in the size of the pelvic spines. Furthermore, other evolutionary pathways leading to the presence of large pelvic spines and the absence of anal spines could have occurred (however, in each case, a problem arises which is similar to or identical with that noted above).

Finally, it should be noted that Diretmus, Anoplogaster, Cleidopus and Monocentris are all highly specialized forms (in terms of their overall morphology). From this standpoint, it does not seem unlikely that the absence of dorsal and/or anal spines in these fishes represents a specialized condition.

Dendrograms #1 and #2 both become more parsimonious if it is assumed that reversal, rather than parallelism, has occurred in character states 74 (presence of dorsal spines) and 78 (presence of anal spines). Thus, dendrograms #1 and #2 each require only two cases of reversal in state 74 (as opposed to four cases of parallelism), and only three cases of reversal in state 78 (as opposed to five cases of parallelism). However, since the amount of reversal (like the amount of parallelism) is the same for both character states in both dendrograms, neither dendrogram emerges as more probable.

Character state 66 (presence of pelvic spines) appears less frequently in dendrogram #1 (four times) than in dendrogram #2 (six times). Thus, dendrogram #1 is more parsimonious in terms of parallelism than dendrogram #2. If it is assumed that in those forms in which pelvic spines are absent [Photoblepharon (species 7), Anomalops (species 8), Polymixia (species 17), Stephanoberyx (species 19) and Anoplogaster (species 26)] the conditions arose secondarily, then neither dendrogram is more parsimonious (four cases of reversal in each). However, in view of the absence of any positive evidence for reversal in these forms, it may be assumed that parallel development of pelvic spines has occurred.

States 47 (fusion of first neural arch) and 51 (absence of epineural ribs).--The vertebral column in teleosts must be flexible enough to permit lateral bending [especially in forms with anguilliform locomotion (Gosline, 1971, p. 19)], but must also be strong enough to resist powerful stresses. Increase in ossification and fusion of vertebral elements (such as fusion of the neural and hemal arches with the centra), as well as development of strong zygapophyses, provide several means by which the vertebral column is capable of resisting these stresses (Patterson, 1964, p. 453). Furthermore, the loss of epineural ribs which occurs in acanthopterygians seems to be a corollary of the increased strength of the vertebral column (Patterson, 1964, p. 453). That is, as the vertebrae become more heavily ossified, and offer more extensive sites for muscle insertion, supplementary sites such as epineural ribs should no longer be necessary (Patterson, 1964, p. 454).

In general, the structure of the axial skeleton in the beryciforms

examined lends support to Patterson's statements. Thus, in Polymixia there is a well-developed series of epineural ribs (present on all of the abdominal and the first seven caudal vertebrae), and the neural arch of the first vertebra is not coossified with the centrum. In all other Recent beryciforms, epineural ribs are absent, and in all except the Holocentridae and Berycidae, the first neural arch is fused to the centrum. It also seems possible that the absence of epineural ribs in non-polymixiid beryciforms reflects more subtle improvements in terms of the strength of the vertebral column.

Character states 47 (fusion of first neural arch) and 51 (absence of epineural ribs) both appear only once in dendrogram #2 (i.e., no parallelism occurs). In dendrogram #1, however, state 47 appears three times (two cases of parallelism) while state 51 appears twice (one case of parallelism). Both character states therefore favor dendrogram #2 over dendrogram #1.

Character states of functional significance in feeding

States 9 (absence of vomerine teeth), 26 (absence of endopterygoid teeth), 27 (absence of ectopterygoid teeth), 28 (absence of palatine teeth), 29 (distal portion of maxilla reduced), 39 (absence of basihyal teeth), 40 (absence of basihyal), 43 (absence of basibranchial teeth), and others.--According to Patterson (1964, pp. 456-459), there is a trend in acanthopterygians toward reduction of the buccal dentition (loss of teeth on the parasphenoid, basibranchials, endopterygoid and ectopterygoid) and increase in the pharyngeal dentition (produced by modification of the gill rakers on the posterior branchial arches into flat tooth plates, and by increase in the size and dentition of the upper and lower pharyngeals). With respect to reduction of the buccal dentition, it should be noted that in various beryciforms teeth have also been lost on the vomer, palatine and basihyal [note: although basihyal and basibranchial teeth are supported by (or fused to) elements of the pharyngeal skeleton, they may be considered to function as buccal teeth, since they oppose the vomerine and parasphenoid teeth, resp.]. Finally, in some beryciforms the basihyal itself has been lost.

The acanthopterygian type of dentition described above seems to be well-adapted for feeding by means of protractile jaws (the presence of protractile jaws is a characteristic feature of acanthopterygians). Thus, Patterson (1964, pp. 456-457) states:

> A protrusile mouth functions as a pipette. The sudden protrusion of the mouth both brings it nearer to the prey and increases the volume of the buccal cavity. The result of this increase in volume is that the water immediately in front of the mouth, together with any contained prey, is sucked in. The size of the prey which can be taken by this method obviously depends on the size of the mouth, but the prey must always be rather small in comparison with the size of the predator. The development of a protrusile mouth thus fits in with the type of feeding

deduced from the dentition. Prey taken by a protrusile mouth would tend to be gulped straight into the pharynx, where the main dentition of acanthopterygians is concentrated.

Certain other features such as loss of maxillary teeth and reduction in the distal portion of the maxilla also seem to be adaptations for feeding with protractile jaws (see discussion below).

In many primitive teleosts [e.g., Elops (Forey, 1973b, p. 19), Salvelinus (Norden, 1961, p. 779), Salmo (Gregory, 1933, p. 152) and Chirocentrus (Gregory, 1933, p. 142)] both the premaxilla and maxilla are toothed, the latter bone forming most of the oral margin of the upper jaw. In typical acanthopterygians, however, it is the premaxilla which is the dominant element of the upper jaw. This has occurred through the development of ascending and articular processes on the premaxilla, and by an increase in the length of its alveolar (tooth-bearing) process. The increase in the length of the alveolar process of the premaxilla during the transition from the primitive teleostean to the acanthopterygian condition required certain changes in the morphology of the maxilla. That is, in order for the alveolar process to grow back beneath the maxilla, it was necessary for the distal portion of the maxilla, along with its dentition, to become reduced.

Although Gregory (1933, p. 242) noted that an increase in the length of the alveolar process of the premaxilla was one of the stages involved in the evolution of protractile jaws, he did not discuss the functional importance of this development in the actual mechanics of jaw protrusion. A consideration of the mechanism of jaw protrusion in fishes such as those of the acanthopterygian family Nandidae, however, provides a possible explanation of the functional significance of the presence of an elongate alveolar process.

K. Liem (1970), through a series of elegant experiments, has shown that jaw protrusion in the Nandidae is a function of depression of the mandible. Thus, lowering of the mandible produces tension in the medial and anterior maxillomandibular ligaments, which pull the distal ends of the premaxillae forward and slightly downward (note: the medial and anterior maxillomandibular ligaments connect the distal ends of the premaxilla and maxilla to the ascending process of the dentary) (K. Liem, 1970, pp. 111-112). In order to obtain maximum speed and efficiency in the transformation of the movement of the mandible to the upper jaw, the medial and anterior maxillomandibular ligaments should be as short as possible (the greater the lengths of the ligaments, the greater the slack) (K. Liem, 1970, p. 113). Thus, any modifications which result in a shortening of the distance between the points of attachment of these ligaments will be of considerable functional advantage. K. Liem (1970, p. 113) suggests that an increase in the height of the ascending process of the dentary represents one such modification. It should be noted, however, that an increase in the length of the alveolar process of the premaxilla would produce the same result.

In summary, the evolution of a highly adapted mechanism for feeding by means of protractile jaws has involved not only reduction of the buccal and increase in the pharyngeal dentition, but also loss of maxillary teeth and reduction in the distal portion of the maxilla, both of which allowed the alveolar process of the premaxilla to increase in length.

Although many beryciforms probably feed by rapidly protruding the jaws and sucking prey directly into the pharynx, generalizations concerning feeding habits should be regarded with some caution. It seems quite clear, for example, that the large, firmly set, fang-like teeth in the upper and lower jaws

of Anoplogaster are used to seize and kill prey before it is passed into the pharynx. Nevertheless, the buccal dentition of Anoplogaster is strongly reduced, the pharyngeal dentition is quite formidable, and the distal portion of the maxilla has lost its teeth and is no longer expanded behind the alveolar process of the premaxilla (which is extremely long)--all features which are of adaptive significance for feeding with protractile jaws (above). The question thus arises as to whether any of the features noted above are also of functional importance in the type of feeding mechanism utilized by forms such as Anoplogaster.

It is probable that at least two of the features, loss of maxillary teeth and reduction of the distal portion of the maxilla, represent modifications which are essential for the development of a highly efficient feeding mechanism in which prey is initially grasped between the jaws. Recall that in primitive teleosts, the teeth of the upper jaw are borne by two bones, the premaxilla and maxilla. This condition is functionally less efficient than the one in which only a single element bears teeth, for the strength of the bite is weaker (providing that all other factors, such as mass of the adductor mandibulae muscle, its point of insertion on the lower jaw relative to the quadrate-mandibular articulation, etc., are equal). However, unless the mouth decreases in size during the evolution of a lineage from an ancestor exhibiting the primitive upper jaw pattern, loss of maxillary teeth is only one step toward the most efficient functional system (loss of maxillary teeth without a concomitant decrease in mouth size would result in an upper jaw in which only a portion of the biting margin bears teeth). It is also necessary for the alveolar or tooth-bearing process of the premaxilla to grow back beneath the maxilla in order to compensate for the loss of the maxillary dentition. As noted above, such an increase in the length of the alveolar process must be preceded not only by the loss of maxillary teeth, but also by a reduction of the distal portion of the maxilla.

Reduction of the buccal dentition would appear to be disadvantageous to fishes in which the prey is initially seized with the jaws. The buccal dentition would assist that of the jaws in the killing and the prevention of escape of prey. In Anoplogaster, however, the strong reduction of the buccal dentition (teeth are absent on the vomer, endopterygoid, ectopterygoid, basihyal and basibranchials, and are only rudimentarily developed on the palatine) may be explained in terms of the hypertrophy of the marginal dentition--that is, the development of large, fang-like teeth on the premaxilla and dentary probably rendered the buccal dentition unnecessary.

A comparison of dendrograms #1 and #2 with respect to the amount of parallelism involved in those character states which are of functional significance in feeding will now be made. State 28 (absence of teeth on the palatine) is of no value in choosing between the dendrograms because it appears an equal number of times (twice) in both. Similarly, absence of teeth on the parasphenoid is a derived character state which does not favor either dendrogram because it occurs in all 26 of the species examined (see footnote on p. 161). It is for this reason that the character, presence/absence of parasphenoid teeth, was omitted from the original data set (see p. 146). If the absence of parasphenoid teeth was to be represented as a derived state in the two dendrograms, it would, of course, be necessary to include it only once in each (i.e., in a lineage leading to all 26 of the species). Character states 9, 26, 27 and 43 (absence of teeth on the vomer, endopterygoid, ectopterygoid and basibranchials, resp.) appear less frequently in dendrogram #1 than in dendrogram #2 (five vs. six, five vs. eight, seven vs. nine and seven vs. eight, resp.).

However, this advantage is offset by the fact that character states 29 (distal portion of maxilla reduced), 39 (absence of teeth on the basihyal) and 40 (absence of basihyal) appear less frequently in dendrogram #2 than in dendrogram #1 (three vs. five, one vs. two[1] and two vs. four, resp.). Furthermore, the presence or absence of teeth on the maxilla is a character which, although not included in the original data set, also favors dendrogram #2. Myripristis (species 12) is the only form in the dendrograms which retains the primitive state of this character (presence of teeth). Thus, if the derived state of this character was represented in the dendrograms, it would appear only five times in dendrogram #2 as compared to seven times in dendrogram #1.

In conclusion, comparison of dendrograms #1 and #2 with respect to the amount of parallelism involved in those character states which are of functional significance in feeding [i.e., states 9, 26, 27, 28, 29, 39, 40 and 43, as well as the two states which were not included in the original data set (absence of teeth on the parasphenoid and maxilla)] reveals that neither dendrogram is more parsimonious. Thus, if all 10 of the character states listed above are considered together, it is found that they appear a total of 45 times in each dendrogram.

Amount of parallelism in functionally important character states--summary

The discussions above have shown that the 15 functionally important character states which were selected for analysis fall into three categories: (1) those which appear less frequently (exhibit less parallelism) in dendrogram #1 (states 9, 26, 27, 43, 66) (2) those which appear less frequently in dendrogram #2 (states 29, 39, 40, 47, 51, absence of teeth on the maxilla) and (3) those which appear an equal number of times in the two dendrograms (states 28, 74, 78, absence of teeth on the parasphenoid).

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[1]Inspection of the two dendrograms reveals that state 39 appears five times in dendrogram #1 and six times in dendrogram #2. However, it is probable (for the reasons discussed below) that this is a misrepresentation of the actual situation.

Due to damage of the visceral skeleton in the specimen of Melamphaes macrocephalus (species 24) which was examined, it was not possible to determine which state of character 31 (basihyal) is present in this species. However, since all of the other species (20-23, 25) of the Melamphaeidae which were examined (including the congeneric M. eulepis) have a toothless basihyal (state 39), it is highly probable that the same state occurs in M. macrocephalus. The presence of a toothed basihyal in M. macrocephalus also seems unlikely in view of the fact that, as in the other melamphaeids examined, the basibranchials and the palatal bones are completely toothless. Thus, if it is assumed that a toothless basihyal is present in M. macrocephalus, state 39 would appear only once in dendrogram #2 [in the lineage leading to the common ancestor of all of the species except Polymixia (species 17)], but would appear twice in dendrogram #1 (in the lineage leading to species 1-16, and in that leading to species 18-26).

The net result of comparing the two dendrograms with respect to all 15 of these character states is that dendrogram #2 is slightly more parsimonious (in dendrogram #2 these 15 states appear a total of 64 times, as compared to 65 appearances in dendrogram #1). This result contrasts with that obtained when the amount of parallelism in all 94 states of the original data set is taken into consideration (i.e., when no attempt is made to evaluate the functional significance of the character states). It must be emphasized, however, that only 13 functionally important character states from the original data set have been analyzed. It is possible that a more extensive analysis would produce a different result.

Number of Groups Defined by the Presence of Unique, Derived States

As noted earlier in the discussion, the strongest evidence that a group is monophyletic is the presence in all of its species of derived character states which do not occur in any species outside that group. In this respect, dendrogram #2 is clearly superior to dendrogram #1. Thus, only two of the groups which form at a level of less than 26 states in dendrogram #1 are defined by the presence of unique, derived states, as compared to five groups in dendrogram #2 (recall that all of the groups which form at a level of 26 or more states are present in both dendrograms). The two groups in dendrogram #1 referred to above are (1) the group Gibberichthyidae + Stephanoberycidae + Melamphaeidae (species 18-25), which forms at a level of 19 states, only one of which is unique to it (13 - absence of orbitosphenoid) and (2) the group Monocentridae + Trachichthyidae + Anomalopidae + Diretmidae + Berycidae + Holocentridae + Polymixiidae (species 1-17), which forms at a level of five states, two of which are unique to it (55 - absence of supraneurals, 76 - presence of two predorsals). The five groups in dendrogram #2 referred to above are (1) the group Gibberichthyidae + Stephanoberycidae + Melamphaeidae (group #1 above) (recall that this is one of the two groups which forms at a level of less than 26 states and which is present in both dendrograms) (2) the group Monocentridae + Trachichthyidae + Anomalopidae + Anoplogasteridae + Diretmidae (species 1-9, 26), which forms at a level of 11 states, two of which are unique to it (8 - small mesethmoid, 59 - one postcleithrum) (3) the group Monocentridae + Trachichthyidae + Anomalopidae + Anoplogasteridae + Diretmidae + Gibberichthyidae + Stephanoberycidae + Melamphaeidae (species 1-9, 18-26), which forms at a level of five states, one of which is unique to it (47 - fusion of neural arch of first vertebra) (4) the group Monocentridae + Trachichthyidae + Anomalopidae + Anoplogasteridae + Diretmidae + Gibberichthyidae + Stephanoberycidae + Melamphaeidae + Berycidae (species 1-11, 18-26), which forms at a level of three states, one of which is unique to it (21 - absence of antorbital) and (5) the group Monocentridae + Trachichthyidae + Anomalopidae + Anoplogasteridae + Diretmidae + Gibberichthyidae + Stephanoberycidae + Melamphaeidae + Berycidae + Holocentridae (species 1-16, 18-26), which forms at a level of two states, both of which are unique to it (51 - absence of epineural ribs, 85 - neural spine of PU2 crest-like[1]).

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[1]State 39 (absence of basihyal teeth) is probably also unique to this group (see fn. 1, p. 199).

Consistency of the Arrangement of the Groups with Additional Morphological Data

Certain characters other than those of the original data set support the arrangement of the groups shown in dendrogram #2. One example concerns the relationship of Anoplogaster. In dendrogram #2, Anoplogaster (species 26) and Diretmus (species 9) share the same number of states with monocentrids, trachichthyids and anomalopids (species 1-8). Consideration of an additional character, the pattern of the frontal crests, indicates that Anoplogaster is more closely related to these groups than Diretmus. The pattern of the frontal crests in Anoplogaster, monocentrids, trachichthyids and anomalopids is ⋊ -like. This pattern is not present in any of the other species examined. The relationship between Anoplogaster and the stephanoberyciforms shown in dendrogram #1 implies that the detailed pattern of the frontal crests in Anoplogaster and in monocentrids, trachichthyids and anomalopids has evolved independently.[1]

Another example which shows that the arrangement of the groups in dendrogram #2 is more consistent with additional morphological data concerns the relationship of Polymixia (species 17). In spite of its peculiar specializations (p. 184), Polymixia is unquestionably the most primitive of the species examined (it possesses only 21 of the 94 derived character states). Additional character states also indicate that Polymixia is more primitive than any of the other species. These character states are listed below:

(1) absence of ornamentation (crests and ridges) and mucous cavities on the frontal bones
(2) presence of a large (elongate) tooth plate over the basibranchials, and an extensive dentition on the vomer (the basibranchial dentition in Polymixia is very similar to that present in the primitive teleost Elops; see Nelson, 1969a, p. 494, fig. 6)
(3) large size of the second ural centrum (U2).

All of these features, in addition to the fact that Polymixia is the only form which retains epineural ribs and a basihyal tooth plate (see footnote 1, p. 199) indicate that Polymixia should be removed from the Order

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[1] A number of other investigators, including Woods and Sonoda (1973), have also suggested that the closest relatives of Anoplogaster are to be found among the non-stephanoberyciform fishes. However, some of the evidence presented by Woods and Sonoda (1973, p. 387) for grouping Anoplogaster with non-stephanoberyciforms deserves comment. Three of the features which are listed as being common to Anoplogaster and "typical berycoids" (but not stephanoberyciforms) are the presence of an orbitosphenoid, the number of caudal rays, and the presence of procurrent spines. Since the presence of an orbitosphenoid is a primitive character state, it is not useful for determining phylogenetic relationships. The number of caudal rays in all beryciforms (including stephanoberyciforms) except Cleidopus and Polymixia is 19 (this is also a primitive character state). The only derived character state is the presence of procurrent spines, but it too occurs in all beryciforms.

Beryciformes.[1] Retention of Polymixia in the Order Beryciformes would result in the persistence of a non-monophyletic group. However, for the reason discussed below, removal of Polymixia from the Order Beryciformes does not ensure that the remaining group of species (1-16, 18-26) is monophyletic.

The derived character states which are present in species 1-16 and 18-26 include not only the six discussed above (presence of ornamentation on the frontal bones, reduction in the extent of the dentition on the vomer and basibranchials, reduction in the size of U2, absence of epineural ribs, absence of a basihyal tooth plate, and presence of a low neural crest on PU2), but all 20 of the states listed in table 3 (pp. 168-169). The total number of derived character states shared by species 1-16 and 18-26 is therefore quite impressive. However, it must be emphasized that since none of these character states is unique to species 1-16 and 18-26 if other teleosts are taken into consideration [for example, most (if not all) of these states occur in various members of the Suborder Percoidei (Order Perciformes)], the monophyly of this group is open to question.

Comparison of dendrograms #1 and #2 in terms of their consistency with certain characters which were discussed by Rosen (1973) in his treatment of beryciform relationships, but which were not analyzed in this investigation, may also be made. Rosen's study of the Beryciformes led him to conclude that it is possible to recognize within this group a trachichthyoid assemblage (including the families Trachichthyidae, Anomalopidae, Monocentridae, Diretmidae and probably the Paradiretmidae, Korsogasteridae and Sorosichthyidae) and a stephanoberycoid assemblage (including the families Barbourisiidae, Rondeletiidae, Gibberichthyidae, Melamphaeidae, Stephanoberycidae, Anoplogasteridae, Cetomimidae, Mirapinnidae, Eutaeniophoridae and Megalomycteridae--the last four families are collectively termed cetomimoids) (Rosen, 1973, p. 505). Although representatives of a number of the families noted above were not examined in this investigation, some of the evidence provided by Rosen regarding their relationships is useful in evaluating the relative merits of dendrograms #1 and #2.

If Rosen's (1973) suggestion of a relationship between Rondeletia (Family Rondeletiidae) and Gibberichthys is correct, the evidence supporting this relationship does not favor either dendrogram. Rosen (1973, p. 492) noted three features shared by Rondeletia and Gibberichthys which suggest that they are related: 1) in both genera there is a wide band of papillate lateral line organs in the dermis 2) their jaw musculature is highly distinctive and of a complex A_1 type and 3) the pharyngobranchial apparatus in both is characterized by having a toothless second pharyngobranchial lying along the dorsolateral surface of the third pharyngobranchial. Rondeletia was not examined in this investigation but the close relationship between Gibberichthys (species

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[1]One of the characters of the caudal skeleton (63 - length of the neural spine of PU2) also indicates that Polymixia is not closely related to the other species examined. The primitive state of this character is the one in which the neural spine of PU2 is one-half the length of that of PU3. All of the species except Polymixia have become specialized from this condition by reducing the neural spine of PU2 to a low crest ($\leq$ one-third the length of the spine of PU3). Polymixia, although not retaining the primitive state of this character, has become specialized in the opposite direction--the neural spine of PU2 is complete (= in length to the spine of PU3).

18) and Stephanoberyx (species 19), shown in both dendrograms #1 and #2, is considered to be based on sound evidence (see pp. 188-189). It should be noted that the third feature listed above is inconclusive in terms of deciding whether Gibberichthys is more closely related to Rondeletia than to Stephanoberyx, because Rosen (1973, p. 496) stated that Stephanoberyx also possesses a toothless second pharyngobranchial which is closely aligned with the dorsolateral edge of the third pharyngobranchial. The significance of the first feature noted above is somewhat questionable since many deep-sea fishes have papillate lateral lines (Ebeling and Weed, 1973, p. 398). The similar jaw musculature of Gibberichthys and Rondeletia therefore appears to be the only strong evidence for a relationship between them. Such a relationship would require independent development of the pattern of frontal crests and the peculiar morphology of the extrascapular bone in Gibberichthys and Stephanoberyx, for these features are not seen in Rondeletia [Parr (1929, p. 40, fig. 16) and Paxton (personal communication) indicate the absence of a ——< pattern of frontal crests in Rondeletia bicolor and R. loricata (resp.), and Paxton (1974, p. 185, fig. 5) shows the extrascapular of R. loricata to be a small element]. A relationship between Rondeletia and Gibberichthys would also require parallel evolution between the former genus and cetomimoids in certain features. For example, cetomimoids are scaleless and have the dorsal and anal fins situated posteriorly and equal and opposite (Rosen, 1973, p. 489), as in Rondeletia (but not Gibberichthys) (Ebeling and Weed, 1973, pp. 398-399). Ebeling and Weed (1973, p. 408, fig. 6) also indicate that Rondeletia and the cetomimoid Cetostomus are specialized in having the caudal vertebrae enclosed by a cartilaginous sheath, in contrast to the condition seen in Gibberichthys.

Rosen (1973, p. 496) noted several characters which he felt indicated that Anoplogaster (species 26) belongs to the stephanoberycoid assemblage (as shown in dendrogram #1, but not dendrogram #2). Thus, Rosen stated that there are similarities between Anoplogaster and Eutaeniophorus in the form of the pharyngobranchial dentition, between Anoplogaster and Cetomimus in the insertion of the retractor arcuum branchialum (RAB) muscle, and between Anoplogaster and cetomimoids, Rondeletia and Gibberichthys in having the third and fourth hypurals articulate with a complete compound centrum (PU1 + U1 + U2) rather than with a second ural centrum (U2). Rosen did not specify the manner in which the pharyngobranchial dentitions of Anoplogaster and Eutaeniophorus are similar, but perhaps he was referring to the position of the tooth plates of the third and fourth pharyngobranchials. Rosen (1973, p. 491, fig. 118) described and illustrated these plates as being laterally oriented in Eutaeniophorus. Although Rosen's figure of the pharyngobranchials of Anoplogaster (fig. 126, which is the same view as that shown for Eutaeniophorus) does not clearly indicate that the tooth plates of the third and fourth pharyngobranchials are laterally oriented in this form, reexamination of my material of Anoplogaster revealed that these tooth plates are somewhat laterally positioned. Aside from this similarity, it should be noted that a comparison of Rosen's figures 118 and 126 reveals certain differences in the pharyngobranchial dentition of these two forms. Thus, Eutaeniophorus is shown to lack teeth on the second pharyngobranchial (present in Anoplogaster) and the tooth plate of the third pharyngobranchial is noticeably smaller than in Anoplogaster.

Rosen's contention that RAB has a similar insertion in Anoplogaster and Cetomimus also appears to be unsupported by his illustrations. Rosen (1973, p. 490, figs. 116 and 117) shows RAB inserting on both the fourth

pharyngobranchial and its tooth plate in Cetomimus, while in Anoplogaster (fig. 126) the fourth pharyngobranchial is not shown (it is absent in the specimens examined for this report) and RAB does not appear to even closely approach the tooth plate of the fourth pharyngobranchial. Even if Anoplogaster resembled Cetomimus in the insertion of RAB, the resemblance would not be indicative of phylogenetic relationship, for Rosen (1973, p. 501) admits that a sole or partial RAB insertion on the fourth arch is primitive for neoteleosteans as a whole.

Rosen's statement that the third and fourth hypurals of Anoplogaster articulate with a complete compound centrum as in cetomimoids, Rondeletia and Gibberichthys is also inconsistent with his illustrations. Rosen's figure of the caudal skeleton of Anoplogaster (fig. 127) shows that U2 is autogenous (not fused) with respect to PU1 + U1, as is also the case in Rondeletia (fig. 121) and the cetomimoid Ataxolepis (fig. 57). Rosen's figure of the cetomimoid Cetostomus regani (fig. 54) does not show an autogenous second ural centrum, but since the last vertebra shown is labelled PU1 + U1, U2 is presumably autogenous or absent in the specimen illustrated [in the specimen of C. regani illustrated by Ebeling and Weed (1973, p. 407, fig. 56) U2 is shown to be a tiny, autogenous element]. The caudal skeleton of Gibberichthys was not illustrated by Rosen, but in Ebeling and Weed's figure (1973, p. 407, fig. 5A) and in the specimen of Gibberichthys examined for this report U2 is autogenous. In short, the cetomimoids Cetomimus and Eutaeniophorus (Rosen, 1973, p. 432, figs. 55 and 56) are the only forms under consideration which are shown to have a complete compound centrum that articulates with the third and fourth hypurals.

Rosen's suggestion of a relationship between Anoplogaster and various stephanoberycoids therefore appears to be based on weak evidence. As noted earlier, the pattern of the frontal crests in Anoplogaster indicates that it is more closely related to trachichthyoids (as shown in dendrogram #2) than to stephanoberycoids.

Five other characters discussed by Rosen (1973) are found to support the arrangement of groups shown in dendrogram #2 (but not dendrogram #1). Four of these involve the relationship between species 1-9, 18-26 (i.e., the species belonging to the trachichthyoid and stephanoberycoid assemblages recognized by Rosen)[1]. The resemblances between trachichthyoids and stephanoberycoids in derived character states are listed by Rosen (1973, p. 498) in the form of statements that represent trends common to both groups, and include:

1) The development of an external process on the third infraorbital (= second infraorbital of this report) representing the bony arch covering the sensory canal (see Rosen, 1973, pp. 477-478, for an explanation as to why this character state is derived).
2) The presence of elongate, diamond-shaped neuromasts distributed on the circumorbitals as follows: lacrimal (3); infraorbital - 1 (io - 1) (2); io - 2 (2); io - 3 (1); io - 4 (1); dermosphenotic (1).
3) The formation of an internal division of the adductor mandibulae to control the maxilla.
4) The formation of a large third pharyngobranchial that has an elevated, posterior cartilaginous apex on which the retractor arcuum branchialum is inserted.

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[1]Patterson (1967, p. 104) also suggested that the families to which species 1-9, 18-26 belong form a related assemblage, although he did not provide any evidence in that publication to support his view.

Another derived feature which supports the arrangement of groups shown in dendrogram #2 is the heteracanth condition of the dorsal fin spines. Rosen (1973, pp. 501-502) found this condition, in which the bases of the dorsal spines are displaced alternately to the right and left so that when the fin is depressed the spines lie recumbent on either side of the midline, to be present only in the Holocentridae, Monocentridae and Perciformes. Although Rosen (1973, p. 501, footnote) notes several differences between the dorsal spines of holocentrids and monocentrids, thereby suggesting to him that the heteracanth condition has been independently acquired in these two groups, he finds holocentrid spines exactly the same as those of perciforms (personal communication). Furthermore, although Rosen (1973, pp. 501-502) did not explicitly state that the Holocentridae should be removed from the Beryciformes and regrouped with the Perciformes, the suggestion that this should be done is clearly evident[1]. Examination of dendrogram #2 reveals that it is more compatible with Rosen's suggestion than dendrogram #1. This is because in dendrogram #2 there are only two character states (51 - absence of epineurals; 85 - neural spine of PU2 crest-like) uniting holocentrids (species 12-16) to their nearest allies (species 1-11 and 18-26), both of which are also found in perciforms[2], whereas in dendrogram #1 there are 14 character states uniting holocentrids to their nearest allies (species 9-11), two of which (62 - presence of anterior process of pelvic bone; 88 - stegural fused) are not present in all perciforms[2]. Thus, if one accepts Rosen's suggestion of a relationship between holocentrids and perciforms, it is necessary to assume that character states 62 and 88 evolved independently in holocentrids and diretmids + berycids (species 9-11), whereas no parallelism would be required (with respect to character states 51 and 85) in the case of dendrogram #2. In short, the Holocentridae is less "integrated" into the phylogeny of dendrogram #2 than into that of dendrogram #1, thereby making dendrogram #2 more compatible with Rosen's suggestion.

It should be noted that some additional evidence for a holocentrid - perciform relationship has recently been presented by Nolf and Taverne (1977). These authors have divided the Holocentridae (as understood in this report) into two families -- the Holocentridae (containing such genera as Adioryx and Holocentrus) and the Myripristidae (containing such genera as Plectrypops and Myripristis). Nolf and Taverne discussed certain similarities in the otoliths and swim bladder between the Myripristidae and the perciform family Sciaenidae. In addition, resemblances in the caudal skeleton between the Myripristidae + Holocentridae and the Sciaenidae were noted. Nolf and Taverne (1977, p. 150) concluded that the evidence suggests a close relationship between the Myripristidae and Sciaenidae. Some of this evidence is not convincing, however. For example, Nolf and Taverne (1977, pp. 152-153, fig. 1) note that the saccular otoliths of the sciaenids Otolithes ruber and Johnieops aneus are very similar to those of the Myripristidae in having a very peculiar outline (i.e., triangular with slightly rounded corners). The significance of this similarity is lessened, however, by their statement on page 158 that this feature is typical of beryciforms (in other words, it is not unique to myripristids and

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[1] Rosen (personal communication) has informed me that he believes that the Holocentridae should indeed be regrouped with the Perciformes.

[2] Based on an examination of the perciform members of the "out-group"-- see character tables in appendix I.

sciaenids). The similarities in the caudal skeleton between the Myripristidae (and Holocentridae) and Sciaenidae which Nolf and Taverne (1977, p. 156) mention include: 1) presence of a neural arch or crest (but no spine) on PU2 2) fusion between PU1, U1 and U2 3) presence of three epurals 4) presence of a stegural which is fused to the terminal vertebra 5) presence of a normal pair of uroneurals and 6) presence of five hypurals. Features #3 and #5 are primitive and are therefore not valid indicators of relationship. The remaining features are present in many beryciforms (other than myripristids and holocentrids), thereby weakening Nolf and Taverne's argument for a myripristid - sciaenid relationship. Thus, of the 26 species appearing in dendrograms #1 and #2, feature #1 is present in species 1-16 and 18-26, #2 is present in species 10-16 and 20-25, #4 is present in species 9-16 and 20-26 and #6 (five or fewer hypural bones) is present in species 9-16 and 20-26.

In summary, it may be stated that although I agree with Rosen (1973, p. 502) that there are only very scant data on derived character states to relate holocentrids to other beryciforms, and that the evidence which he presents [as well as some of that put forth by Nolf and Taverne (1977)] may indicate a holocentrid - perciform relationship, I feel that it would be premature to remove the Holocentridae from the Beryciformes at this juncture. Rather, the evidence discussed by Rosen (1973) and Nolf and Taverne (1977) should be kept carefully in mind by future investigators -- if and when additional characters are discovered which support a relationship between holocentrids and perciforms, then the former should be removed from the Beryciformes.

Comparison of Dendrogram #1 and Dendrogram #2 (Summary)

Comparison of dendrograms #1 and #2 in terms of the amount of parallelism which occurs, the number of groups which are defined by the presence of unique, derived character states, and the consistency of the arrangement of the groups with additional morphological data indicates that dendrogram #2 is a better representation of the phylogenetic relationships of the 26 species examined. Dendrogram #1 is better than dendrogram #2 only with respect to the amount of parallelism which occurs in all 94 derived states of the original data set (32 fewer cases of parallelism) (a preliminary analysis reveals that the amount of parallelism which occurs in the functionally important character states is about the same--i.e., neither dendrogram is strongly favored). When certain additional morphological characters are taken into consideration, the amount of parallelism required in dendrogram #1, but not in dendrogram #2, increases (i.e., the arrangement of the groups in dendrogram #2 is more consistent with this additional data). Perhaps the best reason for selecting dendrogram #2 in favor of dendrogram #1, however, is that more of the groups in dendrogram #2 are defined by the presence of unique, derived states. As has been repeatedly emphasized in the discussion above, the presence of such states in a group is the strongest evidence that it is monophyletic.

Concluding Remarks

It is certainly not an exaggeration to state that "we are further

from a reasonably complete knowledge of living teleosts than we are of any other large, non-piscine, vertebrate group" (Greenwood et al., 1966, p. 347). Hopefully, this investigation represents a substantial contribution to our knowledge of teleostean fishes. It is also hoped that this investigation will provide an adequate basis for future studies concerning the phylogenetic relationships between beryciforms and other groups, such as the Cetomimoidei, Zeiformes, Lampridiformes and Perciformes.

TABLE 6

LIST OF DERIVED CHARACTER STATES USED IN THIS INVESTIGATION

Character State Number	Character State Name
1	nasals large
2	anterolateral portion of nasal does articulate with lateral ethmoid
3	transverse crest on dorsal surface of supraoccipital present
4	supratemporal fossa ends well-behind posterior border of orbit
5	supratemporal fossa ends at posterior border of orbit
6	supratemporal fossa ends at middle of orbit
7	supratemporal fossa ends well-ahead of middle of orbit
8	mesethmoid small
9	vomer toothless
10	distinct postorbital curvature of parasphenoid present
11	ventrolateral flanges on shaft of parasphenoid absent
12	foramen for internal carotid artery does not pierce ascending process of parasphenoid
13	orbitosphenoid absent
14	pterosphenoids meet in midline of orbit
15	basisphenoid absent
16	facet for anterior portion of head of hyomandibula formed within autosphenotic only
17	3 external openings in pars jugularis
18	2 external openings in pars jugularis
19	fenestra in lateral surface of exoccipital present
20	ventrolateral flanges on ventral aspect of posterior end of basioccipital present
21	antorbital absent
22	lacrimal bears ⊂ -shaped process for articulation with lateral ethmoid
23	posterior portion of lacrimal not reduced, and extends back below infraorbital 1 to articulate with infra-orbital 2
24	posterior portion of lacrimal strongly reduced

TABLE 6--cont.

