THE EVOLUTION OF BRANCHIOSTEGAL RAYS IN TELEOSTOME FISHES

B

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THE EVOLUTION OF BRANCHIOSTEGAL RAYS IN TELEOSTOME FISHES

ABSTRACT

The origin, function and evolution of the branchiostegal rays, the related opercular and gular bones and associated hyoid elements were investigated in teleostome fishes. Alizarin, skeletal or alcoholic specimens of over half the living families (over 240) and all the living orders of teleostome fishes with branchiostegals were examined. Literature provided data for most of the remaining living and fossil families and orders.

Several evolutionary trends became apparent; a tendency for number of branchiostegals to decrease, following Williston's Law; increasing separation of mandibular and hyoid arches; and an increase in number and complexity of hyoid elements.

In the development of hyoid elements, but not of branchiostegal rays, the ontogenetic sequence paralleled the phylogenetic sequence. Examination of the unusual adult hyoid relationships in the neotenic Schindleria showed it to resemble the larval condition of normal fishes. The condition in the tiny goby, Mistichthys, is similar.

The structure of the branchiostegal series and hyoid elements proved valuable in tracing the relationships of fishes. Major findings include: Hiodontidae were found not be be closely related to the Notopteridae; the Notopteridae and osteoglossoid families to be related to the mormyriforms; the Neoscopelidae and Myctophidae to differ from other myctophiforms; the ophidioids to require ordinal separation from the Perciformes and placement near the Gadiformes and Ateleopiformes; the Amblyopsidae to belong in the Percopsiformes; the Anabantoidei and Ophicephaloidei to be closely related suborders of common ancestry deserving placement in the same order; the Beloniformes to differ from most other orders in the loss of the interhyal and upper hypohyal; and the Echeneiformes to differ from most Perciformes in the possession of 8-11 branchiostegals. The number of branchiostegals was found to be influenced by posterior extension of the jaws, small body length, feeding habits, gill membrane attachment and deepsea existence.

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McAllister, D.E. 1960. Le *Gasterosteus wheatlandi*, nouvelle espèce de poisson pour la province de Quebéc. Le Naturaliste Canadien, 87(5):117-118.

McAllister, D.E. 1961. The origin and status of the deepwater sculpin, *Myoxocephalus thompsonii*, a nearctic glacial relict. Nat. Mus. Canada, Bull. 172: 44-65.

McAllister, D.E. and C.C. Lindsey. 1961. Systematics of the freshwater sculpins (*Cottus*) of British Columbia. Nat. Mus. Canada, Bull. 172: 66-89.

McAllister, D.E. 1962. Fish remains from Ontario Indian Sites 700 to 2500 years old. Nat. Mus. Canada, Natural Hist. Pap. 17: 2-6.

McAllister, D.E. 1963. A revision of the smelt family, Osmeridae. Nat. Mus. Canada, Bull. 191: 1-53.

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INTRODUCTION

This is a study of the evolution of branchiostegals in teleostome fishes. The study considers the vertical evolution of branchiostegals with special regard to ordinal phylogeny of teleostome fishes. It also considers the horizontal evolution of branchiostegals in regard to the effect of internal and environmental factors. The homologous structures, the opercular bones and gular plates, and the elements of the hyoid arch (except the hyomandibular, urohyal, and the glossohyal)[1] upon which the branchiostegals insert, are also studied, although in less detail. The origin, development, and function of the branchiostegals are also dealt with. The central problem considered is to what extent the branchiostegals reflect the phylogeny of the teleostome fishes.

In the evolution of a group, a morphological structure has three courses. It may remain the same or almost the same. It may do this even if other structures are evolving rapidly. Secondly, it may advance through modification of form, through complication or addition. Thirdly, it may degenerate through simplication, loss or disappearance. All of these courses are of value to the student of phylogeny. Possession of a structure nearly similar by two groups, supposing the similarity is not due to parallelism, suggests relationship and common origin. Differences wrought through evolutionary change towards complexity or simplicity suggest placement in different phylogenetic lines or in different taxa, the closeness of relationship depending on the degree of difference. Through this method a sequence of relationships may be built up, and

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[1] These bones can be important systematically but are not directly associated with the branchiostegals.

through examination of fossils and determination of primitive characters the sequences can be transformed into a phylogenetic tree or dendrogram.

A clear picture of phylogeny cannot be gained through examination of a single character. Because of parallel evolution and because of different rates of evolution in different structures a single character may lead one astray in tracing phylogeny. A clear picture of phylogeny is based on as many firm taxonomic characters as possible. This reduces the probability of confusing homologous and analagous characters and presents a picture of the evolution of the whole animal and not just one part. Therefore, in this study the relationships suggested by the branchiostegal series (operculars, branchiostegals, gulars) and the hyoid arch, are checked with other sound taxonomic characters (from literature or original observations).

The concentration which the study of a single characters complex enables has advantages over the studying of many characters simultaneously. Parallelisms are more readily noted. Smaller differences are less likely to be ignored. Some valuable single character complex studies may be noted: Hubbs (1920) on the branchiostegals, Starks (1930) on the bones of the shoulder girdle and (1926) on the ethmoid bones, Burne (1909) and Derscheid (1924) on the olfactory organ, Whitehouse (1910) and Gosline (1960), (1961) on the caudal skeleton, Emelianov (1935) on the ribs, Frost (1925), (1926), (1927), etc. on the otloliths, Stensio (1947) on the sensory canals of the head, Lindsey (1956) on the vertical fins. Holstvoogd (1963) on the retractores arcuum branchialium and Freihofer on the ramus lateralis accessorius.[1] None of these studies has included all the orders and only one more than 100 families.

It is from the combination of detailed studies such as these and others yet to be done that the ultimate picture of the phylogeny of the Teleostomi will be constructed. Towards this end the present paper hopes to contribute.

Literature

Branchiostegal counts have been used in fish taxonomy even before the time of Linnaeus. The more careful ichthyologists such as Day, Regan, Smitt and Jordan have included branchiostegals in their descriptions and analyses of fishes, as have Gill, Ryder and Starks in their osteological studies.

There have been few studies of branchiostegals on the broad scale however. Bertelsen and Marshall (1956) discuss the number and arrangement of branchiostegals in some of the malacopterygian orders while placing the Miripinnati. The only other study, and the most important one, is that of Hubbs (1920). This concise study enumerates many of the important evolutionary changes in the branchiostegals of living fishes. Hubbs noted the tendency for decrease in branchiostegals during evolution (noted previously as early as 1904), and the differences in shape and arrangement of the branchiostegals of malacopterygians and acanthopterygians. He noted the malacopterygian nature of the branchiostegals in the Synentognathi, and the acanthopterygian nature of the branchiostegals in the Microcyprini, Symbranchia and Opisthomi.

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[1] Two further valuable studies in progress may be noted, that of Quentin Bone, Marine Laboratory, Plymouth on lateral muscle innervation and G. Nelson, University of Hawaii on the branchialarches.

He based his conclusions on the examination of about 140 families distributed in less than twenty orders, but gave no figures, and described only a few in detail.

The hyoid arch, aside from papers on the osteology of single species, has received little attention from the broad comparative point of view in fishes. Corsy (1933) studied the evolution of the hyoid arch of vertebrates but only a small portion of this study was devoted to teleostome fishes. Khanna (1961) described the hyobranchial skeleton of some Indian fishes. Allis (1915) and (1928) and Edgeworth (1926) and (1931) comment on the lower elements in discussions upon the homologies of the hyomandibular.

This paper tries to extend these and other comparative studies by the inclusion of fossil groups, the examination of every order of fishes with branchiostegals and as many families as possible (over half of the living families),[1] the presentation of data in a consistent style, the illustration of many forms, and in the interpretation of the data in terms of phylogeny, adaption and parallelism.

Definitions

To introduce the subject and to clarify the terminology, the technical terms pertinent to the study are here defined, synonyms listed and structures are illustrated (fig. 1). The terminology of Harrington

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[1] Over 240 of the 402 living families and over 330 species and 700 specimens examined. Counts lacking on only 16 living and 42 fossil families (i.e. data (own & literature) available for 452 of total of 510 living and fossil teleostome families). All living orders with branchiostegals were examined.

(1955) is used, as far as it applies. Starks (1901) may be referred to for the older synonyms. Two terms, spathiform and acinaciform are introduced for the first time.

Branchiostegals or branchiostegal rays: These are the struts of dermal bone (sometimes cartilage) below the operculars, that insert on the hyoid arch and support the gill membrane of Teleostomi. The term lateral gulars is sometimes misapplied to the broad branchiostegals of Chondrostei. The branchiostegals are here believed to be homologous with the hyoid rays of Acanthodii and Elasmobranchii (fused into the "opercular plate" of chimaeras).

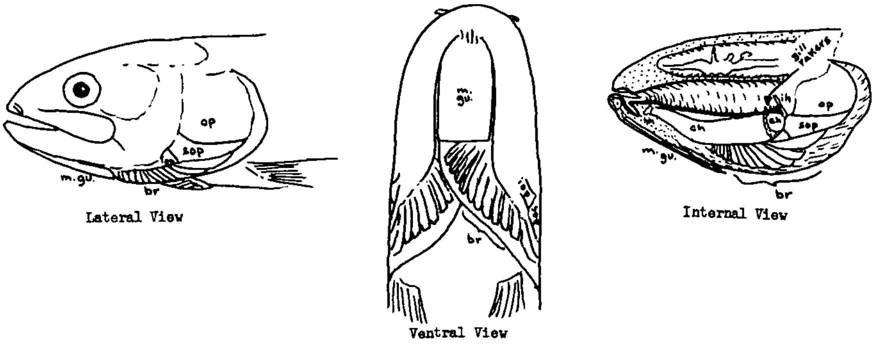
Branchioperculum: This is the enlarged uppermost branchiostegal in *Amia*.

Jugostegelia: These are the branchiostegals free from the hyoid arch and overlapping, found in the anguilliform families, Echelidae, Ophichthidae and Neenchelyidae.

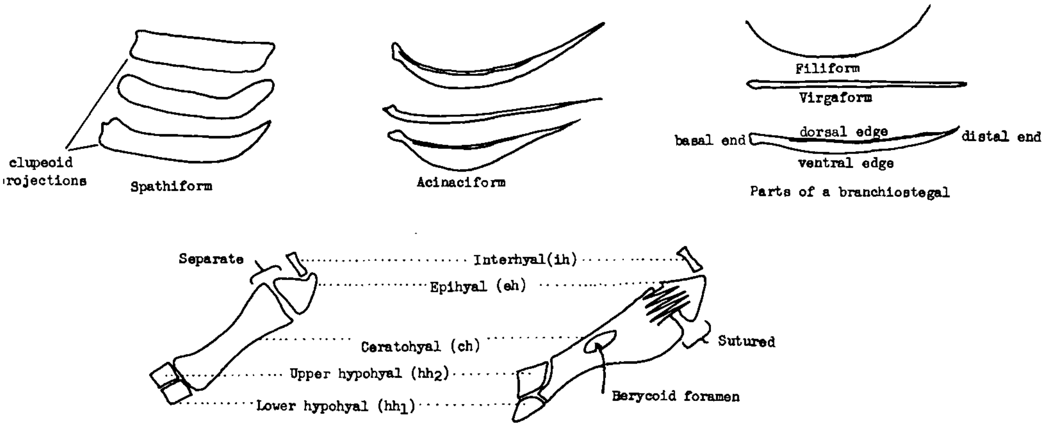
Spathiform: Applies to the broad, laminar, paddle-shaped branchiostegals found in some malacopterygian and most of the more primitive teleostomes. From the Latin *spatha* or spatula. E.g. branchiostegals of *Amia*.

Acinaciform: Applies to the slender, non-laminar, sword or scimitar-like branchiostegals found in some malacopterygians and most actinopterygians. From the Latin *acinaces* or scimitar. E.g. branchiostegals of *Perca*.

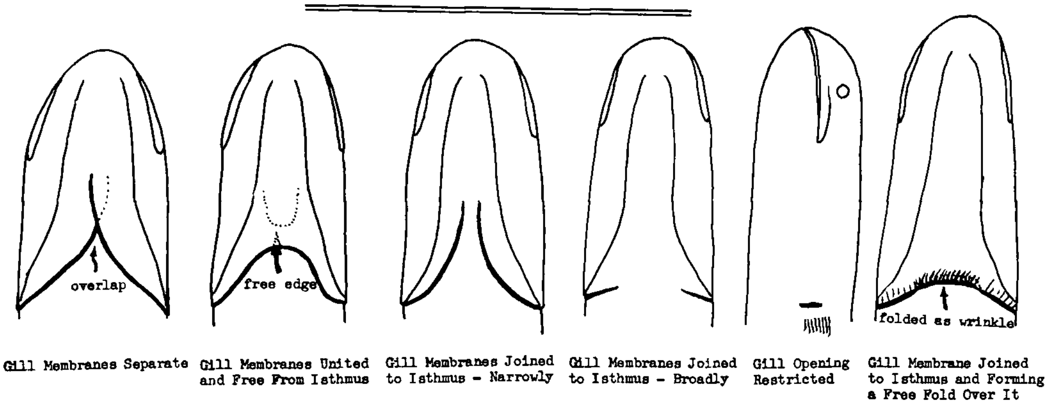
Operculum: The large dermal bony (sometimes cartilaginous) upper element of the gill cover behind the preoperculum and inserting on the hyomandibular in teleostomes. Believed to be an enlarged branchiostegal.



GENERAL VIEWS OF BRANCHIOSTEGALS
(in *Amia calva*)



BRANCHIOSTEGAL AND HYOID ARCH TERMINOLOGY



GILL MEMBRANE ATTACHMENT

Fig. 1. General features and relative positions of branchiostegals, operculars, gulars, hyoid arch and gill membranes.

Suboperculum: The large, dermal, bony (sometimes cartilaginous) gill cover element below the operculum in teleostomes. Believed to be an enlarged branchiostegal.

Interoperculum: The large, dermal, bony (sometimes cartilaginous) element below the lower arm of the preoperculum and anterior to or under the front half of the suboperculum. It typically is connected to the mandible, epihyal and suboperculum. Believed here to be an enlarged branchiostegal. Found only in higher teleostomes (Group II and above).

Operculars: Collective term for the operculum, suboperculum and, if present, the interoperculum.

Gill membrane or branchiostegal membrane: The membrane lying between the operculars and the isthmus which is supported by the branchiostegals. The gill membranes may be variously connected to the isthmus. If the gill membranes are not connected to one another or the isthmus and overlap anteriorly they are termed *separate* (e.g. *Salmo*, *Sphyraena*). If the gill membranes are attached to one another, yet not joined to the isthmus (at least posteriorly), then they are said to be *united and free from the isthmus* (e.g. Polyodontidae, Notopteridae); they may in this case have a small or large free border posteriorly (whether the posterior edge is free may be determined by running a needle under it). In the Synbranchiformes the gill openings are united and free from the isthmus but dorsally attached to the body before the pectoral fin; this gives the appearance of a single ventral gill opening but is really only a special case of being united and free. Lastly, the gill membranes may be *joined to the isthmus* (e.g. most Cyprinidae, Gobiidae). They may be *narrowly joined to the isthmus* (e.g. *Gasterosteus*) or joined to the isthmus anteriorly in which case the gill opening is wide, or they may be broadly joined to the isthmus (e.g. most Cyprinidae) in which case the gill opening is narrow and the space between the gill openings is wide, or the gill opening may be restricted (e.g. Anguillidae) in which case the gill opening is reduced to a small aperture on the side of the head. When the gill membranes are joined to the isthmus a fold may form across the isthmus between the gill slits (e.g. *Myoxocephalus polyacanthocephalus*) which secondarily resembles the gill membranes united and free condition. The preceding terms have not been used consistently by some authors but the definitions and illustrations given here should make the distinctions clear and should help standarize the terminology.

Median gular: A median bony plate extending backwards from the symphysis between the mandibles. It is bordered posteriorly by the lateral gulars or branchiostegals, if present. Primitively it bears a v-shaped pit line. It may be homologous with the branchiostegals. E.g. *Amia*, *Elops*. A second median gular, posterior to the normal median gular is found in some Dipneusti.

Lateral gulars: Pair(s) of bony plates, larger than the branchiostegals, lying between the median gular and branchiostegals (when present), and inserting on the hyoid arch medial to the mandibles. It is believed here to be homologous with the branchiostegals. Primitively bears a transverse pit line. E.g. *Polypterus*, *Calamoichthys*, *Latimeria*. In some Dipneusti there may be two pairs, an anterior and a posterior pair.

Gulars: Collective term for median and lateral gulars.

Branchiostegal series: Collective term for the operculars, branchiostegals and gulars (all branchiostegal derivatives).

Interhyal: Endochondral bony or cartilaginous, usually cylindrical element in teleostomes connecting the lower portion of the hyoid arch to the hyomandibular. It acts as a pivot. It may or may not be homologous with the tetrapod stylohyal, which term has been used for it. The interhyal typically inserts on the lower tip of the hyomandibular. Paired.

Epihyal: Endochondral bony or cartilaginous usually triangular element in higher teleostomes (Group II and III) lying between the ceratohyal and interhyal. Probably derived from the ceratohyal. Paired.

Ceratohyal: Endochondral bony or cartilaginous usually hourglass-shaped element in teleostomes lying between the epihyal, if present, or interhyal and the hypohyal(s). Paired. Found in Acanthodii, Elasmobranchii and Teleostomi.

Hypohyal(s): Endochondral bony or cartilaginous element(s) lying below the ceratohyal and lateral to the glossohyal, in Acanthodii and Teleostomi. In the Crossopterygii, Dipneusti and lower Actinopterygii (Group IIB and lower) the hypohyal is single; in the higher Actinopterygii (except where secondarily degenerate) there is a lower (hypohyal 1) and an upper (hypohyal 2) hypohyal. Called basihyals by some authors.

Hyoid arch: Restricted in this study to include only the interhyal, epihyal, certaohyal and hypohyals (since the other hyoid elements, the hyomandibular and basihyal (= glossohyal) were not included in this study).

Sutured: The epihyal and ceratohyal are termed sutured if they are joined by interdigitating prongs emitted by each bone, while they are termed separate if not so joined.

Clupeoid projection: This is a bulge on the anterior edge of the base of branchiostegals in clupeoids and their derivatives. Percopsoid projection is an angulation on the anterior branchiostegal base (see fig. 3).

Beryciform foramen: This is a perforation above the midsection of the centre of the ceratohyal found in beryciform fishes and some of their derivatives. In some fishes the roof of the foramen is lost and only a notch appears on the dorsal edge of the ceratohyal. The foramen perforates the groove along which the hyoid artery runs on the outer face of the ceratohyal.

Positional terms: Since the hyoid arch may be almost horizontal or almost vertical the branchiostegals towards the interhyal end of the arch may either be called dorsal or posterior branchiostegals. The branchiostegals toward the hypohyal end of the arch may similarly be called ventral or anterior branchiostegals. In numbering the branchiostegals the uppermost (or posteriormost) provided the starting point since the lower (anterior) branchiostegals are the most variable and do not provide as stable a point of enumeration. The portion of the branchiostegal inserting on the hyoid arch is termed basal, the opposite end the distal tip. The two long edges may be called the ventral (anterior) edge and the dorsal (posterior) edge. According to their insertion branchiostegals are divided into epihyal and ceratohyal (sometimes interhyal and hypohyal), external and ventral or internal branchiostegals. When a branchiostegal straddles the epihyal-ceratohyal or a ceratohyal-hypohyal joint a half a branchiostegal is awarded to each (recorded in descriptions and tables as ½).

Classification

The basis of the classification used herein is that of Berg (1947; 1955). Modifications of this classification were made from the later literature. Changes, sometimes considerable, were also made in the classification of living fishes, mainly in the rearrangement of orders and status of certain groups, as suggested by this study and data from other studies. The uniform -iformes ending was adopted for orders, -oidei for suborders, -idae for families and -inea for subfamilies.