Character State Number	Character State Name
25	head of hyomandibula double
26	endopterygoid toothless
27	ectopterygoid toothless
28	palatine toothless
29	distal portion of maxilla not expanded behind tip of alveolar process of premaxilla
30	2 supramaxillae present; posterior supramaxilla without slender process overlying anterior supramaxilla
31	1 supramaxilla present; anterior end of supramaxilla with slender process
32	0 supramaxillae present
33	teeth slightly expanded onto lateral surface of dentary
34	teeth greatly expanded onto lateral surface of dentary
35	ventral border of dentary distinctly notched
36	prominent spine at angle of preopercle present
37	ceratohyal foramen absent
38	ventral border of ceratohyal strongly notched for articulation with heads of branchiostegal rays
39	basihyal toothless
40	basihyal absent
41	8 branchiostegal rays present
42	7 branchiostegal rays present
43	basibranchials toothless
44	anterior end of CB5 does not articulate directly with BB4
45	PB2 toothless
46	tooth plate of PB4 absent
47	neural arch of 1st abdominal vertebra fused
48	pleural ribs begin on 2nd abdominal vertebra
49	pleural ribs begin on 6th abdominal vertebra
50	pleural ribs begin on 7th abdominal vertebra
51	epineural ribs absent

TABLE 6--cont.

Character State Number	Character State Name
52	epipleural ribs absent
53	tympanic plate present
54	1 supraneural present
55	0 supraneurals present
56	extrascapular does cover entire dorsal aspects of epiotic, parietal and much of supraoccipital
57	dorsal portion of supracleithrum not pierced by canal for lateral line
58	ventral border of supracleithrum distinctly notched
59	1 postcleithrum present
60	scapula with 2 foramina
61	4th actinost enlarged, showing evidence of fusion with another (5th) actinost
62	anterior process of pelvic bone present
63	lateral process of pelvic bone present; weakly developed
64	lateral process of pelvic bone present; strongly developed
65	distal portion of posterior process of pelvic bone expanded into a distinct flange or plate
66	pelvic fin spine present
67	7 pelvic rays
68	6 pelvic rays
69	5 pelvic rays
70	3 or fewer pelvic rays
71	10 or more pelvic rays
72	pelvic fin radials present; outermost radial with hook-like process
73	pelvic fin radials absent
74	dorsal fin spine(s) present
75	dorsal fin spines do project strongly in opposite directions
76	2 predorsals present
77	3 predorsals present

TABLE 6--cont.

Character State Number	Character State Name
78	anal fin spine(s) present
79	penultimate anal fin spine enlarged (4th of 5 spines)
80	penultimate anal fin spine enlarged (3rd of 4 spines)
81	U2 fused (to PU1 + U1)
82	distal portions of neural and hemal spines of PU4 (but not PU5) expanded
83	distal portions of neural and hemal spines of PU4 and PU5 expanded
84	hemal arch of PU3 fused
85	neural spine of PU2 crest-like
86	neural spine of PU2 complete
87	neural arch of PU2 fused
88	stegural fused (to underlying centra)
89	single pair of uroneurals present; strongly reduced
90	uroneurals absent
91	parhypural fused (to hypural 1)
92	18 principal rays
93	scales of body very large and thick
94	ventral ridge scales present

TABLE 7

LIST OF SPECIES WHICH APPEAR IN DENDROGRAMS #1 AND #2

Species Number	Species Name
1	Cleidopus gloriae-maris
2	Monocentris japonicus
3	Hoplostethus mediterraneus
4	Gephyroberyx darwini
5	Trachichthys australis
6	Paratrachichthys sp.
7	Photoblepharon palpebratus
8	Anomalops katopteron
9	Diretmus argenteus
10	Centroberyx affinis
11	Beryx splendens
12	Myripristis sp.
13	Ostichthys trachypoma
14	Plectrypops retrospinis
15	Holocentrus rufus
16	Adioryx diadema
17	Polymixia lowei
18	Gibberichthys pumilus
19	Stephanoberyx monae
20	Scopeloberyx sp.
21	Poromitra crassiceps
22	Scopelogadus mizolepis
23	Scopelogadus unispinis
24	Melamphaes macrocephalus
25	Melamphaes eulepis
26	Anoplogaster cornuta

TABLE 8

LIST OF CLEARED AND STAINED MATERIAL EXAMINED

Order Beryciformes	Institution and Catalogue No.	Locality	No. Specimens	Standard Length
Family Anomalopidae				
Anomalops katopteron	USNM 114605	Dutch East Indies	1	76 mm
Anomalops katopteron	AMNH 15360	Dutch East Indies	1	---
Photoblepharon palpebratus	AMNH 15361	Dutch East Indies	1	65 mm
Photoblepharon palpebratus	Gift from Mr. David Fridman	Red Sea	1	62 mm
Family Anoplogasteridae				
Anoplogaster cornuta	FMNH 66620	Gulf of Mexico	2	84, 88 mm
Family Berycidae				
Beryx splendens	FMNH 66446	Gulf of Mexico	1	159 mm
Centroberyx affinis	USNM (uncatalogued)	Australia	1	212 mm
Family Diretmidae				
Diretmus argenteus	FMNH 65303	Off Tortugas, W. coast Fla.	1	72 mm
Diretmus pauciradiatus	FMNH 67002	Caribbean Sea	1	88 mm
Family Gibberichthyidae				
Gibberichthys pumilus	FMNH 66805	Off St. Augustine, Florida	1	50 mm
Gibberichthys pumilus	CAS (uncatalogued)	Gulf of Mexico	1	86 mm
Family Holocentridae				
Adioryx diadema	FMNH 73814	Maldive Islands	2	86, 92 mm
Holocentrus rufus	FMNH 60170	Jamaica	1	74 mm
Myripristis sp.	FMNH (uncatalogued)	S.E. United States	1	165 mm
Ostichthys trachypoma	FMNH 65198	West Indies	2	64, 65 mm
Plectrypops retrospinis	FMNH 48242	Bermuda	2	70,71 mm

TABLE 8--cont.

Family Melamphaeidae				
Melamphaes eulepis	FMNH 77982	Gulf of Mexico	1	42 mm
Melamphaes macrocephalus	FMNH 77983	Eastern Pacific	1	73 mm
Poromitra crassiceps	SIO 70-339	Philippine Sea	1	89 mm
Scopeloberyx sp.	FMNH 77984	Gulf of Mexico	1	88 mm
Scopelogadus mizolepis	FMNH 77985	Indian Ocean	1	88 mm
Scopelogadus unispinis	FMNH 77986	Indian Ocean	1	106 mm
Family Monocentridae				
Monocentris japonicus	FMNH 73560	Japan Seas	1	73 mm
Cleidopus gloriae-maris	AMNH 4768	Western Australia	1	175 mm
Family Polymixiidae				
Polymixia lowei	FMNH 67023	Gulf of Mexico	1	83 mm
Polymixia lowei	FMNH 46387	Gulf of Mexico	1	98 mm
Family Stephanoberycidae				
Stephanoberyx monae	FMNH 77987	Gulf of Mexico	2	97, 102 mm
Family Trachichthyidae				
Gephyroberyx darwini	FMNH 64532	Caribbean Sea	1	65 mm
Gephyroberyx darwini	FMNH 65227	Caribbean Sea	1	74 mm
Hoplostethus mediterraneus	FMNH 66788	Gulf of Mexico	2	88, 102 mm
Paratrachichthys sp.	FMNH (uncatalogued)	Off coast of Somalia	1	70 mm
Trachichthys australis	USNM 197649	---	1	93 mm
NON-BERYCIFORM TELEOSTS				
Family Albulidae				
Albula vulpes	FMNH 4835	Bermuda	1	139 mm
Family Aulopodidae				
Aulopus japonica	FMNH 71831	Nagasaki	1	147 mm
Family Chlorophthalmidae				
Chlorophthalmus agassizi	FMNH 67131	---	1	83 mm

TABLE 8--cont.

Non-beryciform Teleosts	Institution and Catalogue No.	Locality	No. Specimens	Standard Length
Family Cichlidae				
Cichla ocellaris	FMNH 53784	British Guiana	1	---
Cichla ocellaris	FMNH 73531	Peru	1	45 mm
Family Clupeidae				
Etrumeus micropus	FMNH 55780	Korea	1	129 mm
Family Elopidae				
Elops saurus	FMNH 37074	Louisiana Gulf	1	189 mm
Family Hiodontidae				
Hiodon tergisus	FMNH 48066	Illinois	1	105 mm
Family Kyphosidae				
Girella nigricans	FMNH 59036	California	1	82 mm
Family Osmeridae				
Osmerus mordax	FMNH 37338	---	1	133 mm
Family Salmonidae				
Salvelinus fontinalis	FMNH 63441	Michigan	1	128 mm
Family Serranidae				
Morone americanus	FMNH 6534	Potomac River	1	78 mm

Institutional Abbreviations:

AMNH = American Museum of Natural History
CAS = California Academy of Sciences
FMNH = Field Museum of Natural History
SIO = Scripps Institution of Oceanography
USNM = United States National Museum

TABLE 9

LIST OF THE FAMILIES OF BERYCIFORM FISHES, WITH THE NUMBER AND NAMES OF THE GENERA CONTAINED IN EACH FAMILY, THE NUMBER OF SPECIES CONTAINED IN EACH GENUS, AND THE NUMBER OF SPECIES OF EACH GENUS EXAMINED IN THIS INVESTIGATION[a] (Fossil taxa not included)

Family	(Number) and Names of Genera Contained in Each Family		Number of Species Contained in Each Genus	Number of Species of Each Genus Examined in this Investigation
Anomalopidae	(3)	Anomalops	1	1
		Kryptophaneron	2[b]	0
		Photoblepharon	1	1
Anoplogasteridae	(1)	Anoplogaster	1	1
Berycidae	(2)	Beryx	3	1
		Centroberyx	3[c]	1
Diretmidae	(1)[c]	Diretmus	2 or 3[c]	1
Gibberichthyidae	(1)	Gibberichthys	2[d]	1
Holocentridae	(7)	Adioryx	24	1
		Corniger	1[c]	0
		Flammeo	5	0
		Holocentrus	2	1
		Myripristis	18[e]	1
		Ostichthys	3[c]	1
		Plectrypops	5 or 6[c]	1
Melamphaeidae	(5)	Melamphaes	19	2
		Poromitra	4	1
		Scopeloberyx	4 or 5	1
		Scopelogadus	3	2
		Sio	1	0

TABLE 9--cont.

Monocentridae	(2)[c]	Cleidopus	1 or 2[c]	1
		Monocentris	2[c]	1
Polymixiidae	(1)	Polymixia	5[c]	1
Stephanoberycidae	(3)	Acanthochaenus	1	0
		Malacosarcus	1	0
		Stephanoberyx	1	1
Trachichthyidae	(5)	Gephyroberyx	3	1
		Hoplostethus	14-16[c]	1
		Optivus	1[c]	0
		Paratrachichthys	7[c]	1
		Trachichthys	1[c]	1

[a]Unless otherwise indicated, the data concerning the number and names of the genera contained in each family, as well as the number of species contained in each genus, are taken from Ebeling and Weed (1973) for the families Gibberichthyidae, Melamphaeidae and Stephanoberycidae and Woods and Sonoda (1973) for the remaining families. The number of species of each genus examined in this investigation refers only to those species treated in the final phylogenetic analysis [species appearing in dendrograms #1 and #2 (p. 182 and p. 191, resp.)].

[b]Rosenblatt and Montgomery (1976, p. 510).

[c]Woods (personal communication).

[d]de Sylva and Eschmeyer (1977, p. 227).

[e]Greenfield (1974, p. 1).

APPENDIX I

TABLES OF THE CHARACTERS ANALYZED IN THIS INVESTIGATION

Tables of the 70 characters analyzed in this investigation (tables 10-79) are presented on the following pages. In identifying character states which are present in the Beryciformes, all of the Recent species which I examined and all of the Cretaceous species described by Patterson (1964, 1967, 1968) were taken into consideration.

Unless otherwise indicated, the species of the "out-group" are those listed in table 3. The data for the Recent species have been taken from cleared and stained material (table 8), with the exception of Mycteroperca venosa. The data for Mycteroperca were taken primarily from dried skeletal material (FMNH,[1] cat. nos. 51292 and 51378). For the characters of the caudal skeleton (60-68) an additional species, Kuhlia sandvicensis (a member of the Family Kuhliidae of the Suborder Percoidei), was examined. The data for Kuhlia were also taken from dried skeletal material (FMNH, cat. no. 63873). Unless otherwise indicated, the data for the fossil species have been taken from the following sources: Nematonotus longispinus (Rosen and Patterson, 1969); Sardinioides minimus (Goody, 1969); Aulolepis typus and Ctenothrissa radians (Patterson, 1964, 1968); Pattersonichthys delicatus (Gaudant, 1978b).

In each table, a horizontal line is placed between the superorders Protacanthopterygii and Acanthopterygii in order to stress the fact that the members of the "out-group" belonging to the former superorder (as well as those belonging to the Elopomorpha, Clupeomorpha and Osteoglossomorpha) are more primitive than beryciforms in their overall level of structural organization, whereas the members of the "out-group" belonging to the latter superorder are more advanced. The vertical line located next to the myctophoids, ctenothrissiforms and pattersonichthyiform indicates that emphasis was placed on the character states present in these forms when determining the derivativeness of the states present in beryciforms.

In the character state trees, state I always denotes the most primitive condition (for beryciforms). Character states which are unique to fossil taxa are marked with an asterisk (*). Two states enclosed in parentheses and located beside an arrow indicates that intraspecific variation occurs [e.g., I → II].
(I-II)

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[1]Field Museum of Natural History.

TABLE 10

CHARACTER #1. SIZE OF NASAL BONES

States present in the Beryciformes

I - nasals not large (fail to meet in midline)
II - nasals large (meet in midline)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	not large	II
	Albula	not large	↑
			I
Clupeomorpha	Etrumeus	not large	
Osteoglossomorpha	Hiodon	not large	
'Protacanthopterygii'	Salvelinus	not large	
	Osmerus	not large	
	Nematonotus	not large	
	Sardinioides	---	
	Aulopus	not large	
	Chlorophthalmus	not large	
	Pattersonichthys	not large	
	Aulolepis	---	
	Ctenothrissa	not large	
Acanthopterygii	Mycteroperca	not large	
	Morone	not large	
	Girella	not large	
	Cichla	not large	

Remarks: None.

TABLE 11

CHARACTER #2. NASAL--LATERAL ETHMOID ARTICULATION

States present in the Beryciformes

I - anterolateral portion of nasal does not articulate with lateral ethmoid
II - anterolateral portion of nasal does articulate with lateral ethmoid

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	no articulation	II
	Albula	no articulation	↑
			I
Clupeomorpha	Etrumeus	no articulation	
Osteoglossomorpha	Hiodon	no articulation	
'Protacanthopterygii'	Salvelinus	no articulation	
	Osmerus	no articulation	
	Nematonotus	no articulation	
	Sardinioides	---	
	Aulopus	no articulation	
	Chlorophthalmus	no articulation	
	Pattersonichthys	no articulation	
	Aulolepis	---	
	Ctenothrissa	no articulation	
Acanthopterygii	Mycteroperca	no articulation	
	Morone	no articulation	
	Girella	no articulation	
	Cichla	no articulation	

Remarks: None.

TABLE 12

CHARACTER #3. TRANSVERSE CREST OF SUPRAOCCIPITAL

States present in the Beryciformes

I - transverse crest on dorsal surface of supraoccipital absent
II - transverse crest[a] on dorsal surface of supraoccipital (forming anterior wall of supratemporal fossa) present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑
			I
Clupeomorpha	Etrumeus	absent	
Osteoglossomorpha	Hiodon	absent	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	absent	
	Sardinioides	---	
	Aulopus	absent	
	Chlorophthalmus	absent	
	Pattersonichthys	absent[b]	
	Aulolepis	absent	
	Ctenothrissa	absent	
Acanthopterygii	Mycteroperca	absent	
	Morone	absent	
	Girella	absent	
	Cichla	absent	

Remarks: [a]The transverse crest may represent a median, ctenoid scale which is fused to the supraoccipital.

[b]Gaudant (personal communication).

TABLE 13

CHARACTER #4. ANTERIOR EXTENT OF SUPRATEMPORAL FOSSA

States present in the Beryciformes

I - supratemporal fossa absent
II - supratemporal fossa ends well-behind posterior border of orbit
III - supratemporal fossa ends at posterior border of orbit
IV - supratemporal fossa ends at middle of orbit
V - supratemporal fossa ends well-ahead of middle of orbit

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	fossa absent	V
	Albula	fossa absent	↑
			IV
Clupeomorpha	Etrumeus	fossa absent	↑
			III
Osteoglossomorpha	Hiodon	fossa absent	↑
			II
	Salvelinus	fossa absent	↑
	Osmerus	fossa absent	I
	Nematonotus	fossa absent[a]	
	Sardinioides	---	
'Protacanthopterygii'	Aulopus	fossa absent	
	Chlorophthalmus	fossa absent	
	Pattersonichthys	fossa absent[b]	
	Aulolepis	fossa absent	
	Ctenothrissa	post. bdr. orbit	
	Mycteroperca	ant. bdr. orbit	
Acanthopterygii	Morone	well-behind post. bdr. orbit	
	Girella	middle orbit	
	Cichla	middle orbit	

Remarks: [a]The supratemporal fossa in Nematonotus is either absent or extends only very slightly onto the dorsal surface of the skull (Rosen and Patterson, 1969, p. 448, fig. 65).

[b]Gaudant (personal communication).

TABLE 14

CHARACTER #5. SIZE OF MESETHMOID

States present in the Beryciformes

I - mesethmoid large and not confined to a position between the dorsomedial portions of the lateral ethmoids

II - mesethmoid small and confined to a position between the dorsomedial portions of the lateral ethmoids

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	mesethmoid absent[a]	II
	Albula	?[b]	↑
			I
Clupeomorpha	Etrumeus	?[b]	
Osteoglossomorpha	Hiodon	large	
'Protacanthopterygii'	Salvelinus	mesethmoid absent[a]	
	Osmerus	mesethmoid absent[a]	
	Nematonotus	large	
	Sardinioides	large	
	Aulopus	large	
	Chlorophthalmus	large	
	Pattersonichthys	large	
	Aulolepis	large	
	Ctenothrissa	large	
Acanthopterygii	Mycteroperca	large	
	Morone	large	
	Girella	large	
	Cichla	large	

Remarks: [a]The unpaired element in the ethmoid region of Elops, Salvelinus and Osmerus is dermal (Patterson, 1970, p. 262), and therefore not homologous with the mesethmoid of beryciforms.

[b]A large element is present in the ethmoid region of Albula and Etrumeus, but whether it is dermal, endochondral or compound could not be determined.

TABLE 15

CHARACTER #6. VOMERINE TEETH

States present in the Beryciformes

I - vomer toothed
II - vomer toothless

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	toothed	II
	Albula	toothed	↑ (I-II)
			I
Clupeomorpha	Etrumeus	toothed	
Osteoglossomorpha	Hiodon	toothless	
'Protacanthopterygii'	Salvelinus	toothed	
	Osmerus	toothed	
	Nematonotus	---	
	Sardinioides[a]	toothed	
	Aulopus	toothed	
	Chlorophthalmus	toothed	
	Pattersonichthys	toothed	
	Aulolepis	toothed	
	Ctenothrissa	toothed	
Acanthopterygii	Mycteroperca	toothed	
	Morone	toothed	
	Girella	toothless	
	Cichla	toothless	

Remarks: [a]Sardinioides sp. (Goody, 1969, p. 203).

TABLE 16

CHARACTER #7. POSTORBITAL CURVATURE OF PARASPHENOID

States present in the Beryciformes

I - distinct postorbital curvature of parasphenoid absent
II - distinct postorbital curvature of parasphenoid present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑
			I
Clupeomorpha	Etrumeus	present	
Osteoglossomorpha	Hiodon	present	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	---	
	Sardinioides	absent	
	Aulopus	absent	
	Chlorophthalmus	absent	
	Pattersonichthys	present (slight)	
	Aulolepis	absent	
	Ctenothrissa	present (strong)	
Acanthopterygii	Mycteroperca	absent	
	Morone	absent	
	Girella	absent	
	Cichla	absent	

Remarks: None.

TABLE 17

CHARACTER #8. FLANGES ON SHAFT OF PARASPHENOID

States present in the Beryciformes

I - ventrolateral flanges on shaft of parasphenoid present
II - ventrolateral flanges on shaft of parasphenoid absent

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑
			I
Clupeomorpha	Etrumeus	absent	
Osteoglossomorpha	Hiodon	absent	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	present	
	Chlorophthalmus	present[a]	
	Pattersonichthys	present	
	Aulolepis	present	
	Ctenothrissa	present	
Acanthopterygii	Mycteroperca	absent	
	Morone	absent	
	Girella	absent	
	Cichla	absent	

Remarks: [a]The flanges in Chlorophthalmus are partly membranous.

TABLE 18

CHARACTER #9. POSITION OF FORAMEN FOR INTERNAL CAROTID ARTERY

States present in the Beryciformes

I - foramen for internal carotid artery pierces ascending process of parasphenoid

II - foramen for internal carotid artery does not pierce ascending process of parasphenoid (foramen is between ascending process and prootic)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	pierces pr.	II
	Albula	does not pierce pr.	↑
			I
Clupeomorpha	Etrumeus	pierces pr.	
Osteoglossomorpha	Hiodon	pierces pr.	
	Salvelinus	does not pierce pr.	
	Osmerus	does not pierce pr. (probably)	
'Protacanthopterygii'	Nematonotus	---	
	Sardinioides	---	
	Aulopus	pierces pr.	
	Chlorophthalmus	pierces pr.	
	Pattersonichthys	---	
	Aulolepis	pierces pr.	
	Ctenothrissa	pierces pr.	
Acanthopterygii	Mycteroperca	does not pierce pr.	
	Morone	does not pierce pr.	
	Girella	pierces pr.	
	Cichla	---	

Remarks: None.

TABLE 19

CHARACTER #10. ORBITOSPHENOID

States present in the Beryciformes

I - orbitosphenoid present
II - orbitosphenoid absent

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	present	II
	Albula	present	↑
			I
Clupeomorpha	Etrumeus	present	
Osteoglossomorpha	Hiodon	present	
'Protacanthopterygii'	Salvelinus	present	
	Osmerus	---	
	Nematonotus	---	
	Sardinioides[a]	absent	
	Aulopus	absent[b]	
	Chlorophthalmus	absent	
	Pattersonichthys	absent	
	Aulolepis	present	
	Ctenothrissa	present	
Acanthopterygii	Mycteroperca	absent	
	Morone	absent	
	Girella	absent	
	Cichla	absent	

Remarks: [a] Sardinioides sp. (Gaudant, 1978b, p. 119).

[b] A very large orbitosphenoid is present in Aulopus filamentosus, however (Goody, 1969, p. 208, fig. 88).

TABLE 20

CHARACTER #11. PTEROSPHENOIDS

States present in the Beryciformes

I - pterosphenoids separate (do not meet in midline of orbit)
II - pterosphenoids meet in midline of orbit

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	separate	II
	Albula	separate	↑
			I
Clupeomorpha	Etrumeus	meet in midline	
Osteoglossomorpha	Hiodon	separate	
'Protacanthopterygii'	Salvelinus	separate	
	Osmerus	---	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	separate	
	Chlorophthalmus	separate	
	Pattersonichthys	---	
	Aulolepis	separate	
	Ctenothrissa	separate	
———	Mycteroperca	separate/ meet in midline (intrasp. var.)	
Acanthopterygii	Morone	separate	
	Girella	separate	
	Cichla	separate	

Remarks: None.

TABLE 21

CHARACTER #12. BASISPHENOID

States present in the Beryciformes

I - basisphenoid present
II - basisphenoid absent

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	present	II
	Albula	present	↑
			I
Clupeomorpha	Etrumeus	present (arms only)	
Osteoglossomorpha	Hiodon	present (arms only)	
'Protacanthopterygii'	Salvelinus	present	
	Osmerus	---	
	Nematonotus	---	
	Sardinioides	present (only pedicel presvd.)	
	Aulopus	present	
	Chlorophthalmus	present (pedicel only)	
	Pattersonichthys	present	
	Aulolepis	present (but complt. basphnd. unknown)	
	Ctenothrissa	present	
Acanthopterygii	Mycteroperca	present	
	Morone	present	
	Girella	present	
	Cichla	present	

Remarks: None.

TABLE 22

CHARACTER #13. FACET FOR HEAD OF HYOMANDIBULA

States present in the Beryciformes

I - facet for anterior portion of head of hyomandibula (or for anterior head if hyomandibula double-headed) formed within both prootic and autosphenotic (or within cartilage between prootic and autosphenotic)

II - facet for anterior portion of head of hyomandibula (or for anterior head if hyomandibula double-headed) formed within autosphenotic only

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	w/in pro- and auto-	II
	Albula	w/in pro- and auto-	↑
			I
Clupeomorpha	Etrumeus	w/in auto-	
Osteoglossomorpha	Hiodon	w/in pro- and auto-	
	Salvelinus	w/in cartilage between pro- and auto-	
	Osmerus	---	
'Protacanthopterygii'	Nematonotus	---	
	Sardinioides	w/in pter-, auto-, and (?) pro-	
	Aulopus	w/in pter-, pro-, and auto-	
	Chlorophthalmus	w/in auto-	
	Pattersonichthys	w/in auto-	
	Aulolepis	w/in pro- and auto-	
	Ctenothrissa	w/in pro- and auto-	
Acanthopterygii	Mycteroperca	w/in pro- and auto-	
	Morone	w/in pro- and auto-	
	Girella	w/in pro- and auto-	
	Cichla	w/in pro- and auto-	

Remarks: None.

TABLE 23

CHARACTER #14. NUMBER OF EXTERNAL OPENINGS IN PARS JUGULARIS

States present in the Beryciformes

I - 4 external openings in pars jugularis
II - 3 external openings in pars jugularis
III - 2 external openings in pars jugularis

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	4 openings	III
	Albula	4 openings	↑
			II
Clupeomorpha	Etrumeus	3 openings	↑
			I
Osteoglossomorpha	Hiodon	2 openings (probably)	
'Protacanthopterygii'	Salvelinus	3 openings	
	Osmerus	---	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	4 openings	
	Chlorophthalmus	3 openings	
	Pattersonichthys	---	
	Aulolepis	4 openings	
	Ctenothrissa	4 openings	
Acanthopterygii	Mycteroperca	2 openings	
	Morone	2 openings	
	Girella	3 openings	
	Cichla	2 openings	

Remarks: Patterson (1964, pp. 434-438) discusses the morphological changes which have occurred in the trigemino-facialis chamber during the evolution of teleosts. He convincingly demonstrates that there has been a progressive reduction in the number of openings in the pars jugularis.

TABLE 24

CHARACTER #15. EXOCCIPITAL "FENESTRA"

States present in the Beryciformes

I - "fenestra" in lateral surface of exoccipital absent
II - "fenestra" in lateral surface of exoccipital present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑
Clupeomorpha	Etrumeus	absent	I
Osteoglossomorpha	Hiodon	absent	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	absent	
	Chlorophthalmus	absent	
	Pattersonichthys	---	
	Aulolepis	absent	
	Ctenothrissa	absent	
Acanthopterygii	Mycteroperca	absent	
	Morone	absent	
	Girella	absent	
	Cichla	---	

Remarks: None.

TABLE 25

CHARACTER #16. VENTROLATERAL FLANGES OF BASIOCCIPITAL

States present in the Beryciformes

I - ventrolateral flanges on ventral aspect of posterior end of basioccipital absent

II - ventrolateral flanges[a] on ventral aspect of posterior end of basioccipital present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑
Clupeomorpha	Etrumeus	absent	I
Osteoglossomorpha	Hiodon	present	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	absent	
	Chlorophthalmus	absent	
	Pattersonichthys	---	
	Aulolepis	absent	
	Ctenothrissa	absent	
Acanthopterygii	Mycteroperca	absent	
	Morone	absent	
	Girella	absent	
	Cichla	absent	

Remarks: [a]The ventrolateral flanges are associated with the fibrous wall of the swim bladder.

TABLE 26

CHARACTER #17. ANTORBITAL (ACCESSORY NASAL BONE)

States present in the Beryciformes

I - antorbital present
II - antorbital absent

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	present	II
	Albula	present	↑
Clupeomorpha	Etrumeus	present	I
Osteoglossomorpha	Hiodon	absent	
'Protacanthopterygii'	Salvelinus	present	
	Osmerus	present	
	Nematonotus	present	
	Sardinioides[a]	present	
	Aulopus	present	
	Chlorophthalmus	present	
	Pattersonichthys	present	
	Aulolepis	---[b]	
	Ctenothrissa	---[b]	
Acanthopterygii	Mycteroperca	absent	
	Morone	absent	
	Girella	absent	
	Cichla	absent	

Remarks: [a] Sardinioides illustrans (Patterson, 1964, p. 461).

[b] Gaudant (1978b, p. 18) has shown that the bone described by Patterson (1964, p. 223 and p. 250) as an antorbital in Aulolepis typus and Ctenothrissa radians is probably a supraorbital.

TABLE 27

CHARACTER #18. LACRIMAL-LATERAL ETHMOID ARTICULATION

States present in the Beryciformes

I - lacrimal bears concave facet (or flange) for articulation with lateral ethmoid
II - lacrimal bears ⊂-shaped process for articulation with lateral ethmoid
III - lacrimal bears splint-like ascending process for articulation with lateral ethmoid

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	no lac.-lat.eth.art.	II III*[a]
	Albula	no lac.-lat.eth.art.	↑ ↑
			I
Clupeomorpha	Etrumeus	no lac.-lat.eth.art.	
Osteoglossomorpha	Hiodon	no lac.-lat.eth.art.	
'Protacanthopterygii'	Salvelinus	no lac.-lat.eth.art.	
	Osmerus	no lac.-lat.eth.art.	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	no lac.-lat.eth.art.	
	Chlorophthalmus	lac. bears facet	
	Pattersonichthys	---	
	Aulolepis	lac. bears facet	
	Ctenothrissa	lac. bears facet	
Acanthopterygii	Mycteroperca	lac. bears facet	
	Morone	lac. bears facet	
	Girella	lac. bears facet	
	Cichla	lac. bears facet	

Remarks: [a]State III occurs only in the fossil Sphenocephalus fissicaudus (Rosen and Patterson, 1969, p. 401).

TABLE 28

CHARACTER #19. POSTERIOR PORTION OF LACRIMAL

States present in the Beryciformes

I - posterior portion of lacrimal not reduced, and articulates solely with infraorbital 1
II - posterior portion of lacrimal not reduced, and extends back below infraorbital 1 to articulate with infraorbital 2
III - posterior portion of lacrimal strongly reduced (to a series of ossicles which extend from the lacrimal "proper" to infraorbital 1)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	not redcd; art. w/io.1	II III
	Albula	not redcd; art. w/io.1	I
Clupeomorpha	Etrumeus	not redcd; art. w/io.1	
Osteoglossomorpha	Hiodon	not redcd; art. w/io.1	
'Protacanthopterygii'	Salvelinus	not redcd; art. w/io.1	
	Osmerus	not redcd; art. w/io.1	
	Nematonotus	not redcd; art. w/io.1	
	Sardinioides	---	
	Aulopus	not redcd; art. w/io.1	
	Chlorophthalmus	not redcd; art. w/io.1	
	Pattersonichthys	not redcd; art. w/io.1	
	Aulolepis	---	
	Ctenothrissa	not redcd; art. w/io.1	
Acanthopterygii	Mycteroperca	---	
	Morone	not redcd; art. w/io.1	
	Girella	not redcd; art. w/io.1	
	Cichla	not redcd; art. w/io.1	

Remarks: None.

TABLE 29

CHARACTER #20. HEAD OF HYOMANDIBULA

States present in the Beryciformes

I - head of hyomandibula single
II - head of hyomandibula double

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	double	II
	Albula	single	↑
			I
Clupeomorpha	Etrumeus	double	
Osteoglossomorpha	Hiodon	double	
'Protacanthopterygii'	Salvelinus	single	
	Osmerus	single	
	Nematonotus	---	
	Sardinioides	single	
	Aulopus	double	
	Chlorophthalmus	single	
	Pattersonichthys	single[a]	
	Aulolepis	single	
	Ctenothrissa	single	
Acanthopterygii	Mycteroperca	double	
	Morone	double	
	Girella	double	
	Cichla	double	

Remarks: [a]Goody (1969).

TABLE 30

CHARACTER #21. ENDOPTERYGOID TEETH

States present in the Beryciformes

I - endopterygoid toothed
II - endopterygoid toothless

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	toothed	II
	Albula	toothed	↑ (I-II)
			I
Clupeomorpha	Etrumeus	toothed	
Osteoglossomorpha	Hiodon	toothed	
'Protacanthopterygii'	Salvelinus	toothless	
	Osmerus	toothed	
	Nematonotus	---	
	Sardinioides[a]	toothed	
	Aulopus	toothed	
	Chlorophthalmus	toothless	
	Pattersonichthys	---	
	Aulolepis	toothed	
	Ctenothrissa	toothed	
Acanthopterygii	Mycteroperca	toothless	
	Morone	toothless	
	Girella	toothless	
	Cichla	toothless	

Remarks: [a]Sardinioides monasteri (Patterson, 1964, p. 461).

TABLE 31

CHARACTER #22. ECTOPTERYGOID TEETH

States present in the Beryciformes

I - ectopterygoid toothed
II - ectopterygoid toothless

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	toothed	II
	Albula	toothed/toothless (var. in single spec.)	↑ (I-II) I
Clupeomorpha	Etrumeus	toothed (few rudimentary teeth)	
Osteoglossomorpha	Hiodon	toothed	
'Protacanthopterygii'	Salvelinus	toothless	
	Osmerus	toothless	
	Nematonotus	---	
	Sardinioides[a]	toothed	
	Aulopus	toothed	
	Chlorophthalmus	toothless	
	Pattersonichthys	toothed (tooth patch small)[b]	
	Aulolepis	toothed	
	Ctenothrissa	toothed (tooth patch very small)	
Acanthopterygii	Mycteroperca	toothless	
	Morone	toothless	
	Girella	toothless	
	Cichla	toothless	

Remarks: [a] Sardinioides sp. (Patterson, 1964, p. 461).

[b] Gaudant (personal communication).

TABLE 32

CHARACTER #23. PALATINE TEETH

States present in the Beryciformes

I - palatine toothed
II - palatine toothless

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	toothed	II
	Albula	toothed	↑
			I
Clupeomorpha	Etrumeus	toothed	
Osteoglossomorpha	Hiodon	toothed	
'Protacanthopterygii'	Salvelinus	toothed	
	Osmerus	toothed	
	Nematonotus	---	
	Sardinioides[a]	toothed	
	Aulopus	toothed	
	Chlorophthalmus	toothed	
	Pattersonichthys	toothed	
	Aulolepis	toothed	
	Ctenothrissa	toothed	
Acanthopterygii	Mycteroperca	toothed	
	Morone	toothed	
	Girella	toothed	
	Cichla	(2-3 small teeth) toothless	

Remarks: [a]Sardinioides sp. (Patterson, 1964, p. 461).

TABLE 33

CHARACTER #24. DISTAL PORTION OF MAXILLA

States present in the Beryciformes

I - distal portion of maxilla expanded behind tip of alveolar process of premaxilla

II - distal portion of maxilla not expanded behind tip of alveolar process of premaxilla

Out-group	taxon	state	Character state tree
Elopomorpha	Elops[a]	expanded	II
	Albula	expanded	↑
			I
Clupeomorpha	Etrumeus[a]	expanded	
Osteoglossomorpha	Hiodon[a]	expanded	
'Protacanthopterygii'	Salvelinus[a]	expanded	
	Osmerus[a]	expanded	
	Nematonotus	expanded	
	Sardinioides	not expanded	
	Aulopus	expanded	
	Chlorophthalmus	not expanded	
	Pattersonichthys	expanded	
	Aulolepis[a]	expanded	
	Ctenothrissa[a]	expanded	
Acanthopterygii	Mycteroperca	expanded	
	Morone	not expanded	
	Girella	not expanded	
	Cichla	not expanded	

Remarks: [a]In these forms, the maxilla is the dominant element of the upper jaw.

TABLE 34

CHARACTER #25. NUMBER OF SUPRAMAXILLAE

States present in the Beryciformes

I - 2 supramaxillae present; posterior supramaxilla with slender process overlying anterior supramaxilla
II - 2 supramaxillae present; posterior supramaxilla without slender process overlying anterior supramaxilla
III - 1 supramaxilla present; anterior end of supramaxilla with slender process[a]
IV - 0 supramaxilla present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	2 smx.;post.smx.w/pr.	IV
	Albula	1 smx.; ant.end w/pr.	↑
			II III
Clupeomorpha	Etrumeus	1 smx.; ant.end tapered	↑ ↑
			I
Osteoglossomorpha	Hiodon	0 smx.	
'Protacanthopterygii'	Salvelinus	1 smx.; ant. end tapered	
	Osmerus	1 smx.; ant. end w/pr.	
	Nematonotus	2 smx.; post.smx.w/pr.	
	Sardinioides	2 smx.; post.smx.w/pr.	
	Aulopus	2 smx.; post.smx.w/pr.	
	Chlorophthalmus	1 smx.; ant. end tapered	
	Pattersonichthys	2 smx.; post.smx.w/pr.	
	Aulolepis	2 smx.; post.smx.w/pr.	
	Ctenothrissa	2 smx.; post.smx.w/pr.	
Acanthopterygii	Mycteroperca	1 smx.; ant. end tapered	
	Morone	0 smx.	
	Girella	0 smx.	
	Cichla	0 smx.	

Remarks: [a]In Melamphaes macrocephalus, M. eulepis and in the fossil Sphenocephalus fissicaudus (Rosen and Patterson, 1969, p. 401, fig. 29), the anterior end of the supramaxilla is tapered somewhat, but there is no distinct anterior process. State III was assigned to these taxa.

TABLE 35

CHARACTER #26. DENTARY TEETH

States present in the Beryciformes

I - teeth not expanded onto lateral surface of dentary (at symphysis)
II - teeth slightly expanded onto lateral surface of dentary ($\leq$ 1/2 depth at symphysis)
III - teeth greatly expanded onto lateral surface of dentary (>1/2 depth at symphysis)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	slightly expanded (= 1/2 depth)	III
			↑
	Albula	not expanded	II
			↑
Clupeomorpha	Etrumeus	not expanded	I
Osteoglossomorpha	Hiodon	not expanded	
'Protacanthopterygii'	Salvelinus	not expanded	
	Osmerus	not expanded	
	Nematonotus	not expanded	
	Sardinioides	not expanded	
	Aulopus	not expanded	
	Chlorophthalmus	slightly expanded (<1/2 depth)	
	Pattersonichthys	slightly expanded? (<1/2 depth)	
	Aulolepis	not expanded	
	Ctenothrissa	not expanded	
Acanthopterygii	Mycteroperca	not expanded	
	Morone	not expanded	
	Girella	greatly expanded (>1/2 depth)	
	Cichla	not expanded	

Remarks: None.

TABLE 36

CHARACTER #27. VENTRAL BORDER OF DENTARY

States present in the Beryciformes

I - ventral border of dentary (near symphysis) not "notched"
II - ventral border of dentary (near symphysis) distinctly "notched"

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	not notched	II
	Albula	not notched	↑
			I
Clupeomorpha	Etrumeus	not notched	
Osteoglossomorpha	Hiodon	not notched	
'Protacanthopterygii'	Salvelinus	not notched	
	Osmerus	not notched	
	Nematonotus	not notched	
	Sardinioides	not notched	
	Aulopus	not notched	
	Chlorophthalmus	not notched	
	Pattersonichthys	not notched	
	Aulolepis	weakly notched	
	Ctenothrissa	weakly notched	
Acanthopterygii	Mycteroperca	not notched	
	Morone	not notched	
	Girella	not notched	
	Cichla	not notched	

Remarks: None.

TABLE 37

CHARACTER #28. PREOPERCULAR SPINE

States present in the Beryciformes

I - prominent spine at angle of preopercle absent
II - prominent spine at angle of preopercle present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑
			I
Clupeomorpha	Etrumeus	absent	
Osteoglossomorpha	Hiodon	absent	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	absent	
	Sardinioides	absent	
	Aulopus	absent	
	Chlorophthalmus	absent	
	Pattersonichthys	absent	
	Aulolepis	absent	
	Ctenothrissa	absent	
Acanthopterygii	Mycteroperca	absent	
	Morone	absent[a]	
	Girella	absent	
	Cichla	absent	

Remarks: [a]In Morone, there is a gradation of serrations on the preopercle, those at the angle being slightly larger. No prominent spine is present, however.

TABLE 38

CHARACTER #29. CERATOHYAL FORAMEN

States present in the Beryciformes

I - ceratohyal foramen present (ceratohyal perforate)
II - ceratohyal foramen absent (ceratohyal imperforate)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑ (I-II)
			I
Clupeomorpha	Etrumeus	absent	
Osteoglossomorpha	Hiodon	absent[a]	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	absent	
	Sardinioides[b]	absent	
	Aulopus	present	
	Chlorophthalmus	absent	
	Pattersonichthys	present	
	Aulolepis	present	
	Ctenothrissa	present	
Acanthopterygii	Mycteroperca	absent	
	Morone	absent[a]	
	Girella	present	
	Cichla	absent[a]	

Remarks: [a]In Hiodon and Morone, the imperforate condition of the ceratohyal is probably due to the fact that the foramen has become confluent with the dorsal edge of the bone (the dorsal margin is distinctly notched). The same may be true in Cichla, although in this form the margin is only slightly concave.

[b]Sardinioides sp. (Gaudant, 1978b, p. 120).

TABLE 38--cont.

The distribution of states in the non-acanthopterygian members of the "out-group" suggests that the perforate condition is primitive for beryciforms, but that the imperforate condition is primitive for teleosts as a whole. Rosen and Patterson (1969, p. 408), however, present strong evidence that the presence of a ceratohyal foramen is also the primitive teleost condition. Fraser (1972a, p. 50) believes that a perforate ceratohyal is primitive for percoids.

TABLE 39

CHARACTER #30. VENTRAL BORDER OF CERATOHYAL

States present in the Beryciformes

I - ventral border of ceratohyal not strongly "notched" for articulation with heads of branchiostegal rays
II - ventral border of ceratohyal strongly "notched" for articulation with heads of branchiostegal rays (#2-4)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	not notched	II
	Albula	not notched	↑
			I
Clupeomorpha	Etrumeus	strongly notched (#1-8)	
Osteoglossomorpha	Hiodon	not notched	
'Protacanthopterygii'	Salvelinus	not notched	
	Osmerus	not notched	
	Nematonotus	not notched	
	Sardinioides	---	
	Aulopus	not notched	
	Chlorophthalmus	not notched	
	Pattersonichthys	not notched	
	Aulolepis	weakly notched (#1-5)	
	Ctenothrissa	weakly notched (#1-5)	
Acanthopterygii	Mycteroperca	not notched	
	Morone	weakly notched (#2-3)	
	Girella	weakly notched (#2)	
	Cichla	not notched	

Remarks: None.

TABLE 40

CHARACTER #31. BASIHYAL

States present in the Beryciformes

I - basihyal toothed
II - basihyal toothless
III - basihyal absent

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	toothed	III
	Albula	toothless[a]	↑
			II
Clupeomorpha	Etrumeus	toothed	↑ (I-II)
			I
Osteoglossomorpha	Hiodon	toothed	
'Protacanthopterygii'	Salvelinus	toothed	
	Osmerus	toothed	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	toothed	
	Chlorophthalmus	toothed (3 tiny teeth)	
	Pattersonichthys	---	
	Aulolepis	absent?[b]	
	Ctenothrissa	---	
Acanthopterygii	Mycteroperca	toothless	
	Morone	toothless	
	Girella	toothless	
	Cichla	toothless	

Remarks: [a]In Albula, the anterior portion of the basihyal supports a toothless tooth plate.

[b]Patterson (1964, p. 258) states that there is no sign of an ossified basihyal in Aulolepis.

TABLE 41

CHARACTER #32. NUMBER OF BRANCHIOSTEGAL RAYS

States present in the Beryciformes

I - 9 branchiostegal rays present
II - 8 branchiostegal rays present
III - 7 branchiostegal rays present
IV - 6 branchiostegal rays present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	30 rays	IV*[a]
	Albula	11/13 rays	↑
		(var. in single spec.)	III
			↑
Clupeomorpha	Etrumeus	15 rays	II
			↑ (I-II)
Osteoglossomorpha	Hiodon	9 rays	I
'Protacanthopterygii'	Salvelinus	13 rays	
	Osmerus	7 rays	
	Nematonotus	10 rays	
	Sardinioides	8 or 9 rays	
	Aulopus	14 rays	
	Chlorophthalmus	8 rays	
	Pattersonichthys	10 rays	
	Aulolepis	9 rays	
	Ctenothrissa	9 rays	
Acanthopterygii	Mycteroperca	7 rays	
	Morone	7 rays	
	Girella	6 rays	
	Cichla	5 rays	

Remarks: [a]State IV occurs only in the fossils Sphenocephalus fissicaudus (Rosen and Patterson, 1969, p. 402) and Omosoma monasteri (Patterson, 1964, p. 375).

TABLE 42

CHARACTER #33. BASIBRANCHIAL TEETH

States present in the Beryciformes

I - basibranchials toothed
II - basibranchials toothless

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	toothed	II
	Albula	toothed	↑
			I
Clupeomorpha	Etrumeus	toothed	
Osteoglossomorpha	Hiodon	toothed	
'Protacanthopterygii'	Salvelinus	toothless	
	Osmerus	toothed	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus[a]	toothless	
	Chlorophthalmus	toothless	
	Pattersonichthys	---	
	Aulolepis	toothed	
	Ctenothrissa	toothless	
Acanthopterygii	Mycteroperca	toothless	
	Morone	toothless	
	Girella	toothless	
	Cichla	toothless	

Remarks: [a]Although the basibranchials are toothless in the specimen which was examined (A. japonica), Nelson (1969a, p. 501) reports the presence of teeth on BB2 in Aulopus (no species given).

TABLE 43

CHARACTER #34. 5th CERATOBRANCHIAL (CB5)-
4th BASIBRANCHIAL (BB4) ARTICULATION

States present in the Beryciformes

I - anterior end of CB5 articulates directly with BB4
II - anterior end of CB5 does not articulate directly with BB4 (attached to BB4 by a short ligament)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	direct articulation	II
	Albula	---	↑
			I
Clupeomorpha	Etrumeus[a]	---	
Osteoglossomorpha	Hiodon	direct articulation	
'Protacanthopterygii'	Salvelinus	direct articulation	
	Osmerus	---	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	direct articulation	
	Chlorophthalmus	direct articulation	
	Pattersonichthys	---	
	Aulolepis	---	
	Ctenothrissa	---	
Acanthopterygii	Mycteroperca	---	
	Morone	indirect articulation	
	Girella	indirect articulation	
	Cichla	indirect articulation	

Remarks: [a]The anterior end of CB5 articulates directly with BB4 in Chirocentrus dorab (Nelson, 1970b, p. 7, fig. 5B), another primitive member of the Clupeomorpha.

TABLE 44

CHARACTER #35. TEETH ON 2nd PHARYNGOBRANCHIAL (PB2)

States present in the Beryciformes

I - PB2 toothed
II - PB2 toothless

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	toothed	II
	Albula	toothed	↑
			I
Clupeomorpha	Etrumeus	toothed	
Osteoglossomorpha	Hiodon	toothed	
'Protacanthopterygii'	Salvelinus	toothed	
	Osmerus	toothless	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	toothed	
	Chlorophthalmus	toothed	
	Pattersonichthys	---	
	Aulolepis	---	
	Ctenothrissa	toothed	
Acanthopterygii	Mycteroperca	toothed	
	Morone	toothed	
	Girella	toothed	
	Cichla	toothed	

Remarks: None.

TABLE 45

CHARACTER #36. TOOTH PLATE OF 4th PHARYNGOBRANCHIAL (PB4)

States present in the Beryciformes

I - tooth plate of PB4 present
II - tooth plate of PB4 absent

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	present	II
	Albula	present	↑
			I
Clupeomorpha	Etrumeus	present	
Osteoglossomorpha	Hiodon	present	
'Protacanthopterygii'	Salvelinus	present	
	Osmerus	present	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	present	
	Chlorophthalmus	present	
	Pattersonichthys	---	
	Aulolepis	present	
	Ctenothrissa	present[a]	
Acanthopterygii	Mycteroperca	present	
	Morone	present	
	Girella	present	
	Cichla	present	

Remarks: [a]Rosen (1973, p. 464, fig. 80).

TABLE 46

CHARACTER #37. NEURAL ARCH OF 1st ABDOMINAL VERTEBRA

States present in the Beryciformes

I - neural arch of 1st abdominal vertebra autogenous
II - neural arch of 1st abdominal vertebra fused

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	all 77 autog.	II
	Albula	all 71 autog.	↑
			I
Clupeomorpha	Etrumeus	1st 27 autog.	
Osteoglossomorpha	Hiodon	1st 30 autog.	
'Protacanthopterygii'	Salvelinus	1st 28 autog.	
	Osmerus	1st 28 autog.	
	Nematonotus	---	
	Sardinioides	1st few autog. (at least)	
	Aulopus	1st 10 autog.	
	Chlorophthalmus	1st autog.	
	Pattersonichthys	1st 13 autog.[a] (at least)	
	Aulolepis	1st 5 autog.	
	Ctenothrissa	1st 5 autog.	
Acanthopterygii	Mycteroperca	---	
	Morone	1st autog.	
	Girella	1st autog.	
	Cichla	1st fused	

Remarks: [a]Goody (1969).

TABLE 47

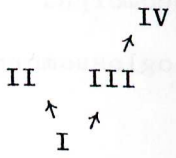
CHARACTER #38. ORIGIN OF 1st PLEURAL RIB

States present in the Beryciformes

I - pleural ribs begin on 3rd abdominal vertebra
II - pleural ribs begin on 2nd abdominal vertebra
III - pleural ribs begin on 6th abdominal vertebra
IV - pleural ribs begin on 7th abdominal vertebra

Out-group	taxon	state
Elopomorpha	Elops	begin on 5th vert.
	Albula	begin on 3rd vert.
Clupeomorpha	Etrumeus	begin on 3rd vert.
Osteoglossomorpha	Hiodon	begin on 3rd vert.
	Salvelinus	begin on 3rd vert.
	Osmerus	begin on 3rd vert.
	Nematonotus	---
	Sardinioides	---
'Protacanthopterygii'	Aulopus	begin on 2nd vert. (probably)
	Chlorophthalmus	begin on 3rd vert.
	Pattersonichthys	begin on 4th vert.
	Aulolepis	begin on 3rd vert.
	Ctenothrissa	begin on 3rd vert.
———	Mycteroperca	begin on 3rd vert. (probably)
Acanthopterygii	Morone	begin on 3rd vert.
	Girella	begin on 3rd vert.
	Cichla	begin on 3rd vert.

Character state tree



Remarks: None.

TABLE 48

CHARACTER #39. EPINEURAL RIBS

States present in the Beryciformes

I - epineural ribs present
II - epineural ribs absent

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	present	II
	Albula	present	↑
			I
Clupeomorpha	Etrumeus	present	
Osteoglossomorpha	Hiodon	present	
'Protacanthopterygii'	Salvelinus	present	
	Osmerus	absent	
	Nematonotus	present	
	Sardinioides	present	
	Aulopus	present	
	Chlorophthalmus	present	
	Pattersonichthys	present	
	Aulolepis	present	
	Ctenothrissa	present	
Acanthopterygii	Mycteroperca	---	
	Morone	absent	
	Girella	absent	
	Cichla	absent	

Remarks: None.

TABLE 49

CHARACTER #40. EPIPLEURAL RIBS

States present in the Beryciformes

I - epipleural ribs present
II - epipleural ribs absent

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	present	II
	Albula	present	↑
			I
Clupeomorpha	Etrumeus	present	
Osteoglossomorpha	Hiodon	absent ?[a]	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	present	
	Nematonotus	present	
	Sardinioides	present	
	Aulopus	present	
	Chlorophthalmus	present	
	Pattersonichthys	present	
	Aulolepis	present	
	Ctenothrissa	present	
Acanthopterygii	Mycteroperca	---	
	Morone	present	
	Girella	present	
	Cichla	present	

Remarks: [a]A small, curved, rib-like element, associated with the first pleural rib, is present in Hiodon. This element may represent a vestigial epipleural rib.

TABLE 50

CHARACTER #41. "TYMPANIC" PLATE

States present in the Beryciformes

I - tympanic plate absent
II - tympanic plate present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑
			I
Clupeomorpha	Etrumeus	absent	
Osteoglossomorpha	Hiodon	absent	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	absent	
	Chlorophthalmus	absent	
	Pattersonichthys	absent	
	Aulolepis	absent	
	Ctenothrissa	absent	
Acanthopterygii	Mycteroperca	---	
	Morone	absent	
	Girella	absent	
	Cichla	absent	

Remarks: None.

TABLE 51

CHARACTER #42. NUMBER OF SUPRANEURALS

States present in the Beryciformes

I - 3 supraneurals present
II - 1 supraneural present
III - 0 supraneurals present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	33 supraneurals	III
	Albula	17 supraneurals	↑
			II
Clupeomorpha	Etrumeus	12 supraneurals	↑
			I
Osteoglossomorpha	Hiodon	30 supraneurals	
'Protacanthopterygii'	Salvelinus	16 supraneurals	
	Osmerus	16 supraneurals	
	Nematonotus	3 supraneurals	
	Sardinioides	4 supraneurals	
	Aulopus	3 supraneurals	
	Chlorophthalmus	2 supraneurals	
	Pattersonichthys	0 supraneurals	
	Aulolepis	---	
	Ctenothrissa	---	
Acanthopterygii	Mycteroperca	---	
	Morone	0 supraneurals	
	Girella	0 supraneurals	
	Cichla	0 supraneurals	

Remarks: Supraneurals represent detached neural spines (Eaton, 1945, p. 205; Rosen and Patterson, 1969, p. 380). Predorsals (character #57) are serially homologous with the proximal radials of the dorsal fin, and may be regarded as vestigial supports of a previously elongate fin (Smith and Bailey, 1961, p. 346).

TABLE 52

CHARACTER #43. EXTRASCAPULAR

States present in the Beryciformes

I - extrascapular does not cover entire dorsal aspects of epiotic, parietal and much of supraoccipital (extrascapular usually small)

II - extrascapular does cover entire dorsal aspects of epiotic, parietal and much of supraoccipital (extrascapular large and plate-like)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	does not	II
	Albula	do not (2 exscplrs.)	↑
			I
Clupeomorpha	Etrumeus	does not	
Osteoglossomorpha	Hiodon	does not	
'Protacanthopterygii'	Salvelinus	do not (4-5 exscplrs.)	
	Osmerus	do not (5 exscplrs.)	
	Nematonotus	does not	
	Sardinioides	does not	
	Aulopus	does not	
	Chlorophthalmus	does not	
	Pattersonichthys	---	
	Aulolepis	does not	
	Ctenothrissa	---	
Acanthopterygii	Mycteroperca	do not (2 exscplrs.)	
	Morone	do not (2 exscplrs.)	
	Girella	do not (2 exscplrs.)	
	Cichla	do not (2 exscplrs.)	

Remarks: None.

TABLE 53

CHARACTER #44. CANAL IN SUPRACLEITHRUM

States present in the Beryciformes

I - dorsal portion of supracleithrum pierced by canal for lateral line
II - dorsal portion of supracleithrum not pierced by canal for lateral line

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	pierced by canal	II
	Albula	pierced by canal	↑
			I
Clupeomorpha	Etrumeus	pierced by canal	
Osteoglossomorpha	Hiodon	pierced by canal	
'Protacanthopterygii'	Salvelinus	pierced by canal	
	Osmerus	pierced by "trough"[a]	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	pierced by canal	
	Chlorophthalmus	pierced by canal	
	Pattersonichthys	---	
	Aulolepis	pierced by canal	
	Ctenothrissa	pierced by canal	
Acanthopterygii	Mycteroperca	pierced by canal	
	Morone	pierced by canal	
	Girella	pierced by canal	
	Cichla	pierced by canal	

Remarks: [a] In Osmerus, the dorsal portion of the supracleithrum bears a deep trough or channel on its lateral surface for the lateral line.

TABLE 54

CHARACTER #45. VENTRAL BORDER OF SUPRACLEITHRUM

States present in the Beryciformes

I - ventral border of supracleithrum not "notched"
II - ventral border of supracleithrum distinctly "notched"

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	not notched	II
	Albula	not notched	↑
			I
Clupeomorpha	Etrumeus	not notched	
Osteoglossomorpha	Hiodon	not notched	
'Protacanthopterygii'	Salvelinus	not notched	
	Osmerus	not notched	
	Nematonotus	not notched	
	Sardinioides	not notched	
	Aulopus	not notched	
	Chlorophthalmus	not notched	
	Pattersonichthys	not notched	
	Aulolepis	not notched	
	Ctenothrissa	not notched	
Acanthopterygii	Mycteroperca	not notched	
	Morone	not notched	
	Girella	not notched	
	Cichla	not notched	

Remarks: None.

TABLE 55

CHARACTER #46. NUMBER OF POSTCLEITHRA

States present in the Beryciformes

I - 2 postcleithra present
II - 1 postcleithrum present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	2 postcleithra	II
	Albula	3 postcleithra	↑
Clupeomorpha	Etrumeus	3 postcleithra	I
Osteoglossomorpha	Hiodon	1 postcleithrum	
'Protacanthopterygii'	Salvelinus	3 postcleithra	
	Osmerus	0 postcleithra	
	Nematonotus[a]	2 postcleithra	
	Sardinioides	2 postcleithra	
	Aulopus	2 postcleithra	
	Chlorophthalmus	2 or 3 postcleithra[b]	
	Pattersonichthys	2 postcleithra	
	Aulolepis	2 postcleithra	
	Ctenothrissa	2 postcleithra	
Acanthopterygii	Mycteroperca	2 postcleithra	
	Morone	2 postcleithra	
	Girella	2 postcleithra	
	Cichla	2 postcleithra	

Remarks: [a] Nematonotus bottae (Goody, 1969, p. 223, fig. 95).

[b] In Chlorophthalmus, there is a scale-like element at the upper end of the postcleithral series. It may represent a scale, or the most dorsal postcleithrum.

TABLE 56

CHARACTER #47. FORAMINA IN SCAPULA

States present in the Beryciformes

I - scapula with 1 foramen
II - scapula with 2 foramina

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	1 foramen[a]	II
	Albula	1 foramen[a]	↑
Clupeomorpha	Etrumeus	2 foramina	I
Osteoglossomorpha	Hiodon	1 foramen	
'Protacanthopterygii'	Salvelinus	1 foramen[a]	
	Osmerus	1 foramen[a]	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	1 foramen	
	Chlorophthalmus	1 foramen	
	Pattersonichthys	1 foramen	
	Aulolepis	1 foramen	
	Ctenothrissa	1 foramen	
Acanthopterygii	Mycteroperca	1 foramen	
	Morone	1 foramen	
	Girella	1 foramen	
	Cichla	1 foramen	

Remarks: [a] In Albula and Osmerus, the scapular "foramen" is large, and confluent with the edge of the bone.

TABLE 57

CHARACTER #48. MORPHOLOGY OF 4th ACTINOST

States present in the Beryciformes

I - 4th actinost normally developed, showing no evidence of fusion with another (5th) actinost

II - 4th actinost enlarged, showing evidence of fusion with another (5th) actinost

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	4 actnsts.; 4th nml.	II
	Albula	4 actnsts.; 4th nml.	↑
			I
Clupeomorpha	Etrumeus	? (homology of actnsts. not clear)	
Osteoglossomorpha	Hiodon	4 actnsts.; 4th nml.	
'Protacanthopterygii'	Salvelinus	4 actnsts.; 4th nml.	
	Osmerus	4 actnsts.; 4th nml.	
	Nematonotus	---	
	Sardinioides	4 actnsts.; 4th nml.	
	Aulopus	4 actnsts.; 4th nml.	
	Chlorophthalmus	4 actnsts.; 4th nml.	
	Pattersonichthys	4 actnsts.; 4th nml.	
	Aulolepis	4 actnsts.; 4th nml.	
	Ctenothrissa	4 actnsts.; 4th nml.	
Acanthopterygii	Mycteroperca	4 actnsts.; 4th nml.	
	Morone	4 actnsts.; 4th nml.	
	Girella	4 actnsts.; 4th nml.	
	Cichla	4 actnsts.; 4th nml.	

Remarks: None.

TABLE 58

CHARACTER #49. ANTERIOR PROCESS OF PELVIC BONE

States present in the Beryciformes

I - anterior process of pelvic bone absent
II - anterior process of pelvic bone present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	probably absent[a]	↑
			I
Clupeomorpha	Etrumeus	absent	
Osteoglossomorpha	Hiodon	absent	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	absent	
	Chlorophthalmus	absent	
	Pattersonichthys	---	
	Aulolepis	---	
	Ctenothrissa	---	
Acanthopterygii	Mycteroperca	present	
	Morone	present	
	Girella	absent	
	Cichla	present	

Remarks: [a]In Albula, the posteromedial portion of the pelvic bone bears a long, slender, well-ossified process. Although this process may be homologous with the anterior process of other forms, it appears to be more medially than anteriorly directed. Elops does not possess an anterior process, but an indistinct medial process is probably present.

TABLE 59

CHARACTER #50. LATERAL PROCESS OF PELVIC BONE

States present in the Beryciformes

I - lateral process of pelvic bone absent
II - lateral process of pelvic bone present; weakly developed
III - lateral process of pelvic bone present; strongly developed

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	III
	Albula	absent	↑
			II
Clupeomorpha	Etrumeus	absent	↑
			I
Osteoglossomorpha	Hiodon	absent	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	present; strongly developed[a]	
	Chlorophthalmus	present; strongly developed	
	Pattersonichthys	absent	
	Aulolepis	---	
	Ctenothrissa	---	
Acanthopterygii	Mycteroperca	present; weakly developed	
	Morone	absent	
	Girella	absent	
	Cichla	present; weakly developed	

Remarks: [a]The lateral process in Aulopus is entirely cartilaginous.

TABLE 60

CHARACTER #51. POSTERIOR PROCESS OF PELVIC BONE

States present in the Beryciformes

I - distal portion of posterior process of pelvic bone not expanded into a distinct flange or plate
II - distal portion of posterior process of pelvic bone expanded into a distinct flange or plate

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	post. pr. absent	II
	Albula	post. pr. absent	↑
			I
Clupeomorpha	Etrumeus	not expanded	
Osteoglossomorpha	Hiodon	not expanded[a]	
'Protacanthopterygii'	Salvelinus	not expanded	
	Osmerus	post. pr. absent	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	not expanded	
	Chlorophthalmus	not expanded	
	Pattersonichthys	not expanded[b]	
	Aulolepis	not expanded	
	Ctenothrissa	not expanded	
Acanthopterygii	Mycteroperca	not expanded	
	Morone	weakly expanded	
	Girella	not expanded	
	Cichla	not expanded	

Remarks: [a]The "posterior process" of the pelvic bone in Hiodon may not be homologous with that of other forms, since it is an unpaired, median element. Furthermore, it is not coossified with the pelvic bones--rather, it is bound to them by connective tissue.

[b]Gaudant (personal communication).

TABLE 61

CHARACTER #52. PELVIC FIN SPINE

States present in the Beryciformes

I - pelvic fin spine absent
II - pelvic fin spine present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑
Clupeomorpha	Etrumeus	absent	I
Osteoglossomorpha	Hiodon	absent	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	absent	
	Sardinioides	absent	
	Aulopus	absent	
	Chlorophthalmus	absent	
	Pattersonichthys	absent	
	Aulolepis	absent	
	Ctenothrissa	absent	
Acanthopterygii	Mycteroperca	present	
	Morone	present	
	Girella	present	
	Cichla	present	

Remarks: A structure at the base of the first ray of the pelvic fin, termed the "splint" by Gosline (1961, p. 18) and the "rudimentary spine" by Patterson (1964, p. 444), is present in many of the members of the "out-group" (Elops, Albula, Hiodon, Salvelinus, Osmerus, Sardinioides, Pattersonichthys and several species of Ctenothrissa). A pelvic splint is also present in the fossil Sphenocephalus fissicaudus (Beryciformes) (Rosen and Patterson, 1969, p. 404). The splint is not considered to represent a fin spine (or a lepidotrichium), because it is asymmetrical to the axis of the fin.

TABLE 62

CHARACTER #53. NUMBER OF PELVIC FIN RAYS

States present in the Beryciformes

I - 8 pelvic rays
II - 7 pelvic rays
III - 6 pelvic rays
IV - 5 pelvic rays
V - 3 or fewer pelvic rays
VI - 10 or more pelvic rays

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	13/14 rays (var. in single spec.)	V
	Albula	10 rays	IV
Clupeomorpha	Etrumeus	8 rays	III
Osteoglossomorpha	Hiodon	7 rays	(II-III) II VI
'Protacanthopterygii'	Salvelinus	8 rays	I*[a]
	Osmerus	8 rays	
	Nematonotus	9 rays[b]	
	Sardinioides	8 rays	
	Aulopus	9 rays	
	Chlorophthalmus	9 rays	
	Pattersonichthys	8 rays[c]	
	Aulolepis	8 rays[d]	
	Ctenothrissa	8 rays	
Acanthopterygii	Mycteroperca	5 rays	
	Morone	5 rays	
	Girella	5 rays	
	Cichla	5 rays	

Remarks: [a]State I occurs only in the fossils Homonotichthys dorsalis and H. pulchellus (Patterson, 1964, p. 297 and p. 301, resp.).

[b]Gaudant (1978b, p. 120).

[c]Gaudant (1978a, p. 202).

[d]Gaudant (personal communication).

TABLE 63

CHARACTER #54. RADIALS OF PELVIC FIN

States present in the Beryciformes

I - pelvic fin radial(s) present; outermost radial without hook-like process
II - pelvic fin radials present; outermost radial with hook-like process[a]
III - pelvic fin radials absent

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	present; w/o pr.	II III
	Albula	present; w/o pr.	I
Clupeomorpha	Etrumeus	present; w/o pr.	
Osteoglossomorpha	Hiodon	present; w/o pr.	
	Salvelinus	present; w/o pr.	
	Osmerus	present; w/o pr.	
'Protacanthopterygii'	Nematonotus	---	
	Sardinioides	---	
	Aulopus	present; w/o pr.	
	Chlorophthalmus	present; w/o pr.	
	Pattersonichthys	---	
	Aulolepis	---	
	Ctenothrissa	---	
Acanthopterygii	Mycteroperca	---	
	Morone	absent	
	Girella	absent	
	Cichla	absent	

Remarks: [a]The process projects into the base of the pelvic fin spine.

TABLE 64

CHARACTER #55. DORSAL FIN SPINES

States present in the Beryciformes

I - dorsal fin spines absent
II - dorsal fin spine(s) present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑
			I
Clupeomorpha	Etrumeus	absent	
Osteoglossomorpha	Hiodon	absent	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	---	
	Sardinioides	present[a]	
	Aulopus	absent	
	Chlorophthalmus	absent	
	Pattersonichthys	present	
	Aulolepis	absent	
	Ctenothrissa	absent	
Acanthopterygii	Mycteroperca	present	
	Morone	present	
	Girella	present	
	Cichla	present	

Remarks: [a]Gaudant (1977, p. 2480).

TABLE 65

CHARACTER #56. PROJECTION OF DORSAL FIN SPINES

States present in the Beryciformes

I - dorsal fin spines do not project strongly in opposite directions
II - dorsal fin spines do project strongly in opposite directions

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	--- (absent)	II
	Albula	--- (absent)	↑
Clupeomorpha	Etrumeus	--- (absent)	I
Osteoglossomorpha	Hiodon	--- (absent)	
	Salvelinus	--- (absent)	
	Osmerus	--- (absent)	
	Nematonotus	--- (no info.)	
'Protacanthopterygii'	Sardinioides	--- (only one spine present[a])	
	Aulopus	--- (absent)	
	Chlorophthalmus	--- (absent)	
	Pattersonichthys	--- (only one spine present)	
	Aulolepis	--- (absent)	
	Ctenothrissa	--- (absent)	
Acanthopterygii	Mycteroperca	do not	
	Morone	do not	
	Girella	do not	
	Cichla	do not	

Remarks: [a]Gaudant (1977, p. 2480).

The fact that the elements of the dorsal fin in the non-acanthopterygian members of the "out-group" are never alternately inclined to the right and left indicates that state I is primitive.

TABLE 66

CHARACTER #57. NUMBER OF PREDORSALS

States present in the Beryciformes

I - 0 predorsals present
II - 2 predorsals present
III - 3 predorsals present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	0 predorsals	III
	Albula	0 predorsals	↑
Clupeomorpha	Etrumeus	0 predorsals	II ↑ (I-II)*[a]
Osteoglossomorpha	Hiodon	0 predorsals	I
'Protacanthopterygii'	Salvelinus	0 predorsals	
	Osmerus	0 predorsals	
	Nematonotus	0 predorsals	
	Sardinioides	0 predorsals	
	Aulopus	0 predorsals	
	Chlorophthalmus	0 predorsals	
	Pattersonichthys	3 predorsals	
	Aulolepis	---	
	Ctenothrissa[b]	3 predorsals	
Acanthopterygii	Mycteroperca	---	
	Morone	3 predorsals	
	Girella	3 predorsals	
	Cichla	2 predorsals	

Remarks: [a] Intraspecific variation between states I and II occurs only in the fossil Hoplopteryx lewesiensis (Patterson, 1964, p. 320).

[b] Ctenothrissa signifer and C. vexillifer (Gaudant, personal communication).

TABLE 67

CHARACTER #58. ANAL FIN SPINES

States present in the Beryciformes

I - anal fin spines absent
II - anal fin spine(s) present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑
			I
Clupeomorpha	Etrumeus	absent	
Osteoglossomorpha	Hiodon	absent	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	---	
	Sardinioides	present ?[a]	
	Aulopus	absent	
	Chlorophthalmus	absent	
	Pattersonichthys	present	
	Aulolepis	absent	
	Ctenothrissa	absent	
Acanthopterygii	Mycteroperca	present	
	Morone	present	
	Girella	present	
	Cichla	present	

Remarks: [a]Gaudant (1977, pp. 2479-2481).

TABLE 68

CHARACTER #59. PENULTIMATE ANAL FIN SPINE

States present in the Beryciformes

I - penultimate anal fin spine not enlarged
II - penultimate anal fin spine enlarged[a] (4th of 5 spines)
III - penultimate anal fin spine enlarged[a] (3rd of 4 spines)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	---(absent)	III
	Albula	---(absent)	↑
			II*[b]
Clupeomorpha	Etrumeus	---(absent)	↑
			I
Osteoglossomorpha	Hiodon	---(absent)	
'Protacanthopterygii'	Salvelinus	---(absent)	
	Osmerus	---(absent)	
	Nematonotus	---(no info.)	
	Sardinioides	---(only one spine present?[c])	
	Aulopus	---(absent)	
	Chlorophthalmus	---(absent)	
	Pattersonichthys	---(only one spine present)	
	Aulolepis	---(absent)	
	Ctenothrissa	---(absent)	
Acanthopterygii	Mycteroperca	spine not enlarged	
	Morone	spine enlarged (2nd of 3 spines)	
	Girella	spine not enlarged	
	Cichla	spine not enlarged	

Remarks: [a]Enlarged = thicker, more robust than last spine.