METHODS

The branchiostegal series and hyoid bones were examined by several methods. The principal method was by clearing and staining with alizarin following the method of Hollister (1934). Specimens preserved in alcohol usually from three to six inches but sometimes as short as one inch (Phallostethidae) or as long as sixteen inches were employed for staining. The stained hyoid arch with the branchiostegals was usually removed and examined. Some were photographed under a binocular microscope. In quite a few cases dermestid-cleaned skeletons were examined; here caution must be employed since branchiostegals may be lost during skeletonizing. Alcoholic specimens were dissected for examination of the arch and branchiostegals. From other alcoholic specimens branchiostegal counts were taken without dissection. In the latter method one must check to see if the uppermost branchiostegal is hidden under the suboperculum or whether the lowest branchiostegal, which may be quite small, is not obscured by the skin. An attempt was made to examine at least one specimen from as many families as possible. Representatives were chosen by availability except that as many families and suborders as possible were examined.

Branchiostegals were counted on the left. When the branchiostegals were abnormal (see Crossman, 1960, for examples) the counts were not recorded. E.g. fused, bent, or irregularly placed branchiostegals.

For families not examined and to supplement families examined, counts were obtained from the literature. Information on fossils was wholly obtained from the literature. These sources are included in References under the family. Synonyms of taxa follow enclosed in parentheses. Fossil groups are indicated by the sign "†".

Observations were made at the Vancouver Public Aquarium to gain an understanding of the movements of the elements in a living fish.

The principal sources of material were the National Museum of Canada, Ottawa (NMC), and the museum of the Institute of Fisheries, University of British Columbia (BC). Other material was borrowed from Stanford University (SU), and Royal Ontario Museum (ROM), British Museum (BM), Scripps Institution of Oceanography (SIO), and University of Michigan Museum of Zoology (UMMZ), or examined at the United States National Museum (USNM). Acknowledgements note other sources.

EMBRYOLOGY

The hyoid arch develops from the second visceral arch, the first becoming the jaws, the more posterior ones supporting gills. The following, from de Beer (1937), Wade (1962) and original observations on Amia appear to be the usual order of development: 1) ventral extension of a cartilaginous hyomandibular-symplectic rod from the auditory capsule and appearance of a ceratohyal cartilage below this, 2) separation of the hyomandibular-symplectic cartilage from the auditory capsule, 3) appearance of the interhyal half or three quarters of the way up the lower side of the hyomandibular-symplectic cartilage and appearance of a hypohyal, 4) appearance of the upper, then the lower branchiostegals, appearance of the median gular, operculum, suboperculum and interoperculum, 5) ossification of the ceratohyal in the anterior and epihyal in the posterior end of the ceratohyal cartilage, and of the symplectic and the hyomandibular in their cartilage, 6) ossification of the upper and lower hypohyal in the hypohyal cartilage, 7) suturing of epihyal and ceratohyal (delayed till adult in Anarhichas). In different groups the exact sequence may vary and of course not all of these elements are found in all teleostomes.

It is interesting to compare the ontogenetic and phylogenetic appearance of the hyoid elements. This is done below:

	Ontogeny	Phylogeny
1)	ceratohyal cartilage	hypohyal and ceratohyal
2)	a hypohyal and interhyal cartilage	interhyal
3)	epihyal and ceratohyal ossification	epihyal

4)	upper and lower hypohyal ossification	upper and lower hypohyal
5)	suturing of epihyal and ceratohyal	suturing of epihyal and ceratohyal

In comparing the sequence of appearance of the hyoid elements in the table above it may be seen that the embryonic sequence of appearance of every element follows the phylogenetic sequence of origin in every case except that of the hypohyal which is delayed to the next stage in embryonic development.

The embryonic development of the hyoid arch is also valuable because it suggests the two hypohyals develop from a single precursor, the cartilaginous hypohyal, a point which the positional relationships of the two adult hypohyals would tend to confirm. The embryonic development of the epihyal from the ceratohyal would also appear to be a morphologically and phylogenetically plausable development.

The development of the branchiostegals does not appear to recapitulate phylogeny. In the higher teleosts numerous branchiostegals do not appear and then secondarily diminish to a reduced number, perhaps because of selection at the embryonic stage. Nor do the embryonic branchiostegals of higher teleosts commence embryonically as spathiform and then change to acinaciform shape: instead, they commence as acinaciform.

Embryology enables one to explain one of the unusual characters of the Schindlerioidei. Gosline (1959) states the Schindlerliidae were, as far as he knew, unique in having the epihyal inserting on the upper head of the hyomandibular. However, as noted above, the interhyal commonly inserts high up on the lower side of the hyomandibular-symplectic cartilage embryonically; the point at which it inserts marks the later point of division of the lower end of the hyomandibular and the upper end of the symplectic. Development in the neotenic Schindleria appears to have ceased at a point before the cartilage differentiated into the hyomandibular and symplectic; the epihyal therefore appears to insert on the upper head of the "hyomandibular" (= hyomandibular-symplectic cartilage). Thus, the position of the hyoid arch and "hyomandibular" is unique only that it is found in the adult, and this is not surprising since one expects to find larval conditions in a neotenic fish. An unusual condition is that a hypohyal is not present, although the epihyal has made its appearance. A similar condition is found in the minute goby, Mystichthys luzonensis where the interhyal inserts above the ventral end of the hyomandibular.

Another unusual condition that embryology elucidates is the origin of the mental barbels in the Mullidae. Here there are only 3 normal branchiostegals on the external face of the hyoid arch. At the anteriormost end of the ceratohyal close to the symphysis in the adult is a slightly twisted osseous ray which becomes attenuate and cartilaginous distally. This ray has been suggested to be a branchiostegal (Starks, 1904), thus accounting for the missing fourth branchiostegal one expects on the external face of the hyoid arch. Lo Bianco (1907) and Caldwell (1962) investigated the development of mullids. At 6-8 mm. 4 slender branchiostegals were found in the normal position, at 11-15 mm. the fourth branchiostegal thickened, at 22 mm. the branchiostegal began moving anteriorly and medially, to achieve at 30 mm.

nearly the adult mental condition. Here the study of development confirms the theory that the mental hyoid ray is indeed a branchiostegal. It would be interesting to follow the development of Polymixia, an unrelated form which has a hyoid barbel believed to be supported by branchiostegals. Another worthy problem would be the close following of the development of the median gular to compare it with branchiostegals development for evidence on whether or not they are homologous.

A series of young Amia calva were examined from two Ontario collections (NMC58-192-S, Pt. Pelee, Lake Erie, 20.6-26.7 mm. standard length; NMC58-209, Georgian Bay, Lake Huron, 44.5-50.1 mm. length). The following relationship between standard length and number of branchiostegals was found:

Standard Length (mm.)	21	23	25	26	27	44	46	47	48	49	50
No. Branchiostegals	5	7	7-8	8-9	9	8-13	12	13	12	12	10-12

These data would suggest that by 46 mm. standard length the adult number of 10-13 branchiostegals is attained. Gasterosteus at 25 mm. have attained the adult number of 6 (Runyan, 1961); Neostethus of 25 mm. had attained the adult complement of 5 (own observation). It would seem advisable not to take branchiostegal counts as representative of the adult condition from very young specimens.

FUNCTION OF THE BRANCHIOSTEGAL SERIES

The bones of the branchiostegal series may function in five ways, in respiration, in feeding, in sensing, in protection of the gills and in protection or defense of the fish. These functions are discussed below.

Respiration

Respiration in teleosts is accomplished by maintaining an almost continuous flow of water over the gill filaments. The buccal cavity creates a positive pressure before the gills and the operculum and branchiostegals create a negative pressure behind the gills. The cycle is summarized (from Hughes and Shelton, 1958) in four phases: 1) Water is drawn into the mouth past the open buccal valves by negative pressure created by dropping the lower jaw, which then starts to close. As this happens the operculum is abducting with the opercular cavity closed by the branchiostegal membrane (opercular valve), thus creating a negative pressure and drawing water through the gills from the buccal cavity. 2) As the mouth closes the buccal cavity is reduced; water leaves the mouth until the buccal valves close, causing a rise in pressure. As this happens pressure in the opercular cavity is less negative because of flow through the gills. As the operculum reaches the end of its abduction the pressure within the opercular cavity equals the external pressure and the branchiostegal membrane opens. 3) The operculum begins to abduct with a gap between it and the flank, through which water exits. The mouth closes increasing buccal cavity pressure, forcing water over the gills with little loss out the mouth as the lips are close and the buccal valves effective. 4) The mouth begins to open increasing the volume of the buccal cavity and opening the buccal valves, and dropping the pressure in the buccal cavity. The operculum continues to abduct raising the opercular cavity pressure as the gap between the operculum and flank decreases. At this point there is a tendency for reversal of water flow across the gills. From this resume it may be seen that the branchiostegal membrane functions as a valve to seal the gill opening during abduction of the operculum. Secondly, it acts as an expansable wall (comparable to the rib cage) which permits the volume of the opercular cavity to enlarge and allows a greater volume of water to be drawn through the gills. This is accomplished by spreading the branchiostegals (much like unfolding a fan).

Intermittently the branchiostegals take part in a coughing reflex. Here water flow is reversed through the gills to clean them of debris.

It is possible that branchiostegals function also in aerial respiration. Under conditions of low oxygen, surface dwelling physostomous fishes may inhale air bubbles. It is possible that abduction of the branchiostegals may assist in this process. It is notable that the branchiostegals of surface dwelling physostomous fish are broad imbricating structures while those of deepwater or physoclistous fish are slender and non-imbricating. It is possible that reflexing the spathiform branchiostegals assists in inhaling bubbles of air. Depression of gular bones may assist in inhaling air also.

Feeding

Many fish feed by inhaling the food particles into the mouth. In macrophagus fish this probably takes place mainly by dropping the floor of the buccal cavity, although the creation of negative pressure in the opercular cavity by the operculum and branchiostegal membrane may take some part in this. It is in the microphagus or plankton feeders that these latter actions are more important. Here water is drawn through the sieving apparatus of the gills, the gill rakers and out the long gill slit. A long gill membrane with numerous, branchiostegals is necessary to open and close the long gill slit during feeding and respiration.

Curry-Lindahl (1956) reports that the lungfish, Protopterus, sucks its food into the mouth. He quotes an author saying this is accomplished by depression of the hyoid bone. It may be that this behavior is a holdover from ancestors which had gular plates. Gulars would help in sudden depression of mouth floor and hence sucking in of prey.

Behavior

The branchiostegals and their membranes have been shown to play a part in behavior of fishes by modern ethologists. The branchiostegal membranes are commonly employed in agonistic displays by fishes. Here the branchiostegals are spread and thrust laterally. For example in cichlids, "fighting begins with lateral display in which the fishes, in breeding colors, hold themselves parallel to each other, with the median fins and eventually the branchiostegal membranes erected". (Baerends, 1957). This aggressive component, raising the branchiostegals, may be employed in territorial behavior, in establishing social hierarchies (Allee, 1952) and in courtship (Morris, 1954). It may be noted that the erecting of the operculum and branchiostegal membrane has the effect of enlarging the head. This type of display is known in such fishes as Gasterosteidae, Cottidae, Cichlidae, and Anabantidae.

Another behavioral function of the branchiostegal membrane can be suggested, although not yet proven. Differences exist in coloration of related forms. Red slashes occur in the hyoid cleft on the lower side of the head in Salmo clarkii. In other species of Salmo this cleft is light colored. In Thymallus arcticus on the other hand it is black. In other groups there are differences in photophore pattern on the branchiostegal membrane. In Porichthys species may have U-shaped or V-shaped patterns of photophores (Hubbs and Schultz, 1939). Differences in the number of photophores on the branchiostegals of sternoptychids are given by Schultz (1961): Argyropelecus and Polyipnus 6, Sternoptyx 3. It is possible that the role of color is important only in agonistic behavior. However, the fact that the membrane is used in courtship and that there are interspecific differences suggests that these forms use the patterns in species recognition. By analogy it is suggested that photophores have a function parallel to that of color. A further function is suggested by Tavolga (1958). In Bathygobius soporator the males make low-pitched grunting sounds to attract the female, apparently by forcible ejection of water through the gill openings (in which the branchiostegals would take part).

Sensory

In some fishes modified branchiostegals have a sensory function. In both Mullidae and Polymixiidae the anterior branchiostegal becomes free from the branchiostegal membrane and forms a long barbel-like structure. Of the Mullidae, Herald (1961) says "The long, tactile barbels under the chin, constantly working in the same way as a mine detector as they are dragged over the bottom, enable the goatfishes to locate small items of food that might otherwise be missed. These barbels are highly flexible, often moving back and forth even when the goatfish is at rest. When not in use, the barbels can be pulled under the throat, where they are fairly inconspicuous." According to Andriashev (1944) the barbels in Mullus are also employed in digging and chemoreception.

As the polymixiids are deepwater forms, living between 600 and 1200 feet, their habits are not well known. Through analogy with the barbels of Mullidae it is possible to suggest that they also have a sensory function. It is difficult to conceive of any other function.

In Linophryne coronata the hyoid barbel was found to be formed of a nerve issuing from the hind corner of the mandible and of a strand of the interhyoideus muscle.

Protection of Gills

The branchiostegal series serve to protect the gills. In some forms lacking branchiostegals, scales have assumed the protective function (Mesturus), in others the lateral gulars have expanded to replace them (Polypterus).

Defense and Protection

In certain eleotrids such as Belobranchus, the base of one or more branchiostegals is pointed and projects from the skin. By analogy it is conceivable that this spine or spines is used as a deterrent defensive mechanism (similar to the suborbital spines in Cobitidae, maxillary spines of Notacanthidae, caudal peduncle spines of Acanthuridae). Many acanthopterygian fishes have spines on the opercular bones, probably of similar function. Other fishes, such as Denticipitidae have small spinules on the branchiostegals. The function of these is more difficult to understand. Morris (1955) has experimentally demonstrated the protective value of dorsal spines in sticklebacks. A pike which had been pricked in attempting to swallow a stickleback was less likely to make the attempt again.

THE ORIGIN OF THE BRANCHIOSTEGAL SERIES

The Branchiostegals

In exploring the origin of branchiostegal rays it is necessary first to examine the earliest teleostome fossils. Although fragmentary fossil teleostomes are found in the Lower Devonian deposits, it is not until the Middle Devonian that adequate specimens are known. In the Middle Devonian the three major early teleostome subclasses, Actinopterygii, Crossopterygii and Dipneusti are already clearly distinguished (the subclass Brachiopterygii not being known until the Eocene). In all of these we find broad, flat, spathiform branchiostegals, a median gular and a pair of lateral gulars and operculum and a sub-operculum. The branchiostegal series of these subclasses are much more similar than in modern representatives of the groups, as the later Actinopterygii tend to lose the gulars while the Dipneusti and Crossopterygians lose the branchiostegals. It is also notable that the opercle and particularly the subopercle are more similar to the branchiostegals, than are the opercle and subopercle in more modern teleosts. However, it is evident that the branchiostegal series is already quite well developed in the earliest teleostome remains and that it is therefore necessary to examine the forerunners of teleostomes to determine the origin of the branchiostegal series. The forerunners of the teleostomes are not known with certainty. However, most evidence points towards origin from the Acanthodii or a closely related group. The Acanthodii are sufficiently ancient to be ancestral to the teleostomes (unlike the Elasmobranchii). The Acanthodii agree with the Teleostomi in possession of true bone in the skeleton, jaws, circumorbital bones, ganoid type scales, similar neurocrania (Watson, 1938), shaped branchial arches, small olfactory organs and large anterior orbits. Berg (1947) indicated the two otoliths in Acanthodes are similar to palaeoniscid otoliths. Of the similarity of the scales of Acanthodii and Actinopterygii Aldinger (1937, translation) states "In contrast (to important differences between Acanthodii and Rhipidistia) the scales of Acanthodii are built after the same plan as those of the oldest Elonichthyiformes and of Cheirolepis". Both the Acanthodii and early Teleostomi are found in freshwater deposits. Arambourg (1958a), Romer (1955), Hills (1943) agree that the Acanthodii or forms close to it gave rise to the Teleostomi. Berg (1947) considers ... "that the Acanthodii are allied to the Teleostomi." Watson (1938), in a revision of the Acanthodii, considered that the Acanthodians had no close relationship with the bony fish, while admitting, "Nevertheless there is a most curious set of qualities in which the members of two great groups agree." But he did regard the Teleostomi as derived from the Class Aphetohyoidea in which he included the Acanthodii. In summary then it is quite probable that acanthodians or close gnathostome relatives were ancestral to the Teleostomi, and it is thus then in the Acanthodii that the origins of branchiostegals rays are here sought.

From the visceral arches in the Acanthodii extend rows of bony splints. It is possible that from these the branchiostegal rays developed, as has been suggested by Gregory (1951). The anteriormost of these rows bony splints is well developed, the rays being large and rod-like or paddle-like and forming an operculum. Watson (1938) believed that this row of rays was carried by the mandible, (the rays being retained from a time when the jaws were gill bars) and that a full gill slit separated the mandibular and hyoid arches. He supported this theory by showing the hyoid arch had a set of gill rakers along its whole length and suggesting that these guarded a full gill slit before the hyoid arch. If there was a full slit between the hyoid arch and mandibular arch and not just a small or large dorsal spiracle, then the well developed row of visceral rays must have proceeded from the mandibles.

It is not, however, definite that this operculum was mandibular. In certain of Watson's photographic plates (plate 5 of Climatius and plate 7 of Euacanthus) the hyoid arch has been displaced posteriorly and has carried with it the operculum. In Davis (1894, pl. 27, fig. 1 and 1a of Acanthodes) the hyoid rays are seen to insert on the ventral face of the hyoid arch. If the rays were closely applied to the mandible it would appear they would interfere with opening of the jaws as opening the jaws meet with resistance as the rays were forced upon one another. The branchiostegals of palaeoniscids appear in lateral view to insert upon the mandible while they are actually inserting on the underlying hyoid arch. Stensio (1947) doubted that there was a full hyoid gill slit and that the principal operculum was mandibular. He also mentions that Holmgren has come to a similar conclusion.[1]

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[1] A further paper has just been published which also supports this view. Westoll, T.S. 1963. The hyomandibular problem in placoderm fishes. Proc. XVI Int. Zool. Congress 1: 176.

From the above arguments three hypotheses may be made. If the principal operculum is mandibular the branchiostegals may be derived from: i) the smaller hyoid rays behind the principal operculum, the principal operculum later being lost, or ii) the rays of the principal operculum which became attached to the hyoid arch on closure of the spiracular slit. But if the rays of the principal operculum were indeed hyoidal it can be suggested: iii) that they remained and developed into the branchiostegals. To the author the third hypothesis seems most economical and preferable. However, through sectioning of the hyoid-mandibular region of acanthodian fossils it would be readily determinable which theory is true.

The operculum and suboperculum

The operculum and suboperculum, found in the first known teleostomes, are probably expansions of branchiostegals or their hyoid ray homologues, as has been suggested by Traquair (in Ridewood, 1904) and by Hubbs (1920). Little difference but size may be seen between the opercular, subopercular and branchiostegals of primitive teleostomes. The embryological development of the operculum and suboperculum is very similar. One can see in some acanthodians (e.g. Euthacanthus) a tendency towards expansion of certain opercular rays. It does not seem unreasonable, therefore, to suggest derivation of the operculum and suboperculum from branchiostegals or hyoid rays.

With the expansion of branchiostegals into opercular bones larger muscles might insert upon them and a stronger branchial pump develop. A stronger branchial pump may have developed purely for the sake of efficiency or because of greater respiratory demands. Greater activity would require more oxygen. The acanthodians are known, through a fortunate fossilization (Watson, 1959) to have cyclostome type myomeres with a low central vertex and no horizontal septum. It might be suggested that this type of myomere indicates a lower activity level than would the more highly developed piscine myomere type (Nursall, 1956) found in teleostomes. It might alternately be suggested that during teleostome evolution, conditions of lower oxygenation due to warmer climate produced selection for a more efficient branchial pump. Either of these two factors might explain the evolution of opercular bones from branchiostegals.

The Interoperculum

The interoperculum is absent from the Dipnoi, Crossopterygii, Brachiopterygii and lower Actinopterygii. It is first found in the Ospiiformes of the Lower Triassic. Regan (1929) suggested that the forward migration of the mandible and quadrate dragged the suboperculum down, perhaps causing the lower end of the suboperculum to be fractured and pulled forward to form the interoperculum. This explanation appears rather Lamarkian. The following hypothesis would appear to be preferable. Several authors have suggested that the interoperculum developed from a forwardly displaced branchiostegal (Cole and Johnstone 1902 in Ridewood, 1904; Westoll, 1944; Saint-Seine, 1955).