[b]State II occurs only in the fossil Stichocentrus liratus (Patterson, 1967, p. 94).

[c]Gaudant (1977, pp. 2479-2481).

TABLE 68--cont.

The fact that none of the elements of the anal fin in the non-acanthopterygian members of the "out-group" is enlarged indicates that state I is primitive.

The sequence I → II* → III seems more probable than I → III → II*. The first alternative implies that the first anal spine of Stichocentrus has been lost. This seems probable in view of its extremely small size (Patterson, 1967, p. 94). Furthermore, since loss of anterior elements in the dorsal fin is known to occur (Smith and Bailey, 1961), it seems reasonable to assume that the same situation may occur in the anal fin.

TABLE 69

CHARACTER #60. 2nd URAL CENTRUM (U2)

States present in the Beryciformes

I - U2 autogenous (with respect to PU1 + U1)
II - U2 fused (to PU1 + U1)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	autogenous	II
	Albula	autogenous	↑ (I-II)
			I
Clupeomorpha	Etrumeus	fused (to U1)	
Osteoglossomorpha	Hiodon	autogenous	
'Protacanthopterygii'	Salvelinus	autogenous	
	Osmerus	fused	
	Nematonotus	autogenous	
	Sardinioides	autogenous	
	Aulopus	autogenous	
	Chlorophthalmus	autogenous	
	Pattersonichthys	autogenous	
	Aulolepis	autogenous	
	Ctenothrissa	autogenous	
Acanthopterygii	Mycteroperca	fused	
	Morone	fused	
	Kuhlia	fused	
	Girella	fused	
	Cichla	fused	

Remarks: None.

TABLE 70

CHARACTER #61. NEURAL AND HEMAL SPINES OF 4th AND 5th PREURAL VERTEBRAE (PU4 AND PU5)

States present in the Beryciformes

I - distal portions of neural and hemal spines of PU4 and PU5 not expanded
II - distal portions of neural and hemal spines of PU4 (but not PU5) expanded
III - distal portions of neural and hemal spines of PU4 and PU5 expanded

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	not expanded	III
	Albula	not expanded	↑
			II*[a]
Clupeomorpha	Etrumeus	not expanded	↑
			I
Osteoglossomorpha	Hiodon	not expanded	
'Protacanthopterygii'	Salvelinus	not expanded	
	Osmerus	not expanded	
	Nematonotus	not expanded	
	Sardinioides	not expanded	
	Aulopus	not expanded	
	Chlorophthalmus	not expanded	
	Pattersonichthys	not expanded	
	Aulolepis	---	
	Ctenothrissa	---	
Acanthopterygii	Mycteroperca	not expanded	
	Morone	not expanded	
	Kuhlia	not expanded	
	Girella	not expanded[b]	
	Cichla	not expanded	

Remarks: [a]State II occurs only in the fossil Stichocentrus liratus (Patterson, 1968, p. 77).

[b]The absence of a hemal spine on PU4 in the specimen of Girella nigricans which was examined probably represents an anomaly.

TABLE 71

CHARACTER #62. HEMAL ARCH OF 3rd PREURAL VERTEBRA (PU3)

States present in the Beryciformes

I - hemal arch of PU3 autogenous
II - hemal arch of PU3 fused

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	autogenous	II
	Albula	autogenous	↑ (I-II)*[a]
			I
Clupeomorpha	Etrumeus	fused	
Osteoglossomorpha	Hiodon	fused	
'Protacanthopterygii'	Salvelinus	autogenous	
	Osmerus	autogenous	
	Nematonotus	autogenous	
	Sardinioides	---	
	Aulopus	autogenous	
	Chlorophthalmus	autogenous[b]	
	Pattersonichthys	autogenous	
	Aulolepis	autogenous/fused (intrasp. var.)	
	Ctenothrissa	fused	
Acanthopterygii	Mycteroperca	autogenous	
	Morone	autogenous	
	Kuhlia	autogenous	
	Girella	autogenous	
	Cichla	fused	

Remarks: [a]Intraspecific variation between states I and II occurs only in the fossil Berycopsis elegans (Patterson, 1968, p. 57).

[b]Gaudant (personal communication).

TABLE 72

CHARACTER #63. LENGTH OF NEURAL SPINE OF 2nd PREURAL VERTEBRA (PU2)

States present in the Beryciformes

I - neural spine of PU2 1/2 length neural spine of PU3
II - neural spine of PU2 crest-like (≤ 1/3 length neural spine of PU3)
III - neural spine of PU2 complete (= length neural spine of PU3)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops Albula	= 1/2 length complete	II III I*[a] (I-III)*[b]
Clupeomorpha	Etrumeus	complete	
Osteoglossomorpha	Hiodon	complete	
'Protacanthopterygii'	Salvelinus	complete	
	Osmerus	complete	
	Nematonotus	slightly >1/2 length	
	Sardinioides	slightly >1/2 length	
	Aulopus	slightly >1/2 length	
	Chlorophthalmus	= 1/2 length	
	Pattersonichthys	crest-like (1/3)	
	Aulolepis	= 1/2 length	
	Ctenothrissa	= 1/2 length	
Acanthopterygii	Mycteroperca	crest-like (1/4)	
	Morone	crest-like (1/3)	
	Kuhlia	crest-like (1/3)	
	Girella	crest-like (1/4)[c]	
	Cichla	crest-like (1/4)	

Remarks: [a]State I occurs only in the fossils Aipichthys velifer and Pharmacichthys venenifer (Patterson, 1968, p. 63 and p. 65).

[b]Intraspecific variation between states I and III occurs only in the fossil Aipichthys minor (Patterson, 1968, pp. 63-65, figs. 11A-C).

[c]The specimen of Girella nigricans which was examined is perhaps anomalous in that the neural spine of PU3 is crest-like (1/4 the length of the neural spine of PU4). In this specimen, the neural crests of both PU2 and PU3 are 1/4 the length of the neural spine of PU4.

TABLE 72--cont.

Patterson (1968, pp. 88-89) discusses the ways in which a complete neural spine on PU2 can develop: (1) through elongation of a short neural spine (i.e., a spine 1/2 the length of that of PU3), (2) through fusion of the first epural with a low neural crest on PU2 and (3) through fusion between the second and third preural centra (the neural spine of PU3 would then appear to be that of PU2).

There is no evidence (such as the partial or complete doubling of the neural or hemal spine of the centrum anterior to PU1) that the complete neural spine of PU2 in some beryciforms arose through a fusion between the second and third preural centra (possibility 3). With respect to the first two possibilities, it is important to note that all beryciforms with a complete neural spine on PU2 have three epurals, except Sphenocephalus fissicaudus (Patterson, 1968, p. 62, fig. 10), S. brachypterygius (Rosen and Patterson, 1969, p. 405, fig. 35) and possibly Omosoma simum (Rosen and Patterson, 1969, p. 369). These latter forms have only two epurals. Since the presence of three epurals is undoubtedly primitive for beryciforms (the myctophoids, ctenothrissiforms and the pattersonichthyiform of the "out-group" all possess three epurals), there is strong evidence that the complete neural spine of PU2 in those beryciforms with three epurals arose through elongation of a short neural spine (possibility 1). This interpretation is further supported by the fact that intraspecific variation between states I and III occurs in Aipichthys minor.

Whether the complete neural spine of PU2 in those forms with only two epurals is primary (i.e., the result of elongation of a short neural spine followed by the loss of an epural) or secondary (i.e., the result of fusion of the first epural with a low neural crest on PU2) is questionable. Rosen and Patterson (1969, pp. 367-368) believe that the spine in Sphenocephalus is primary. Fraser (1972b, pp. 234-235), however, discusses the weaknesses of Rosen and Patterson's argument, and concludes that no final decision concerning the nature of the neural spine of PU2 in Sphenocephalus can be reached at this time. Since I agree with Fraser's conclusion, I have not assigned an additional character state to represent the condition present in Sphenocephalus.

TABLE 73

CHARACTER #64. NEURAL ARCH OF 2nd PREURAL VERTEBRA (PU2)

States present in the Beryciformes

I - neural arch of PU2 autogenous
II - neural arch of PU2 fused

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	autogenous	II
	Albula	autogenous	↑ (I-II)
Clupeomorpha	Etrumeus	fused	I
Osteoglossomorpha	Hiodon	fused	
'Protacanthopterygii'	Salvelinus	autogenous	
	Osmerus	autogenous	
	Nematonotus	autogenous	
	Sardinioides	---	
	Aulopus	autogenous	
	Chlorophthalmus	fused	
	Pattersonichthys	autogenous	
	Aulolepis	fused	
	Ctenothrissa	fused	
Acanthopterygii	Mycteroperca	fused	
	Morone	fused	
	Kuhlia	fused	
	Girella	fused	
	Cichla	fused	

Remarks: None.

TABLE 74

CHARACTER #65. STEGURAL

States present in the Beryciformes

I - stegural autogenous (with respect to underlying centra)
II - stegural fused (to underlying centra)

	Out-group taxon	state	Character state tree
Elopomorpha	Elops	stegural absent	II
	Albula	stegural absent	↑ (I-II)
Clupeomorpha	Etrumeus	stegural absent	I
Osteoglossomorpha	Hiodon	stegural absent	
'Protacanthopterygii'	Salvelinus	stegural absent	
	Osmerus	fused	
	Nematonotus	autogenous	
	Sardinioides	---	
	Aulopus	autogenous	
	Chlorophthalmus	autogenous[a]	
	Pattersonichthys	autogenous	
	Aulolepis	autogenous	
	Ctenothrissa	autogenous	
Acanthopterygii	Mycteroperca	autogenous	
	Morone	autogenous	
	Kuhlia	autogenous	
	Girella	autogenous	
	Cichla	autogenous	

Remarks: [a]Gaudant (personal communication).

TABLE 75

CHARACTER #66. NUMBER OF URONEURALS

States present in the Beryciformes

I - single pair of uroneurals present; not reduced
II - single pair of uroneurals present; strongly reduced[a]
III - uroneurals absent

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	3 pr.	III
	Albula	2 pr.	↑
			II
Clupeomorpha	Etrumeus	2 pr.	↑
			I
Osteoglossomorpha	Hiodon	3 pr.	
'Protacanthopterygii'	Salvelinus	3/4 pr. (intrasp. var.)	
	Osmerus	2 pr.; not redcd.	
	Nematonotus	1 pr.; not redcd.	
	Sardinioides	1 pr.; not redcd.	
	Aulopus	1 pr.; not redcd.	
	Chlorophthalmus	1 pr.; not redcd.	
	Pattersonichthys	1 pr.; not redcd.	
	Aulolepis	1 pr.; not redcd.	
	Ctenothrissa	1 pr.; not redcd.	
Acanthopterygii	Mycteroperca	absent	
	Morone	1 pr.; not redcd.	
	Kuhlia	1 pr.; not redcd.	
	Girella	absent	
	Cichla	absent	

Remarks: [a]Strongly reduced = uroneurals barely extend past the tip of the spinous process of the stegural.

TABLE 76

CHARACTER #67. PARHYPURAL

States present in the Beryciformes

I - parhypural autogenous (with respect to hypural 1)
II - parhypural fused (to hypural 1)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	autogenous	II
	Albula	autogenous	↑
			I
Clupeomorpha	Etrumeus	autogenous	
Osteoglossomorpha	Hiodon	autogenous	
'Protacanthopterygii'	Salvelinus	autogenous	
	Osmerus	autogenous	
	Nematonotus	autogenous	
	Sardinioides	autogenous	
	Aulopus	autogenous	
	Chlorophthalmus	autogenous	
	Pattersonichthys	autogenous	
	Aulolepis	autogenous	
	Ctenothrissa	autogenous	
Acanthopterygii	Mycteroperca	autogenous	
	Morone	autogenous	
	Kuhlia	autogenous	
	Girella	autogenous	
	Cichla	autogenous	

Remarks: None.

TABLE 77

CHARACTER #68. NUMBER OF PRINCIPAL CAUDAL RAYS

States present in the Beryciformes

I - 19 principal rays (inner 17 branched)
II - 18 principal rays (inner 16 branched)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	19 (17)	II
	Albula	19 (17)	↑
Clupeomorpha	Etrumeus	19 (17)	I
Osteoglossomorpha	Hiodon	18 (16)	
	Salvelinus	19 (17)	
	Osmerus	19 (17)	
	Nematonotus	19 (17)	
	Sardinioides	19 (17)	
'Protacanthopterygii'	Aulopus	19 (17)	
	Chlorophthalmus	19 (17)	
	Pattersonichthys	19 (17)	
	Aulolepis	---	
	Ctenothrissa	19 (17)	
	Mycteroperca	17 (15)	
	Morone	17 (15)	
Acanthopterygii	Kuhlia	17 (15)	
	Girella	17 (15)	
	Cichla	16 (14)	

Remarks: None.

TABLE 78

CHARACTER #69. BODY ARMOR

States present in the Beryciformes

I - scales of body not greatly enlarged and thickened (no armor)
II - scales of body very large and thick (armor present)

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	no armor	II
	Albula	no armor	↑
Clupeomorpha	Etrumeus	no armor	I
Osteoglossomorpha	Hiodon	no armor	
'Protacanthopterygii'	Salvelinus	no armor	
	Osmerus	no armor	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	no armor	
	Chlorophthalmus	no armor[a]	
	Pattersonichthys	no armor	
	Aulolepis	no armor	
	Ctenothrissa	no armor	
Acanthopterygii	Mycteroperca	no armor	
	Morone	no armor	
	Girella	no armor	
	Cichla	no armor	

Remarks: [a]Goody (1969).

TABLE 79

CHARACTER #70. VENTRAL RIDGE SCALES (SCUTES)

States present in the Beryciformes

I - ventral ridge scales absent
II - ventral ridge scales present

Out-group	taxon	state	Character state tree
Elopomorpha	Elops	absent	II
	Albula	absent	↑
			I
Clupeomorpha	Etrumeus	absent	
Osteoglossomorpha	Hiodon	absent[a]	
'Protacanthopterygii'	Salvelinus	absent	
	Osmerus	absent	
	Nematonotus	---	
	Sardinioides	---	
	Aulopus	absent	
	Chlorophthalmus	absent	
	Pattersonichthys	absent[b]	
	Aulolepis	---	
	Ctenothrissa	absent	
Acanthopterygii	Mycteroperca	absent	
	Morone	absent	
	Girella	absent	
	Cichla	absent	

Remarks: [a]In Hiodon, the ventral midline of the body is keeled. Scales cover the lateral aspects of this keel. Median ventral ridge scales comparable to those of beryciforms are not present in Hiodon.

[b]Gaudant (personal communication).

TABLE 80

CHARACTERS AND SPECIES IN WHICH INTRASPECIFIC VARIATION OCCURS

The categories < 50%, = 50% and > 50% refer to the frequency of occurrence of the most derived state. + denotes a fossil taxon.

< 50%	= 50%	> 50%
60 - +Aipichthys minor (Patterson, 1968, p. 63)	6 - Hoplostethus mediterraneus	6 - Diretmus argenteus
63 - +Aipichthys minor (Patterson, 1968, p. 63)	29 - Anoplogaster cornuta	21 - Monocentris japonicus
64 - Hoplostethus mediterraneus	29 - Stephanoberyx monae	22 - Monocentris japonicus
	29 - Scopelogadus unispinus	32 - Anoplogaster cornuta
	31 - Adioryx diadema	32 - Stephanoberyx monae
	53 - Photoblepharon palpebratus	
	60 - Holocentrus rufus	
	60 - Ostichthys trachypoma	
	60 - +Stichocentrus liratus (Patterson, 1968, p. 77)	
	62 - +Berycopsis elegans (Patterson, 1968, p. 57)	
	65 - Ostichthys trachypoma	

Note: Intraspecific variation also occurs in character 57 (+Hoplopteryx lewesiensis), but no information on the frequency of occurrence of the states involved is available (Patterson, 1964, p. 320).

TABLE 81

TYPES OF CHARACTER STATE TREES ENCOUNTERED IN THIS INVESTIGATION

Number of States	Number of Characters	Character State Tree
		UNIDIRECTIONAL
2	52	I → II
3	9	I → II → III
4	1	I → II → III → IV
5	1	I → II → III → IV → V
		MULTIDIRECTIONAL
3	4	I → II ↘ III
4	2	I → II ↘ III → IV
6	1	I → II → III → IV → V ↘ VI
166	70	
(70 primitive + 96 derived)		

TABLE 82

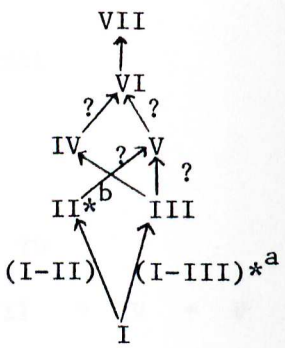
EXAMPLE OF A CIRCULAR CHARACTER STATE TREE
(Number of Hypurals)

States present in the Beryciformes

I - 6 bones (H1, H2, H3, H4, H5, H6)
II - 5 bones (H1, H2, H3+H4, H5, H6)
III - 5 bones (H1, H2, H3, H4, H5, --)
IV - 4 bones (H1+H2, H3, H4, H5, --)
V - 4 bones (H1, H2, H3+H4, H5, --)
VI - 3 bones (H1+H2, H3+H4, H5, --)
VII - 2 bones (H1+H2, H3+H4+H5, --)

Out-group	taxon	state
Elopomorpha	Elops	7 (H1 - H7)
	Albula	6 (H1 - H6)
Clupeomorpha	Etrumeus	6 (H1 - H6)
Osteoglossomorpha	Hiodon	7 (H1 - H7)
'Protacanthopterygii'	Salvelinus	6 (H1 - H6)
	Osmerus	6 (H1 - H6)
	Nematonotus	6 (H1 - H6)
	Sardinioides	6 (H1 - H6)
	Aulopus	6 (H1 - H6)
	Chlorophthalmus	6 (H1 - H6)
	Pattersonichthys	6 (H1 - H6)
	Aulolepis	6 (H1 - H6)
	Ctenothrissa	6 (H1 - H6)
Acanthopterygii	Mycteroperca	5 (H1 - H5)
	Morone	5 (H1 - H5)
	Girella	5 (H1 - H5)
	Cichla	5 (H1 - H5)

Character state tree



Remarks: [a]Intraspecific variation between states I and III occurs only in the fossil Pycnosteroides levispinosus (Patterson, 1968, p. 66).

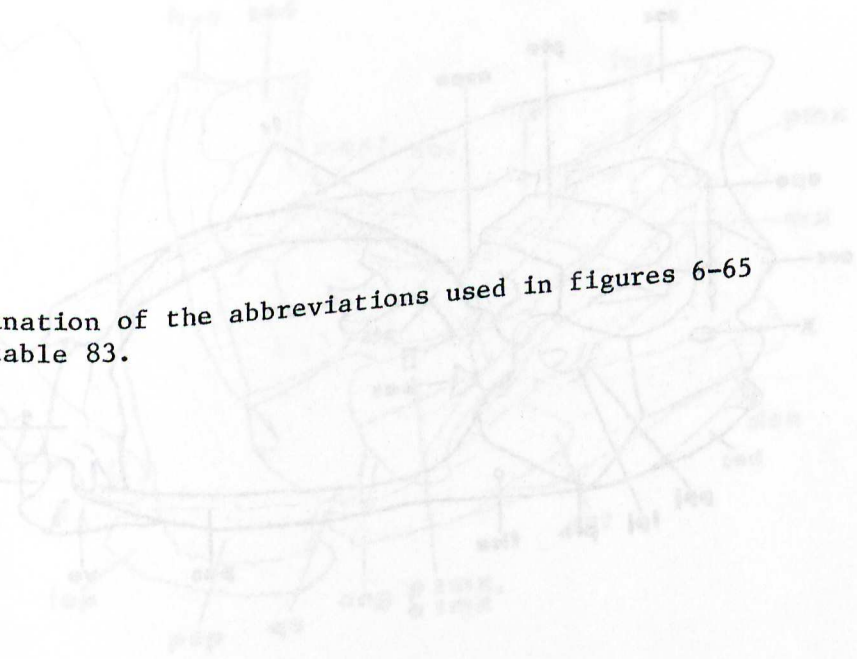
[b]State II occurs only in the fossil Caproberyx superbus (Patterson, 1968, p. 77).

TABLE 82--cont.

The number of hypurals in the caudal skeleton is a character which was analyzed but which was not included in the data set because its tree is circular (the Combinatorial Method does not permit the use of circular character state trees). State V, for example, could have been derived from state II through loss of the sixth hypural or from state III through fusion of the third and fourth hypurals. Both possibilities seem equally probable.

APPENDIX II

ANATOMICAL ILLUSTRATIONS



An explanation of the abbreviations used in figures 6-65 is given in table 83.

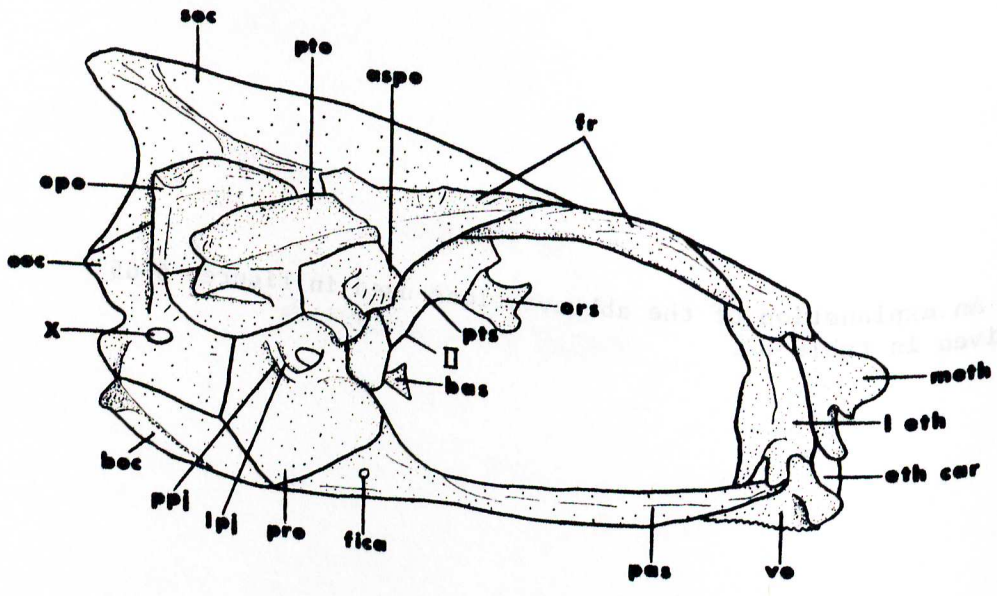


Fig. 6.--Polymixia lowei. Neurocranium, lateral view, x 3.1.

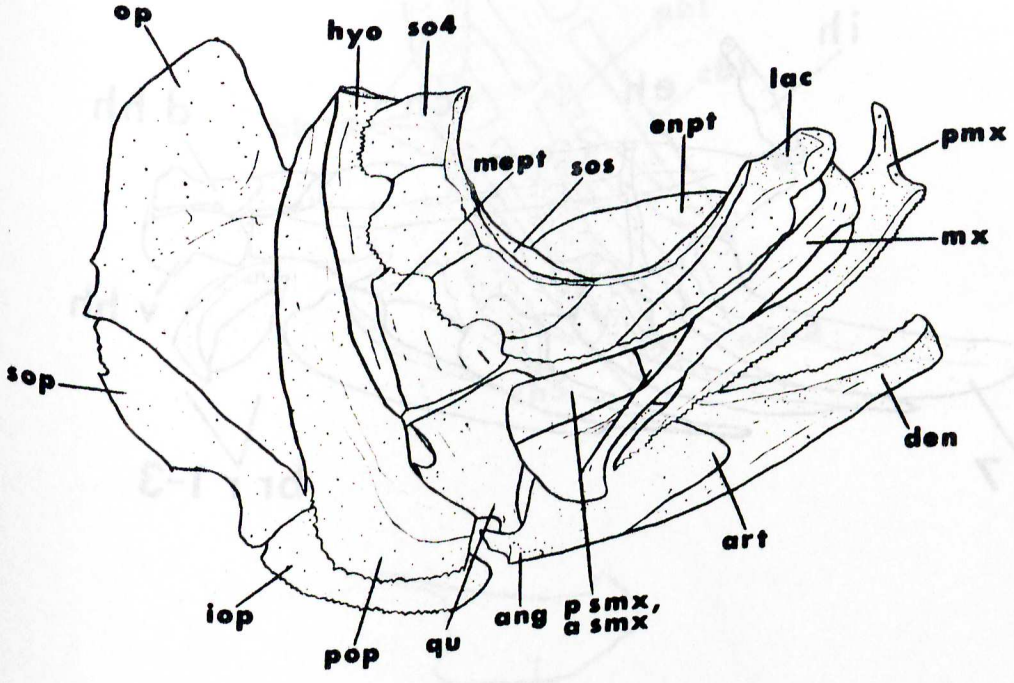


Fig. 7.--Polymixia lowei. Face bones, lateral view, x 1.9.

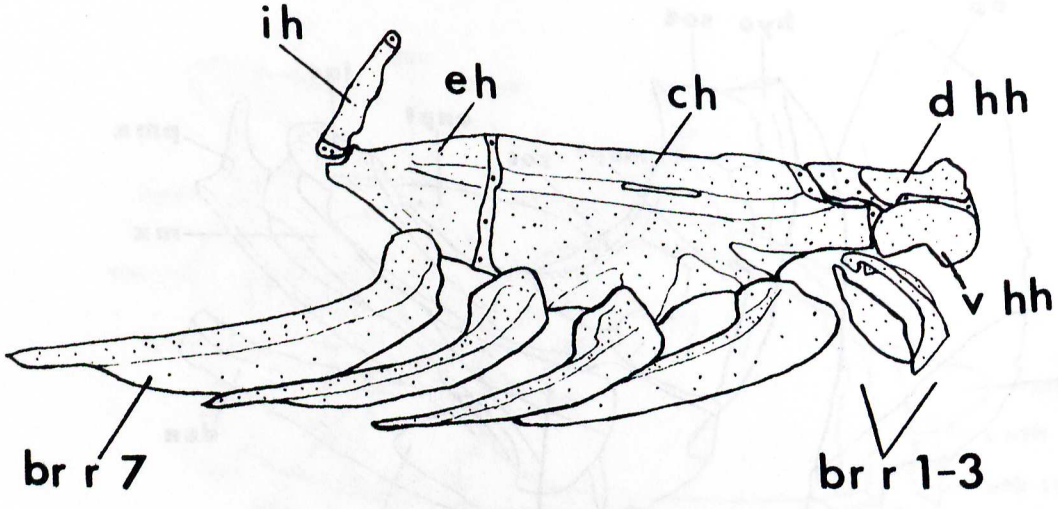


Fig. 8.--Polymixia lowei. Right hyoid arch and branchiostegal rays, lateral view, x 6.

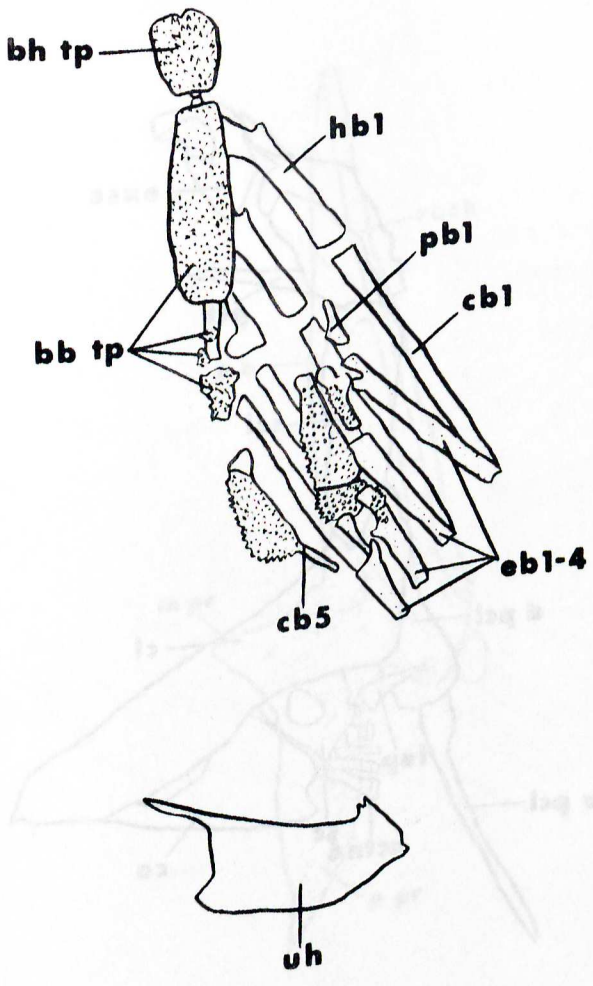


Fig. 9.--Polymixia lowei. Above: branchial arches of right side, dorsal view, x 5.4. Below: urohyal, lateral view, x 5.4.

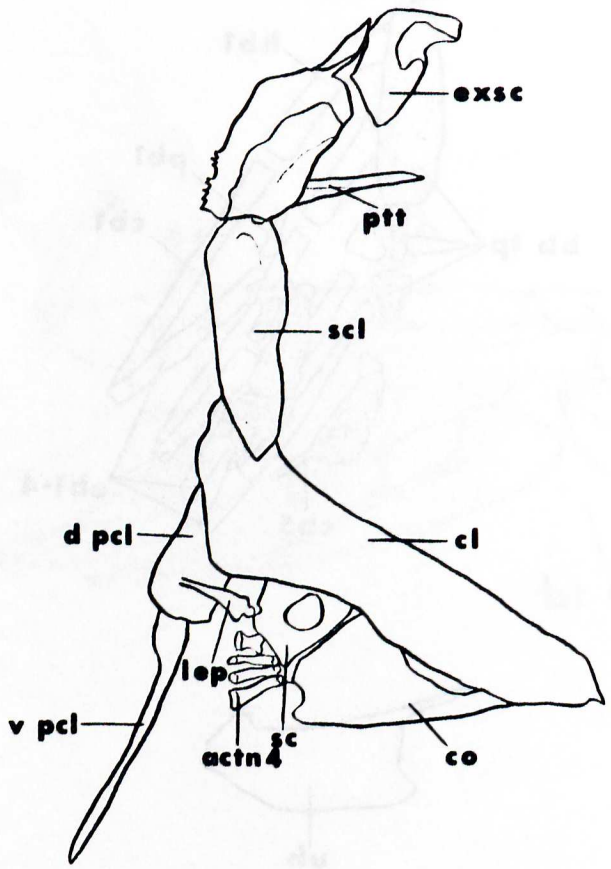


Fig. 10.--Polymixia lowei. Right pectoral girdle, lateral view, x 4.8.

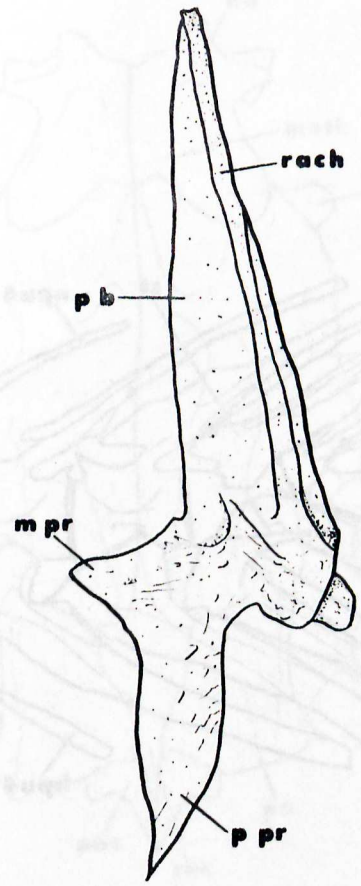


Fig. 11.--Polymixia lowei. Right pelvic girdle, dorsal view, x 6.7.

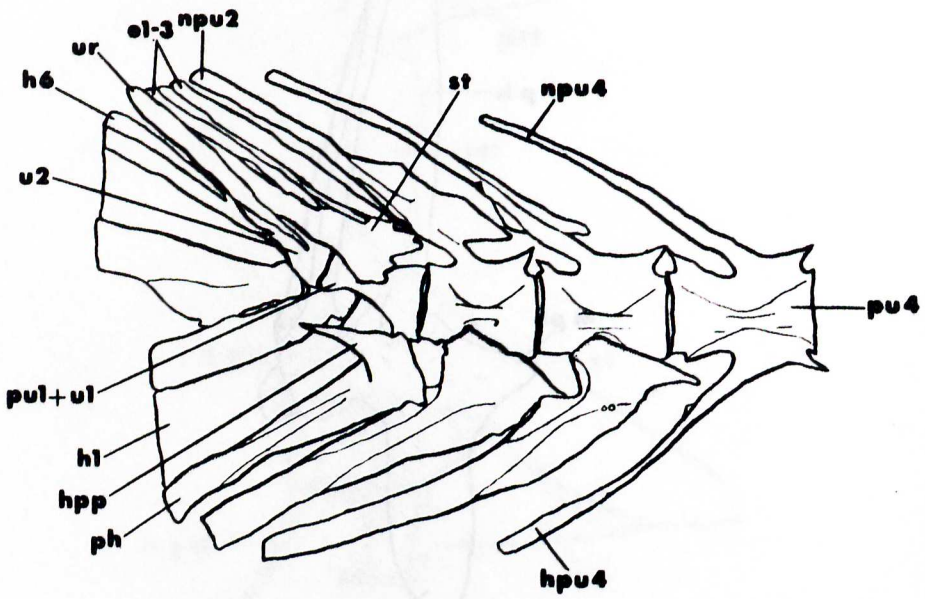


Fig. 12.--Polymixia lowei. Caudal skeleton, lateral view, x 8.5.

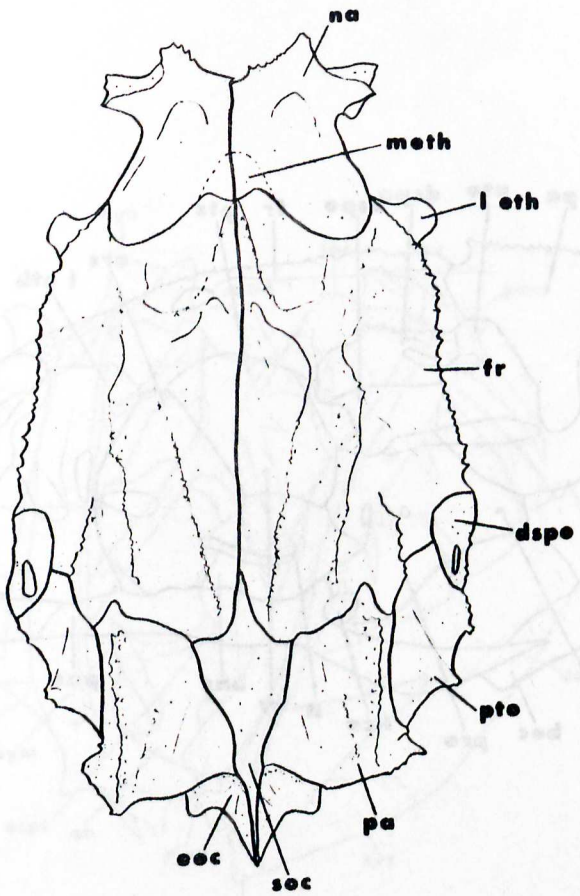


Fig. 13.--Anoplogaster cornuta. Neurocranium, dorsal view, x 4.0.

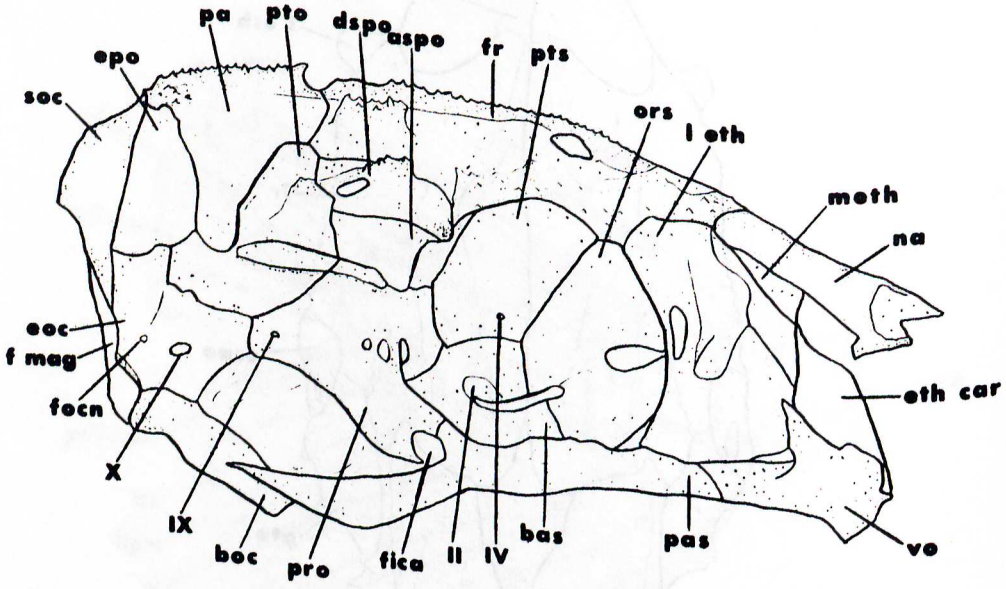


Fig. 14.--Anoplogaster cornuta. Neurocranium, lateral view, x 3.2.

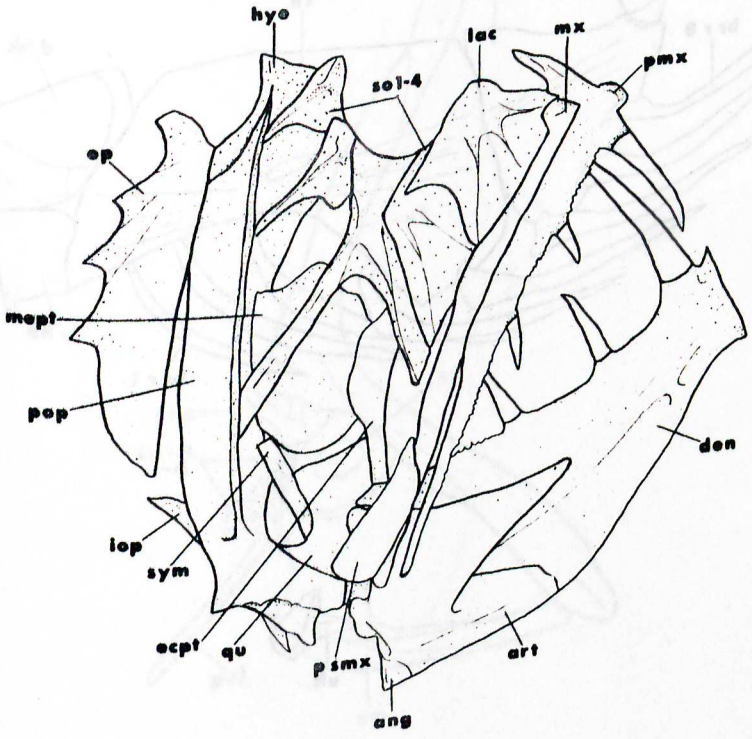


Fig. 15.--Anoplogaster cornuta. Face bones, lateral view, x 1.3.

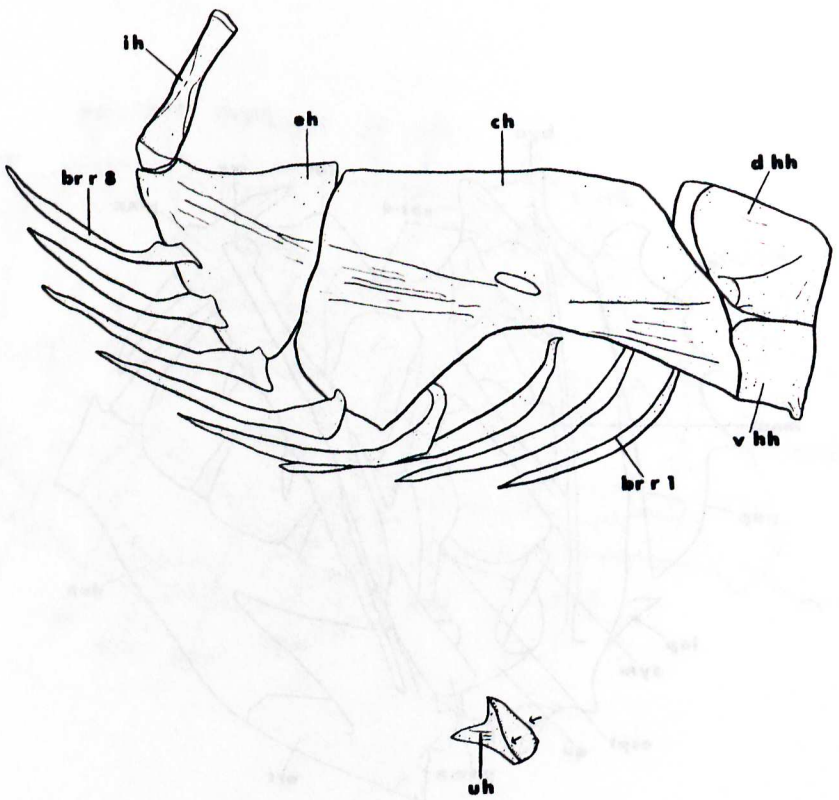


Fig. 16.--Anoplogaster cornuta. Above: right hyoid arch and branchiostegal rays, lateral view, x 3.4. Below: urohyal, anterolateral view, x 3.4. Arrows indicate sites of attachment of urohyal-hypohyal ligaments.

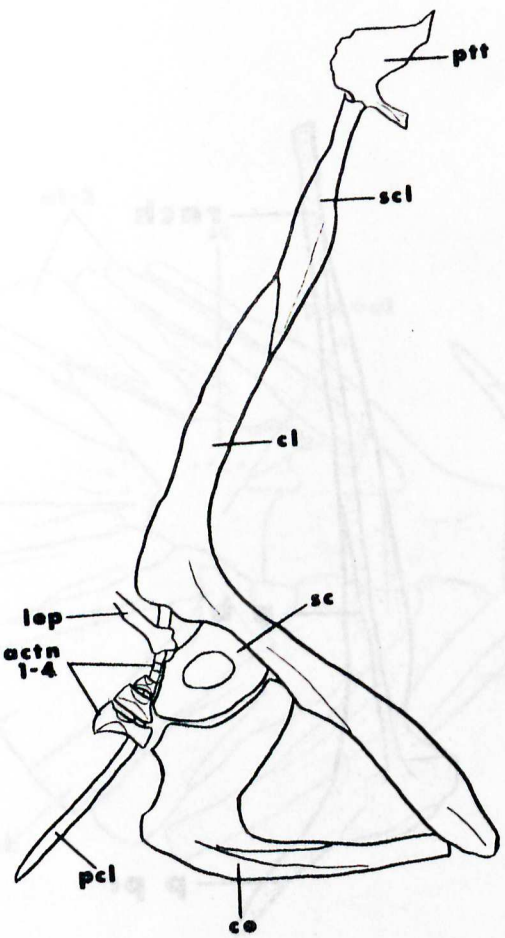


Fig. 17.--Anoplogaster cornuta. Right pectoral girdle, lateral view, x 1.6.

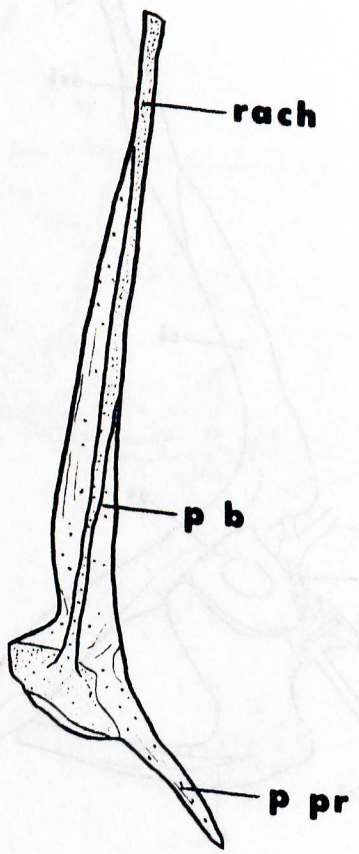


Fig. 18.--Anoplogaster cornuta. Left pelvic girdle, dorsal view, x 4.7.

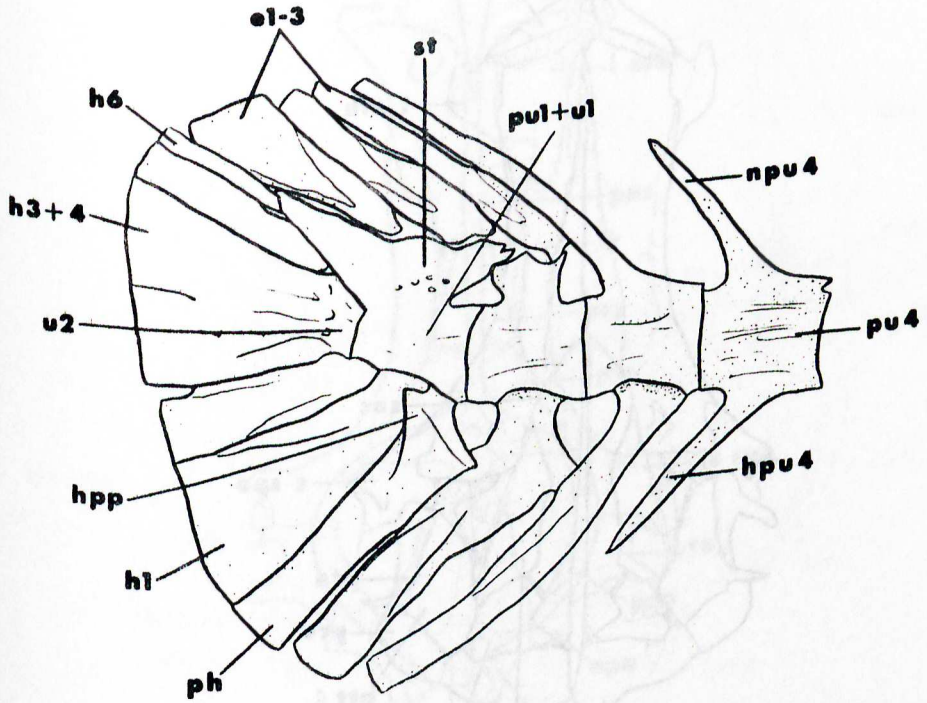


Fig. 19.--Anoplogaster cornuta. Caudal skeleton, lateral view, x 8.7.

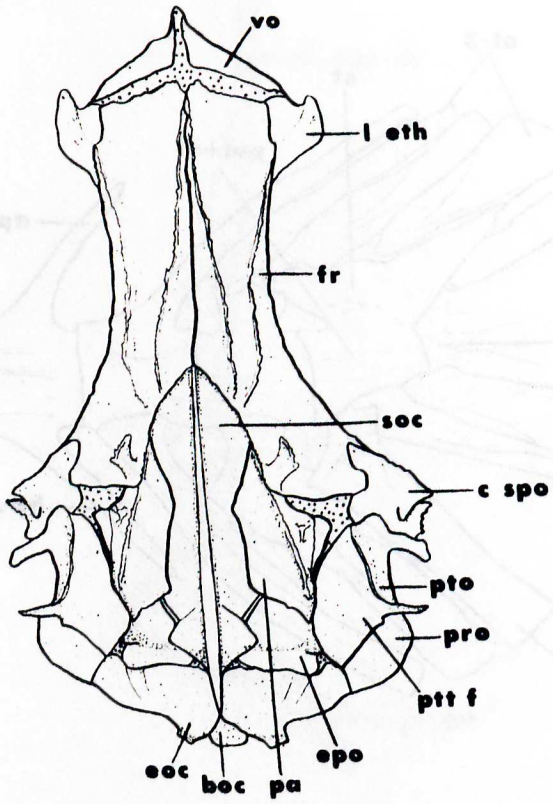


Fig. 20.--Diretmus argenteus. Neurocranium, dorsal view, x 4.2.

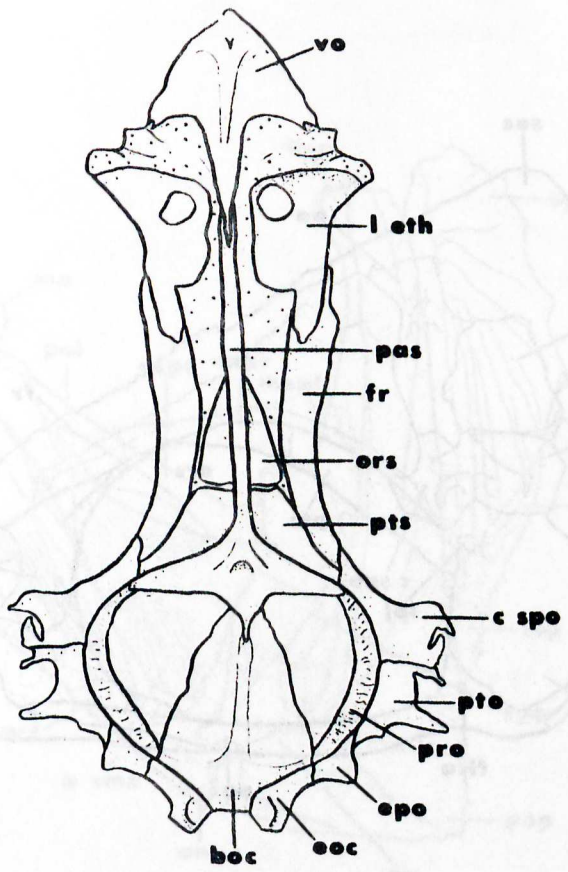


Fig. 21.--Diretmus argenteus. Neurocranium, ventral view, x 4.2.

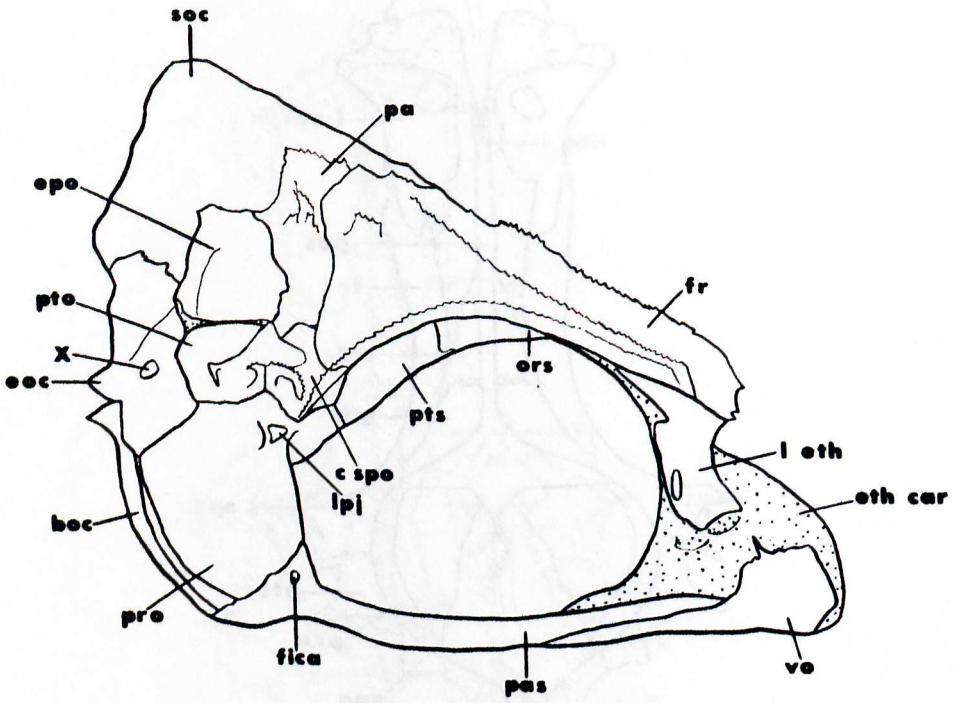


Fig. 22.--Diretmus argenteus. Neurocranium, lateral view, x 3.9.

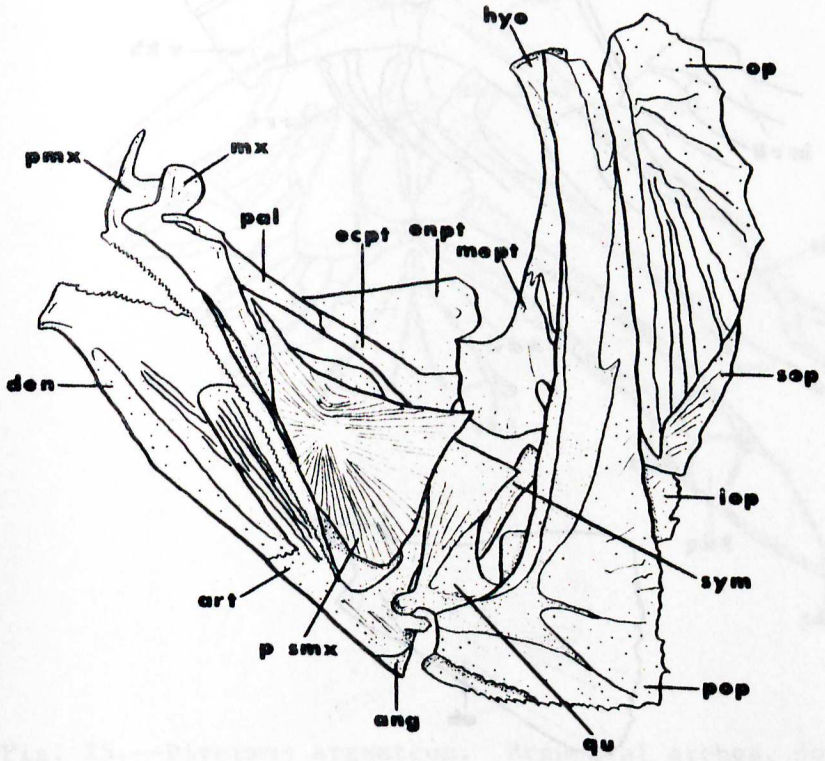


Fig. 23.--Diretmus argenteus. Face bones, lateral view, x 1.5.

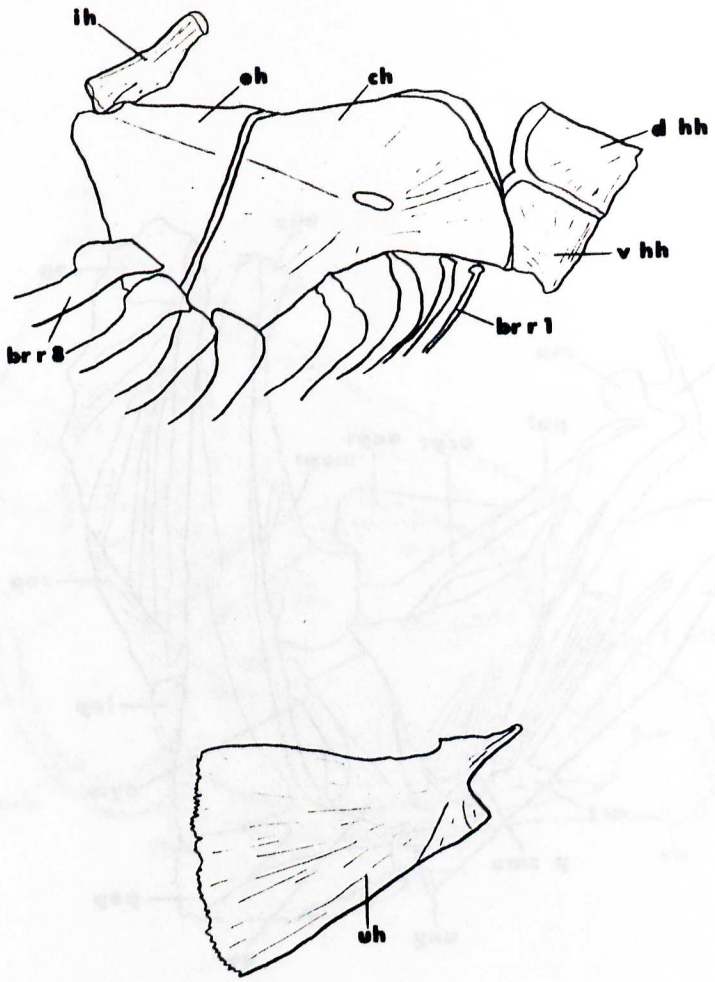


Fig. 24.--Diretmus argenteus. Above: right hyoid arch and branchiostegal rays, lateral view, x 3.9. Below: urohyal, lateral view, x 3.9.

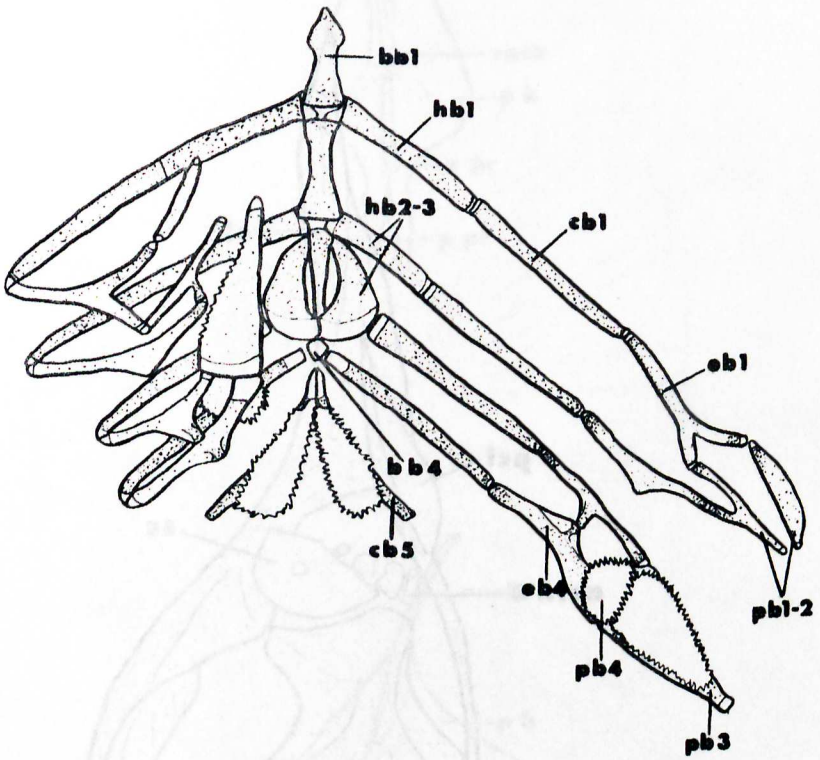


Fig. 25.--Diretmus argenteus. Branchial arches, dorsal view (except upper elements of right side, which are reflected back to expose ventral aspect), freehand sketch.

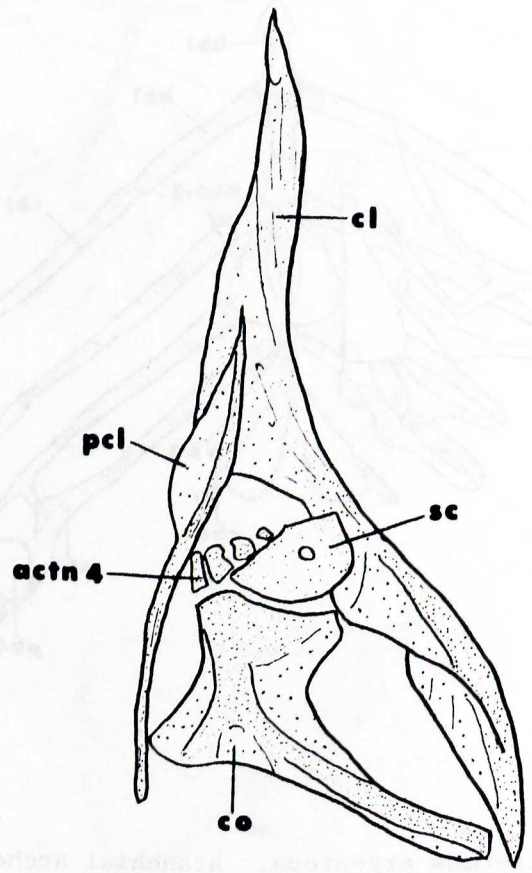


Fig. 26.--Diretmus argenteus. Left pectoral girdle, medial view, x 2.0.

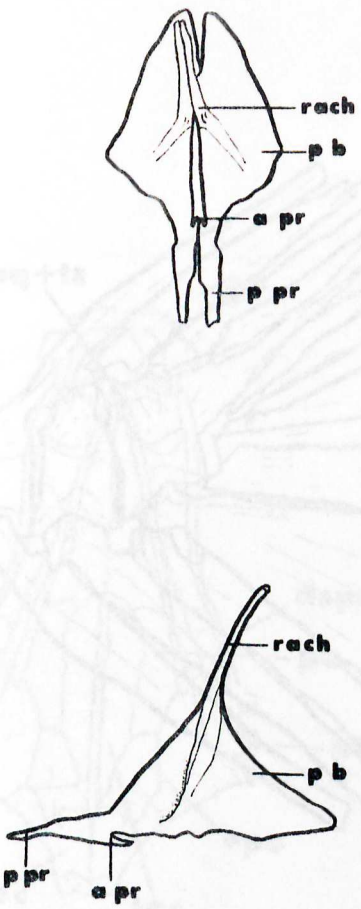


Fig. 27.--Diretmus argenteus. Above: pelvic girdles, dorsal view, x 3.9. Below: right pelvic girdle, lateral view, x 3.9.

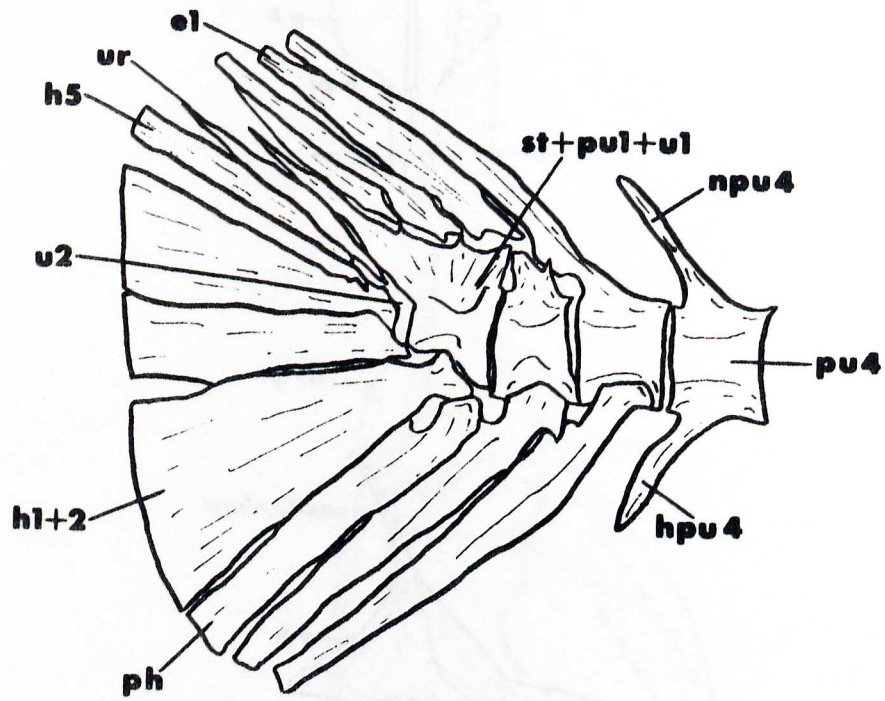


Fig. 28.--Diretmus argenteus. Caudal skeleton, lateral view, x 10.8.

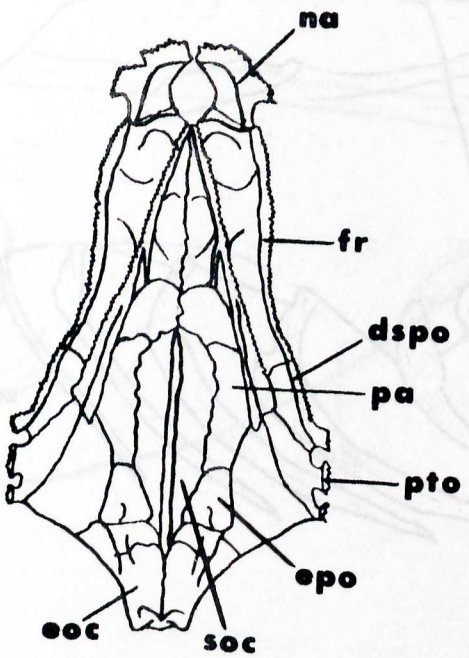


Fig. 29.--Centroberyx affinis. Neurocranium, dorsal view. After Patterson (1964).

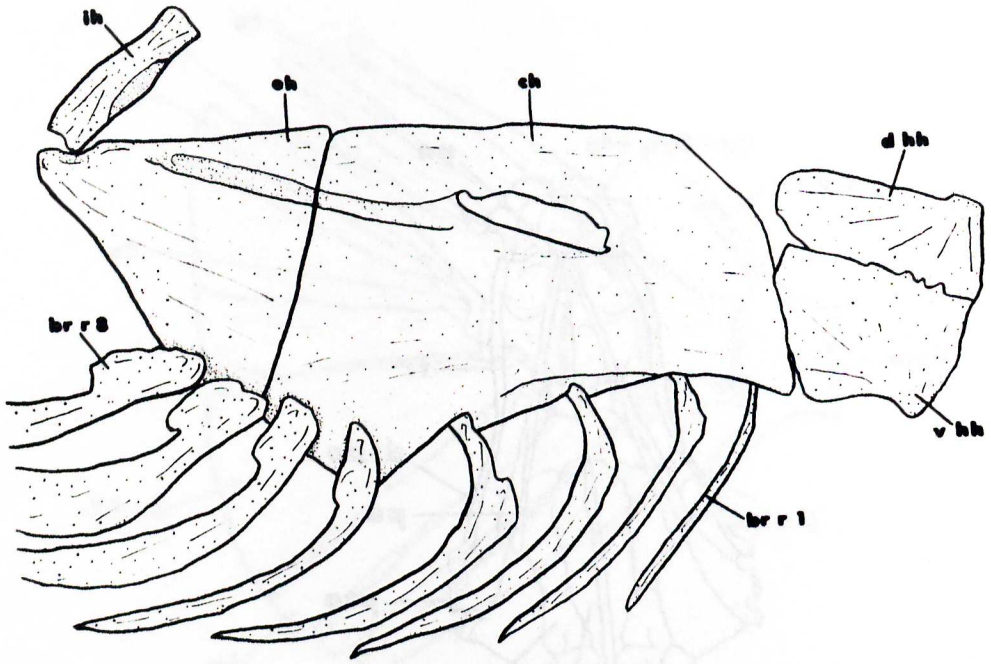


Fig. 30.--Centroberyx affinis. Right hyoid arch and branchiostegal rays, lateral view, x 1.4.

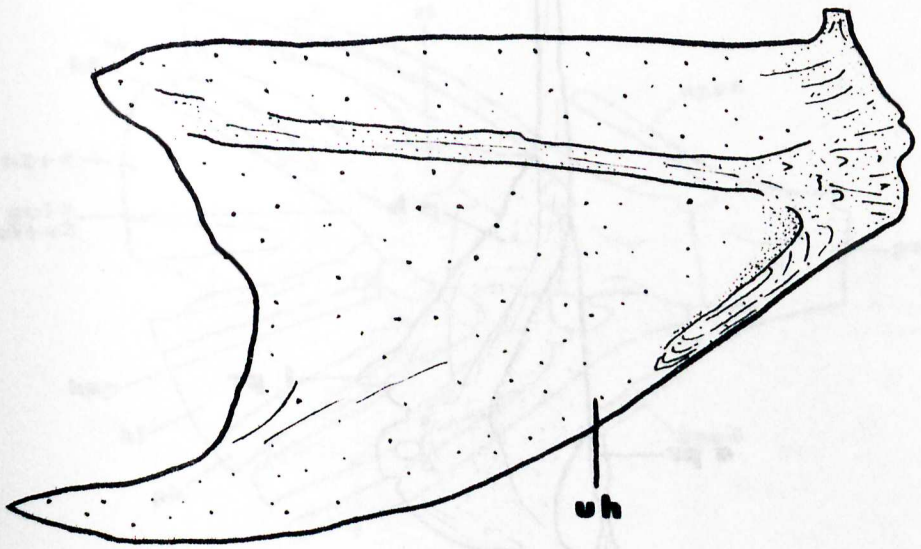


Fig. 31.--Centroberyx affinis. Urohyal, lateral view, x 2.2.

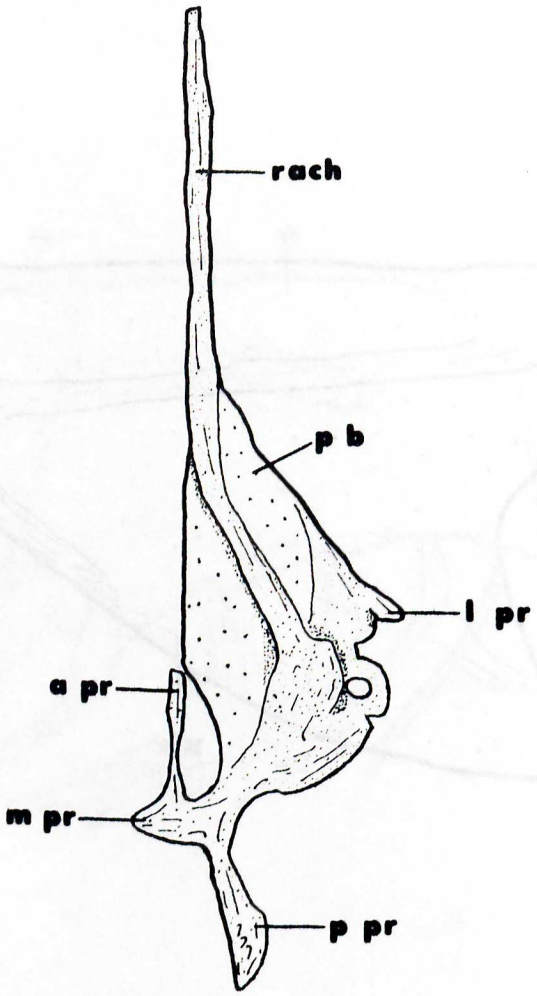


Fig. 32.--Centroberyx affinis. Right pelvic girdle, dorsal view, x 2.0.

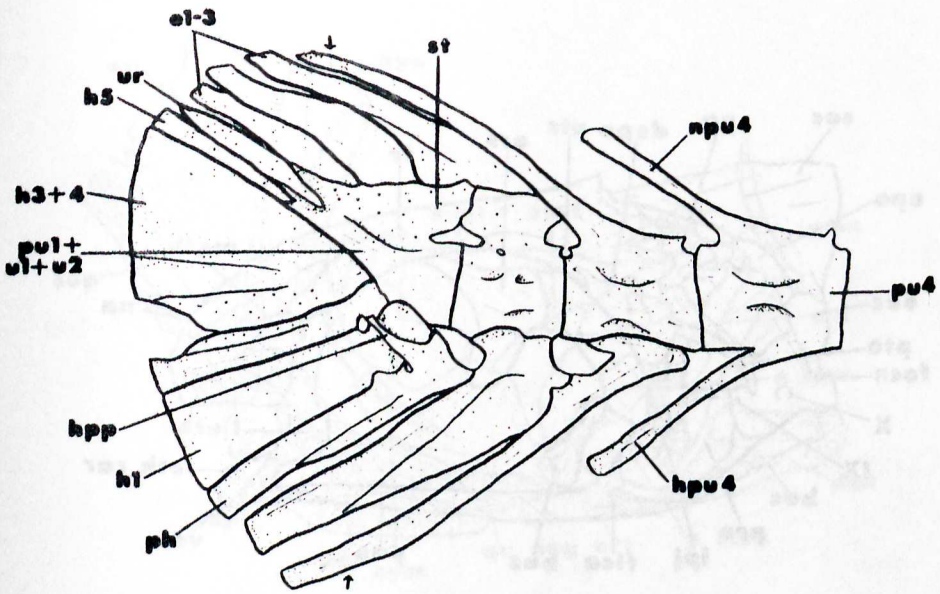


Fig. 33.--Centroberyx affinis. Caudal skeleton, lateral view, x 1.6. Arrows indicate position of foremost procurrents.