The development of an interoperculum seems to have been a further development in the separation of the mandibles and operculum. The preoperculum developed in the teleostome ancestors, partially separating the jaw and opercular movements. With the freeing of the maxillary in the Holostei the need again arose to increase separation of the jaws and operculum to make their movements more independent from one another. The evolutionary solution was the interpolation of the uppermost branchiostegal between the jaws and the suboperculum; thus, the uppermost branchiostegal became the interoperculum. Schaeffer (1956) has shown there is a high degree of correlation between the freeing of the maxillary and the presence of an interoperculum.

An element in the chondrostean Platysiagum has been termed by Brough (1939) a modified branchiostegal or an incipient interoperculum. This element lies in a slight concavity under the front two thirds of the suboperculum. The element cannot be identified as an interoperculum since it does not separate the jaws from the suboperculum, nor is it broadly bordered by the preoperculum. It is very similar to the uppermost branchiostegal of the chondrosteans Ptycholepis and Brookvalia which lie in a slight emargination of the suboperculum. It therefore seems inadvisable to call this element an incipient interoperculum.

The Gular Plates

Both median and lateral gular plates are found in the earliest of the actinopterygian, crossopterygian and dipnoan teleosts. The lateral gulars are hardly distinguishable (only by being slightly larger and bearing a pit line) from the adjacent branchiostegals in the earliest teleost fossils (Cheirolepidae). Indeed there is no reason to suppose that the lateral gulars are not simply expanded branchiostegal rays. The lateral gulars are already characteristically large in the earliest crossopterygians. As the crossopterygians evolve the lateral gulars eventually supplant both the median gular plate and the branchiostegals. The branchiostegals and median gular are also lost during the evolution of the Dipnoi. The Brachiopterygii also lack a median gular and branchiostegals, the large lateral gulars have supplanted them.

The pit lines are of great value in tracing the gular elements. The median gular of Crossopterygians and Actinopterygians may be identified by a V-shaped pit line. The lateral gulars of all four sub-classes, at least primitively bear a transverse pit line. In the Crossopterygians (osteolepids) one or two of the branchiostegals under the end of the mandible may bear a short pit line. These appear to have been retained in the dipnoans where the anterior of the two marked branchiostegals has moved to the medial edge of the posterior branchiostegals. In the Dipnoi there are primitively two pairs of lateral gulars, the posterior pair of which bears the pit line and which is thus identifiable with the lateral gulars of the other suborders. The second pair of gulars may have formed by division of the single crossopterygian pair, or by expansion of one of the anterior branchiostegals. The first suggestion is favoured since the gular pit lines still retain a position (at the anterior end of the posterior gulars) that would be in the centre of the single gular, although it is now divided into two. If the anterior gulars were formed from expanded branchiostegals one might expect the pit lines on the posterior gulars to be in the middle of the gular rather than at the anterior end.

The origin of the median gular is less certain. There is no bone from which it can be derived. However, it is possible that it arose from a branchiostegal close to the midline. This is difficult to conceive as the median gular overlies the branchiostegals and is not in the same plane. It is possible that it arose <u>de nouveau</u> from dermal tissue. Or perhaps it evolved from the hyoid rays of the Acanthodii. The hyoid rays are continuously distributed around the hyoid arches in the Acanthodii, not restricted bilaterally as in the Teleostomi. Possibly the median hyoid ray of the Acanthodii gave rise to the median gular.

PHYLOGENETIC OR VERTICAL EVOLUTION

The phylogenetic or vertical evolution of branchiostegals as opposed to adaptive or horizontal evolution is traced in this section. The phylogeny of the operculars, gulars and hyoid arch elements is also traced but in less detail. The groups are treated in phylogenetic order, as closely as is possible in a linear series. For the best picture of phylogeny see plate XVIII. Evolution is followed down to family level, although occasionally comments may be made on lessor taxa. An attempt is made to illustrate at least one example of every order, (see plates I, II, III, etc.).

CLASS TELEOSTOMI (OSTEICHTHYES INCLUDING DIPNOI)

Branchiostegals (0-2)3-20(21-50). One (or two) median gulars, one or two pairs of lateral gulars present or absent. Operculum, suboperculum and (in higher groups) interoperculum usually present, but sometimes absent. Interhyal, epihyal (in higher groups), ceratohyal and one or two (in higher groups) hypohyals usually present but sometimes lost. Lower Devonian to present. Four subclasses and 66 orders, 38 of which are living.

Although the subclass Actinopterygii is considered most primitive, then the Crossopterygii, Dipneusti and Brachiopterygii, the latter are placed first because they are more primitive than the higher Actinopterygii. The Brachiopterygii might best be placed as a chondrostean order of the Actinopterygii. But until its affinities are known with certainty it would appear preferable to leave it in a separate subclass.

The Dipneusti are often included in the same class as the other bony fishes, but Berg isolates them in their own class. Since the Dipneusti are derivable from the Crossopterygii and since they are not distinguished to a higher degree than the other subclasses of teleostomes they are included in the Teleostomi, not in a separate class.

KEY TO TELEOSTOMI BASED ON THE BRANCHIOSTEGAL SERIES AND HYOID ARCH

The following key outlines the major events in the evolution of the Teleostomi. While it follows the phylogeny rather closely, for the best picture of phylogeny of the Teleostomi see the evolutionary dendrogram. For the keying out of groups and determining of relationships one cannot depend on one set of characters, so that some orders cannot be separated in this key. The key demonstrates that at many points in evolution that the branchiostegals and hyoid arch provide sharp division between related groups. For example the Beloniformes are separated from all other malacopterygians by the lack of an interhyal and non-filiform branchiostegals, the Cyprinodontiformes and Gobiesociformes differ from all other acanthopterygians (except a genus of Gobiidae and Syngnathidae) in having lost one hypohyal, a different one in each case. The Tarasiiformes, Chondrosteiformes and Peltopleuriformes are neatly separated by branchiostegals. Just as important are the similarities shown among orders which cannot be conveniently separated on the basis of branchiostegals. Thus, is indicated the closeness of the great proportion of the acanthopterygians.

Key to the Classes of Gnathostomes

A With jaws, laterally paired nostrils, 3 semicircular canals.

  B Without rays on the hyoid arch ... Pterichthyes, Coccostei.

  BB With rays on the hyoid arch.

    C Lacking gular plates, an interhyal and opercular bones. ("Opercular plate" of holocephalans composed of fused hyoid rays).

      D Hypohyal and ceratohyal present. Class Acanthodii.

      DD Only ceratohyal present. Class Elasmobranchii (including Holocephali).

    CC With or without gular plates, with an interhyal (lost in some orders), with opercular bones (completely lost only in Giganturiformes and Saccopharyngiformes). Class Teleostomi.

Key to Subclasses of Teleostomi

The subclasses are difficult to separate in a convenient manner because the primitive members are so similar and because of the convergence between the Coelacanthiformes and Brachiopterygii.

A With one large pair of gulars longer than 2/3 of the mandible or with 2 pairs of gulars (except gulars absent in Ceratodiformes and Lepidosirenformes these recognizable because of cartilaginous disk under tip of operculum).

B With or without median gular and branchiostegals. Medium-sized subquadrate or subtriangular operculum with a broad or triangular suboperculum. Where suboperculum is triangular opercular fold passes behind it ... Crossopterygii.

BB With or without a median gular and branchiostegals. Operculum large and pentagonal (or reduced to a slender ray with a cartilaginous disk under its tip). Narrow elongate suboperculum below ... Dipneusti.

BBB Without median gular or branchiostegals. Operculum and suboperculum medium-sized and subtriangular; opercular fold in front of suboperculum ... Brachiopterygii (contains a single order Polypteriformes).

AA With one pair of gulars shorter than ½ of length of mandible or without gulars ... Actinopterygii

Key to Orders of Crossopterygii

A Branchiostegals and sometimes median gular present. Lateral gulars taper along whole length towards anterior tip. Suboperculum completely ventral to operculum. Supraorder Osteolepides.

B Branchiostegals 10. Suboperculum with ventral edge on the dorsal edge of the lowest preoperculum (third) ... Hoploptychiformes.

BB Branchiostegals 4-8. Suboperculum with ventral edge not on dorsal edge of lowest preoperculum ... Osteolepiformes.

AA Branchiostegals and median gular absent. Lateral gulars of even breadth, do not taper through whole length towards anterior tip. At least dorsal portion of suboperculum opposite front of lower portion of operculum. Supraorder Coelacanthi ... Coelacanthiformes.

Key to Orders of Dipneusti

The following is a tentative key based on the assumption that the Uronemiformes have gular plates and that they and the Ctenodontiformes have less than three branchiostegals.

A Gular plates and usually branchiostegal(s) present. Operculum large and circular or pentagonal in shape. Supraorder Dipteri.

B Branchiostegals 3 ... Dipteriformes.

BB Branchiostegals less than 3.

C Suboperculum 1/3 to ½ of size of operculum ... Phaneropleuriformes.

CC Suboperculum smaller.

D Operculum oval ... Uronemiformes.

DD Operculum scallop-edged, roughly circular ... Ctenodontiformes.

AA Gular plates and branchiostegals absent. Operculum small and elongate.

Supraorder Ceratodi.

E Operculum arrowhead-shaped; suboperculum a slender ray ... Ceratodiformes.

EE Operculum a slender ray; suboperculum chevron-shaped ... Lepidosireniformes.

Key to Orders of Actinopterygii

Due to paucity of information, the orders Cephaloxeniformes, Aethodontiformes, Luganoiformes, and Ptycholepiformes must be omitted from this key.

A Interoperculum absent. Lateral gulars may be present. Group I (Chondrostei). (Maxillary not free from cheek, except Dorypteriformes).

  B With a pair of lateral gulars and usually with a median gular. Always with a suboperculum.

    C With 4 or more branchiostegals

      D With pit line on lateral gulars ... Palaeonisciformes, Perleidiformes.

      DD Without pit line on lateral gulars ... Pholidopleuriformes.

    CC With 1-3 branchiostegals ... Haplolepiformes.

  BB Without lateral and median gulars. With or without suboperculum.

    E With suboperculum (except Polydontoidei).

      F Branchiostegals 3 or more.

        ..... Tarasiiformes 15 branchiostegals.

        ..... Platysiagiformes 12 branchiostegals.

..... Phanerorhynchiformes "series" of branchiostegals.

..... Chondrosteiformes 9-10 branchiostegals.

..... Peltopleuriformes 6-7 branchiostegals.

FF Branchiostegals 0-1.

G Operculum smooth ... Redfieldiiformes.

GG Operculum grooved or incised ... Acipenseriformes.

EE Without suboperculum

H Operculum deeper than long ... Dorypteriformes, Bobasatraniiformes, Pycnodontiformes.

HH Operculum as long as deep ... Saurichthyiformes.

AA Interoperculum present (secondarily absent in Lepidosteiformes, some Mormyriformes, Giganturiformes, Saccopharyngiformes, some Anguilliformes). Lateral gulars never present. (Maxillary free from cheek).

I A single hypohyal present, a median gular often present. Group II (Holostei).

J Median gular present.

K Branchiostegals 30 or fewer ... Ospiiformes, Amiiformes, Pholidophoriformes.

KK Branchiostegals 30-50 ... Pachycormiformes.

JJ Median gular absent.

Branchiostegals 3 ... Lepisosteiformes.

Branchiostegals 12-13 ... Aspidorhynchiformes.

II Two hypohyals present (except Lycopteridae, Phractolaemidae, Mormyriformes, Amphiliidae, Chacidae, Anguilliformes, Stylephoridae, Beloniformes, some Syngnathidae, Cyprinodontiformes, Gobiesociformes). Median gular only in Elopoidei and Albuloidei. Group III (Teleostei).

L Branchiostegals 0-36, one or more of upper branchiostegals often spathiform (except Stomiatoidei, Myctophiformes, Mormyriformes, some Cypriniformes, Notacanthiformes, Anguilliformes). Epihyal and ceratohyal sutured together only in Siluroidei and Beloniformes. Never spines on opercular bones. Branchiostegals usually inserting on external face of hyoid arch with a minority below on the ventral or internal, sometimes all on ventral edge; only sporadically in Clupeiformes (Hiodontidae, Chanidae, Gonorhynchidae, Osmeridae, Argentinidae) and commonly in the Myctophiformes is the acanthopterygian pattern of the 4 upper branchiostegals on the external face and 0-5 lower ones on the ventral (or internal) face of the hyoid arch found. Group IIIA Malacopterygi.

M With branchiostegals, hyoid arch and operculum.

N Hypohyals 2 (except Phractolaemidae, Amphiliidae and Chacidae).

O One or more upper branchiostegals spathiform, at least distally ... Clupeiformes, Cypriniformes.

OO Branchiostegals not spathiform.

P Branchiostegals not straight, curve up behind gill cover ... Myctophiformes.

PP Branchiostegals nearly straight, do not curl up behind gill cover ... Notacanthiformes.

NN Hypohyals 0-1

Q Branchiostegals not filiform and not curled up around dorsal edge of operculum.

R With interhyal ... Mormyriformes.

RR Without interhyal ... Beloniformes.

QQ Branchiostegals filiform and curled around operculum ... Anguilliformes.

MM Without branchiostegals or operculum ... Giganturiformes, Saccopharyngiformes.

LL Branchiostegals 1-9 (10) (except 8-11 in Echeneiformes). Branchiostegals acinaciform, sometimes filiform, never spathiform (except Molidae). Epihyal and ceratohyal usually sutured together (but suture secondarily lost in several groups). Often spines on operculum, sometimes on suboperculum and interoperculum. The upper 4 branchiostegals on the external face of the hyoid arch, the other 0-7 (usually 2-3) on the ventral or internal face. Group IIIB Acanthopterygi.

S Hypohyals 2 (except in one genus of Syngnathidae, Gobiidae and Stylephoridae and all the Phallostethidae).

T Branchiostegals modally 7 or more. Gill membranes usually separate (except some Gadiformes) ... Beryciformes, Zeiformes, Lampridiformes, Bathyclupeiformes, Ophidiiformes, Gadiformes, Ateleopiformes, Echeneiformes.

TT Branchiostegals modally 6 or less. Gill membranes separate, united and free from isthmus, or joined to isthmus ... Percopsiformes, Syngnathiformes, Perciformes, Pleuronectiformes, Tetraodontiformes, Icosteiformes, Gasterosteiformes, Mastacembeliformes, Synbranchiiformes, Batrachoidiformes, Lophiiformes, Pegasiformes.

SS Hypohyals 1

U Lower hypohyal present. With epihyal-ceratohyal suture ... Cyprinodontiformes.

UU Upper hypohyal present. Without epihyal-ceratohyal suture ... Gobiesociformes.

SUBCLASS CROSSOPTERYGII

Branchiostegals 10 or fewer; median gular present or absent, primitively with a V-shaped pit line; a single pair of large gulars at least 2/3 the length of the mandible; operculum present; usually suboperculum present; hypohyal, ceratohyal and interhyal present. Lower Devonian to present. Two superorders with three orders and 12 families.

SUPERORDER OSTEOLEPIDES

Branchiostegals and median gular present (median gular in Hoploptychiformes?). The lateral gulars taper along their whole length towards the anterior tip. Suboperculum ventral to operculum and taking normal part in movement of gill cover. Lower Devonian to Upper Carboniferous. Two orders. Thomson (1962) would reduce the status of these two orders.

† ORDER HOPLOPTYCHIFORMES

Branchiostegals 10; median gular unknown; a pair of large lateral gulars with an arc-shaped pit line; operculum and suboperculum present lower edge of suboperculum on upper edge of third preoperculum. Lower to Upper Devonian. Two families.

† Porolepidae

Branchiostegals: No data available.

† Hoploptychidae

Branchiostegals: In *Hoploptychius flemingi* about 10. The first six are elongate and situated in a series below the suboperculum. The remaining four are very short and lie between the gulars and the mandibles; the first of these bears a short vertical pit line. At least two of these short branchiostegals are known in Glyptolepis.

Gulars: One of Woodward's specimens of Hoploptychius flemingi shows the lateral gulars but no median gular nor does his text report a median gular in Glyptolepis. The lateral gulars in Hoploptychius are large, about the same length as the mandible. The posterior edge of the lateral gulars curve inward and anteriorly, leaving a V-shaped gap. At the centre of each gular is a short arc-shaped pit line with apex anteriormost.

Operculars: The operculars of Hoploptychius are rather different from those in Osteolepis since they insert on the diagonal base of the upper preopercular (squamosal), rather than on the vertical base of the lower preoperculum as in Osteolepis. Thus the opercular bones are more dorsal in Hoploptychius and their bases diagonal. The operculum is larger than the suboperculum. The jaw of Hoploptychius is shorter than in Osteolepis and the triangular lowest preoperculum acts an interoperculum of the holostean type, a piviting point for the opercular bones.

Relationships: The more numerous branchiostegals would indicate this order to be more primitive than the Osteolepiformes. The opercular bones and number of branchiostegals separate the two orders. Yet the two orders share features which separate them from the Coelacanthi: their gular plates taper anteriorly, they possess branchiostegals and the suboperculum is below rather than anterior to the operculum.

References: Jarvik (1948), Woodward (1891), Stensio (1947).

† ORDER OSTEOLEPIFORMES (RHIZODONTIFORMES)

Branchiostegals 4-8; usually a median gular with pit line; one pair of large lateral gulars with pit line; suboperculum not with lower edge on upper edge of third preoperculum; operculum and suboperculum present. Six families. Middle Devonian to Lower Permian.

Taxonomy: The operculars, gulars, branchiostegals and other skull bones of Rhizodontiformes are so similar in form and arrangement I feel constrained to return this order to the Osteolepiformes, as Arambourg (1958) has done.

† Gyroptychiidae

Branchiostegals: In Gyroptychius branchiostegals 6-8. The first is almost quadrangular but expands distally. The remainder are short and broad and bridge the gap between the gulars and the mandible. The second is characterized by a diagonal pit line somewhat anterior to the center. The last two branchiostegals may fuse into a single large plate.

Gulars: The diamond-shaped median gular bears a broad V-shaped pit line. The lateral gulars are large, narrow anteriorly to a point and bear a short arc-shaped pit line at the centre of the side next to the mandibles. The posterior edges of the plates curve anteriorly and medially, leaving a wedge-shaped gap between them. The gulars are about $\frac{3}{4}$ the length of the mandibles. The anterolateral portion of the gulars contacts the mandibles (a primitive character).

Operculars: The operculum and suboperculum are small and rectangular. The operculum is slightly larger. The opercular bones are slightly shorter than in Osteolepis.

Taxonomy: This family erected by Berg (1955).

Relationships: The branchiostegal series speak for a very close relationship to the Osteolepidae.

References: Berg (1955), Jarvik (1948).

† Osteolepidae

Pl. I

Branchiostegals: In Osteolepis macrolepidotus about 7 spathiform branchiostegals. The first, broad but elongate, is under the suboperculum, which it much resembles. The remainder of the branchiostegals are short and wide; they span the gap between the gulars and the mandible. The second and sometimes the third branchiostegal bear a small arc-shaped pit line. These two pit lines are important because they act as labels. They provide evidence that these two branchiostegals are homologous to the two pit-line-bearing branchiostegals between the gulars and the mandible in Dipterus and further that the bone called suboperculum in Dipterus is indeed that bone. The pit line on the third branchiostegal of O. macrolepidotus is apparently in the process of being lost, since it is often not present.

In Osteolepis panderi there are only 4 branchiostegals, the anterior ones being displaced by the lateral gulars; in Thursius there are 5-6 much as in Osteolepis, the second with a pit line. The branchiostegals narrow anteriorly as the lateral gular approaches the jaw, until the first branchiostegal becomes pointed.

Gulars: In *Osteolepis* a small diamond-shaped median gular is located in the fork of the mandibular rami. It bears a V-shaped pit line, the arms of which curve slightly outward. The very large lateral gulars nearly equal the length of the mandibles. They taper only slightly anteriorly. The posterior edge curves inward and anteriorly. In the middle of each lateral gular is a short arc-shaped pit line whose apex faces anteriorly. The width of the lateral gulars enters about 3 times in their length. In *Thursius* the gulars are pointed anteriorly and about .9 of the mandibular length. They bear a pit line and their posterior edges curve medially and anteriorly.