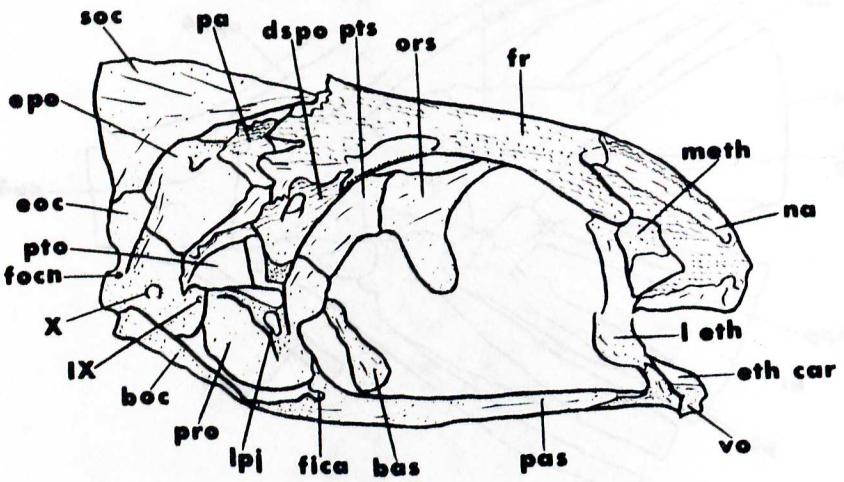


Fig. 34.--Photoblepharon palpebratus. Neurocranium, lateral view, x 3.5.

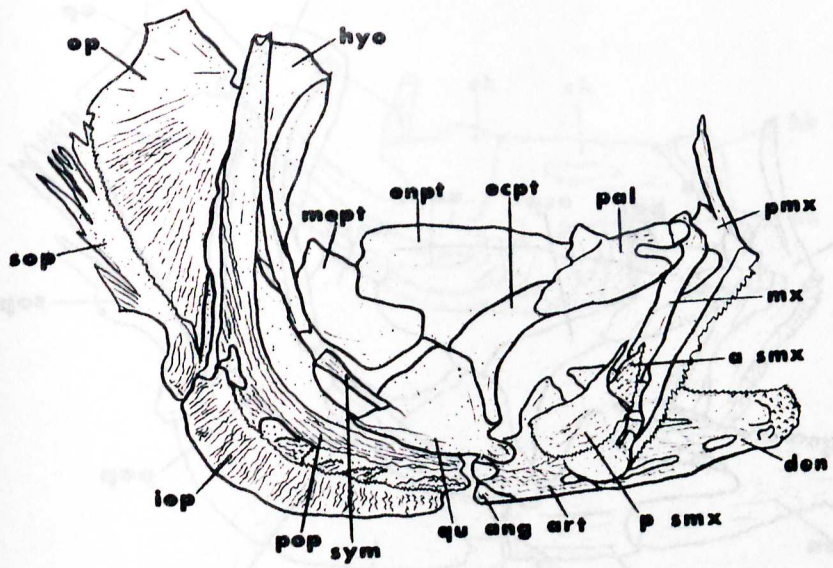


Fig. 35.--Photoblepharon palpebratus. Face bones, lateral view, x 3.1.

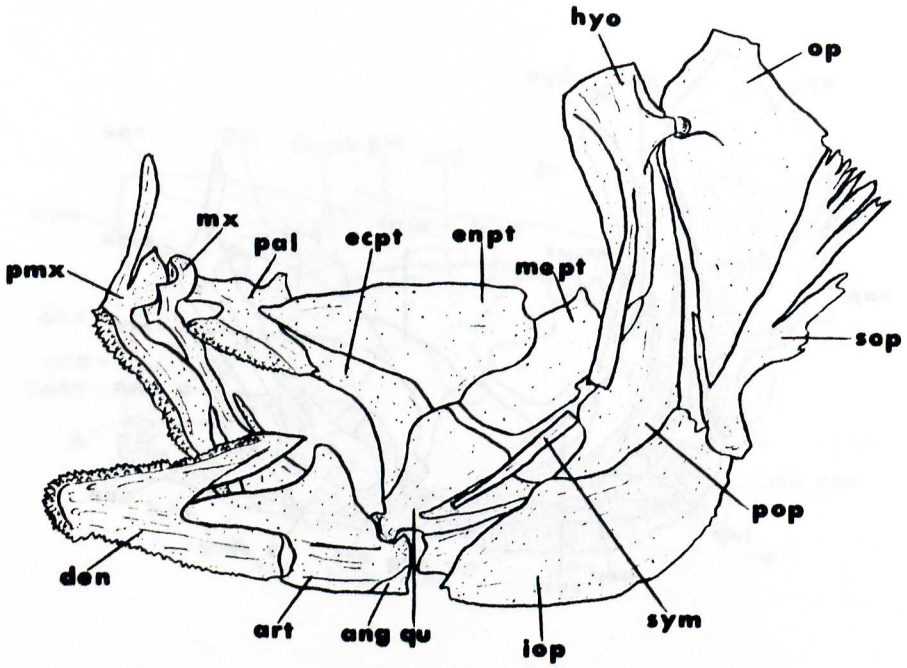


Fig. 36.--Photoblepharon palpebratus. Face bones, medial view, x 3.5.

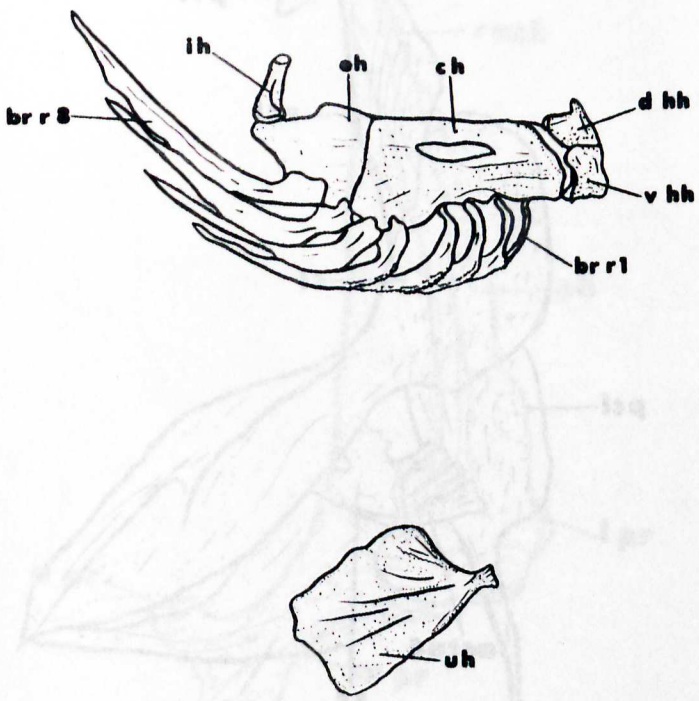


Fig. 37.--Photoblepharon palpebratus. Above: right hyoid arch and branchiostegal rays, lateral view, x 3.1. Below: urohyal, lateral view, x 3.1.

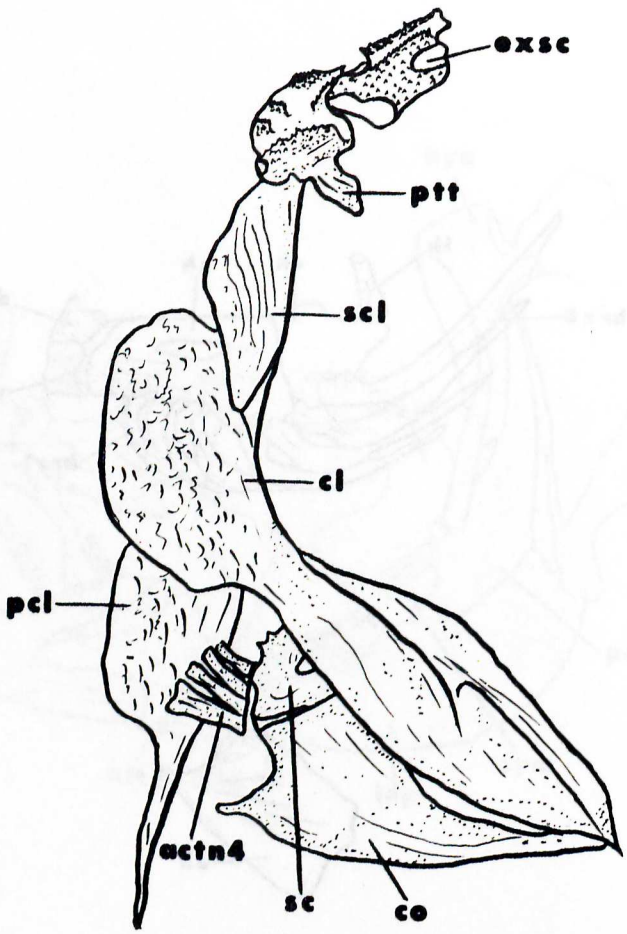


Fig. 38.--Photoblepharon palpebratus. Right pectoral girdle, lateral view, x 3.9.

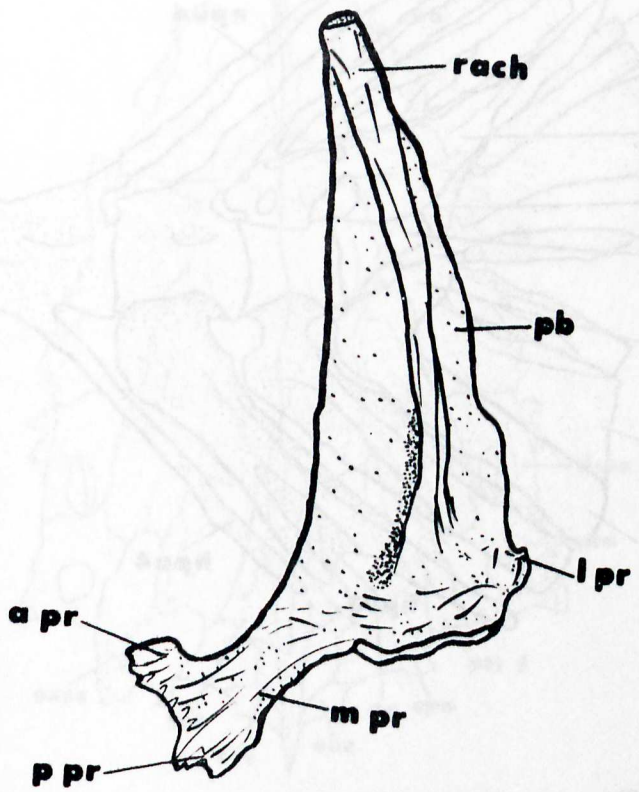


Fig. 39.--Photoblepharon palpebratus. Right pelvic girdle, dorsal view, x 8.7.

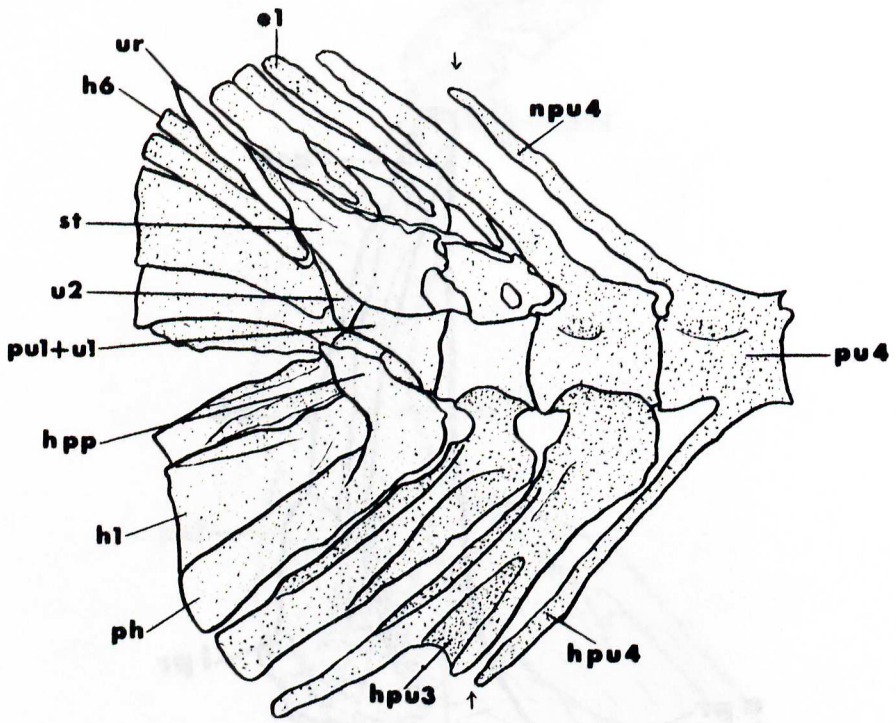


Fig. 40.--Photoblepharon palpebratus. Caudal skeleton, lateral view, x 7.0. Arrows indicate position of foremost procurrents.

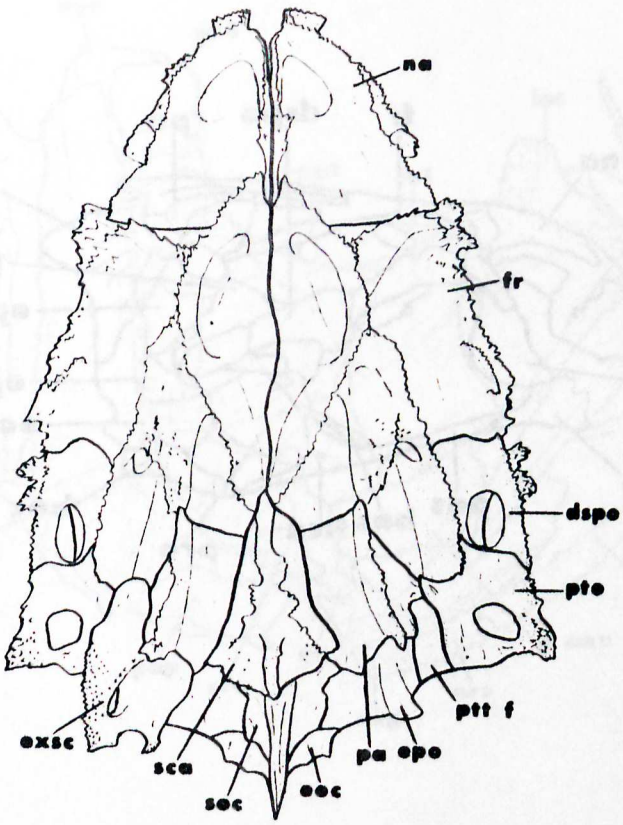


Fig. 41.--Monocentris japonicus. Neurocranium, dorsal view, x 3.0.

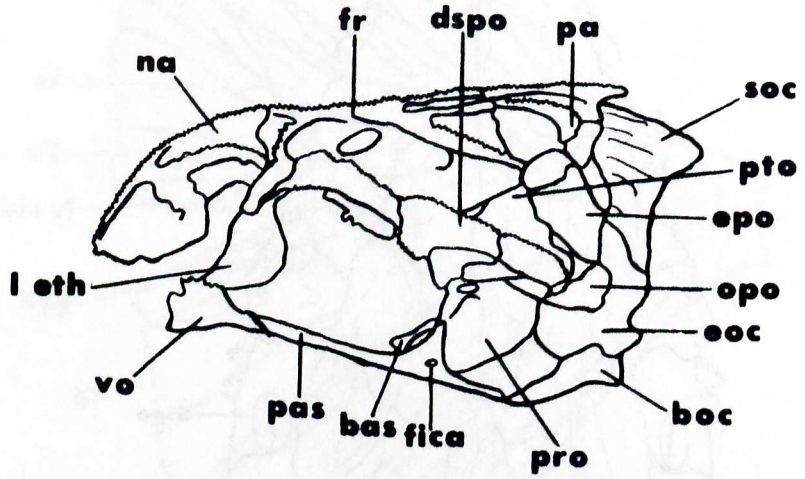


Fig. 42.--Monocentris japonicus. Neurocranium, lateral view. After Starks (1904).

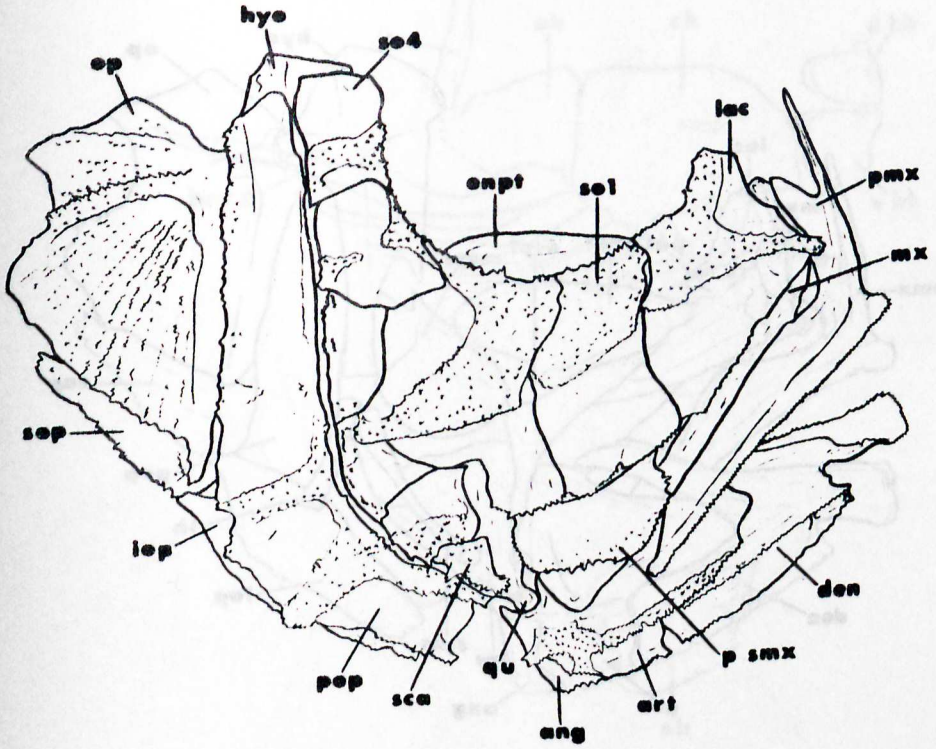


Fig. 43.--Monocentris japonicus. Face bones, lateral view, x 3.1.

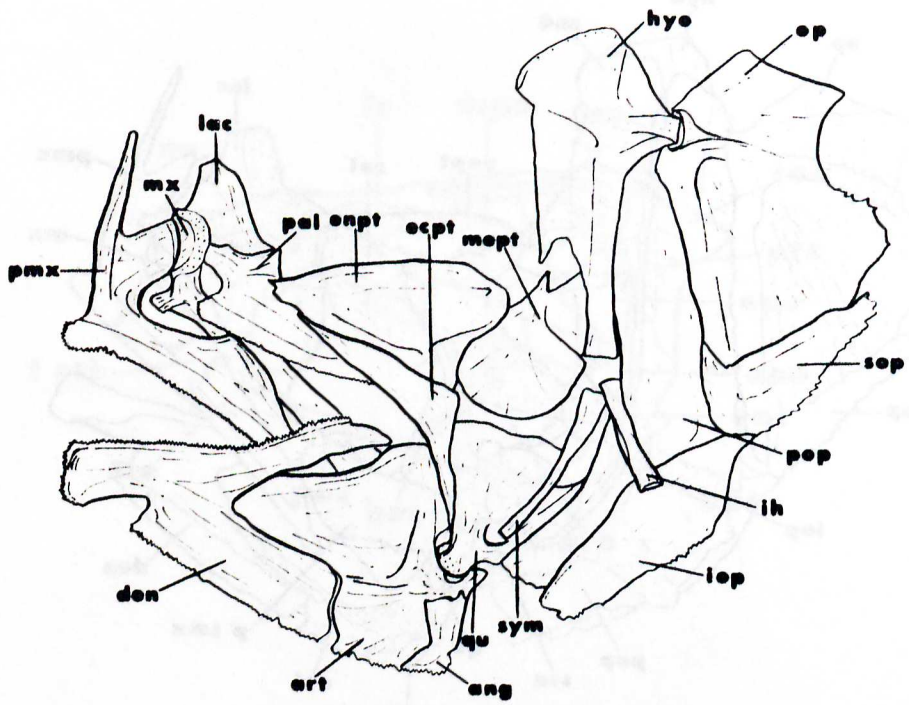


Fig. 44.--Monocentris japonicus. Face bones, medial view, x 2.9.

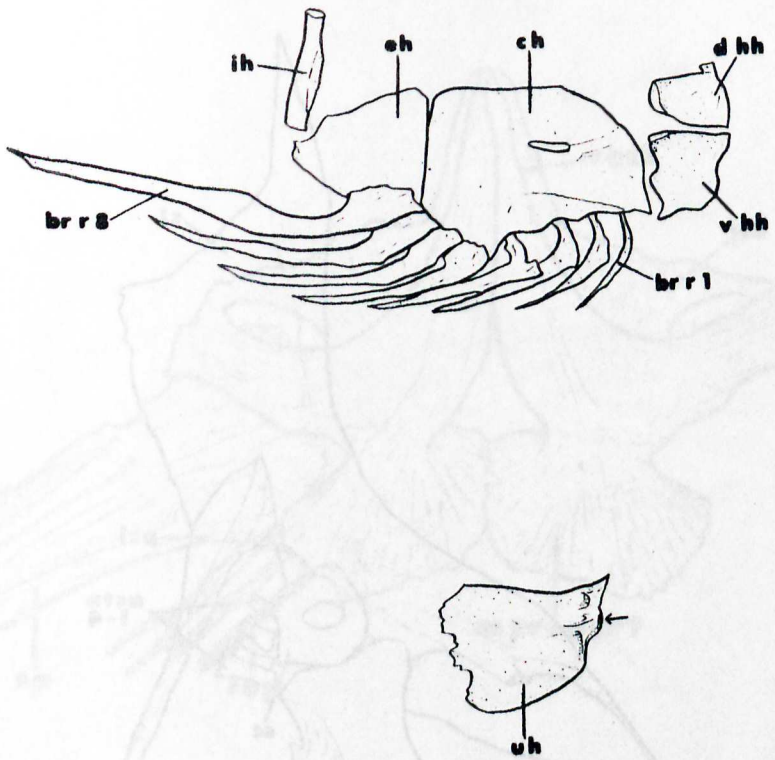


Fig. 45.--Monocentris japonicus. Above: right hyoid arch and branchiostegal rays, lateral view, x 3.9. Below: urohyal, lateral view, x 3.9. Arrow indicates site of attachment of urohyal-hypohyal ligament.

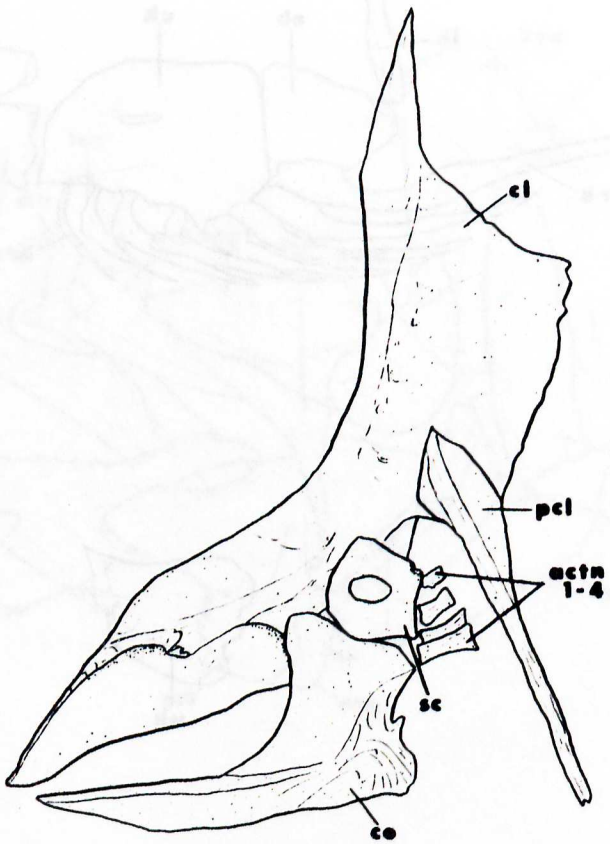


Fig. 46.--Monocentris japonicus. Lower portion of right pectoral girdle, medial view, x 3.1.

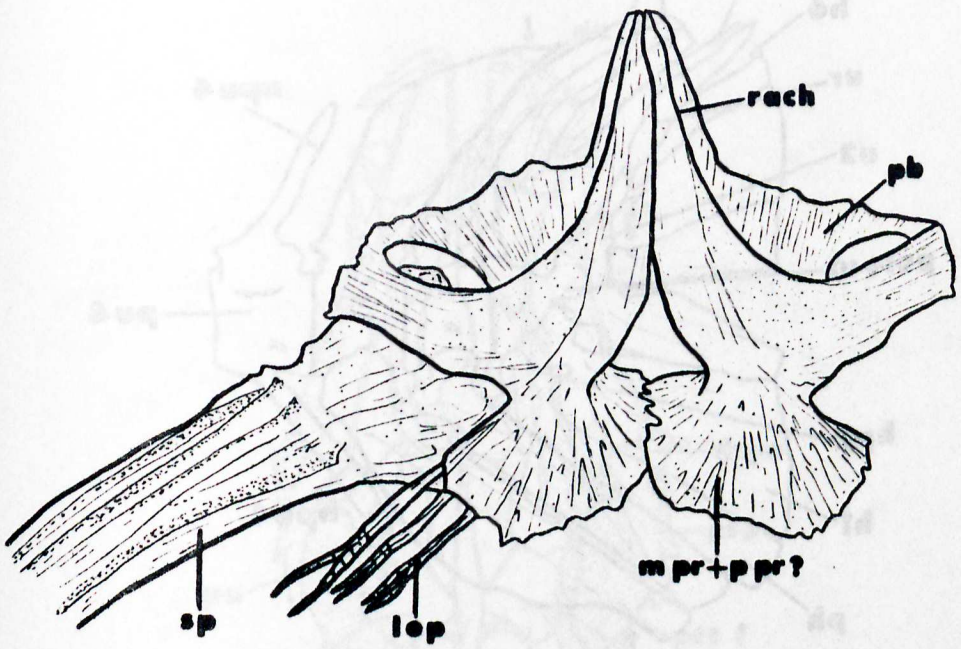


Fig. 47.--Monocentris japonicus. Pelvic girdles and pelvic fin (left side), dorsal view, x 4.0.

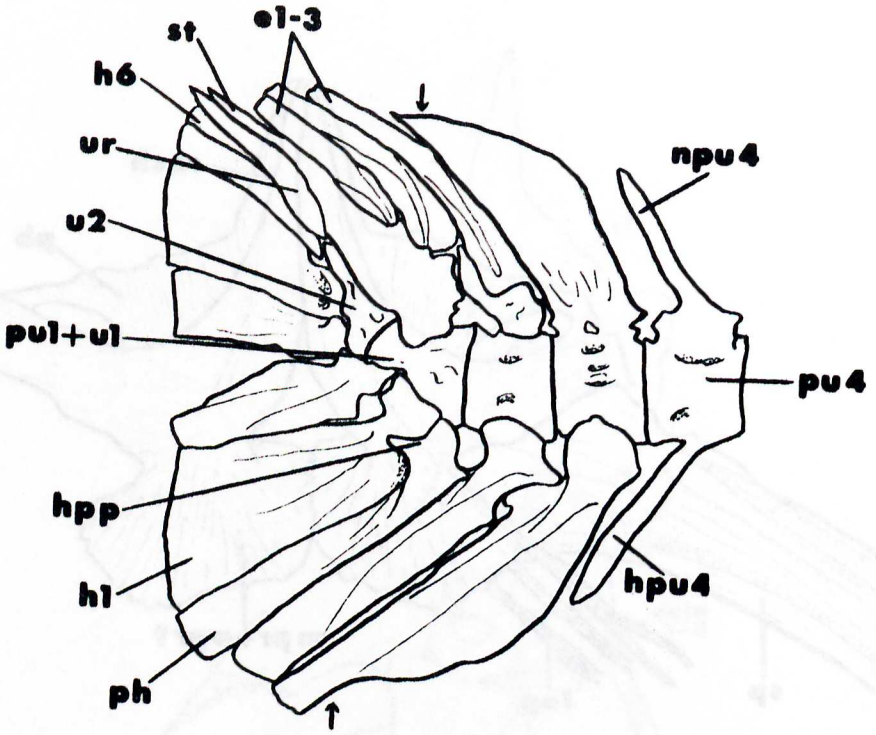


Fig. 48.--Monocentris japonicus. Caudal skeleton, lateral view, x 11.0. Arrows indicate position of foremost procurrents.

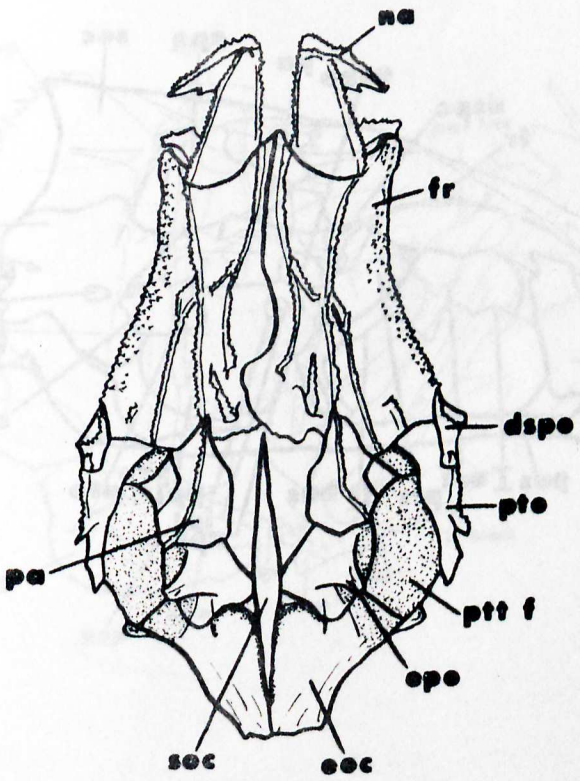


Fig. 49.--Paratrachichthys sp. Neurocranium, dorsal view, x 4.9.

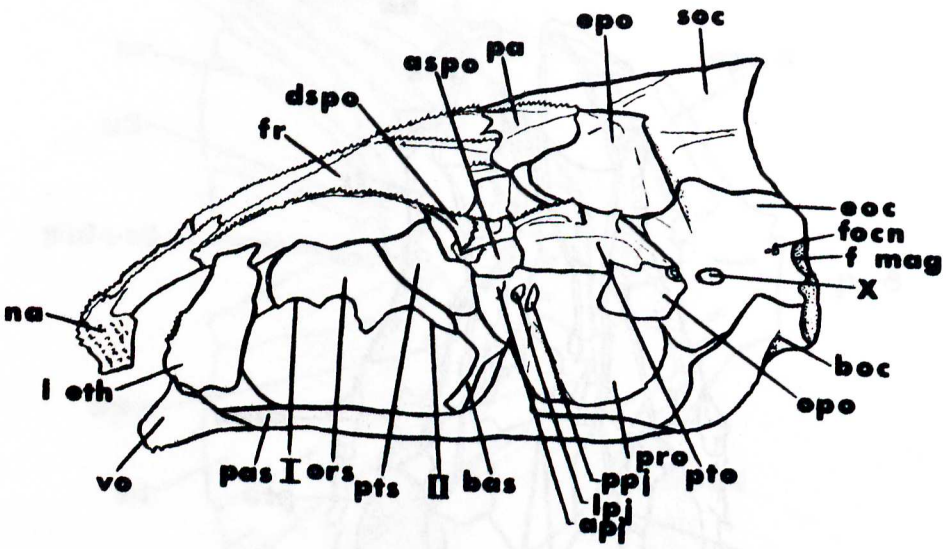


Fig. 50.--Paratrachichthys sp. Neurocranium, lateral view, x 5.0.

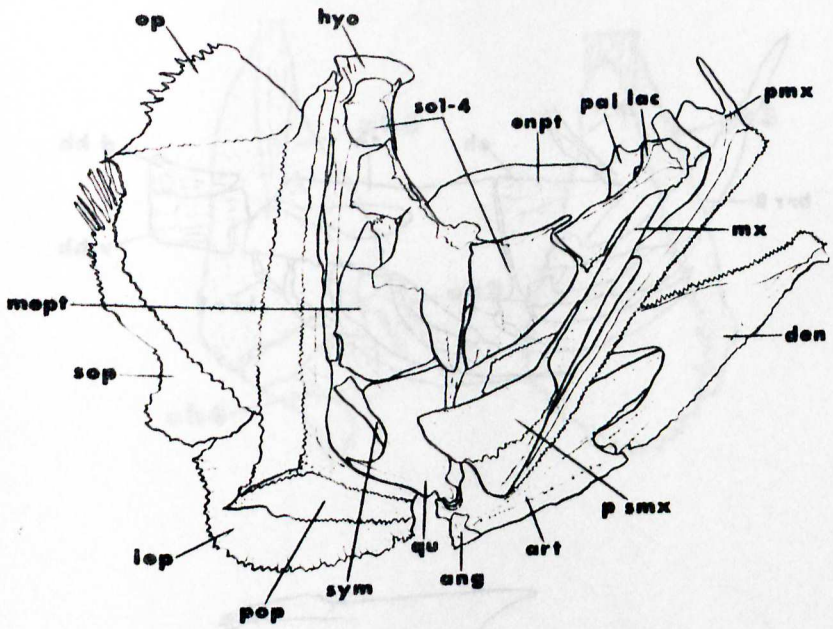


Fig. 51.--Paratrachichthys sp. Face bones, lateral view, x 3.8.

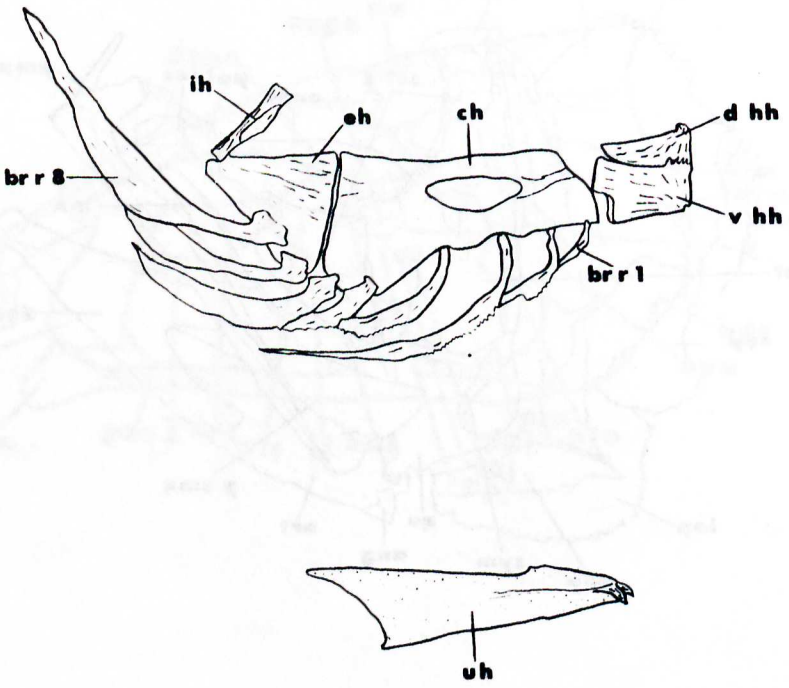


Fig. 52.--Paratrachichthys sp. Above: right hyoid arch and branchiostegal rays, lateral view, x 3.8. Below: urohyal, lateral view, x 3.8.