Operculars: In *Osteolepis* the operculum is slightly larger than the suboperculum; both are elongate in horizontal direction and very similar in shape. The operculum of *Thursius* is said to be deeper than broad and the suboperculum smaller and to be broader than deep.

References: Woodward (1891), Berg (1947, 1955), Jarvik (1948).

† Eusthenopteridae

Pl. I.

Branchiostegals: In *Eusthenopteron foordi* 8 branchiostegals. The first is elongate and lies below and slightly anterior to the suboperculum. The remainder are very short and are situated between the gulars and the mandible; the first of these bears a vertical pit line; the last is triangular. In *Eusthenodon* 8.

Gulars: A small median gular with an arc-shaped pit line with apex anteriormost is present, an unusual shape for this pit line. The lateral gulars are relatively small--about 2/3 of the length of the mandible. They are narrow (their width entering 4.5 times in the length) and fail to touch the mandible anteriorly. Slightly anterior to their centre is a J-shaped pit line, instead of the usual arc-shaped or straight line.

Operculars: The operculum and suboperculum are of about equal size and trapezoidal in shape.

Taxonomy: Berg (1955) erected this family.

Relationships: This family differs from other Osteolepiformes by the shorter and narrower lateral gulars. It is closest to Osteolepidae in this respect.

References: Berg (1955), Jarvik (1944, 1952), Bryant (1919).

† Rhizondontidae

Branchiostegals: In *Rhizodopsis sauroides* there are 5 branchiostegals. The first of these is elongate and situated under the suboperculum. The remaining 4 lie between the lateral gulars and the mandibles; they narrow anteriorly until the first is triangular.

Gulars: In *Rhizodopsis* a small anterior median gular is followed by a large pair of gulars. The median gular, situated in the fork of the mandibles, is egg shaped with apex anteriormost. Behind it are the pair of large lateral gulars whose length almost equals that of the mandible. Their posterior edge curves inward and anteriorly. The left is shown to overlap the right in Woodward's fig. 57. The anterior tip of the lateral gular touches the mandible. The length of the gular is about 2½ times its width.

Operculars: The operculum in *Rhizodopsis ornatus* is scallop-shaped (with hinge uppermost) and heavily decorated. The operculum is large and pentagonal in *Rhizodopsis*. The smaller suboperculum is approximately trapezoidal.

Relationships: The operculars, gulars and branchiostegals are very similar to those in other Osteolepiformes.

References: Woodward (1891), Traquair (1883).

† Parabatrachidae

Branchiostegals: No data available.

Gulars: A pair of lateral gulars, each about 2½ times as long as wide, abruptly truncated posteriorly or rounded in *Parabatrachus* (= *Megalichthys* Agassiz).

Operculars: Operculum nearly as broad as deep.

References: Woodward (1891).

SUPRAORDER COELACANTHI (ACTINISTIA)

Branchiostegals and median gular absent. Lateral gulars of even breadth, tapering only at tips. Suboperculum at least partially opposite lower portion of operculum, and apparently not taking part in movement of gill cover. Middle Devonian to present. One order.

ORDER COELACANTHIFORMES

A large pair of lateral gulars of even breadth bearing an arc-shaped pit line. Suboperculum at least partially opposite lower portion of operculum. Suboperculum apparently not taking part in movement of the gill cover. Interhyal and ceratohyal present. Middle Devonian to present. Three suborders, four families.

Taxonomy: There are no notable differences in the branchiostegal series between the three suborders of Coelacanthiformes, but they may be separable on other grounds. Arambourg (1958) does not employ the suborders in his classification.

Relationship: The Coelacanthiformes are more similar to the Osteolepiformes than to the Hoploptychiformes in that the suboperculum is next to the third preoperculum, in that the branchiostegals are fewer in Osteolepiformes and in that the sensory canals of the head, as portrayed by Stensio (1947), are of a more similar pattern.

† SUBORDER DIPLOCERCIDOIDEI

Middle Devonian to Upper Devonian. A single family.

† Diplocercidae

Gulars: In Nesides schmidti a pair of large lateral gulars, length about 5/6 of the mandible. Posterior end protruding slightly beyond mandible.

Operculars: Operculum large and triangular, concave where it meets the upper preoperculum. Between the lower portion of the operculum and the preoperculo-quadrajugal is a small presumably triangular suboperculum. The suboperculum is anterior and not ventral to the operculum.

Taxonomy: Romer (1955) is followed as to the limits of this family.

References: Stensio (1947).

† SUBORDER LAUGIOIDEI

Lower Triassic. A single family.

† Laugiidae

Gulars: A pair of large lateral gulars 7/8 of the length of the mandibles. Breadth even, about 3½ times their length. Little gap posteriorly between the gulars.

Operculars: Operculum medium sized and triangular. Antero-dorsal corner pointed, without notch. Suboperculum not known, presumably absent.

Relationships: The opercular bones are little different from those in the Coelacanthoidei.

References: Stensio (1932).

SUBORDER COELACANTHOIDEI

Lower Carboniferous to present. Two families.

Coelacanthidae

Pl. I

Gulars: There are a pair of large lateral gular plates in members of this family. In *Rhabdoderma elegans* the gulars are about 4/5 the length of the mandible and do not protrude posteriorly beyond the end of the mandible. In *R. aldingeri* the width is 4½ times the length and the main body of the plate is of even breadth, tapering only at the tips. In *Holophagus* (=*Undina*) the gulars are of even breadth--about 3 times in length; they are about equal to the length of the mandible and just posteriorly from it. In *Macropoma* the gulars are almost equal to the length of the mandible and bear arc-shaped pit lines centrally. In *Diplurus* the gulars are long and narrow, the width 4½ in length. In *Whiteia* the gulars occupy only about 2/3 of the mandibular length; they are of even breadth. They bear a short straight pit line centrally. Their posterior ends are rounded but they soon meet on the midline so there is not a V-shaped gap between them.

Operculars: In *Rhabdoderma* the operculum is of middling size and triangular; it has a notch where the antero-dorsal corner meets the spiracular bone. The suboperculum is small and triangular and the upper half is opposite the lower end of the operculum. In *Holophagus* (=*Undina*) the operculum is longer, extending further ventrally than in *Rhabdoderma* and the suboperculum is a long or short triangle, 2/3 or more of which is below the operculum. The operculum is also larger in Wimania (has an antero-dorsal notch) and Axelia (lacks notch). In Macropoma the operculum is of middling size and has a small concavity on its dorso-anterior edge; a small rectangular suboperculum is present. In Mylacanthus the large operculum has a lobate or spinous posterior margin. In Whiteia the operculum is medium sized, triangular, and has a slight concavity on its dorso-anterior corner where it contacts the postspiracular. A small suboperculum is present. In Diplurus the operculum is medium sized, triangular, and without an antero-dorsal notch; the dorso-posterior edge is crenulate; the suboperculum unknown.

Hyoid arch: In Macropomus ceratohyal with postero-ventral projection; cylindrical interhyal.

References: Moy-Thomas (1937), Zittel (1887), Stensio (1921, 1932), Lehman (1952), Schaeffer (1952), Goodrich (1909), Gardiner (1960).

Latimeriidae

Gulars: In Latimeria chalumnae a pair of large lateral gulars is present. These are only slightly less than the length of the mandible. They are of even breadth, and taper at the ends to a point. Width is a little more than 3 times in length. An arc-shaped pit line is present in the centre of each gular; as usual the apex of the arc is anteriormost.

Operculars: Operculum middle sized, a rounded triangle without antero-dorsal notches. Suboperculum small and forming a narrow triangle the apex uppermost. The suboperculum lies entirely in front of the lower half of the operculum.

The opercular fold in Latimeria, unlike in other orders of fishes, passes between the operculum and the suboperculum. The close attachment of the suboperculum to the dorsal operculum and the passage of the opercular fold behind, rather than in front of the suboperculum, would seem to forbid the suboperculums taking part in the movement of the gill cover. From the similar arrangement of the opercular bones in other families of the order Coelacanthiformes one would conclude that the rigidity of the suboperculum also pertains to them. In this character the Coelacanthiformes differ from other crossopterygians and other teleostomes. J. L. B. Smith, from a poorly preserved specimen, reported an interoperculum. This bone is known only from the higher Actinopterygii. Schaeffer suggests Smith's interoperculum may be modified scales in the opercular membrane. Millot and Anthony do not report an interopercular in their study of well preserved specimens and it seems most unlikely it occurs in Latimeria.

Schaeffer (1952) interprets the suboperculum as a preopercular bone in the Coelacanthoidei. This suggestion has the merit of explaining the rigidity of the "suboperculum" and its unusual anterior position in this group. In the other crossopterygian orders the suboperculum is directly ventral.

Hyoid arch: Consists of a short cylindrical hypohyal, a ceratohyal, epihyal and hyomandibular.

References: Millot and Anthony (1959), Smith, J. L. B. (1940).

SUBCLASS DIPNEUSTI

Branchiostegals three or less; median gular present or absent; 1-2 pairs gulars present or absent (combined length of lateral gulars exceeds one half mandible length); operculum present and suboperculum present (probably inserting on hyomandibular); a hypohyal present or absent; a ceratohyal always present; an interhyal may be present. From late Early Devonian to present. The dipneustians are divided into two superorders, the Dipteri and the Ceratodi, 6 orders and 12 families.

The Ceratodi have a complete branchiostegal series and full-sized operculars while the Dipteri have lost the gulars and branchiostegals and have reduced operculars. The Dipteri are readily distinguished from other fishes by their greatly expanded pentagonal operculum while the Ceratodi are distinguished by their very reduced operculum. The differences in the branchiostegal series alone certainly justify the supraordinal separation of the Ceratodi and Dipteri. The differences between the two make it difficult to characterize the subclass Dipnoi as a whole. However, the differences should be not unduly weighted, since they are concerned mainly with a loss or reduction in characters.

The suboperculum rests on the ceratohyal unlike other fishes, in which it usually rests on the hyomandibular or preoperculum. Further the suboperculum is much more slender than in other teleostomes, except in Scaumenacia. It might therefore be questioned whether or not the dipneustian subopercle is not a branchiostegal. However the condition of the subopercle in Scaumenacia, where it is of normal size and shape, would seem to oppose this thesis. Further, the unusual insertion of the suboperculum may be accounted for by supposing that the great expansion of the operculum in the Dipteri has necessitated a lower insertion of the suboperculum and that it has thus been displaced down from the hyomandibular to the ceratohyal. This position has been conservatively retained in the Ceratodi even though the size of the operculum has been reduced.

The possession of branchiostegals, operculum, suboperculum, median and lateral gulars by primitive dipnoans shows clearly that they are related to the other subclasses of teleostomes. But when they first appear in the fossil record they are already quite specialized, most branchiostegals are already lost and the gulars are more modified than primitive representatives of the other subclasses, and the operculum is considerably enlarged. Although these features distinguish them, they certainly do not warrant class distinction and the many similarities of the primitive members of the subclasses confirm their placement in a single class.

The arrangement of branchiostegals and gulars in primitive dipnoans enable them to be derived from primitive Crossopterygii, but not vice versa. This opinion is in agreement with that of Westoll (1949) who believed that the Dipnoi either stemmed from the Rhipidistia, or that both groups have a common ancestor. To points listed by Westoll for such a common ancestor may be added: a median gular, a pair of lateral gulars with a pit line and broad short branchiostegals.

† SUPERORDER DIPTERI

Gular plates present (Uronemiformes ?). Branchiostegals present in at least Dipteriformes and Phaneropleuriformes. Operculum large, roughly pentagonal. Middle Devonian to present. Ceratohyal present. Four orders.

† ORDER DIPTERIFORMES (RHYNCHODIPTERIFORMES)

Branchiostegals three, a small median gular and two pairs of gular plates, the posterior bearing pit lines; a large pentagonal operculum and a small elongate suboperculum present. From the late Early Devonian to Upper Devonian. Three families.

† Dipnorhynchidae

Branchiostegals: Two branchiostegals in *Dipnorhynchus*. An elongate branchiostegal lies below the suboperculum, which it much resembles (in fact Westoll calls it suboperculum 2). Laterally between the anterior and posterior gulars lies a second triangular branchiostegal (called by Westoll a lateral gular).

Gulars: Consists of a small anterior median gular, a pair of oval anterior gulars which slightly overlap a larger posterior pair of gulars, and between the two pairs of gulars lies a second median gular.

Operculars: A large subrectangular operculum lies above a narrow suboperculum, the latter much like the branchiostegal which lies below it.

Relationships: The gulars and branchiostegals are very similar to those in Dipteridae although there is one less branchiostegal. The possession of a pineal foramen, unique amongst the Dipneusti, shows this family is well separated. It may, according to Berg (1947), deserve a separate order. Westoll considers this family very primitive and shows indications of relationship to the Rhipidistia. It may be noted that the primitive crossopterygians also possessed a pineal foramen.

References: Hills (1933), Westoll (1949).

† Rhynchodipteridae

Branchiostegals: Not preserved.

Gulars: Not preserved.

Operculars: Operculum large, roughly quadrangular. Suboperculum not preserved.

Taxonomy: Berg (1947) provisionally placed this family in its own order; Arambourg and Guibe (1958) place it in the Dipteriformes.

References: Save-Soderbergh (1937).

† Dipteridae

Pl. II

Branchiostegals: In *Dipterus* 3 branchiostegals. Between the posterior gulars and the suboperculum lies a single spathiform elongate branchiostegal. It resembles the suboperculum except that it is somewhat expanded distally, while the suboperculum tapers. Just anterior to this branchiostegal, between the gular and the angle of the jaw, are two very short accessory branchiostegals (about a quarter the length of the other).

The position of these is such that they do not fit into a series with the branchiostegal; the second of these is below the first, not anterior to the first next to the mandible. A pit line runs across these two accessory branchiostegals and onto the posterior gular plate. This reminds one strongly of the situation in the Crossopterygii where the second and third branchiostegals and the gular plate bear pit lines. But in the Crossopterygii the third branchiostegal is anterior, not ventral and the pit lines on the three bones are separate, not in a straight line with one another. However, the relationships seem sufficiently close to suggest that the accessory branchiostegals are homologous with the second and third branchiostegal in primitive Crossopterygii and therefore that they are really branchiostegals and not displaced mandibular elements. And finally it appears that the posterior pair of gulars in Dipterus are derived from the lateral gulars of the Crossopterygii. The anterior pair of gulars in Dipterus may have arisen by division of the lateral crossopterygian gulars into an anterior and posterior pair. Enlargement of the anterior pair of gulars would result in the posterior displacement of the posterior pair of gulars and the accessory branchiostegals and explain why they are out of line with the positions in the Crossopterygii.

Gulars: A small median anterior gular lies in the fork of the mandibular rami. It is not known to bear a V-shaped pit line as in some Crossopterygii and Actinopterygii; nevertheless it seems logical to consider it homologous. The median gular is followed by a medium-sized pair of rhombic gulars. The anterior pair of gulars lacks a pit line;

the posterior pair of gulars are somewhat larger. Their posterior edges curve anteriorly much as those in Crossopterygii, but they overlap more. The left gular overlaps the right in both the anterior and posterior pairs. The posterior gular bears a short straight pit line anteriorly; apparently a continuation of the one running across the accessory branchiostegals. A posterior median gular lies between the two paired gulars.

References: Graham-Smith and Westoll (1937); Watson and Gill (1923), Westoll (1949).

† ORDER PHANEROPLEURIFORMES

Branchiostegals two; a small median gular and two large pairs of gulars present; a large operculum and medium-sized suboperculum present; ceratohyal known. Upper Devonian. Three families.

† Phaneropleuridae

Branchiostegals: No data available.

Gulars: A pair of long gulars, pointed anteriorly.

Operculars: Operculum large and circular; suboperculum small and elongate.

References: Woodward (1891), Whiteaves (1889).

† Scaumenacidae

Pl. II

Branchiostegals: In *Scaumenacia* two branchiostegals. One short wide spathiform branchiostegal which widens distally, and another anteriorly between the two paired gulars ("accessory branchiostegal"). These correspond to the two in *Dipterus*.

Gulars: A small median gular lies in the fork of the mandible. Behind this is a relatively small anterior and a larger pair of posterior gulars. The gulars all correspond with those in *Dipterus*, although differing somewhat in form, being less elongate.

Operculars: There is a large pentagonal operculum with a curved evacuation on its dorsal edge. The small wide suboperculum curves up from its lower edge to meet the operculum posteriorly. The suboperculum of *Scaumenacia* is nearly ½ the size of the operculum, the largest suboperculum in the superorder.

Relationships: The close correspondence of all the branchiostegal series to *Dipterus* leaves little doubt that it is related to the Dipteridae. It may be distinguished by its larger suboperculum and the presence of only one accessory branchiostegal.

Reference: Stensio (1947).

† Fleurantiidae

Branchiostegals: Not preserved.

Gulars: In fig. 3 of *Fleurantia* in Graham-Smith and Westoll, are bones which apparently represent a large oval posterior paired gular and a branchiostegal (or suboperculum ?). A paired gular in another specimen bears an arc-shaped pit line.

Operculars: Operculum large and pentagonal.

Hyoid arch: Ceratohyal short, stout, hour-glass shaped and much expanded at the posterior end, only slightly anteriorly.

Relationships: Poorness of preservation of the branchiostegals enables little to be deduced from them. Graham-Smith and Westoll believe *Fleurantia* to be a secondary development from the normal dipnoan ancestor, such as *Dipterus*, *Scaumenacia* being more advanced in fin structure.

References: Graham-Smith and Westoll (1937).

† ORDER URONEMIFORMES

Branchiostegals and gulars not known; a large oval operculum and a small elongate suboperculum present; ceratohyal known. Lower Carboniferous to Upper Permian. Two families.

Taxonomy: Romer does not distinguish the Uronemidae from the Dipteridae. Arambourg and Guibe synonymize the Conchopomidae with the Uronemidae and the Uronemiformes with the Ctenodontiformes. Berg's classification is provisionally retained here.

† Uronemidae

Branchiostegals: Not known.

Gulars: Not known.

Operculars: A large oval operculum is found in *Uronemus splendens*. It has a small dorsal projection. A small bone figured below may represent a suboperculum.

Hyoid arch: Bones resembling the centre portion of ceratohyals have been illustrated.

References: Watson and Gill (1923), Woodward (1891).

† Conchopomidae

Branchiostegals: Not known.

Gulars: Not known.

Operculars: In *Conchopoma gadiformis* a large oval vertical operculum is known. It bears a small dorsal projection. A small angulated wing-like bone may represent a suboperculum.

Hyoid arch: The ceratohyal is of even breadth anteriorly, but is much expanded posteriorly.

References: Watson and Gill (1923).

† ORDER CTENODONTIFORMES

Branchiostegals not known; one pair of gular plates known; large scallop-shaped operculum; small elongate suboperculum. Lower Carboniferous to Lower Triassic. One family.

† Ctenodontidae

Pl. II

Branchiostegals: Not known.

Gulars: A pair of crescentic gular plates situated anteriorly in the fork between mandibular ramii is described for *Sagenodus*. Mesial flanges projecting from these look as if designed to support a pair of gulars posteriorly.

Operculars: Operculum present in *Ctenodus* and *Sagenodus*. It is large, roughly circular, scallop-shaped, and bears, where it inserts, a curved depression dorsally. On its antero-ventral border lies a small elongate suboperculum; a ridge runs along its length externally.

Relationships: Except for a dorsal evacuation the operculum of *Sagenodus* much resembles that of *Dipterus*. The anterior pair of gular plates is, however, of quite different conformation from that of *Dipterus*, being more cresentic.

References: Woodward (1891), Watson and Gill (1923).

SUPERORDER CERATODI

Gular plates and branchiostegals absent. Operculum reduced to an elongate ray which rests on the supratemporal-intertemporal (squamosal). The slender suboperculum rests on the ceratohyal. Ceratohyal and sometimes hypohyal present. Interhyal absent except in larvae. Upper Carboniferous to present. Two orders.

Taxonomy: Arambourg and Guibe (1958) synonymize, without discussion, the Lepidosirenformes with the Ceratodiformes. These two orders are retained here; hyoid arch differences support their separation.

ORDER CERATODIFORMES

A reduced operculum and suboperculum present; hypohyal, ceratohyal (expanded greatly at the upper end) and interhyal present in larvae. Upper Carboniferous to present. One family which includes a living representative *Neoceratodus forsteri* in Australia.

Ceratodidae

Pl. II

Operculars: In *Neoceratodus* operculum reduced in size and shaped like an arrow head pointing posteriorly. The elongate oval suboperculum inserts on the expanded distal end of the ceratohyal. Under the distal end of the suboperculum is an oval cartilaginous plate. Gill opening restricted to side of head.

Hyoid arch: Composed of a small rectangular cartilaginous hypohyal and a large ossified ceratohyal. The ceratohyal is shaped as in Conchopomidae, that is of even breadth anteriorly and expanding greatly at its posterior end. Figures in Gregory, Goodrich and Holmgren and Stensio show no other hyoid bones (except a small cartilaginous hyomandibular). De Beer shows three bones, the "stylohyal", the ceratohyal and the hypohyal in a larval specimen. In the adult specimen here examined only a ceratohyal was present; the cartilaginous hypohyal, if present, was shrivelled and there was no sign of an interhyal.

References: Ridewood (1894), Gregory (1951), Holmgren and Stensio (1936), Goodrich (1958), de Beer (1937).

Material examined: *Neoceratodus forsteri*, skeletal specimen, uncatalogued NMC, Queensland, Australia.

ORDER LEPIDOSIRENIFORMES

Operculum and chevron-shaped suboperculum reduced to a slender ray; only the ceratohyal (slightly expanded at the upper end) present in hyoid arch. Two families, Lepidosirenidae with a single living species in Brazil and Protopteridae with four living species in Africa; both in freshwater. Upper Carboniferous to present.

Taxonomy: Arambourg and Guibe (1958) synonymize Protopteridae with Lepidosirenidae and Lepidosireniformes with Ceratodiformes. These groups are provisionally retained following Berg's classification.

Lepidosirenidae

Pl. II

Operculars: Operculum reduced to an elongate flat ray bearing a small cartilage under its distal tip in *Lepidosiren*. It inserts on the supratemporal-intertemporal (squamosal), the hyomandibular being absent. The suboperculum is shorter but wider than the operculum. The suboperculum is a chevron-shaped bone which inserts on the upper ceratohyal. It is underlain by a broader cartilaginous base. This base is called an interoperculum by Bridge, but it can hardly be that bone which unknown in the dipneustians (found only in the more advanced Actinopterygii). Nor are the cartilaginous distal tips of the operculum and suboperculum likely to be a remnants of a hyoid ray, as he suggests, but are rather unossified portions of the operculum and suboperculum. Gill opening restricted to side of head.

Hyoid arch: Only a ceratohyal is present (even embryologically), the hypohyal, interhyal and hyomandibular being absent. The ceratohyal is large, bowed slightly downwards and expanded slightly at each end. It is attached to the parasphenoid by a ligament (the hyomandibular wanting). There is an odd patch of cartilage on the outer surface of the distal portion of the ceratohyal.

Relationships: The reduced operculum and ceratohyal with posterior end unexpanded of the Lepidosireniformes are doubtless derived from the less reduced operculum and ceratohyal with expanded posterior end of the Ceratodiformes. That is the Ceratodiformes are more primitive than the Lepidosireniformes.

References: Gregory (1951), Ridewood (1894), Bridge (1898), Holmgren and Stensio (1936), de Beer (1937).

Material examined: None.

Protopteridae

Operculars: The operculum tapers posteriorly to a point in Protopterus; it appears to insert on the supratemporal-intertemporal (squamosal). The operculum bears an inner cartilage as in Neoceratodus. The suboperculum is essentially similar to that in Lepidosiren, being an elongate chevron-shaped bone over a cartilaginous base. It inserts on the posterior end of the ceratohyal. Gill opening restricted to side of head.

Hyoid arch: Only a ceratohyal is present, the basihyal, hypohyal, interhyal and hyomandibular are lacking. The ceratohyal is large and slightly expanded at each end. There is a patch of cartilage on the outer surface of the anterior end of the ceratohyal. This is called a vestigial hyoidean ray by Bridge, but its position does not confirm this suggestion. Ligaments connect the ceratohyal to the skull and to the lower jaw, as in *Lepidosiren*.

Relationship: The correspondence of the operculars and ceratohyal in Lepidosirenidae and Protopteridae suggest they are closely related.

References: Ridewood (1894), Bridge (1898), Dean (1895).

Material examined: None.

SUBCLASS BRACHIOPTERYGII

ORDER POLYPTERIFORMES

Branchiostegals absent; median gular absent; a very large pair of lateral gulars (longer than 2/3 of mandible length); large operculum; small suboperculum present - or absent; interoperculum absent. Lower Tertiary (Eocene) to present. A single order and family. It is the only actinopterygian derived group with lateral gulars and lacking branchiostegals.

Polypteridae

Pl. IV

Branchiostegals: Absent.

Gulars: Median gular absent. A pair of large lateral gulars which extend from the symphysis to slightly past the posterior end of the mandibles, extending to the midventral line to a point just before the posterior end of mandibles. A short transverse pit line in the form of an arc is found near the middle of each. According to Daget (1958) the gular pit line is innervated by a nerve extending posteriorly from the middle of the *ramus mandibularis facialis*. In *Calamoichthys* the gulars are slightly shorter, and the tip of the right overlaps the tip of the left. The large gular plates are reminiscent of those in Crossopterygii.

Operculars: Operculum oval and larger than the triangular suboperculum, in *Polypterus*. Subopercle absent in *Calamoichthys*. Gill membranes separate, with right over left.

Hyoid arch: A partially ossified hypohyal, a ceratohyal and interhyal are present. The ends of the ceratohyal and interhyal are not ossified.

Taxonomy: The family Polypteridae consists of two living African freshwater genera *Polypterus* and *Calamoichthys* (= *Erpetoichthys*).

Relationships: The absence of an interoperculum relates it to the lower Actinopterygii. The enlarged lateral gulars recall those of *Pyritocephalus* and *Haplolepis* (Haplolepiformes). These forms also have pit lines on the lateral gulars, the branchiostegals reduced and the operculum larger than the suboperculum. The similarity of the lateral gulars to the Crossopterygii and Dipnoi is doubtless a parallelism. The lateral gulars expanded to cover the region exposed by the loss of the branchiostegals.

Evidence on its relations also comes from its sensory lines (Stensio, 1947). The sensory line of the cheek is of the actinopterygian type. In its principal features it is much as in advanced lower ganoids, but in some respects it has reached the stage of holostean ganoids. The postmaxillary line is similar in its connection with the dermal bones to lower ganoids and parasemionotids. They are probably derived from some sub-holostean ancestor (Stensio, 1947).

References: Devilliers (1958), Daget (1958), Allis (1922), Berg (1947).

Material examined: *Calamoichthys* sp., alcoholic specimen, ROM 18877, Nigeria.

SUBCLASS ACTINOPTERYGII

Branchiostegals 0-50; median gular present or absent, primitively with a V-shaped pit line; lateral gulars, if present, with length less than one half of mandible length; operculum and suboperculum usually present; in higher forms interoperculum usually present; interhyal, epihyal (in higher forms), ceratohyal and hypohyal(s) usually present. Lower Devonian to present. Five supraordinal groups with 56 orders 34 of which are living.

It has been made apparent by various authors, Stensio, Berg, Schaeffer, Gardiner, etc., that the Chondrostei, Holostei and Teleostei (as constituted) are not natural groups, that the Holostei are polyphyletic and that some of the characters which have been used to distinguish the Holostei occur in certain chondrosteans. This has been interpreted as meaning that the Chondrostei, Holostei and Teleostei are not valid groups.

However, other interpretations are possible. Firstly, that some orders have been placed in the wrong group. Secondly, that some of the characters previously used to define the groups have not been diagnostic, although they may tend to be more frequent in one group than the other. According to this interpretation the groups, if reconstituted and redefined, would be natural.

The interoperculum is an important character in diagnosing the Holostei. It is absent in the Chondrostei, present in the Holostei and present in the Teleostei (except in a few groups of the latter where it is secondarily lost). One group presently placed in the Holostei, the Lepisosteiformes lacks and interoperculum, but has a maxillary free from the cheek. However, the jaws have moved far forward, decreasing the need for an interoperculum and the preoperculum has expanded ventrally supplanting the position normally occupied by one. It may safely be suggested therefore that the interoperculum has been secondarily lost. The Platysiagiformes have been suggested to bear an incipient interoperculum. This has been demonstrated not to be so. Further, it bears a maxillary fixed to the cheek and clearly belongs in the Chondrostei. Brough (1939) considered that the maxilla of the subholostean Luganoia was free, but his figure 15 shows the end of the maxilla snugly fitted against the large plate-like preoperculum; in other figures it appears displaced from this notch. It is concluded the maxilla was not free. This and the lack of an interoperculum places it in the Chondrostei. The Ospiiformes have been considered chondrosteans but their maxillary is free and it is now clear that they possess an interoperculum (Stensio, 1932; Lehman, 1952). There now appears to be no good reason not to place the Ospiiformes in the Holostei. The Pycnodontiformes lack an interoperculum and yet have been placed in the Holostei. But recent authors (Rayner, 1941 and Gardiner, 1960) and the present author are in agreement as to their placement in the chondrosteans near the platysomoids or bobasatraniiforms.

When the above changes have been made the Chondrostei and the Holostei comprise homogeneous groups. All of the Holostei have a free maxillary and an interoperculum (except that the interoperculum is lost in the Lepisosteiformes) and all of the Chondrostei have a fixed maxillary (except Dorypterus where the maxillary has shortened and become secondarily free) and lack an interoperculum. That there are other characters which would support this grouping is suggested by Schaeffer's fine association analysis of differential characters. It is also certain that some characters, previously employed to characterize the groups (such as the relation of rays to their supports) do not definitively separate the two groups (however it might still be possible to state that in chondrosteans fin rays exceed or equal pterygiophores and in holostei equal pterygiophores).

The Teleosti may be separated from the Chondrostei and Holostei by the lack of lepidosteid tubules either in their scales or skeleton, and the primitive presence of intermuscular bones and two hypohyals.

For the above reasons the modified supraordinal groups Chondrostei (Group I), Holostei (Group II) and Teleostei (Group III) are therefore reinstated. The Teleostei are further subdivided into the Malacopterygii (Group IIIA) and the Acanthopterygii (Group IIIB). The group Mesichthyes is discarded, as will be discussed later.

GROUP I. CHONDROSTEI

Without interoperculum. Lateral gulars present or absent. A single hypohyal. Lower Devonian to Present.

† ORDER PALAEONISCIFORMES (AEDUELLIFORMES, GYMNONISCIFORMES)

Branchiostegals (1)4-23, spathiform; median and a pair of lateral gulars; operculum and suboperculum present, interoperculum absent; interhyal, epihyal, ceratohyal and a hypohyal known. Lower Devonian to Lower Cretaceous. Several families.

Following Lehman (1958), Berg's Gymnonisciformes are included in the Palaeonisciformes. The Palaeonisciformes are a diverse group which will probably be broken up into other orders when a detailed taxonomic revision is made. However, the practice of removing poorly known families from Palaeonisciformes and raising them to ordinal status does not seem advisable.

SUBORDER PALAEONISCOIDEI

† Cheirolepidae

Pl. III

Branchiostegals: 11-13 branchiostegals are found in Cheirolepis; these are short, wide and spathiform.

Gulars: A median gular has not previously been reported in this group. In Traquair's (1875) figure of the ventral view of the jaws a diamond-shaped, bilaterally symmetrical bone is seen overlying the lateral gular of the right side. It seems likely that this element is a displaced median gular. As median gulars are found in other Palaeonisciformes, dipnoans and coelacanths it would not be surprising to find one in Cheirolepis. A pair of wide lateral triangular gulars each with a pit line are found next to the last branchiostegal.

Operculars: Operculum inclined forwards and much longer than the suboperculum.

Relationship: The branchiostegals and opercular bones of Cheirolepis are little different from those of the palaeoniscid, Glaucolepis; most other characters are in accord with this. The small scales, as pointed out by Aldinger (1937) are however, very similar to those of acanthodians. Cheirolepis thus forms a connecting link between the

Teleostomi and Acanthodii.

References: Traquair (1875), Watson (1925), Woodward (1898), Lehman (1947).

† Palaeoniscidae

Pl. III

Branchiostegals: (1) 4-23 usually 9-15 branchiostegals, short, wide and spathiform. In *Glaucolepis* at least, the last 5 branchiostegals insert on the ceratohyal, none on the hypohyal; presumably rays also seat on the epihyal (see Nielsen's excellent photo pl. 11 and 16, 1942). *Palaeoniscus* 8-9, *Oxygnathus* 12, *Gonatodus* 10, *Boreosomus* 7-8, *Hyllingea* 23, *Plegmolepis* ca. 16, *Watsonichthys* 15, *Acrolepis* 14, *Diaphorognathus* 7-9, *Pygopterus* 20, *Pteronisculus* 12-22, *Stegotrachelus* 6, *Glaucolepis* 13-15, *Cornuboniscus* 16, *Rhadinichthys* 10-11, *Cycloptychius* 10, *Canobius* 4-6, *Mesopoma* 5-7, *Nematoptychius* 20, *Aeduella* 1.

Gulars: A median gular is known from most forms which are sufficiently preserved to show its presence. In *Hyllingea* only scales are found in the gular region. In some forms a second gular is found, a small anterior gular near the symphysis overlying a larger median gular which projects posteriorly to the branchiostegals; in these the lateral gulars are absent (*Boreosomus*, *Diaphrognathus*). In most other adequately represented forms a pair of small lateral gulars is present (*Pteronisculus*, *Palaeoniscus*, *Gonatodus* etc.). In *Aeduella* is a large diamond-shaped gular with V-shaped pit line. The adjacent "branchiostegal" is identifiable as a lateral gular by the arc-shaped pit line. These occupy less than a quarter or third of the length of the mandibles.

Operculars: Operculum and suboperculum present, the operculum generally larger and inclined forwards, except in the short-jawed forms.

Hyoid arch: Watson (1925) did not find an ossified epihyal in any palaeoniscid. He described a short hypohyal and a long ceratohyal in Elonichthys. A hypohyal, long ceratohyal and short element (called 2nd ceratohyal (=epihyal, separate ceratohyal ?) by Nielsen, (1942) are evident in Glaucolepis. The ceratohyal and this element bear a lateral groove for the afferent hyoid arteries. Acrorhabdus is known to have a long hourglass-shaped ceratohyal and a triangular epihyal (?) (shaped similarly to the epihyal in higher forms such as Salvelinus); another bone, possibly the interhyal is present.

Taxonomy: Palaeoniscidae is here used in the sense of Berg (1947) and includes the families Thrissonotidae (Oxygnathidae), Rhadinichthyidae, Canobiidae, Elonichthyidae, Pygopteridae, Acrolepidae, Amblypteridae, Scanilepidae, Dicellopygidae, Boreolepidae, Cocconiscidae, Cornuboniscidae, Tegeolepidae, Styracopteridae, Aeduellidae (the latter raised to ordinal status in a classification outline in Traite de Zoologie, vol. XIII, fasc. 3, 1958). Gymnoniscidae (Gymnonisciformes of Berg) is included in Palaeoniscidae following Lehman (1958); Westoll (1944) believed it to be only the young of Sceletophorus, a palaeoniscid.

Berg's lumping of so many diverse forms into the family Palaeoniscidae does not seem reasonable. Perhaps Romer's recognition of many families would be more acceptable, although he fails to segregate any of the lower Chondrostei into orders. However, the author did not feel in a position to accept all of these families, many monotypic, without analysis. Nielsen (1949) felt that Aldinger had gone somewhat too far in subdivision of the old palaeonisciid group. Berg's classification was therefore provisionally followed, rather than inadvisedly raising groups to family status.

In looking at the variation of the branchiostegal series in a few of the many known paleoniscids, family recognition of certain forms seem to be suggested. Proper delimitation into families will of course require examination of all forms and looking at more than one set of characters. The two median gulars of Boreosomus and Diaphrognathus set them well aside from other palaeoniscids. Several forms have sufficiently numerous branchiostegals to separate them from other palaeoniscids: Agecocephalus, Hyllingea, Nematophychius and Pygopterus have 20 or more branchiostegals. On the other hand the few highly curved branchiostegals in Canobius and Mesopoma would seem partly to justify the family Canobiidae. Aeduella is distinct in having only a single branchiostegal. Although most of the other genera examined are united in having a median gular, a pair of lateral gulars, and 9 to 15 branchiostegals, family delimitation on other bases is of course possible.

References: Berg (1947, 1955), Nielsen (1942), Moy-Thomas and Dyne (1937), Aldinger (1937), Woodward (1891), Woodward and White (1926), Lehman (1958), Brough (1933), White (1933), Gregory (1951), White (1939).

† Coccolepidae

Branchiostegals: About 14 in *Coccolepis macropterus*. The branchiostegals are short, spathiform and slightly curved, similar to those of palaeoniscids.

Reference: Berg (1947).

† Birgeriidae

Branchiostegals: About 14 in *Birgeria*. These are of medium length and spathiform.

Gulars: A small oval median gular and a pair of small lateral gulars which are almost identical to the adjacent branchiostegals were found. Pit lines absent.

Operculars: The opercular bones are separated. The operculum is horizontal and oval; the suboperculum consists of 4 to 6 vertical triangular rays which are fused ventrally, a unique feature in the Palaeonisciformes.

Hyoid arch: A long ceratohyal and a short hypohyal are known.

Taxonomy: *Birgeria* may be a synonym of *Xenestes*; this, according to present rules, need not result in a change of the family name.

Relationships: The unique, fan-like subopercle distinguishes this family from other palaeonisciforms. The branchiostegals and gulars are consistant with a palaeoniscid derivation. Nielsen (1949) believed the body skeleton and dermal bones of the head point to a fairly close relationship to the Palaeoniscidae. Watson (1925), Stensio (1932) and Aldinger (1937) believed the chondrocranium, spiracle, position of nostril and reduced endoskeleton indicate an approach to the sturgeons.

References: Nielsen (1942).

† Holuridae

Branchiostegals: 12 in *Holurus parki*, 8 in *Holuropsis yavorskii*, these short, spathiform with lower edge curved.

Operculars: Operculum and suboperculum present, rectangular.

References: Moy-Thomas (1937), Berg (1955).

† Urosthenidae

Branchiostegals: Head not known. Lehman (1958) would reduce this family to a subfamily of Palaeoniscidae.

References: Berg (1947, 1955).

† Turseoidae

Branchiostegals: 6-7 in *Gwynoddichtis*. Wide, slightly curved spathiform rays.

Gulars: The small median gular is considerably behind the symphysis and sits on top of the lateral gulars. The lateral gulars extend to the symphysis.

Operculars: Operculum a slender rectangle longer than the trapezoidal suboperculum.

Relationship: The Turseoidae differ from the palaeoniscids in the arrangement of the gular plates and in the reduced number of branchiostegals, but not so highly as to preclude immediate derivation from them.

References: Bock (1959).

SUBORDER PLATYSOMOIDEI

Although platysomoids tend to have fewer branchiostegals and more vertical operculars than the palaeoniscoids, both of these characters overlap. The two characters seem to be associated with a shortening of the jaws, requiring fewer branchiostegals to cover the throat and with erecting the suspension, making the operculars more vertical. They are doubtless palaeoniscoid derivatives.

† Platysomidae

Branchiostegals: 6-7 in *Platysomus*, about 4 in *Paramesolepis tuberculata*. Wide, spathiform, with ventral edge curved upwards.

Operculars: Operculum and suboperculum are vertical and about equal in size.

References: Lehman (1958), Moy-Thomas and Dyne (1937), Woodward (1898).

† Amphicentridae

Branchiostegals: About 5 in *Cheirodopsis*, 6 in *Eurynotus geikei*, about 7-9 in *Amphicentrum*, elongate, spathiform, widening distally, ventral edge straight.

Operculars: Operculum and suboperculum high, and oval or rectangular, about equal in size and vertically oriented.

References: Lehman (1958), Woodward (1891), Romer (1955), Dyne (1939).

† ORDER TARRASIIFORMES

Branchiostegals 15, spathiform; gulars not known; operculum and suboperculum present, interoperculum absent. Lower Carboniferous. A single family.

† Tarrasiidae

Pl. III

Branchiostegals: 15 in *Tarrasius problematicus*. Spathiform, lower edge curving upward, upper ones elongate, lower short.

Gulars: Text and figures make no mention of gulars. The anterior branchiostegal is figured as broader and may possibly represent a lateral gular.