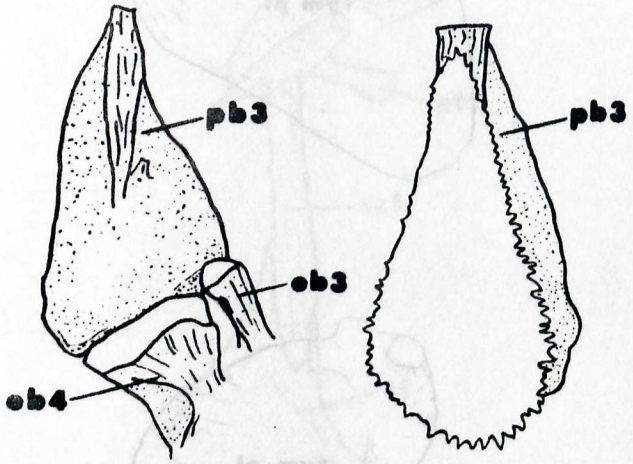


Fig. 53.--Paratrachichthys sp. Left: articulation of third and fourth epibranchials with third pharyngobranchial, dorsal view, x 9.9. Right: third pharyngobranchial (tooth patch shown in outline), ventral view, x 9.9.



Fig. 54.--Paratrachichthys sp. Above: tympanic plate, lateral view, x 7.8. Arrow indicates site of ligamentous attachment to dorsal edge of tympanic plate. Below: tympanic plate, medial view, x 7.8.

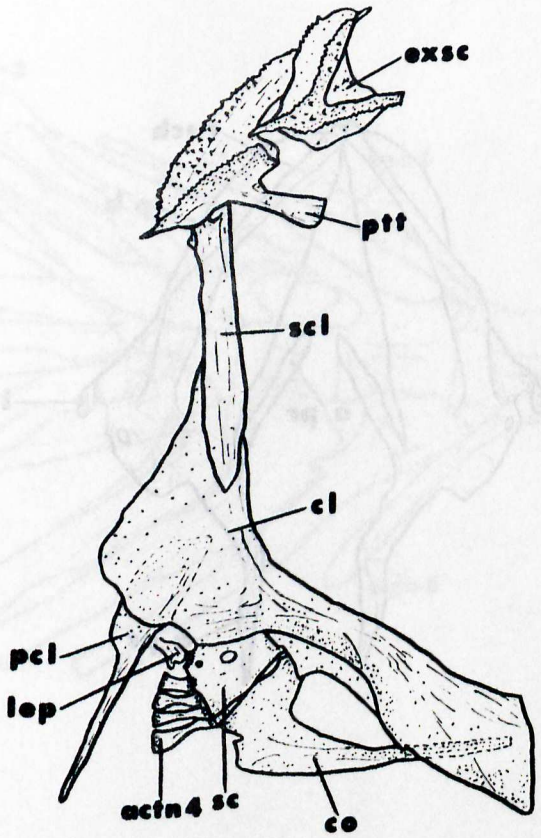


Fig. 55.--Paratrachichthys sp. Right pectoral girdle, lateral view, x 4.9.

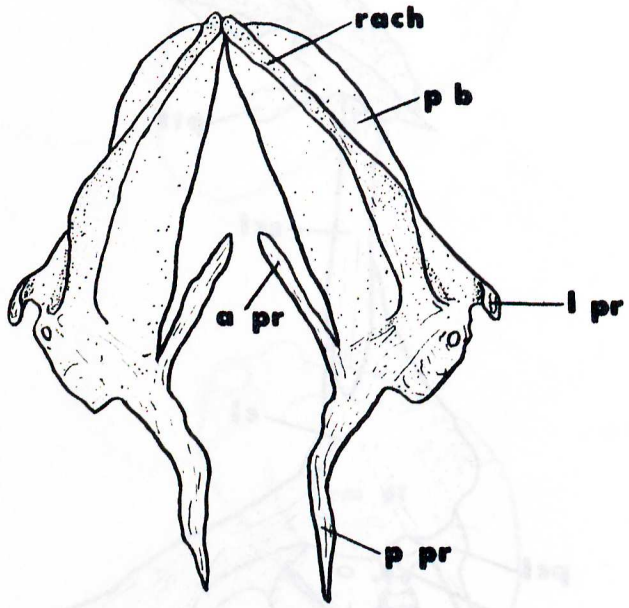


Fig. 56.--Paratrachichthys sp. Pelvic girdles, dorsal view, x 9.7.

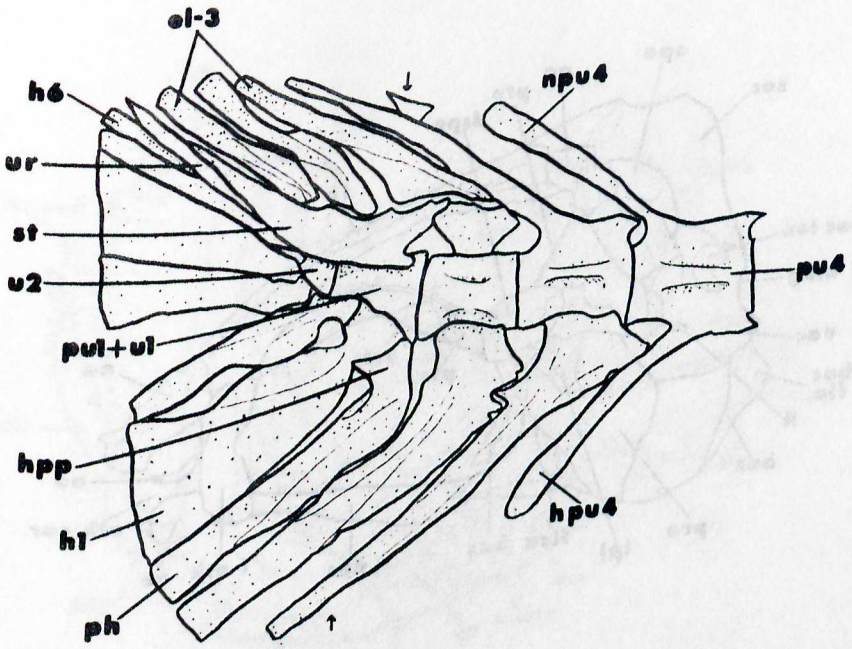


Fig. 57.--Paratrachichthys sp. Caudal skeleton, lateral view, x 9.0. Arrows indicate position of foremost procurrents.

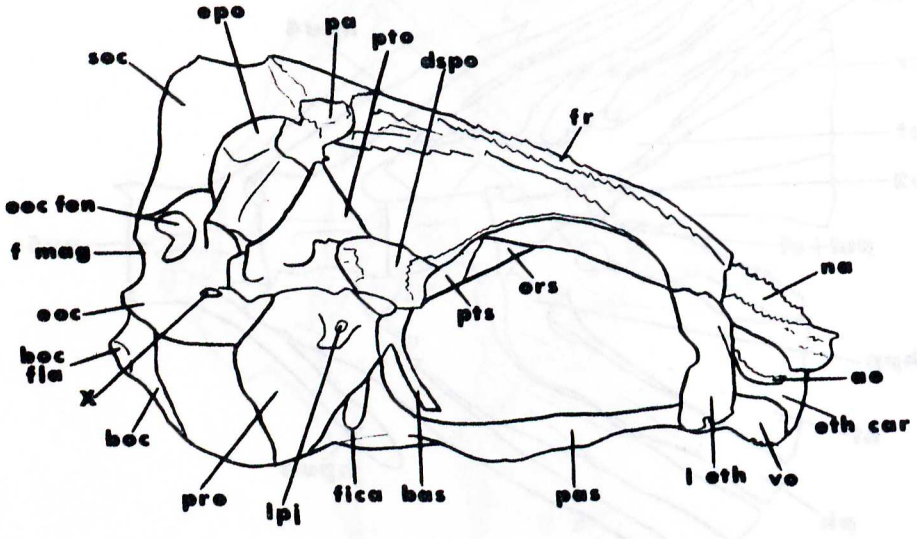


Fig. 58.--Ostichthys trachypoma. Neurocranium, lateral view, x 3.2.

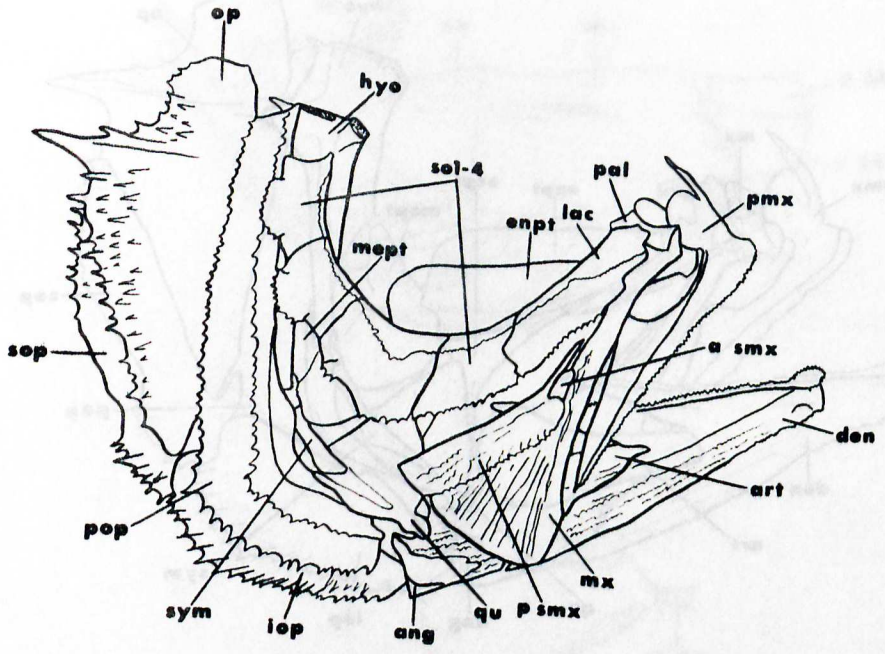


Fig. 59.--Ostichthys trachypoma. Face bones, lateral view, x 2.9.

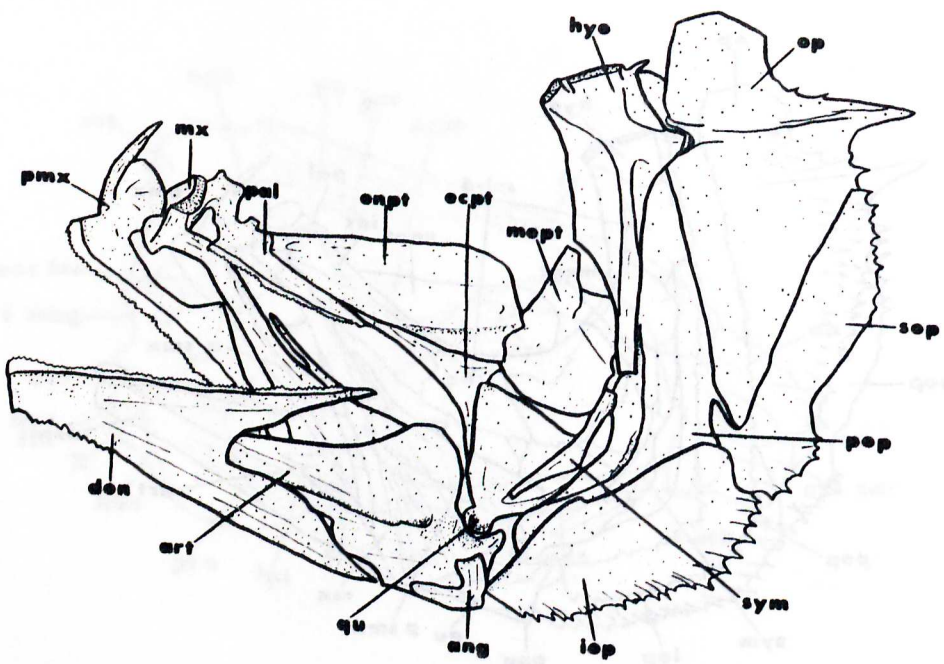


Fig. 60.--Ostichthys trachypoma. Face bones, medial view, x 2.9.

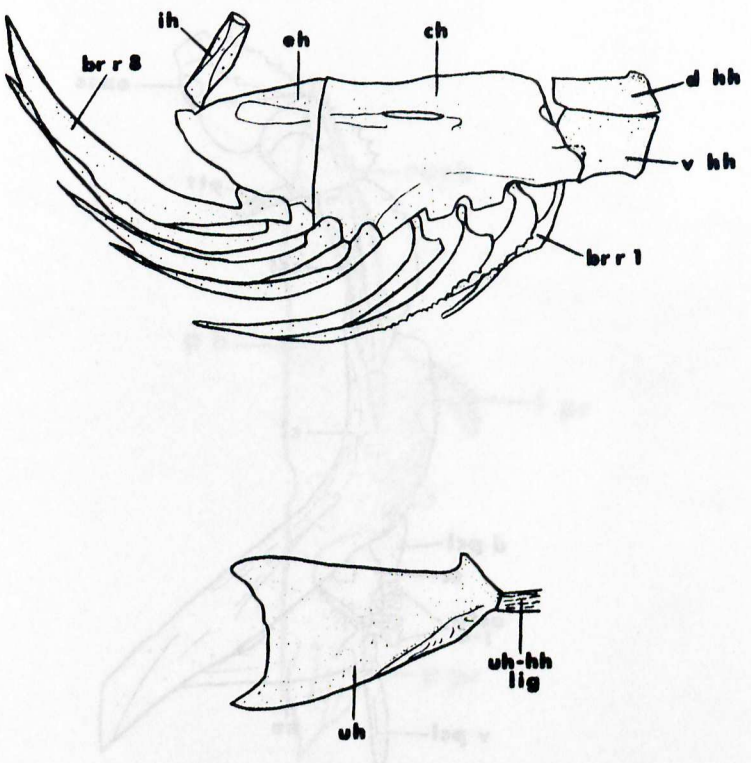


Fig. 61.--Ostichthys trachypoma. Above: right hyoid arch and branchiostegal rays, lateral view, x 3.8. Below: urohyal, lateral view, x 3.8.

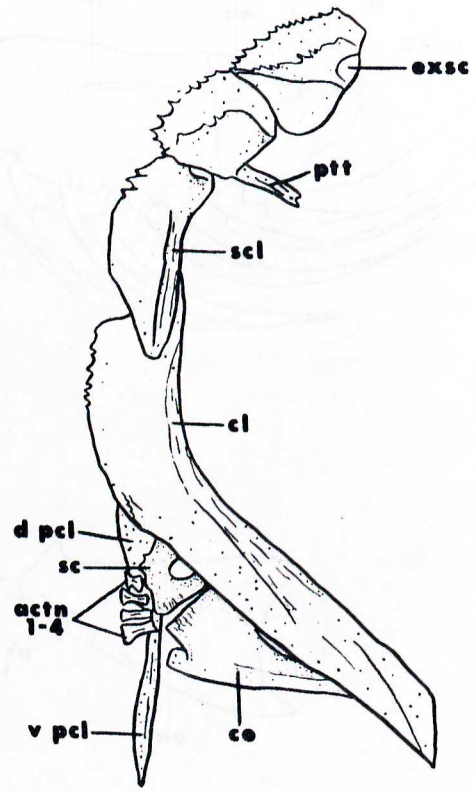


Fig. 62.--Ostichthys trachypoma. Right pectoral girdle, lateral view, x 3.2.

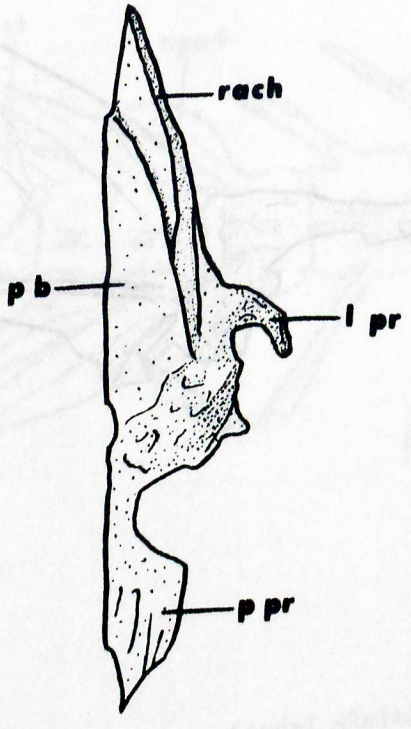


Fig. 63.--*Ostichthys trachypoma*. Right pelvic girdle, dorsal view, x 7.9.

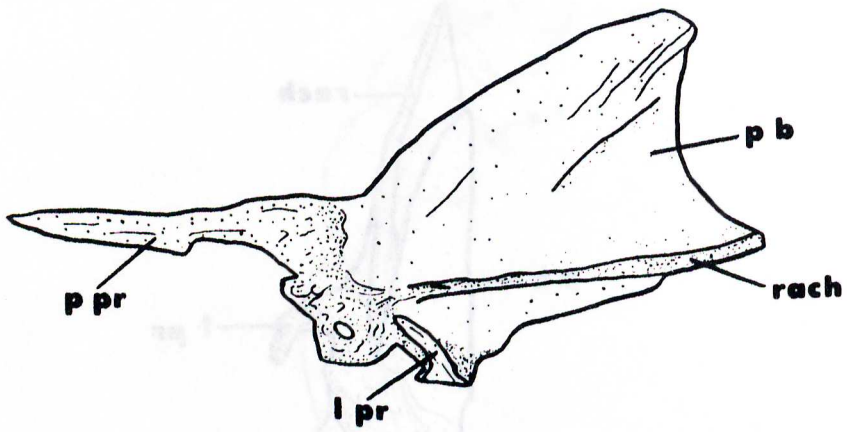


Fig. 64.--Ostichthys trachypoma. Right pelvic girdle, dorso-lateral view, x 7.9.

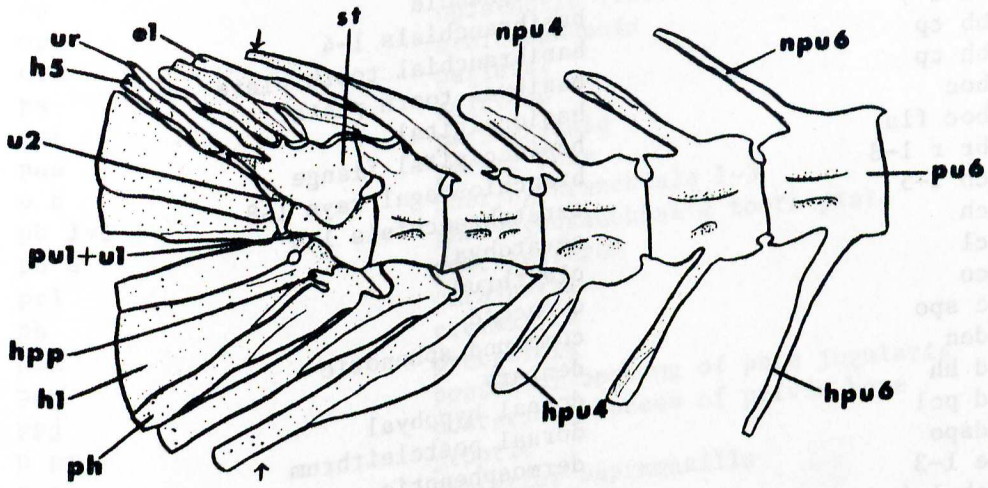


Fig. 65.--Ostichthys trachypoma. Caudal skeleton, lateral view, x 9.0. Arrows indicate position of foremost procurrents.

TABLE 83

ABBREVIATIONS USED IN FIGURES

actn 1-4	actinosts 1-4
ang	angular (retroarticular)
ao	antorbital
apj	anterior opening of pars jugularis
a pr	anterior process of pelvic bone
art	articular (angulo-articular)
a smx	anterior supramaxilla
aspo	autosphenotic
bas	basisphenoid
bb 1-4	basibranchials 1-4
bb tp	basibranchial tooth plate
bh tp	basihyal tooth plate
boc	basioccipital
boc fla	basioccipital flange
br r 1-8	branchiostegal rays 1-8
cb 1-5	ceratobranchials 1-5
ch	ceratohyal
cl	cleithrum
co	coracoid
c spo	compound sphenotic
den	dentary
d hh	dorsal hypohyal
d pcl	dorsal postcleithrum
dspo	dermosphenotic
e 1-3	epurals 1-3
eb 1-4	epibranchials 1-4
ecpt	ectopterygoid
eh	epihyal
enpt	endopterygoid
eoc	exoccipital
eoc fen	exoccipital fenestra
epo	epiotic
eth car	ethmoid cartilage
exsc	extrascapular
fica	foramen for internal carotid artery
f mag	foramen magnum
focn	foramina for occipital nerves
fr	frontal
h 1-6	hypurals 1-6
hb 1-3	hypobranchials 1-3
hpp	hypurapophysis
hpu 3-6	hemal spines of preural centra 3-6
hyo	hyomandibula
ih	interhyal
iop	interopercle

TABLE 83--cont.

lac	lacrimal
lep	lepidotrichium
l eth	lateral ethmoid
lpj	lateral opening of pars jugularis
l pr	lateral process of pelvic bone
mept	metapterygoid
meth	mesethmoid
m pr	medial process of pelvic bone
mx	maxilla
na	nasal
npu 2-6	neural spines of preural centra 2-6
op	opercle
opo	opisthotic (intercalar)
ors	orbitosphenoid
pa	parietal
pal	palatine
pas	parasphenoid
p b	pelvic bone
pb 1-3	pharyngobranchials 1-3
pb 4	pharyngobranchial 4 tooth plate
pcl	postcleithrum
ph	parhypural
pmx	premaxilla
pop	preopercle
ppj	posterior opening of pars jugularis
p pr	posterior process of pelvic bone
pro	prootic
p smx	posterior supramaxilla
pto	pterotic
pts	pterosphenoid
ptt	posttemporal
ptt f	posttemporal fossa
pu 1-6	preural centra 1-6
qu	quadrate
rach	rachis
sc	scapula
sca	scale
scl	supracleithrum
so 1-4	suborbitals 1-4 (infraorbitals 1-4)
soc	supraoccipital
sop	subopercle
sos	subocular shelf
sp	spine
st	stegural
sym	symplectic
tym pl	tympanic plate
u 1-2	ural centra 1-2
uh	urohyal
uh-hh lig	urohyal-hypohyal ligament

TABLE 83--cont.

ur	uroneural
v hh	ventral hypohyal
vo	vomer
v pcl	ventral postcleithrum
I	foramen for olfactory nerve
II	foramen for optic nerve
IV	foramen for trochlear nerve
IX	foramen for glossopharyngeal nerve
X	foramen for vagus nerve

Combinations of symbols linked by plus signs indicate compound elements formed by fusion of the bones indicated.

APPENDIX III

PICTORIAL SURVEY OF REPRESENTATIVE SPECIES OF THE ORDER BERYCIFORMES

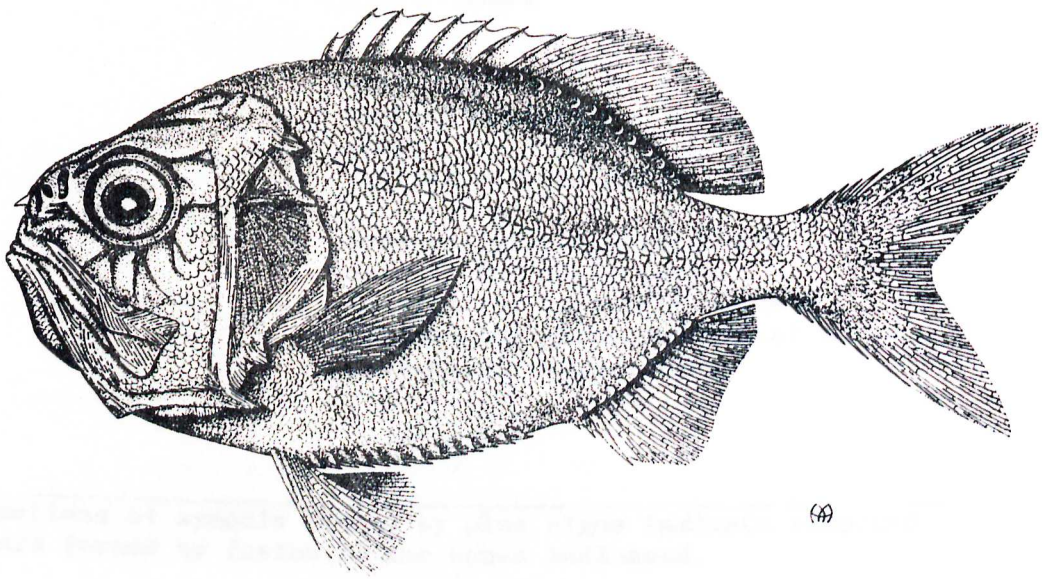


Fig. 66.--Gephyroberyx darwini. (After Woods and Sonoda, 1973)

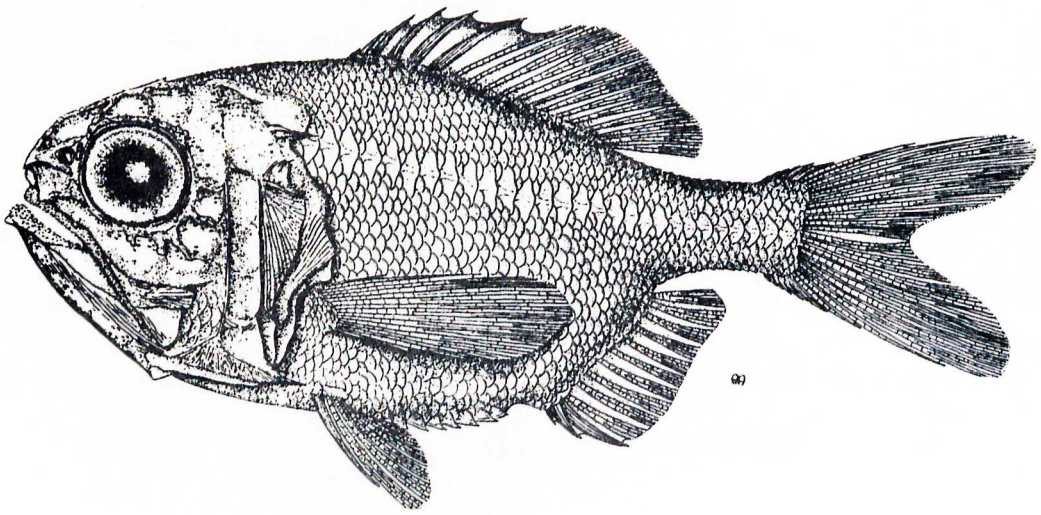


Fig. 67.--Hoplostethus mediterraneus. (After Woods and Sonoda, 1973)

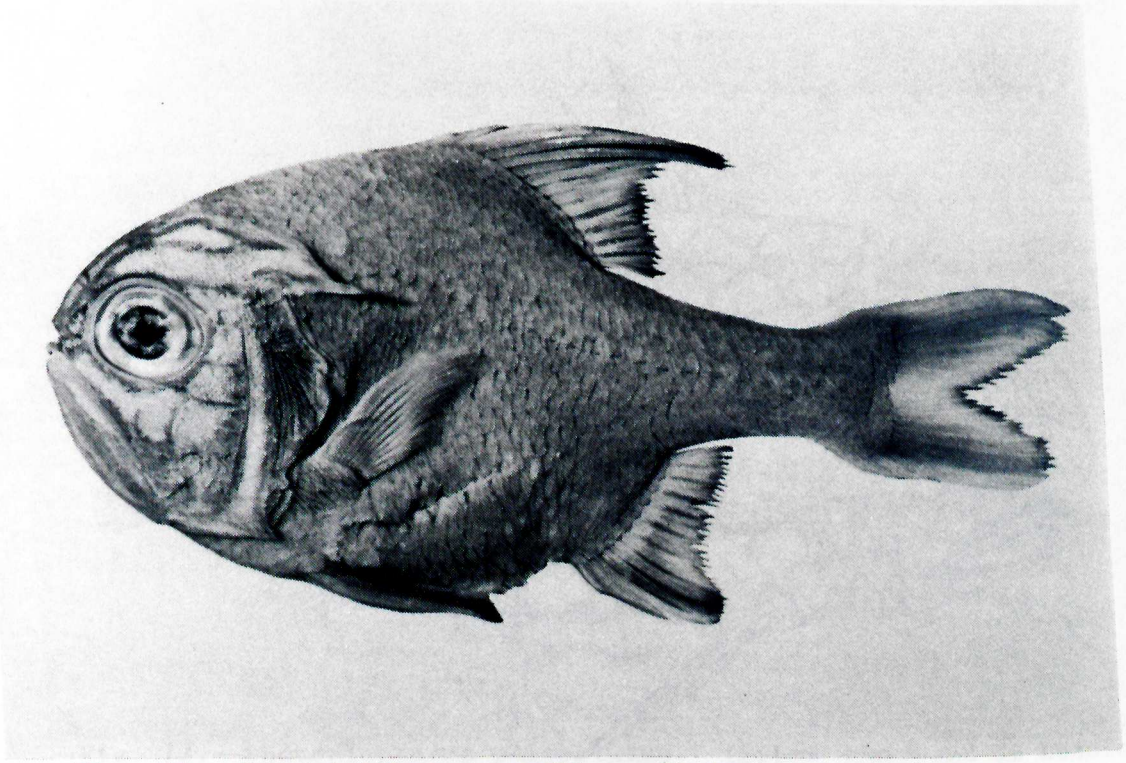


Fig. 68.--Trachichthys australis. (Actual specimen)

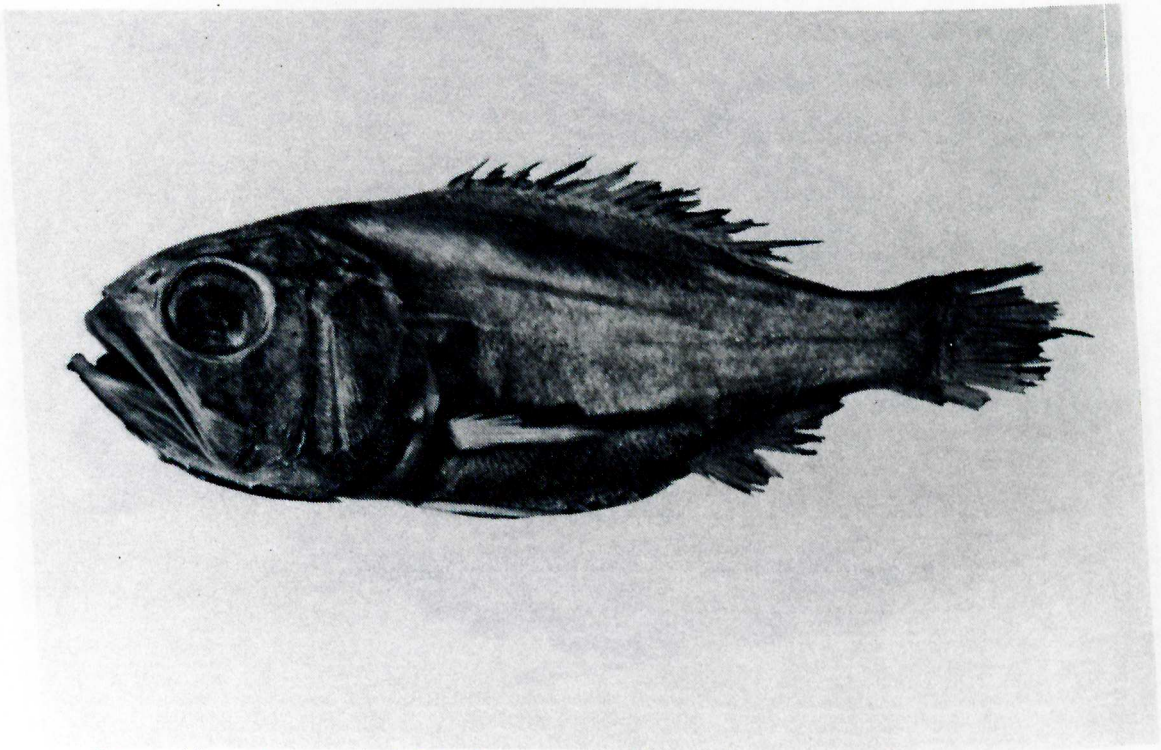


Fig. 69.--Paratrachichthys sp. (Actual specimen)

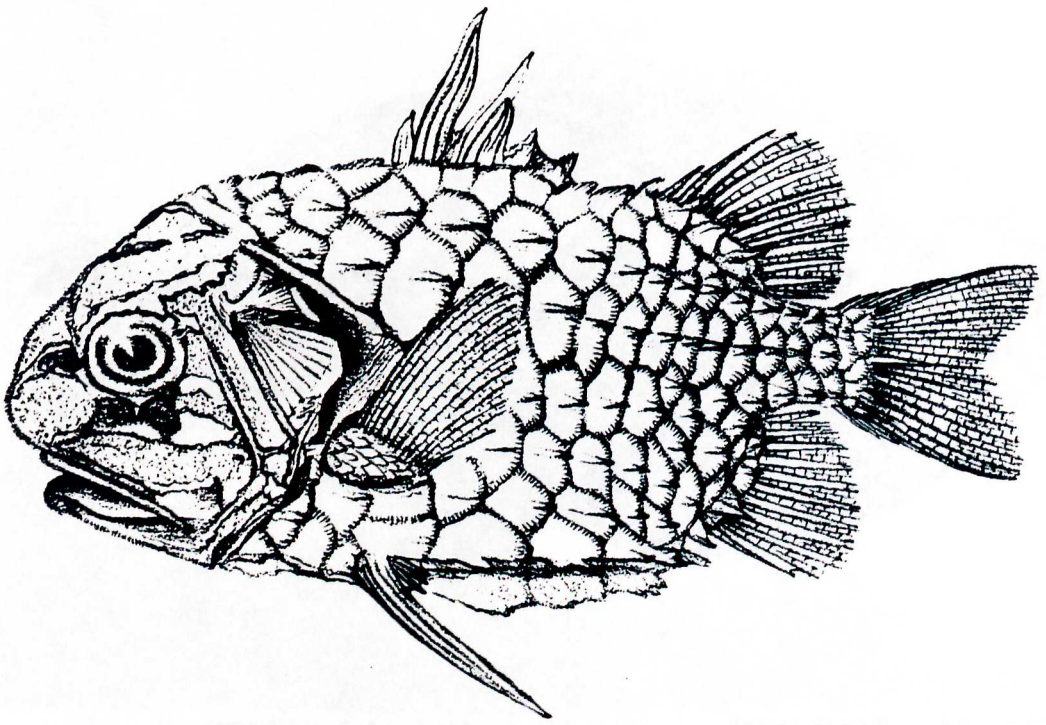


Fig. 70.--Monocentris japonicus. (Artist unknown)