Operculars: Operculum and interoperculum subrectangular and horizontally oriented.

Relationships: *Tarrasius* differs from most palaeonisciforms in the opercle and subopercle being long horizontally and the operculum not being greatly inclined forwards. Unlike other short-jawed forms the number of branchiostegals has not been reduced but they have been bunched closely together. The shortening of the jaws may be associated with the durophagus habit indicated by the teeth. The number and form of the branchiostegals are not out of line with a palaeonisciform derivation. According to Moy-Thomas, "*Tarrasius problematicus* is certainly a Palaeoniscid, as shown by the characteristic arrangement of the bones of the skull, axial skeleton, supporting the skeleton of the median fins and microscopic structure of the scales. It is however, specialized in having continuous dorsal and ventral fins, and a diphycercal tail, loss of scales on the main body and shagreen-like scales on the caudal region, the peculiar shape of the pectoral, and loss of the pelvic fins". One might add to these specializations the elongate, blenny-like form.

References: Traquair (1881), Moy-Thomas (1934).

† ORDER PHANERORHYNCHIFORMES

A long series of branchiostegals; gulars not known; operculum and suboperculum present; interoperculum absent. Middle Carboniferous. A single family.

† Phanerorhynchidae

Branchiostegals: *Phanerorhynchus* is described as having a long series of branchiostegals. The two branchiostegals depicted appear narrow, pointed and quite small.

Gulars: It was impossible to see whether lateral or median gulars were present in the specimen.

Operculars: A long and slightly oblique operculum with sparse longitudinal ridges and a small subopercular present.

Taxonomy: Romer (1955) places *Phanerorhynchus* in the Haplolepidae, apparently on the basis of the scales. But *Phanerorhynchus* is quite different from Haplolepidae in the possession of a long sturgeon-like snout. Westoll (1944) in a revision of the Haplolepidae states that *Haplolepis* is sharply distinct from *Phanerorhynchus* and that the possession of deep flank scales by these two groups is most feasibly regarded as parallelism. *Phanerorhynchus* is thus here placed in its own order, as in Berg.

Relationships: The branchiostegal series are too poorly known to shed light on relationships. Gill and Watson believed the skull and shoulder girdle showed conclusive evidence of palaeoniscid affinities, but the build, character of the caudal peduncle, short-based pelvics, few large dermal rays in the fins and long undivided rostral bone were distinctive. Stensio (1932) placed it in the vicinity of Saurichthyidae. But as Berg (1947) noted the Phanerorhynchidae are so specialized as regards to fin structure that they cannot be regarded as ancestors either of Saurichthyidae or Acipenseridae. It thus seems preferable to regard them as an independently evolved sturgeon-like form derived from the Palaeonisciformes.

References: Gill and Watson (1923), Stensio (1932).

† ORDER HAPLOLEPIFORMES

Branchiostegals 1-3 spathiform, the one next to the lateral gular expanded; large median and lateral gulars; V-shaped pit line on median gular; opercle and subopercle present; interoperculum absent. Upper Carboniferous. A single family.

† Haplolepidae

Pl. III

Branchiostegals: 1-3 in Haplolepis; 1 in Pyritocephalus. The branchiostegal behind the lateral gular (present in all forms) is large, rectangular or triangular and may be as large as one third of the size of the lateral gulars. The second and third branchiostegals, when present, are very broad with rectilinear edges. The exposed portion of the branchiostegals is very short. In Pyritocephalus there is a gap between the single branchiostegal and the suboperculum.

Gulars: A large median gular 1/3 - ½ the length of the mandible is present; it bears a V-shaped pit line with the apex facing posteriorly. A large pair of lateral gulars occupy about 1/3 the length of the jaws. A short transverse pit line is found in the middle of each lateral gular. The enlarged anterior branchiostegal, referred to in the literature as a posterior paired gular, is here considered a branchiostegal.

Operculars: Either the operculum or the suboperculum may be larger. These are vertically oriented in this small-jawed form.

Taxonomy: After Westoll's thorough revision of the family, Lehman raised it to ordinal status.

Relationships: The short jaws, vertically oriented operculars and few branchiostegals in the Haplolepidae remind one of Catopterus and Mesopoma, although the large median and lateral gulars of Haplolepidae do not appear to be present in these forms. However, the similarities in operculars and branchiostegal rays may not be an indication of close common ancestry, but only parallel evolution following a reduction in jaw length. The large size of the gulars and the few branchiostegals distinguish the Haplolepidae from the palaeoniscids, perhaps at the ordinal level, although it is, no doubt, derived from them.

References: Westoll (1944), Lehman (1958).

† ORDER REDFIELDIIFORMES

One large spathiform branchiostegal (sometimes split) below the suboperculum, perhaps absent in some; gulars absent; opercle and subopercle present; interoperculum absent. Lower to Upper Triassic. A single family. Following Lehman (1958) Brookvaliidae is synonymized with Redfieldiidae.

† Redfieldiidae

Pl. V

Branchiostegals: 1 large trapezoidal branchiostegal (called infraoperculum by some authors) below the subopercle in Brookvalia; a triangular one in Geitichthys, Atopocephala, Helichthys and Phylctaenichthys. In Daedalichthys is a curious oval plate (overlying the suboperculum) which is divided into two by a horizontal joint, the lower part larger. Doubtless the plate represents a single split branchiostegal. Redfieldius on the other hand, according to the figure in Berg (1955), has a longer suboperculum and lacks a branchiostegal.

The term infraoperculum is equivalent to the branchioperculum of Hubbs; both refer to an enlarged uppermost branchiostegal.

Gulars: A small narrow median bone may represent a gular in Brookvalia.

Gular plates do not appear to be present in other genera.

Opercular bones: Opercle and subopercle approximately equal, subquadrangular, almost vertical.

Taxonomy: Catopteridae was first applied to the family in 1890. In 1899 Hay discovered Catopterus Redfield 1837 was a junior homonym of Catopterus Agassiz 1833. Hay proposed a replacement name, Redfieldius for Catopterus Redfield. Then he proposed a new family name Dictopygidae, based on Dictopyge (a genus in the same family) to replace Catopteridae. But, according to Article 39a of the International Code of Zool. Nomenclature, the family name must be changed to one based on the valid name of the original nominal type-genus, in order to preserve the taxonomic concept. That is, the new family name must be based on the substitute name Redfieldius (there being no junior synonyms available), rather than on another genus in the same family, Dictopyge. Berg was therefore correct in applying Redfieldiidae and Redfieldiiformes to this group and the name Dictopygidae is therefore a junior subjective synonym. Catopteridae has been used by most authors for this family: Stensio (1921, 1932), Wade (1935), Brough (1934), and Lehman (1958), although Romer (1955) used Dictopygidae. Most of these authors were apparently unaware of the homonymy of Catopterus. The last section of Article 39 ("The provisions of this section are not to be applied so as to upset a widely accepted family-group name that was established before 1961 under a different procedure") does not apply to Catopteridae although it might have applied to Dictopygidae had it been widely accepted. So Redfieldiidae and Redfieldiiformes are the proper familial and ordinal names for this group.

Relationships: Lehman (1958) considered the Perleidae and Catopteridae quite close, differing principally in dentition and fin anatomy. He therefore synonymized the two orders employed for them by Berg under Perleidiformes. The present study shows the branchiostegals of Berg's two orders differ markedly. In Redfieldiiformes there is one broad branchiostegal. In Perleidiformes on the other hand there are 7-12 branchiostegals. Gulars are unknown in Redfieldiiformes, median and lateral gulars are found in Perliediformes. Brough (1931) presents a table giving 9 differences but Schaeffer (1955) indicates that only two of these, excess of rays over radials and the number of branchiostegals are consistent and taxonomically important.

The dilated branchiostegals of Redfieldiiformes are suggestive of those in Haplolepidae, which also has very few branchiostegals (one to three). Haplolepidae differ in the possession of large well developed lateral and median gulars.

References: Berg (1955), Wade (1935), Brough (1931, 1934).

† ORDER PERLEIDIFORMES

Branchiostegals 7-12, spathiform; a median gular with a V-shaped pit line and a pair of lateral gulars; operculum and suboperculum present; interoperculum absent; ceratohyal known. Lower Triassic to Upper Triassic. A single family.

Teleopterina (=*Pyritocephalus*) is included in the Haplolepidae following Westoll (1944). Cleithrolepidae is included in the Perleidae following Lehman (1958).

† Perleidae

Pl. III

Branchiostegals: 7 broad spathiform in Perleidus (not including the lateral gular); 10 narrow spathiform in Meridensia; 12 narrow spathiform in Cleithrolepis and Colobodus; at least 2 or 3 in the fragmentary specimen of Manlietta. On the left, but not the right side, of Lehman's figure of Perleidus madagascariensis is a small branchiostegal half the length of the others; presumably this is teratological.

Gulars: An oval or diamond-shaped median gular of moderate size is present. In Perleidus it bears a V-shaped pit line, with the apex facing posteriorly. The median gular of Manlietta is very large, about as long as the mandible. The lateral gulars are identical in form to the adjacent branchiostegals, which are short and wide in Perleidus; but the lateral gulars bear pit lines.

Operculars: Suboperculum larger than the operculum. These are not deep.

Hyoid arch: In Perleidus the ceratohyal is short and expanded at both ends in the usual hourglass-shape.

Relationships: Differences between this order and Redfieldiiformes are discussed under the latter order. Wade (1935) indicates that Cleithrolepis is probably derived from the platysomids. However, the more numerous branchiostegals of Cleithrolepis cast doubt on this view. The V-shaped pit lines on the median gulars of Haplolepiformes and Perleidiformes would seem to indicate a common ancestory, probably from the Palaeonisciformes. Because of the more numerous branchiostegals of

Perleidiformes it is unlikely that they were directly derived from the Haplolepiformes. The sensory canal system is very close to that of Glaucolepis (Palaeoniscoidei) (Lehman 1952).

References: Lehman (1952), Brough (1939), Wade (1935), Stensio (1921), Schaeffer (1955).

† ORDER DORYPTERIFORMES

Branchiostegals absent; gulars absent; operculum, suboperculum and interoperculum absent. Upper Permian. A single family.

† Dorypteridae

Pl. V

Branchiostegals: Absent.

Gulars: Absent.

Operculars: Absent, although a small bone has been tentatively identified as an operculum in one specimen.

Hyoid arch: A long rectangular bone has been termed the ceratohyal but Westoll suggests that it is an ectopterygoid.

Relationships: The reduction in the branchiostegal series suggests derivation from the Platysomoidei rather than the Palaeoniscoidei. Westoll believed only the Platysomidae could have given rise to them. Lehman (1958) places the order in the family Platysomidae. While it is possible that Dorypterus should not be ordinally separated from the platystomids it requires at least familial separation on the basis of:

absence of branchiostegals, absence of scales on all but the abdomen, the skull being roofed by a single bone and the well developed ventrals. Further, Westoll states that Gill's recognition of its remarkable specialization can only be more strongly endorsed. In the relation of the number of fin rays to pterygiophores Dorypterus is intermediate between platysomids and Bobasatrania according to Stensio (1932). The order Dorypteriformes is thus provisionally retained.

References: Berg (1947), Stensio (1932), Gill (1925), Westoll (1941).

† ORDER BOBASATRANIIFORMES

Branchiostegals, if present, 1-2 or to 4; gulars unknown; operculum present; suboperculum and interoperculum absent. Lower Triassic. A single family.

† Bobasatraniidae

Pl. V

Branchiostegals: One or two, if present; in some, oval or quadrate in shape, in others there appears to be traces of at least 4 elongate spathiform branchiostegals.

Gulars: Unknown.

Operculars: A small narrow operculum present. Suboperculum absent; appears to have coalesced with the lower preopercular plate.

Hyoid arch: A small hourglass-shaped ceratohyal.

Relationships: In the reduction of the branchiostegal series Bobasatraniiformes would appear to be related to but not immediately derived from the Dorypteriformes. They probably share a derivation from the platysomoids (Stensio, Westoll).

References: Berg (1947), Stensio (1932), Lehman (1958), Lambe (1914), Westoll (1941).

† ORDER PYCNODONTIFORMES

Branchiostegals at least 2-5, acinaciform or spathiform; gulars absent; elongate vertical operculum; suboperculum replaced by preoperculum; interoperculum absent. Upper Triassic to Eocene. Three families.

Relationships: The phylogenetic position of this order has been something of an enigma. Berg and Romer place it among the holosteans, Arambroug and Bertin in their enlarged order Amiiformes. Stensio (1947), until the question of holostean classification has been solved, provisionally retains them in the Holostei. Gardiner (1960) derives them, with the Bobasatraniiformes, from an offshoot of the Dorypteriformes. Rayner (1941) places them in the subholosteans and regards them as derived from the platysomids.

Because of the absence of an interoperculum they are here placed in Group I. Their skull and body structure shows similarities to the Dorypteriformes and Bobasatraniiformes. With them the Pycnodontiformes share a large ventral preoperculum which replaces the suboperculum; a dorsal preoperculum; interoperculum absent; operculum elongate and vertically suspended; branchiostegals reduced; about 32-35 neural spines; vertebral centra absent; a postabdominal bone; dorsal and anals long; median fin rays tend to equal radials; body deep. In Gyrodus and

Bobasatrania a lateral line branch runs from the skull to the dorsal origin. However the Pycnodontiformes differ in possession of teeth and branchiostegals and in their abdominal pelvic fins whereas in the Dorypteriformes they are thoracic. In some Pycnondontiformes the supra- and infra-orbital canals join (*Microdon*, *Eomesodon*), unlike *Bobasatrania*. It therefore seems necessary to regard the Pycnodontiformes as an offshoot of the line which gave rise to the Dorypteriformes and Bobasatraniiformes. This opinion is in agreement with that of Rayner and close to that of Gardiner (1960). Their slender curved branchiostegals, graduating to a point, distinguish them from other orders in Group I.

† Gyrodontidae

Pl. V

Branchiostegals: Unknown in *Macromesodon* (= *Mesodon*). One or two long curved sabre-like branchiostegals under the preopercle in *Mesturus*. Two elongate narrow rectilinear branchiostegals in *Gyrodus*.

Gulars: Unknown in *Macromesodon*. Absent in *Mesturus* where the intermandibular region and throat is covered by polygonal plates.

Operculars: An elongate vertically suspended operculum in *Mesturus* and *Macromesodon*; suboperculum replaced by large backwardly extending preoperculum. Stensio (1947) believed the suboperculum and preoperculum were fused and called the bone the preoperculo-suboperculum.

Hyoid arch: Poorly known but the ceratohyal is deep and a small hypohyal is known in *Mesturus*.

References: Woodward (1895), Berg (1947), Arambourg and Bertin (1958), Arambourg (1954), Eastman (1914).

† Coccodontidae

Branchiostegals: Data on branchiostegals of Coccodus has not been found in Woodward (1895) or in any other available literature. Zittel (1887) reports the operculum is large in Zenophilus; possibly his operculum represents the preoperculo-suboperculum.

† Pycnodontidae

Branchiostegals: 4 long narrow curved sabre-like branchiostegals are apparent in one specimen of Pycnodus (plate 72, Agassiz, 1833-1843). Remains of 5 spathiform ones known in Palaeobalistum.

Gulars: Unknown, presumably absent.

Operculars: Operculum apparently small with ventro-posterior projection. Preoperculo-suboperculum large as in Gyrodontidae.

Relationships: The available material does not indicate great differences between the three families of the order. Indeed Romer includes them in one family.

References: Woodward (1895), Agassiz (1833-43).

† ORDER PTYCHOLEPIFORMES

Several spathiform branchiostegals; a median gular present; operculum and suboperculum present; interoperculum absent; ceratohyal known. Lower Triassic to Lower Jurrasic. A single family.

† Ptycholepidae

Pl. V

Branchiostegals: Number not exactly indicated. In Ptycholepis first branchiostegal ornamented and wedge-shaped. Ventral to it there are a series of more normal branchiostegal rays, which are moderately large and elongate.

Gulars: A large median gular present.

Operculars: Operculum larger than the suboperculum.

Hyoid arch: Ceratohyal is a rather long flat bone somewhat constricted in the middle.

Taxonomy: Brough demonstrated that Ptycholepis did not belong in the Eugnathidae and placed it in its own family, Ptycholepidae. Lehman (1958) raised the family to ordinal status.

Relationships: Brough places Ptycholepis in the Subholostei. Lehman indicates it is probable that Ptycholepis is a descendent of the Triassic palaeoniscid genus Boreosomus or of a genus close to Boreosomus. The paucity of data on the branchiostegal series prevents further suggestions being made except to say that the absence of an interoperculum precludes placement among the holostean fishes.

References: Brough (1939), Lehman (1958), Woodward (1895).

† ORDER PHOLIDOPLEURIFORMES

Branchiostegals 6-14, spathiform; a small median gular and a pair of large lateral gulars are known; operculum and suboperculum present;

interoperculum absent; hypohyal and ceratohyal known. Lower to Upper Triassic. A single family.

† Pholidopleuridae

Branchiostegals: 6-14. *Australosomus* with 6-8 short wide branchiostegals which become shorter and broader anteriorly; *Macroaethes* with 14 (19 in figure) elongate branchiostegals with curved edges and rounded tips; *Arctosomus* with about 12; *Pholidopleurus* with at least 4 (series incomplete) branchiostegals which are elongate, fairly broad and resemble those in *Amia*. In *Australosomus* the lower 3 branchiostegals and lateral gular appear to insert on the ceratohyal.

Gulars: A small median gular in *Australosomus* situated anterior to the lateral gulars. A large triangular lateral gular triangular in outline in *Australosomus*. A large triangular lateral gular in *Macroaethes*. A lateral gular is not shown in the figure of *Arctosomus* (Berg in Nielsen, 1949). No pit lines are found on the median or lateral gulars.

Operculars: Operculum somewhat higher than the suboperculum in *Australosomus* but equal in *Macroaethes* and *Pholidopleurus*.

Hyoid arch: In *Australosomus* a small curved hypohyal is placed at the upper anterior corner of the long compressed ceratohyal which is grooved for the afferent hyoid artery.

Taxonomy: The few short broad branchiostegals of *Australosomus* appear to differ sufficiently from those of *Macroaethes* and *Arctosomus* to suggest placement in a different family or subfamily.

Relationships: Lehman (1952) criticizes the view that Australosomus is closely related to the Saurichthyidae. Nielsen and Lehman agree that the common characters of the two groups are those shared by most primitive palaeoniscid-type fishes. The few branchiostegals and absence of a suboperculum in Saurichthys indicate it does not have close affinities with Pholidopleurus. The branchiostegal series of the Pholidopleuriformes would seem to indicate an origin either from the Perleidiformes or from the Palaeonisciformes. Stensio (1932) considers it an offshoot from primitive palaeoniscids specialized in the direction of higher ganoids and teleosts.

References: Nielsen (1949), Lehman (1952), Wade (1935).

† ORDER CEPHALOXENIFORMES

Poorly known, see under description of single Upper Triassic family.

† Cepaloxenidae

Pl. V

Branchiostegals: Unknown, the lower portion of the head not being represented.

Gulars: Unknown.

Operculars: Operculum larger than suboperculum. Presumably no interoperculum.

Taxonomy: Lehman (1958) raises Brough's family to ordinal status.

Relationships: Brough states the fins are of the holostean type, the check bones are essentially palaeoniscid. He places them in the Subholostei between Platysiagidae and Peltopleuridae. The deep flank scales resemble those of the Luganoiidae and Peltopleuridae.

References: Brough (1939).

† ORDER AETHODONTIFORMES

Poorly known, see under description of single Upper Triassic family.

† Aethodontidae

Branchiostegals: Not preserved.

Gulars: An oval median gular plate is known. Lateral gulars unknown.

Operculars: Operculum and suboperculum about equal in size. Interoperculum presumably absent.

Taxonomy: Brough's family was raised to ordinal status by Lehman (1958), although only fragmentary remains of the fish are known.

Relationships: The hemiheterocercal tail and fins with reduced rays are subholostean in character while the cheek bones and sensory canals are palaeoniscid (supraorbital line ends on the frontal). The crushing dentition is unique among the subholosteans.

References: Brough (1939).

† ORDER LUGANOIIFORMES

Poorly known, see description of the single Upper Triassic family.

† Luganoiidae

Pl. V

Branchiostegals: Unknown.

Gulars: Unknown.

Operculars: The operculum and suboperculum are about equal and triangular in Luganoia, while the suboperculum is smaller and rectangular in Besania. Interoperculum absent.

Taxonomy: Lehman (1958) raised Brough's family to ordinal status.

Relationships: Brough states that all the characters are holostean except a) the absence of an interoperculum and the gill cover of almost equal operculum and suboperculum, b) the plate-like preoperculum. They are amongst the most developed of the subholosteans. Subholostean characters are: the rounded, hemiheterocercal tail and the well spaced rays of dorsal and anal which equal in number the endoskeletal supports. The deep body scales resemble those of the Peltopleuridae and Cephaloxenidae.

† ORDER PELTOPLEURIFORMES

Branchiostegals 6-7 elongate spathiform; gulars unknown; operculum and suboperculum present; interoperculum absent. Upper Triassic. A single family.

† Peltopleuridae

Pl. III

Branchiostegals: In Peltopleurus about 6-7 elongate spathiform branchiostegals, the uppermost of which is not enlarged.

Gulars: Unknown.

Operculars: A large triangular operculum and a smaller rectangular suboperculum.

Taxonomy: Lehman (1958) raised Brough's family to ordinal status.

Relationships: From the branchiostegals it can be said that it is unlikely that the Peltopleuriformes arose from the Ptycholepiformes, Redfieldiiformes, Bobasatraniiformes, Haplolepiformes or Dorypteriformes; origin is possible from the Palaeonisciformes, Perleidiformes, or Pholidopleuriformes. According to Lehman (1958) the scales of Peltopleurus recall a little those of Australosomus; however to the present author the scales seem more similar to those of Cephaloxenus or even Luganoia. Lehman then states that the bones of the cranial roof, with the square parietals and the externally homocercal tail recall those of the Perleidae. Altogether, a perleidiform ancestory of the Peltopleuriformes on a common line with the Cephaloxeniformes seems not improbable.

References: Brough (1939), Lehman (1958).

† ORDER PLATYSIAGIFORMES

Branchiostegals about 13, spathiform; gulars unknown; operculum and suboperculum present; interoperculum absent. Upper Triassic and Lower Jurassic. A single family.

† Platysiagidae

Pl. IV

Branchiostegals: Number about 13 in *Platysiagum minus* (text, not figure of Brough). These are broad, short and spathiform. The first branchiostegal is subrectangular. There is a gap, probably a result of preservation, between this branchiostegal and the others.

Gulars: Unknown.

Operculars: The large operculum sends a wedge-shaped projection into the about equal-sized suboperculum. A small concavity on the anterior half of the lower edge of the suboperculum provides for the presences of a small branchiostegal (called by Brough a modified branchiostegal or incipient interoperculum). It has been shown that this is an ordinary branchiostegal.

Hyoid arch: Unknown.

Taxonomy: Brough erected this family and Lehman raised it to ordinal status.

Relationships: The presence of about 13 branchiostegals suggests origin from the Pholidopleuriformes or Palaeonisciformes.

References: Brough (1939), Lehman (1958).

† ORDER CHONDROSTEIFORMES

Branchiostegals about 9-12, spathiform; gulars absent; operculum and suboperculum present; interoperculum absent. Lower Jurassic. Two families.

† Chondrosteidae

Pl. IV

Branchiostegals: 9-10 in *Chondrosteus acipenseroides*, about 12 in *C. lindenburgi*; the uppermost is slightly enlarged and the upper 6 and suboperculum are serrate basally on the ventral edge.

Gulars: Gulars absent. A pair of small curved plates above the anterior end of the ceratohyal, are believed to be lateral gulars by Watson (1925), but appear to the author more likely to be hypohyals.

Operculars: Operculum considerably smaller than the subopercular and shaped like an inverted comma. Suboperculum large and subquadrate and serrate on the anterior ventral corner.

Hyoid arch: The "anterior branchiostegal" of Watson appears to be a hypohyal. An ordinary medium sized hourglass ceratohyal is present. The remains of an interhyal is suggested in some figures (Woodward, Watson). It was perhaps unossified.

Relationships: Discussions under the Acipenseriformes show that Chondrosteidae cannot be closely related or immediately ancestral to the Acipenseriformes.

From the point of view of the number and form of the branchiostegals the Chondrosteidae could have developed from the Palaeonisciformes, the

Perleidiformes, the Ptycholepiformes, or the Platysiagiformes. But the dorsal and anal fin rays equal the basals in the Perleidiformes, Platysiagiformes and Ptycholepiformes and the caudal is symmetrical or nearly symmetrical in Pholidopleuriformes. The latter groups are thus excluded from the ancestry of Chondrosteidae, leaving the Palaeonisciformes. Because of the number of branchiostegals, origin is most likely from the suborder Palaeoniscoidei. This conclusion is in agreement with Watson (1925) who states ... "it shows in its skull structure clear evidence of Palaeoniscid origin."

Lehman (1958) isolates the Chondrosteidae in their own order. This separation may be justified by the lack of a preoperculum in the Chondrosteidae.

References: Woodward (1895), Hennig (1925), Watson (1925).

† Errolichthyidae

Branchiostegals: Four elongate spathiform branchiostegals are known. There may have been more. The distal half of the branchiostegals is divided by three or four grooves - a character unique in teleostomes.

Gulars: Not known.

Operculars: A large operculum and suboperculum are known. These bear grooves on their posterior half similar to those on the branchiostegals. Interoperculum absent.

Hyoid arch: Unknown.

Relationships: The exact phylogenetic position of this family is uncertain. The absence of an interoperculum indicates its placement in the chondrostean fishes (Group I). The discussion under Acipenseriformes demonstrates that it is not closely related or ancestral to that group. Lehman (1952) is followed in placing the Errolichthyidae in the Chondrosteiformes.

† ORDER SAURICHTHYIFORMES

Branchiostegals about 1-3; gulars absent; large semicircular operculum; suboperculum and interoperculum absent. Lower Triassic to Lower Jurassic. A single family.

† Saurichthyidae

Pl. IV

Branchiostegals: One long slender lanceolate branchiostegal in *Saurichthys ornatus*. About three long wide branchiostegals questionably figured for *S. madagascarensis*; in this species they are indicated as being at an angle of about 45° to the mandible, unlike *S. ornatus* where the single branchiostegal is parallel to the mandible.

Gular: Absent.

Operculars: Operculum large and semicircular in *Saurichthys*, smaller in the Lower Jurassic species. Suboperculum absent (or may be incorporated into the operculum).

Hyoid arch: A short curved hypohyal and a very long slender ceratohyal with the middle slightly constricted, are known to be present.

Relationships: The branchiostegal form in S. madagascarensis is uncertain. That of S. ornatus is unlike that of any other chondrostean in its extremely elongate form. From the number of branchiostegals it is unlikely that the Saurichthyiformes are related to the Dorypteriformes, Bobasatraniiformes, Redfieldiiformes or Haplolepiformes. Stensio (1925) indicated that many osteological characters and sensory canal characteristics indicate a close relationship to the Acipenseriformes and concludes they are intermediate between the Palaeonisciformes and the Acipenseriformes. However, the Saurichthyiformes, lacking a suboperculum, cannot have given rise to Acipenseriformes which possesses one. Further the supraorbital canal of Saurichthyiformes ends on the frontal while in Acipenser it joins the infraorbital canal. Thus the Saurichthyiformes cannot be immediately ancestral to the Acipenseriformes and the long rostra may be a parallelism.

References: Stensio (1925), (1932), Lehman (1952), (1958), Berg (1947), Griffith (1962).

ORDER ACIPENSERIFORMES

One branchiostegal; operculum deeply engraved or incised; suboperculum present or absent; interoperculum absent; gulars absent; interhyal, ceratohyal and a hypohyal present. Upper Cretaceous to present. Two families.

Several authors, Traquair (1887), Watson (1925), Aldinger (1937), Stensio (1932) and Lehman (1952), (1958) have forwarded views that Chondrosteidae are intermediate between the palaeoniscoids and sturgeons or that they were ancestral to sturgeons. Wilimovsky (1956) on the other hand expressed doubt that the unarmoured Chondrosteidae were ancestral to the armoured Acipenseridae. There are further difficulties to supposing that Chondrosteidae were ancestral, since they lack a suboperculum, clavicle, preoperculum and ribs, all of which are found in Acipenseridae. The caudal is symmetrical in Chondrosteidae, heterocercal in Acipenseriformes. The supraorbital canal according to Traquair's figures of Chondrosteidae ends on the parietal while in the Acipenseriformes it joins the infraorbital canal (MacAlpin, 1947). Thus it seems doubtful that the Chondrosteidae were ancestral to the Acipenseriformes (although it is possible, though not likely, that they had a common ancestor not in the distant past).

Lehman (1952) described a new fossil fish, Errolichthys which he placed in a separate family in association with Chondrosteidae and Acipenseridae, while (1958) he stated that it was a representative of an order having characters in common with the Chondrosteidae and Palaeoniscidae. However, like Chondrosteidae the supraorbital canal fails to join the infraorbital canal and so cannot be close to the Acipenseriformes.

The only chondrosteans in which the infraorbital and supraorbital canals unite are the Redfieldiiformes. The large eyes, short snout, terminal mouth, developed teeth of the Redfieldiiformes differ from Acipenseriformes. The Phanerorhynchiformes considerably resemble the Acipenseriformes in their long snout, mouth and rows of scutes but are too specialized in their fins to have been ancestral. However, it is possible that a less specialized ancestor of either of these two orders gave rise to the Acipenseriformes.

Finally the presence of an operculum, suboperculum, interhyal and hypohyal argue strongly against Severtzoff's association of the Acipenseriformes with the Selachii. These bones are not known in the Selachii (although *Pleurocanthus* has a hypohyal), but are found in the Teleostomi. As ably pointed out in Stensio's (1932) critique of Severtzoff, the "selachian" characters of Acipenseriformes such as the heterocercal tail and spiracle are primitive characters also shared by generalized Actinopterygii.

Acipenseridae

Pl. IV

Branchiostegals: Most previous authors have stated that branchiostegals are absent. However, examination of a specimen of *Acipenser fulvescens* shows a chevron-shaped bone exposed below the operculum. It is stubby but definitely a branchiostegal. Dissection reveals a plate of slightly larger extent which sends a slight dorsal flange up under the suboperculum, which is completely skin-covered in this species. Holmgren and Stensio (1936) describe and figure the branchiostegal and suboperculum as being at least partly exposed in *Acipenser sturio*. The chevron-shaped branchiostegal of *Acipenser* is quite reminiscent of the forked branchiostegal found in Polyodontidae. The branchiostegal appears to seat on the interhyal.

Gulars: Absent.

Operculars: A large grooved circular operculum with an anterior projection, partly skin covered, is found. Below this is a small, narrow, cartilage, the suboperculum. Its dorsal end underlies the operculum. There has been debate as to whether the large upper bone was an operculum or suboperculum. But the discovery by Holmgren and Stensio (1936), of a lower gill cover bone, the suboperculum, clearly identifies the large upper element in Acipenser as an operculum. Gill membranes joined to isthmus.

Hyoid arch: The hyoid arch is unossified. A short hypohyal, a short ceratohyal, round in cross-section, and cylindrical interhyal are found.

Relationships: The extra-ordinal relationships have already been discussed. Although the families Acipenseridae and Polyodontidae are quite ancient, both reaching back to the Upper Cretaceous, the branchiostegal apparatus shows considerable similarity. The deeply grooved operculum of Acipenser is reminiscent of the incised operculum of Polyodon which has degenerated further. The single chevron-shaped branchiostegal of Acipenser is not unlike the lone forked branchiostegal of Polyodon. The hyoid arches of both contain the same elements and are more or less unossified. Acipenser does differ in the possession of small suboperculum. The ceratohyal of Polydon is longer, a point doubtless related to its longer mandible. Despite the similarities there are many profound differences--scales, rostrum etc. which are found in the oldest fossil forms known and subordinal status may be warranted.

Material examined: Acipenser fulvescens, NMC alizarin specimen, Ontario.

Polyodontidae

Pl. IV

Branchiostegals: In Polyodon a single stout branchiostegal which divides distally, after a slight upward bend, into four prongs. MacAlpin (1947) reports three or four branchiostegals in the fossil Palaeosephurus. From his photographic plate of the specimen and his drawing, it would appear that he may have mistaken the distal divisions of the branchiostegal as separate branchiostegals. It is therefore suggested that Palaeosephurus possessed only a single branchiostegal.

Gulars: Absent.

Operculars: A much incised large cartilaginous operculum is known in Polyodon and Palaeosephurus. A suboperculum is absent but by comparison with Acipenser the gill cover bone can safely be identified as an operculum.

Hyoid arch: A short hypohyal, a long ceratohyal and a large quadrate interhyal comprise the hyoid arch. The centre portion of the ceratohyoid is ossified.

Relationships: Discussion of relationships is found under Acipenseridae and the order.

References: MacAlpin (1947), Berg (1947), Gregory (1933), Lehman (1952), Holmgren and Stensio (1932), Holly (1936).

Material examined: Polyodon spathula, UMMZ alcoholic specimen, U. S. A.

GROUP II. HOLOSTEI

With interoperculum (or secondarily lost). Lateral gulars absent. One or two hypohyals (or secondarily lost). Lower Triassic to present.

† ORDER OSPIIFORMES

Branchiostegals 9-12, spathiform; one or two median gulars present, primitively with V-shaped pit line; operculum and suboperculum of about equal size and interoperculum present. Lower to Upper Triassic. A single family.

† Ospiidae (Parasemionotidae, Tungusichthyidae)

Pl. IV

Branchiostegals: Number 9-12. *Watsonulus* 11 with lower short, upper 3 elongate; *Parasemionotus* 12 short and broad; *Stensioenotus* ca. 11; *Ospia* ca. 11; *Jacobulus* 11; *Tungusichthys* 9; *Promecosomina* 10. Branchiostegals with straight or curved edges and spathiform. About 8 of the 10 branchiostegals insert on the ceratohyal, the other 2 presumably on the epihyal.

Gulars: *Watsonulus* has an 8-shaped median gular. In *Parasemionotus* the gular appears to have separated into two portions, a small triangular anterior one and an elongate posterior one slightly notched for reception of the anterior element. The posterior element bears a V-shaped pit line anteriorly; there are irregular traces of this pit line on the gular of *Watsonulus*. The gular of *Jacobulus* also bears a V-shaped pit line, as does the large gular (4/5 of the mandible length) of *Promescosomina*.

Operculars: Operculum and suboperculum about equal-sized. The interoperculum appears for the first time in the Ospiidae. The interoperculum is well illustrated in Lehman's fine (1952) photographs of specimens (pls. 39, 40). Here the shape of the interoperculum is identical to that of the adjacent branchiostegal, both having a downcurving expanded anterior end. The interoperculum differs only in that it is shorter, in that its posterior end is in contact with the front half of the suboperculum, and in that it separates the suboperculum from the jaws. The surface pattern of the interoperculum lacks the concentric pattern of the suboperculum. The form, position and decoration all militate in favor of development of the interoperculum from the uppermost branchiostegal, rather then from fragmentation of an arm of the suboperculum. In Parasemionotus the interoperculum has assumed a more advanced form, being triangular and being more broadly in contact with the suboperculum, thus resembling the interoperculum of the Amiiformes. But its position and form still suggest a branchiostegal origin (pl. 42, Lehman, 1952).

Hyoid arch: In Broughia the elongate ceratohyal expands posteriorly without the usual constriction in the middle; it is connected via the "stylohyal" (= interhyal) directly to the hyomandibular. In Parasemionotous the ceratohyal is much shortened. In Promecosomina it is heavy, non-constricted and trapezoidal; it is in contact with a triangular epihyal.

Taxonomy: Lehman (1952) unites the Ospiidae and Parasemionotidae, an action which the author agrees with. Romer (1955) is followed in including the Tungusichthyidae in the Parasemionotidae. Ospiidae has priority.

Promecosomina was raised to family level out of the Semionotidae by Wade. Westoll (1944) doubtfully placed it in his order Amioidae with the Eugnathidae, Amiidae and Macrosemiidae. Gardiner (1960) believes it deserves a separate family. Lehman (1952) however, believes that its characters conform to those of the Parasemionotidae (=Ospiidae). The author concurs with the latter view; the large gular, the 10-12 branchiostegals, and V-shaped gular pit line of Promecosomina agree closely with the Ospiidae. Although a very large gular plate is also found in the Eugnathidae, they apparently lack the V-shaped pit line on the gular. But it is also possible that it could be associated with the Catervariolidae of the Amiiformes which have such a V-shaped pit line or with the Semionotidae which also have a V-shaped pit line. It is difficult to tell with which family it should be associated as the specimen of Promecosomina is incomplete, but the number of branchiostegals would suggest placement with Ospiidae (9-12) rather than Semionotidae (4-6) or Catervariolidae (6).

Relationships: The V-shaped pit line and fairly numerous branchiostegals (7-12) of the Ospiiformes recall those of the Perleidiformes. The relations of the fin rays to radials, reduction or absence of the clavicle, scales of lepisosteid type but with vestiges of cosmine layer, a single row of ossified dorsal radials, caudal abbreviate-heterocercal, hyomandibular with opercular process and foramen for truncus hyoideomandibularis n. facialis, sensory canals basically paleoniscid, all common to both groups also suggest that the Ospiiformes are derived from the Perleidiformes. Stensio has proposed that this group evolved from

Perleidae or perleid-like Chondrostei. The Parasemionotiformes probably gave rise to the Amiiformes.

References: Lehman (1952), Stensio (1932), Berg (1955), Wade (1935).

ORDER AMIIFORMES (SEMIONOTIFORMES)

Branchiostegals 5 or 6-30; median gular present, with or without V-shaped pit line; lateral gulars absent; operculum, suboperculum and interoperculum present. Lower Triassic to present. Ten families, one living.

The number of branchiostegals, shape of opercular bones and large gular are characters indicating that the Amiiformes were derived from the Ospiiformes or had a common ancestor with them. In the lower Amiiformes (Furidae, Semionotidae, Catervariolidae, Signeuxellidae) the supraorbital canal ends on the parietal as in the Parasemionotiformes. Both Semionotidae and Catervariolidae possess a V-shaped pit line on the gular, as the Ospiiformes. In both groups there is a supramaxillary and the lower jaw is complex; the fins are holostean; postrostrals are absent; the nasals meet on the midline. But in the Ospiiformes a clavicle is lacking and the preoperculum is platelike. It would seem most likely that the Ospiiformes and Amiiformes descended from a common ancestor. Brough (1939) and Gardiner (1960) are also of this opinion.

† Furidae (Caturidae, Eugnathidae)

Pl. V

Branchiostegals: 6-24. *Furo* (=*Eugnathus*) with 6-12; *Euognathus* 8 or 10; *Macrepistius* about 10; *Isopholis* 12; *Megalurus* about 14; *Lophiostomus* 13; *Brachichthys* (=*Heterolepidotus*) 16; *Caturus* 16-30. In *Lophiostomus* about 13 with 3 epihyal and 10 ceratohyal; in Caturus 25 with about 4 epihyal and 21 ceratohyal. The upper branchiostegal (branchioperculum) of Brachichthys and Caturus is expanded. Branchiostegals spathiform, elongate and with curved tips.

Gulars: A large median gular present, apparently lacking a v-shaped pit line. In Furo it almost covers the space between the mandibular rami, in Caturus it is about 1/3 to 5/8 the length of the mandible, in Isophilis it is about ½ the length of the mandible, in Euognathides it is diamond-shaped, 1/3 of the length of the mandible and without a pit line. Said to be small in Brachichthys. Large, about 4/5 of the mandible, in Lophiostomus. Lateral gulars undescribed and presumably absent.

Operculars: Operculum tending to be larger than suboperculum, the border between them straight or curved, not wedge-shaped, (except in Heterolepidotus). Interoperculum present and triangular. The figure of Heterolepidotus (Stensio, 1947) appears to show two interopercula.

Hyoid arch: A small hypohyal, large, deep ceratohyal and a triangular epihyal known in Furo. In Lophiostomus the ceratohyal is angled and at the anterior end is expanded.

Relationships: The range of branchiostegals in this family is quite large. Brachichthys and Caturus with 16-30 have more than the other genera known which have 14 or less. These two genera provide one of the few examples in which the number of branchiostegals have apparently increased. Rayner believed that the Furidae were the most primitive of the holosteans.