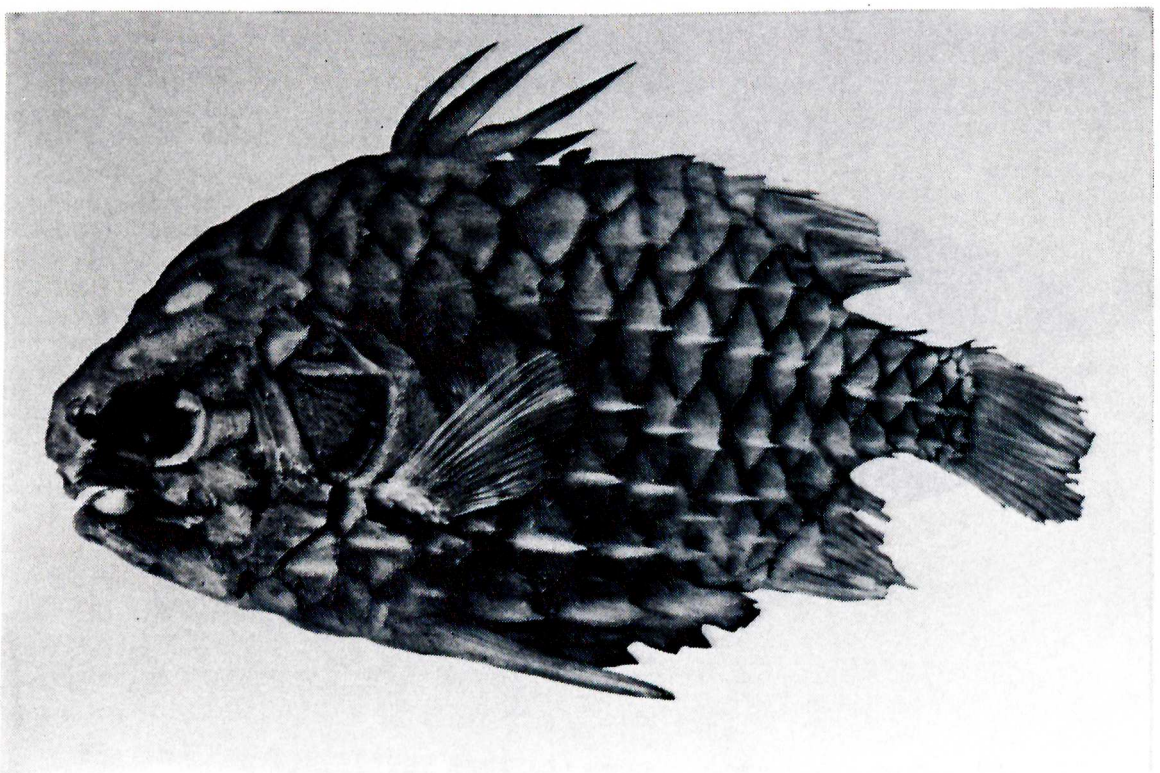


Fig. 71.--Cleidopus gloriae-maris. (Actual specimen)

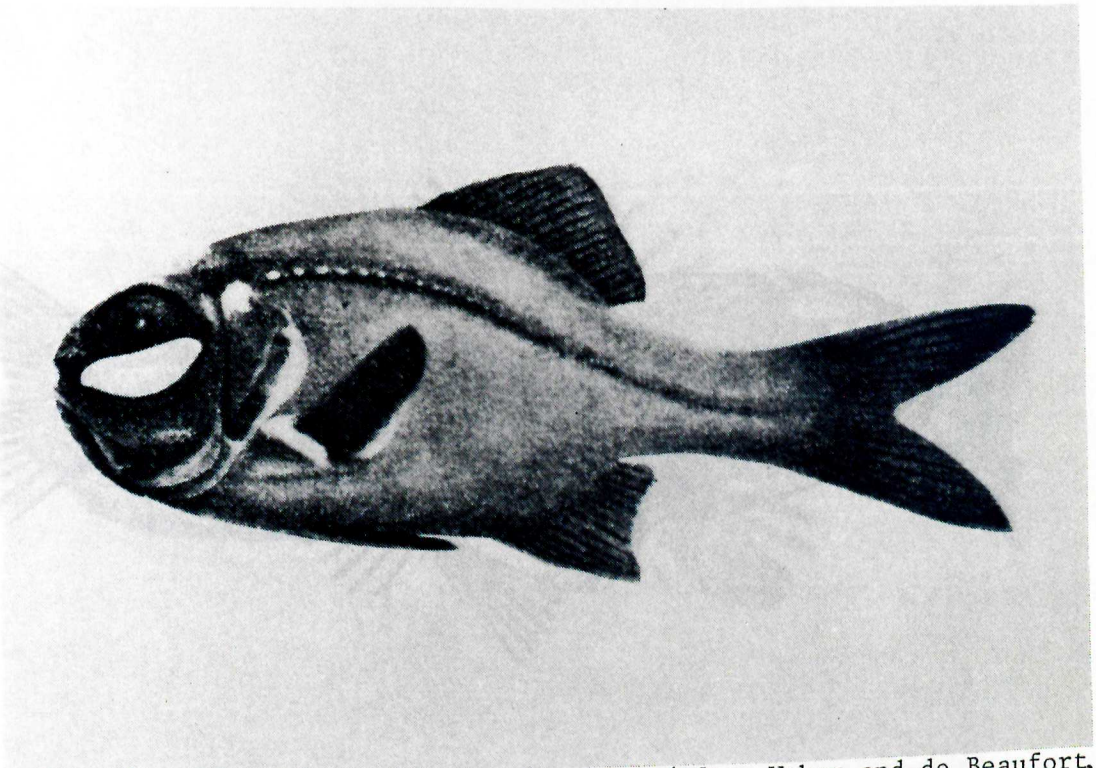


Fig. 72.--Photoblepharon palpebratus. (After Weber and de Beaufort, 1929)

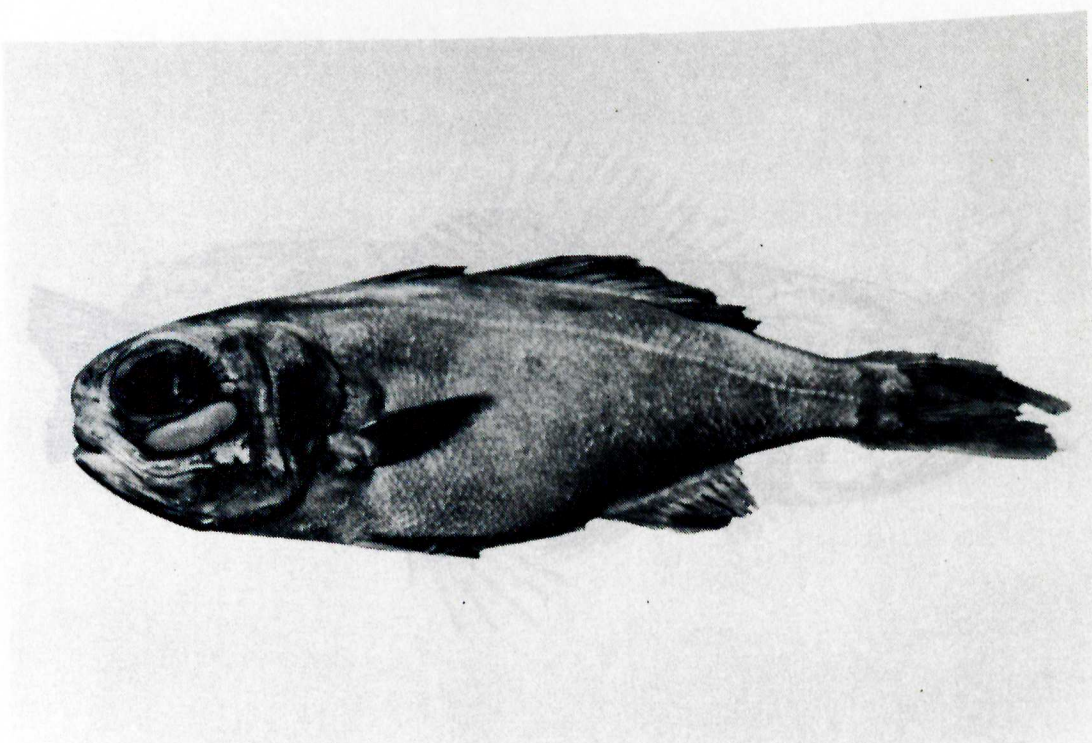


Fig. 73.--Anomalops katopteron. (Actual specimen)

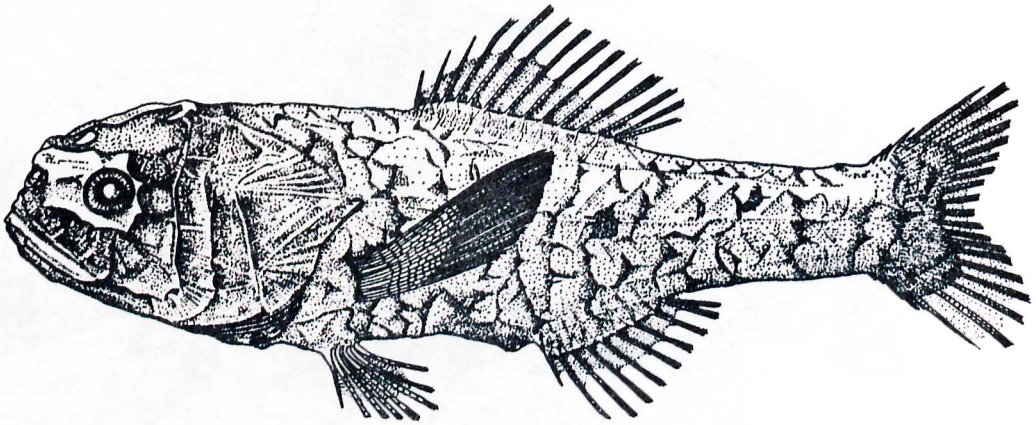


Fig. 74.--Scopelogadus mizolepis. (After Ebeling and Weed, 1973)

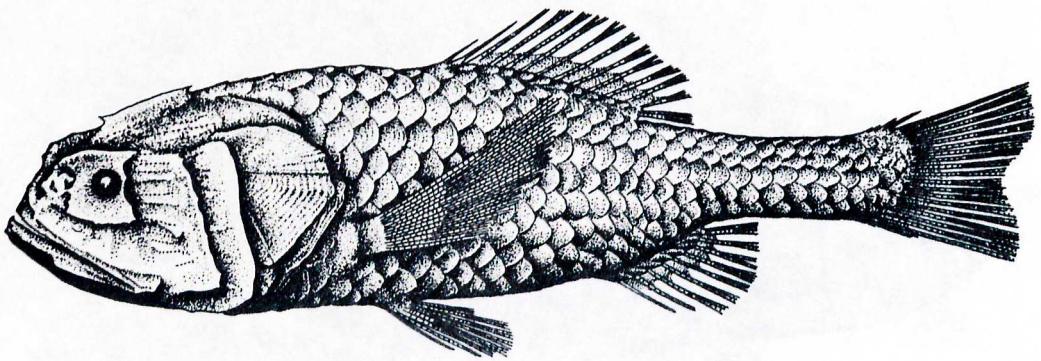


Fig. 75.--Scopeloberyx robustus. (After Ebeling and Weed, 1973)

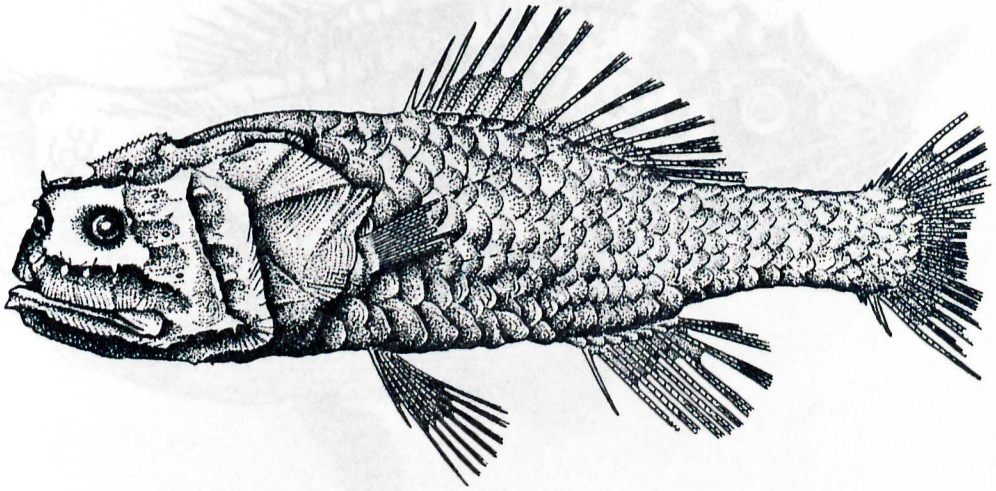


Fig. 76.--Poromitra crassiceps. (After Ebeling and Weed, 1973)

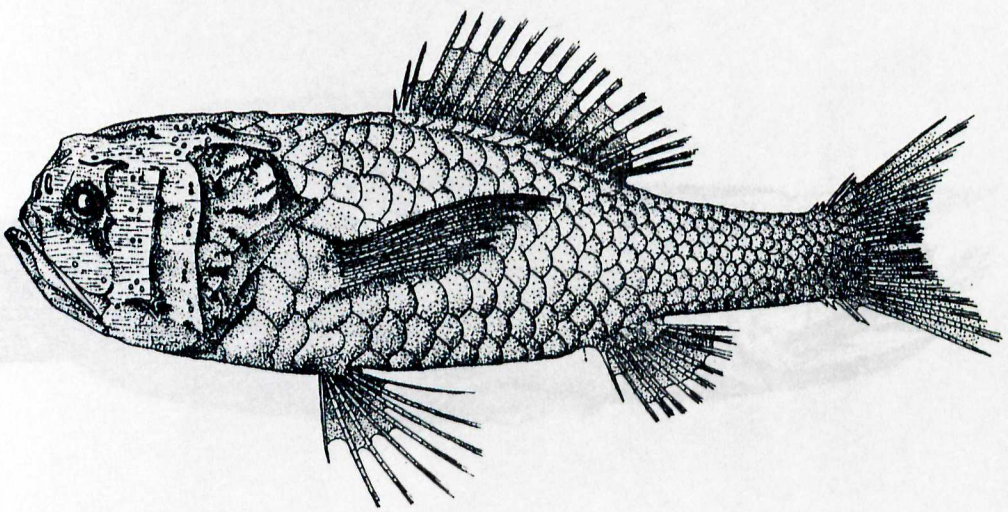


Fig. 77.--Melamphaes eulepis. (After Ebeling and Weed, 1973)

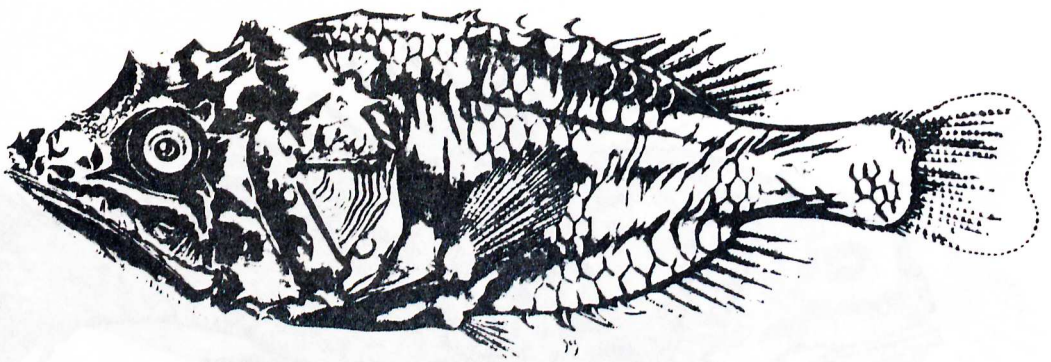


Fig. 78.--Gibberichthys pumilus. (After de Sylva and Eschmeyer, 1977)

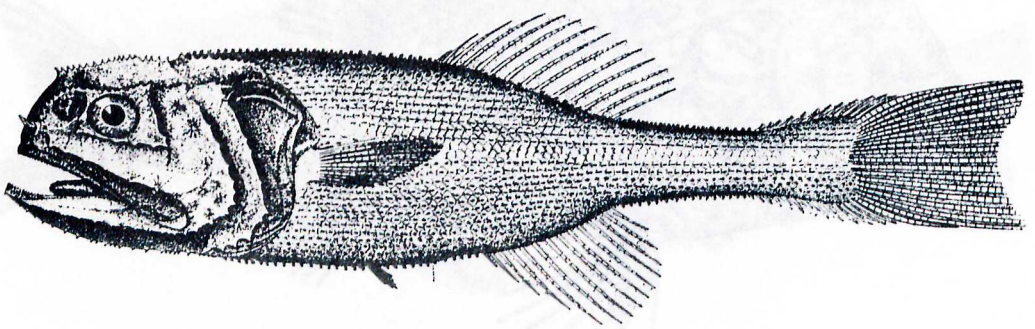


Fig. 79.--Stephanoberyx monae. (After Ebeling and Weed, 1973)

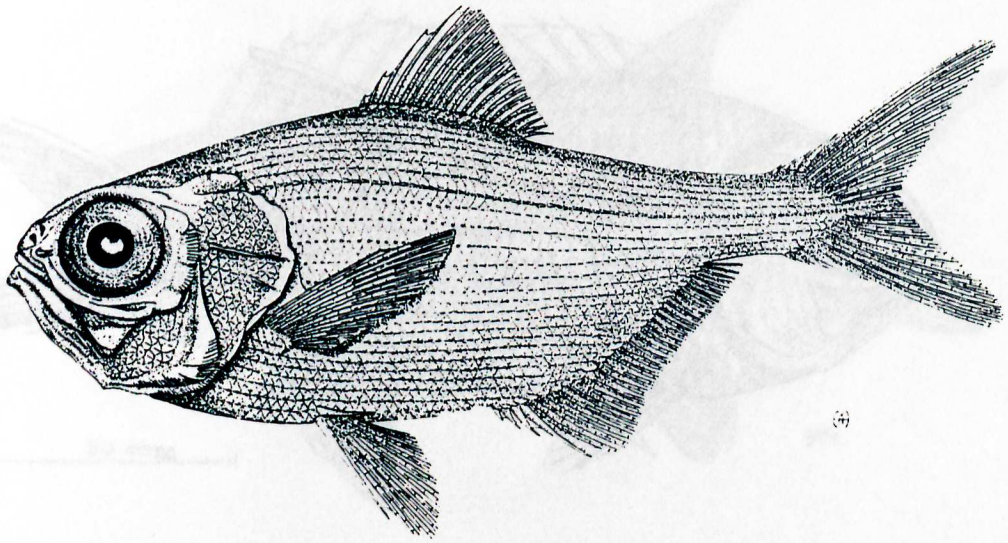


Fig. 80.--Beryx splendens. (After Woods and Sonoda, 1973)

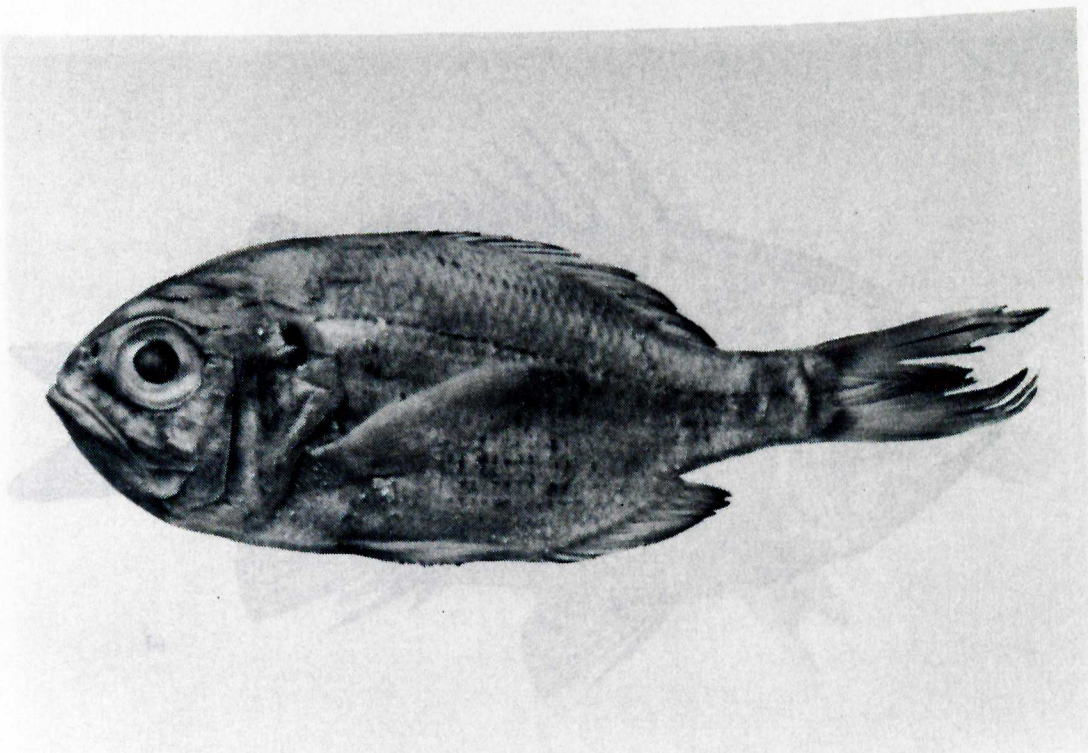


Fig. 81.--Centroberyx affinis. (Actual specimen)

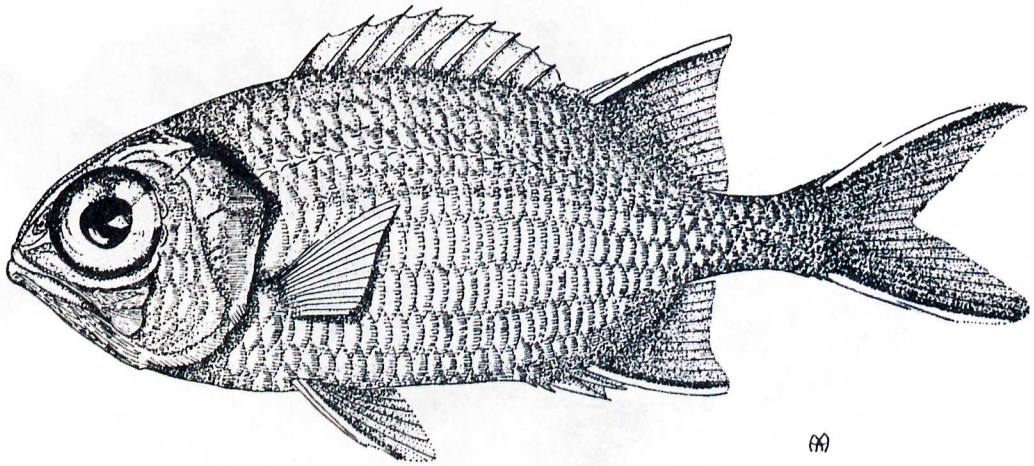


Fig. 82.--Myripristis jacobus. (After Woods and Sonoda, 1973)

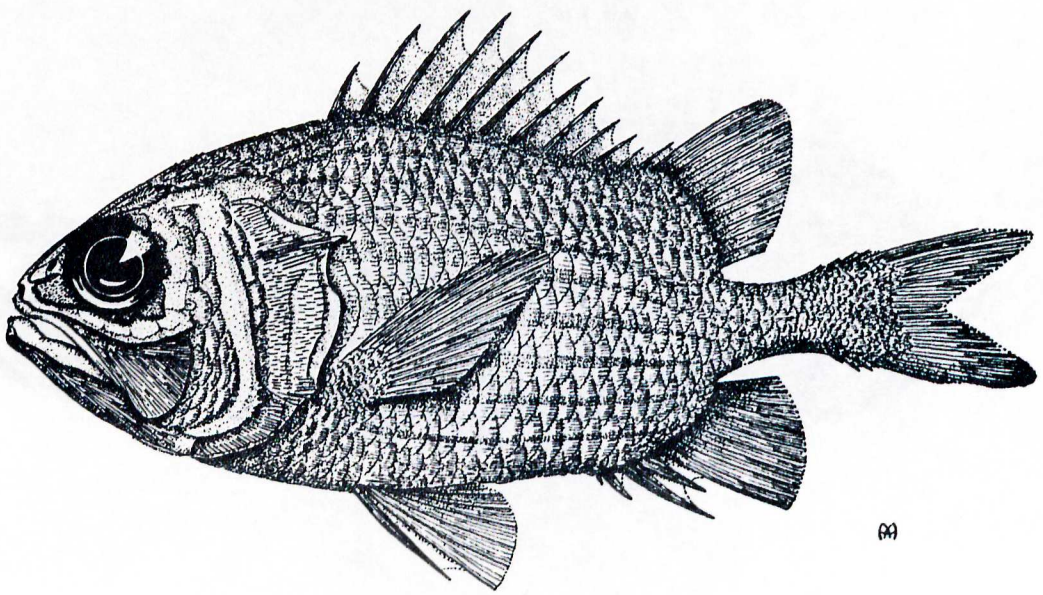


Fig. 83.--Ostichthys trachypoma. (After Woods and Sonoda, 1973)

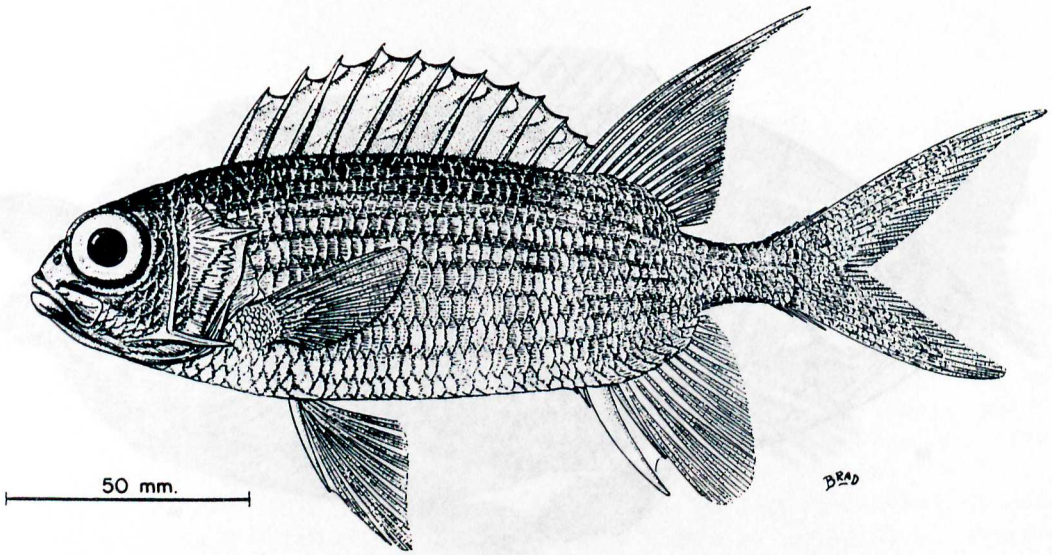


Fig. 84.--Holocentrus rufus. (After Woods and Sonoda, 1973)

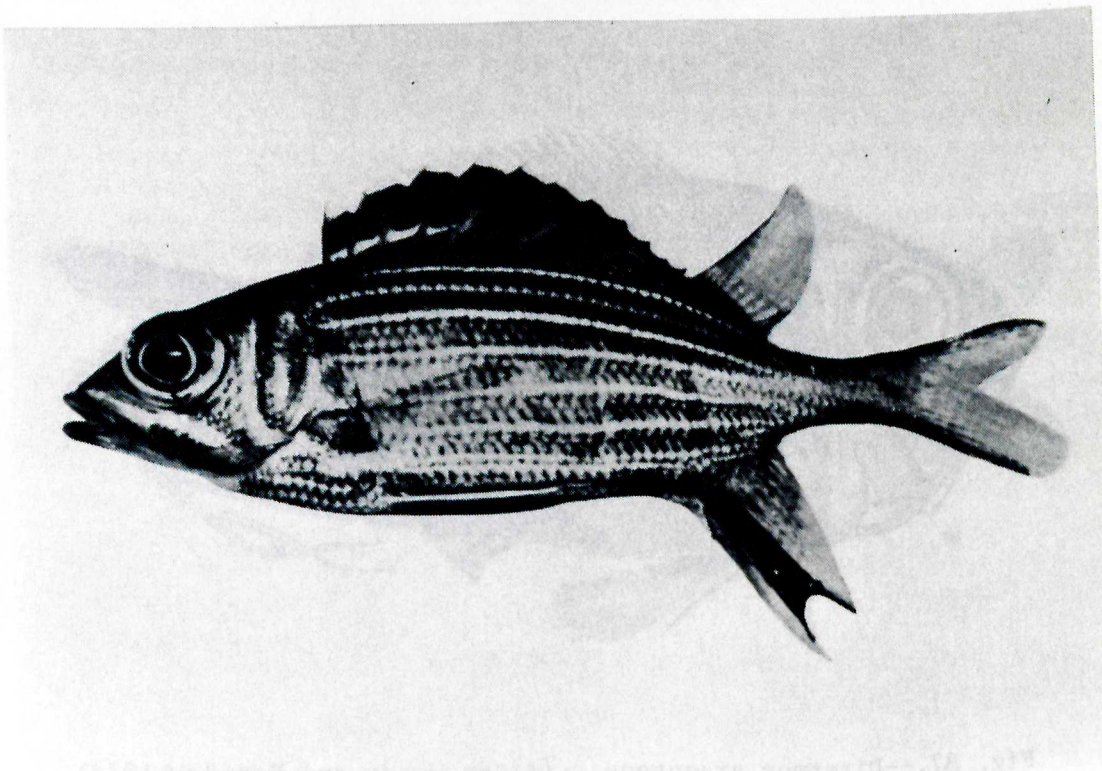


Fig. 85.--Adioryx diadema. (After Woods, 1953)

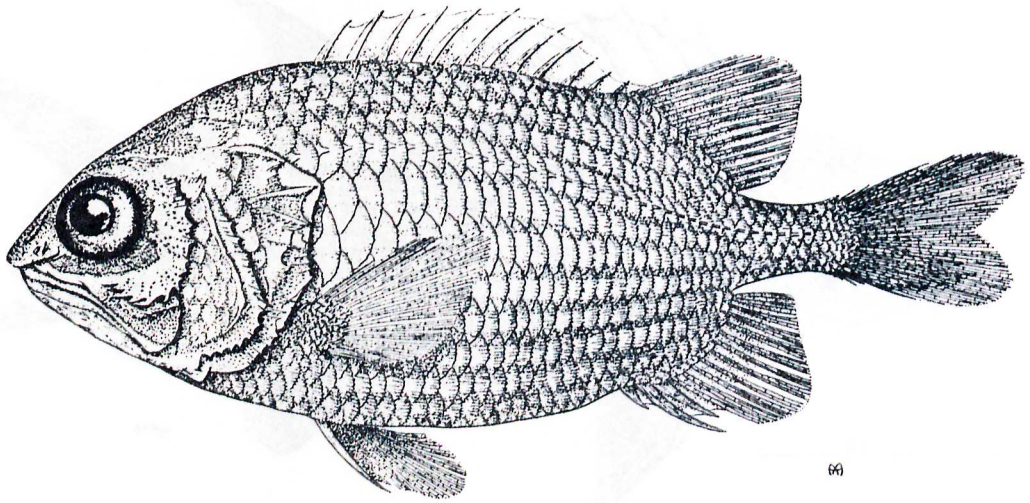


Fig. 86.--Plectrypops retrospinis. (After Woods and Sonoda, 1973)

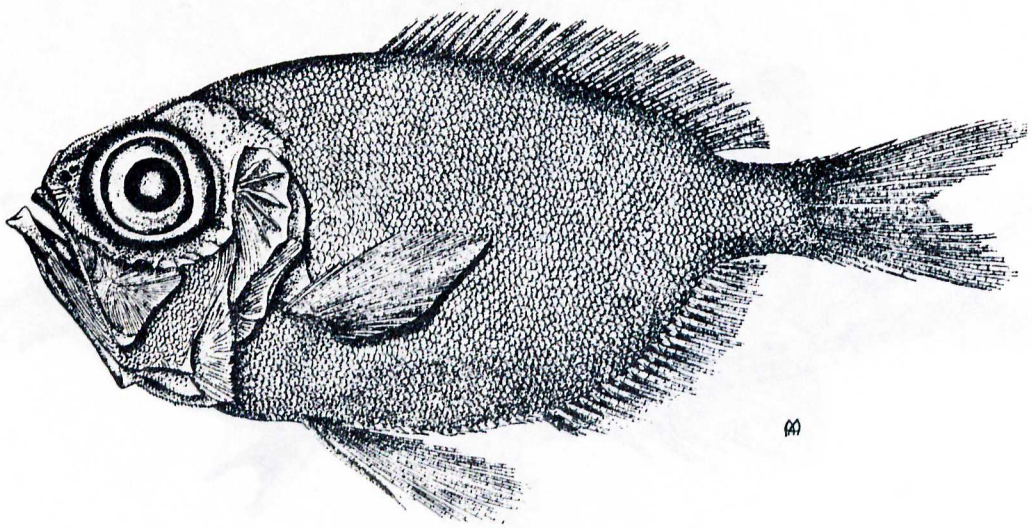


Fig. 87.--Diretmus argenteus. (After Woods and Sonoda, 1973)

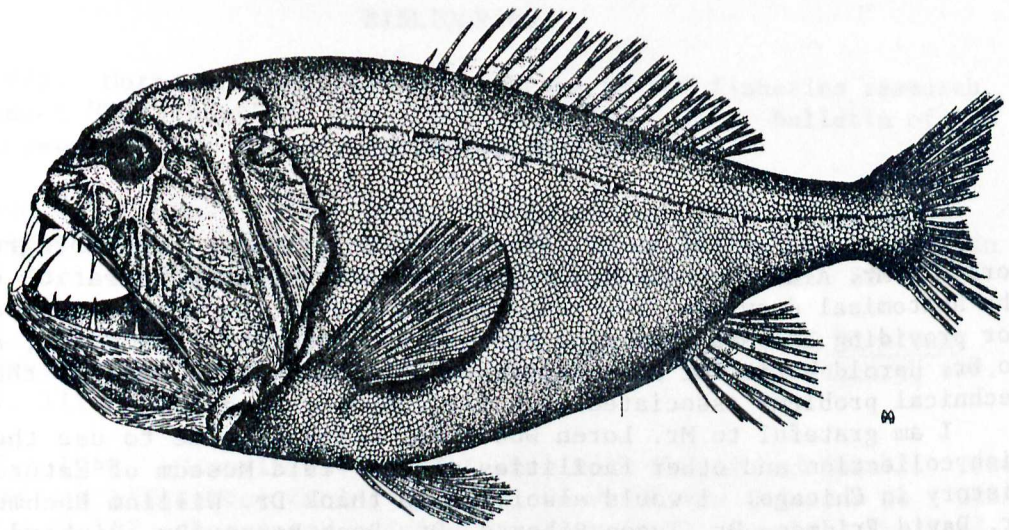


Fig. 88.--Anoplogaster cornuta. (After Woods and Sonoda, 1973)

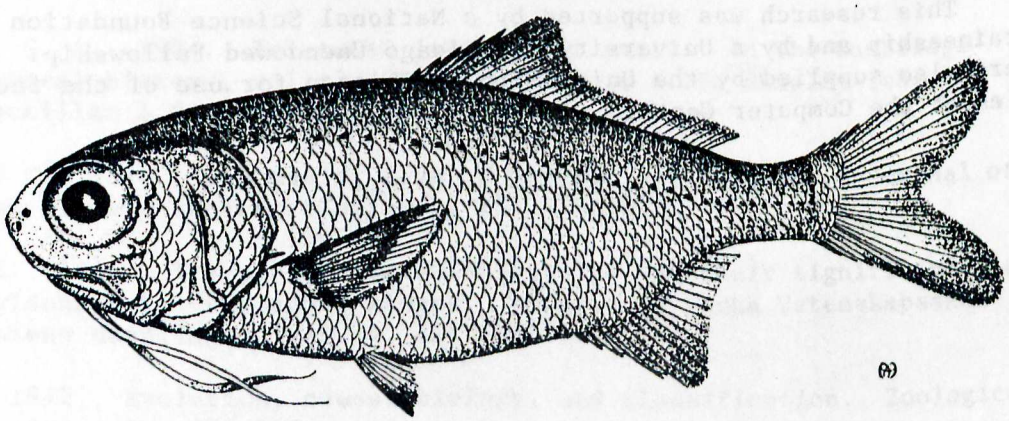


Fig. 89.--Polymixia lowei. (After Woods and Sonoda, 1973)

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