References: Arambourg and Bertin (1958), Berg (1955), Brough (1939), Eastman (1914), Gregory (1923), Lehman (1949), Rayner (1941), Romer (1955), Schaeffer (1960), White and Moy-Thomas (1940), Woodward (1895), Woodward (1902-12), Zittel (1887).

† Acentrophoridae

Branchiostegals: 9-10 curved, elongate, spathiform branchiostegals in *Acentrophorus*. The branchiostegals all insert on the ceratohyal.

Gulars: Gulars have not been reported in this group though the bone "x" in fig. 13 of Gill may represent one.

Operculars: Operculum and suboperculum of about equal size; operculum not sending wedge-shaped projection into suboperculum. Interoperculum small, triangular.

Hyoid arch: A hypohyal and a large, elongate, hourglass-shaped ceratohyal are known. The triangular posterior tip of the ceratohyal in Gill's fig. 7 may represent an epihyal.

Relationships: Gill states that correspondence of fins and supports, preoperculum, opercular apparatus and absence of an infra-clavicle place this genus in the Semionotidae (this was before Berg's erection of the Acentrophoridae). The branchiostegal series do not disagree with such an alignment but indicate that the Acentrophoridae are more primitive than the Semionotidae.

References: Berg (1947), Gill (1923).

† Paracentrophoridae

Branchiostegals: 10 spathiform branchiostegals in *Paracentrophorus*.

Gulars: Not reported.

Operculars: Operculum and suboperculum of equal size, the former sending a wedge-shaped projection to the latter. Interoperculum small and triangular.

Relationships: According to Piveteau (1941 in Gardiner, 1960) belongs in Semionotidae, but according to Gardiner deserves its own family.

References: Gardiner (1960).

† Semionotidae

Branchiostegals: In *Lepidotes* (*Lepidotus*) about 6, the uppermost very broad; in *Dapedius* 6 broad; in *Semionotus* at least 4 to 14. A figure of *Lepidotes montelli* shows at least 6 slender branchiostegals attached to the epihyal.

Gulars: Missing in *Lepidotes*. *Dapedius* with a large median gular plate half the length of the mandible and bearing a V-shaped pit line.

Operculars: The operculum larger than the suboperculum and extending into the suboperculum in a curve or a wedge. Interoperculum a primitive triangle, (*Lepidotus*) or a rectangle (*Dapedius*).

Hyoid arch: A triangular hypohyal, an hourglass-shaped ceratohyal and an epihyal in *Lepidotes*. In *Dapedius* epihyal much contracted at proximal end and ceratohyal remarkably short and deep (in association with its short jaws).

Taxonomy: Berg (1947) states the Semionotidae are doubtless a heterogeneous assemblage and separates them from the Acentrophoridae. Romer places Acentrophoridae in Semionotidae.

Relationships: The close similarity of fins, form and skull bones leave little doubt of the very close affinity of *Acentrophorus* to *Lepidotes*. But Berg gives presumably adequate characters to separate them as families: frontals fused or paired; caudal heterocercal or abbreviate heterocercal; pectorals high or low. To these differences may be added the connection of the supraorbital canal with the temporal canal and the form of operculum (in *Acentrophorus* operculum equal to suboperculum and not sending a wedge into it; in *Lepidotus* operculum larger than suboperculum and sending a wedge into it). Geologically *Acentrophorus* is older (Upper Permian) than Semionotidae (Lower Triassic to Lower Cretaceous). Gardiner (1960) derives *Semionotus* and *Acentrophorus* separately from the palaeoniscid fishes, not from the amiiform line. This derivation seems unlikely as it would call for a second parallel development of the interoperculum.

References: Woodward (1895), Romer (1955), Gardiner (1960), Eastman (1914).

† Catervariolidae

Branchiostegals: 6 small, elongate, spathiform branchiostegals in *Catervariolus hornemani*. The uppermost is covered basally by the interoperculum.

Gulars: A large median gular occupies at least half the length of the mandible. A V-shaped pit line, apex posteriormost, is found on the anterior end. A pair of wide lateral gulars, with width occupying about 1/3-½ of the mandible, may be present. Saint-Seine states they are probably present and dots in their outline in his figures. If so, they are the only family of Amiiformes or Group II known to possess lateral gulars.

Operculars: Interoperculum denticulate.

Hyoid arch: A ceratohyal and a large short wide ephihyal are known.

Taxonomy: This family was recently created by Saint-Seine.

Relationships: Saint-Seine placed this family in association with the Amiidae. The V-shaped pit line, number of branchiostegals, supraorbital pit line ending on the parietal all indicate relationship with the Semionotidae, rather than the Amiidae.

References: Saint-Seine (1955), Arambourg and Bertin (1958).

† Signeuxellidae

Branchiostegals: A single elongate curved spathiform branchiostegal is seen in an incompletely preserved specimen; probably there were several.

Gulars: Unknown.

Operculars: A large operculum sends a wedge into the smaller suboperculum. Below is a fairly large triangular primitive interoperculum.

Hyoid arch: Unknown.

Taxonomy: Saint-Seine erected this family in 1955.

Relationships: Other than placing the Signeuxellidae in the holostean stage Saint-Seine was uncertain of the affinities. Dorsal views of the opercular bones in *Signeuxella* look very similar to those in *Catervariolus*. The supraorbital line ceases on the parietal in both genera. These and other characters suggest they may be related.

References: Saint-Seine (1955), Arambourg and Bertin (1958).

† Macrosemiidae

Branchiostegals: 5-6, perhaps to 9 in *Macrosemius rostratus*; these shaped like a scimitar and inserting on the ceratohyal. Four spathiform branchiostegals with rounded tips known in *M. helenae*, the upper inserting on the epihyal, the others on the ceratohyal. About 10 in *Ophiopsis*, at least 7 in *Propterus*.

Gulars: A gular plate has been observed only in *Ophiopsis* and *Eusemius*.

Operculars: Operculum larger than the suboperculum and sending a wedge down into it. Interoperculum fairly large, and triangular.

Hyoid arch: Epihyal, ceratohyal and hypohyal present.

Relationships: The Macrosemiidae were doubtless derived from a semionotid such as *Lepidotus*, as was discussed under that family, although Rayner and Bertin and Arambourg suggest derivation from Eugnathidae (=Furidae). Although the infraorbital and supraorbital canals join in Sinamiidae, Lombardinidae and Amiidae, as well as in Macrosemiidae, Macrosemiidae does not seem closely related to any of these families. Macrosemiidae retains the branch of the supraorbital canal which terminates on the parietal, unlike the other families, a character which would seem to be primitive. The scales are rhomboid and thus more primitive than those in *Amia*. But on the other hand it has fewer branchiostegal rays than *Amia*.

References: Woodward (1895), Arambourg and Bertin (1958), Zittel (1887), Rayner (1941), Eastman (1914).

† Sinamiidae

Branchiostegals: Branchiostegals questionably suggested by dotted lines to number about 14 in restoration figure of Berg (after Stensio).

Gulars: Unknown.

Operculars: Operculum larger than suboperculum and sending a slight wedge into it. Interoperculum a long triangle. The opercular bones much resemble those in *Amia*.

Hyoid arch: Unknown.

Taxonomy: Although Romer (1955) and Arambourg and Bertin (1958) place *Sinamia* in Amiidae, *Sinamia* is here retained in its own family for the reasons given by Berg.

Relationships: The close similarities of Sinamia and Amia leave little doubt that they are related. However, the fused condition of the parietals in Sinamia indicate that Sinamia was not directly ancestral to Amia. Their similarities must thus arise from having a close common ancestor.

References: Berg (1947).

† Lombardinidae

Branchiostegals: Unknown.

Gulars: Unknown.

Operculars: Large vertical rectangular operculum, small, elongate, horizontal suboperculum, small primitive interoperculum.

Hyoid arch: Unknown.

Taxonomy: This family was recently erected by Saint-Seine (1955).

Relationships: Although the form of the opercular bones does not differ greatly from Catervariolidae and Signeuxellidae, the figure seems to indicate juncture of the infraorbital and supraorbital sensory canals, as in the more advanced Amiiformes. The tail is almost heterocercal, the scales rhomboid. Lack of data on the branchiostegals enables little further statement to be made.

References: Saint-Seine (1955), Arambourg and Bertin (1958).

Amiidae

Pl. V

Branchiostegals: In *Amia* 10-13; in †*Megalurus* 11-12. Form elongate and spathiform with curved tips. The branchiostegals all insert on the ceratohyal. The uppermost branchiostegal is dilated and has been termed the branchiosperculum by Hubbs.

Gular: A large median gular is present in *Amia*. Its length is about 2/3 that of the mandibles. It is bereft of a pit line.

Operculars: Operculum larger than the suboperculum and sending a wedge down into it. Interoperculum small, elongate, and triangular.

Hyoid arch: A triangular hypohyal, angulate large ceratohyal, triangular epihyal with a prong inserting on outer ceratohyal and small cylindrical unossified interhyal.

Relationships: As stated under Sinamiidae, the Amiidae probably share a close common ancestor with that family. The ancestral form was probably near to the Furidae, judging by the branchiostegals and median gular plate.

References: Berg (1947), Jordan and Everman (1896), Hubbs (1920), Agassiz (1833-43).

Material examined: *Amia calva*, 11 alizarin specimens, NMC58-192-S, Pt. Pelee, Ontario; 12 alizarin specimens, NMC58-209, Georgian Bay, Ontario; alcoholic specimen, BC59-426, Illinois.

ORDER LEPISOSTEIFORMES (LEPIDOSTEIFORMES)

Branchiostegals 3, spathiform; gulars absent; operculum and sub-operculum present; interoperculum absent. Upper Cretaceous to present. A single family.

Lepisosteidae

Pl. V

Branchiostegals: 3 small spathiform branchiostegals. The upper two are attached to the epihyal, the other to the ceratohyal. The uppermost is broad, the lower two attenuate.

Gulars: Absent.

Taxonomy: The generic name was originally spelled Lepisosteus by Lacepede. This spelling has been incorrectly emended to Lepidosteus by some authors. Arambourg and Bertin (1958) include the Lepisosteidae in the same order as Amia. The many skeletal oddities of Lepisosteidae would, in the authors opinion, justify its ordinal separation.

Relationships: The modifications of the skull of Lepisosteiformes make its placement difficult. Most authors include it in Holostei. The non-platelike form of the preoperculum, rudimentary clavicle, absence of cosmine layer in the scales, maxillary not immovably connected with the preoperculum and dorsal and anal pterygiophores each supporting a single ray, and tail not heterocercal, are characters indicating holostean placement. However, the fin rays are completely segmented and some of the above holostean characters might be modifications resulting from the peculiar jaws. So the question of placement is not entirely settled.

Rayner (1948), from neurocranial study, believes the Lepisosteidae are derivable from the Semionotidae. Gardiner (1960) also considers such an origin likely.

References: Berg (1947), Arambourg and Bertin (1958), Boulenger (1904), Regan (1923), de Beer (1937).

Material examined: *Lepisosteus osseus*, alizarin specimen, NMC60-478-A, Ontario; skeletal specimen, USNM 110191, U. S. A.

Operculars: An operculum and suboperculum of approximately equal size are present, the first sends a wedge into the latter.

The absence of an interoperculum in this presumably holostean fish has caused a number of authors to identify other elements as the interoperculum. The preoperculum has been identified as an interoperculum by Regan (1923). The passage of the preoperculo-mandibular canal through this bone clearly identifies it as the preoperculum however. Holmgren and Stensio (1936) call the small bone above the anterior end of the preoperculum, the interoperculum. However, that this bone develops in this position, lies above the preoperculo-mandibular canal and is far from the epihyal and suboperculum which true interopercula contact. It is therefore probably the quadrato-jugal as suggested by Hammarberg (in Arambourg and Bertin, 1958). The upper branchiostegal has also been identified as the interoperculum (de Beer, 1937). But this element does not lie in the same horizontal fold as the suboperculum, does not lie over the outer face of the epihyal, and does not insert on the suboperculum or jaw, all relationships which make it difficult to identify as an interoperculum. The interoperculum must therefore be considered to have been lost (or was never present in which case Lepidosteiformes should be placed in the Chondrostei). The very anterior jaws and the downward expansion of the preoperculum into the normal position of the interoperculum are both changes which could have lead to the loss of the interoperculum.

Hyoid arch: Consists of a hypohyal, a short ceratohyal round in cross section, and a short epihyal with a small backward projection on which sits the upper branchiostegal. A small cartilage on top of the epihyal may represent the interhyal.

† ORDER ASPIDORHYNCHIFORMES

Branchiostegals 12-13 spathiform; gulars absent; large operculum and small suboperculum present; advanced interoperculum present. Middle Jurassic to Upper Cretaceous. A single family.

† ORDER ASPIDORHYNCHIFORMES

Branchiostegals 12-13 spathiform; gulars absent; large operculum and small suboperculum present; advanced interoperculum present. Middle Jurassic to Upper Cretaceous. A single family.

† Aspidorhynchidae

Pl. V

Branchiostegals: 12-13 elongate spathiform branchiostegals in *Aspidorhychus acutirostris*; several large branchiostegals in *Belonostomus*.

Gulars: Apparently absent.

Operculars: In Aspidorhynchus operculum large, suboperculum small; together forming a hemicircle. Interoperculum completely under the preoperculum; without dorsal projection posteriorly; subrectangular.

Hyoid arch: Ceratohyal very large, epihyal small.

Relationships: The branchiostegals and opercular bones are most similar to those of the Amiiformes, particularly those of the Amiidae. There are two large postorbital bones, fulcra are lacking, and the lower jaw complex is as in Amia. Berg states the sensory canal system on the head is as in adult Amia. Differences in the scales, dorsal fins, rostrums indicate that Amia cannot be directly ancestral to Aspidorhynchus which therefore must have descended from a common ancestor. In this regard Berg points out the parietals are fused in Aspidorhynchus, as in Sinamia and it may be noted that the opercular bones of Aspidorhynchus are more similar to those in Sinamia. Further, the scales of Sinamia are rhombic and supraorbitals are present as in Aspiorhynchus but unlike Amia. It therefore seems that Aspidorhynchus is more closely related to the sinamiid line than to the amiid line. The advanced form of the interoperculum is probably associated with the L-shape of the preoperculum. Gardiner (1960), however, suggests that the Aspidorhynchiformes maybe derived from the Pholidophoriformes; the branchiostegal series do not argue against this.

References: Assman (1906; in Berg, 1947); Woodward (1895); Agassiz (1833-43).

† ORDER PACHYCORMIFORMES

Branchiostegals (6+) 30-50, spathiform; median gular present; lateral gulars appear absent; equal sized operculum and suboperculum; triangular fairly advanced interoperculum present. Upper Triassic to Upper Cretaceous. A single family.

Taxonomy: Following Romer (1955) and Arambourg and Bertin (1958) Protosphyraenidae is synonymized with Pachycormidae. Woodward (1895) said that *Protosphyraenus* differed little from *Hypsocormus* (Pachycormidae). However, contrary to Arambourg and Bertin, the Pachycormidae is not placed in the same order as the Amiidae. In addition to the characters by which Berg distinguished the Pachycormiformes, there are the greatly enlarged lower postorbital and the numerous branchiostegals.

† Pachycormidae

Branchiostegals: In *Pachycormus* 40-50 with about 22 on the epihyal and 20 on the ceratohyal. Figures of *Hypsocormus* show a complement, presumably incomplete, of about 6. Zittel (1887) gives the number for the family as 30-45. Branchiostegals elongate, rectilinear and spathiform.

Gulars: A large median gular about ½ the length of the mandible is found in *Pachycormus*, a smaller oval one in *Hypsocormus*. A gular is present in *Protosphyraena*. Lateral gulars have not been reported.

Operculars: Operculum very large and triangular, suspended vertically by the apex, larger in *Hypsocormus* than in *Pachycormus*. Suboperculum equally large. Interoperculum small triangular and fairly advanced in *Pachycormus*. An interoperculum is not mentioned in *Protosphyraena* or

Hypsocormus nor is it present in figures of the latter. Presumably specimen(s) of *Hypsocormus* are incomplete, as the interoperculum and some branchiostegals appear to be lacking.

Hyoid arch: Epihyal, a broad more or less straight ceratohyal and a hypohyal are known in *Pachycormus*. A longitudinal groove is found on the meeting ends of the ceratohyal and epihyal.

Relationships: It seems likely that the Pachycormiformes arose from the Eugnathidae which also had numerous branchiostegals (up to 24). The large postorbitals of the Eugnathidae also suggest this. Since more branchiostegals are found in Pachycormiformes this provides a second example of the rare phenomena of the branchiostegal number increasing along a phylogenetic sequence; although it might be taken as one example, the branchiostegals increasing in the eugnathid-pachycormid line. In any case where parts are numerous and unspecialized the ability to increase is often retained.

References: Woodward (1895, 1898), Zittel (1887), Lehman (1949).

† ORDER PHOLIDOPHORIFORMES

Branchiostegals 1 (?) 6-18+; narrow gular plate; operculum larger than suboperculum; interoperculum small; opercular bone borders entire; Middle Triassic to Upper Cretaceous. Six families.

† Pholidophoridae

Pl. V

Branchiostegals: 7-10 in Pholidophorus, curved and spathiform. The upper branchiostegal is expanded distally in some species. Woodward (1895) reports at least 17 pairs of branchiostegals in Pholidophorus (?) dubius.

Gulars: A narrow median gular with a median ridge in Pholidophorus bechi. Gulars unknown in other forms.

Operculars: Large triangular operculum with apex ventral; triangular suboperculum with apex dorsal, slightly smaller than operculum. Interoperculum primitive and triangular.

Relationships: The Ospiiformes show some resemblances but differ in the form of the preoperculum and interoperculum. Gardiner (1960) believes the Ospiiformes gave rise to the pholidophorids. A closer resemblance is seen in the Amiiformes such as Semionotidae and Eugnathidae. Although the Macrosemiidae also resemble the Pholidophoridae they are precluded from ancestry by the fusion of the supra- and infraorbital canals which end on the parietal without fusing with the infraorbital canal in the family Pholidophoridae, Pleuropholidae and Majokiidae. The close resemblance of the opercular apparatus, cephalic sensory canals, postorbitals, irregular median line of the paired roofing bones of the skull suggest a eugnathid origin as most likely.

References: Woodward (1895).

† Pleuropholidae

Branchiostegals: At least 2 branchiostegals in Parapleuropholis. These are spathiform, straight, elongate and broaden distally.

Gulars: Unknown and presumably absent in Pleuropholis.

Operculars: Operculum very large and vertically rectangular; suboperculum small. Interoperculum long and advanced, sending a dorsal arm up behind the preoperculum and about on level with the suboperculum.

Relationships: The branchiostegals and operculars are slightly different in form from those in Pholidophoridae. According to Arambourg and Bertin Pleuropholidae are very close to Pholidophoridae. The number of branchiostegals is considerably lower in Pleuropholidae, but it is not certain that the series is incomplete.

References: Arambourg and Bertin (1958).

† Liguellidae

Branchiostegals: In Liguella there is at least one elongate, curved, spathiform branchiostegal which expands distally.

Gulars: Unknown and presumably absent.

Operculars: Large rectangular operculum; small suboperculum. Interoperculum not preserved, but presumably present.

Taxonomy: Family erected by Saint-Seine.

Relationships: From the fragmentary remains preserved little can be said. The branchiostegals are curved, rather than straight as in Pleuropholidae, but in both they expand distally.

References: Saint-Seine (1955), Arambourg and Bertin (1958).

† Majokiidae

Branchiostegals: Not preserved.

Gulars: Not known.

Operculars: Operculum large, quadrate; subopercular small, triangular and denticulate. Interoperculum ending posteriorly in a spine.

Taxonomy: Family erected by Saint-Seine.

Relationships: Fragmentary remains enable little to be said about this group.

References: Saint-Seine (1955), Arambourg and Bertin (1958).

† Oligopleuridae

Branchiostegals: In *Oligopleurus* at least 6 elongate, curved, spathiform branchiostegals distally expanded, in *Oeonoscopus* about 13.

Gulars: Not observed.

Operculars: Opercular large, quadrate; suboperculum small. Lower limb of preoperculum large and obscuring interoperculum, if present.

Hyoid arch: Ceratohyal and epihyal present.

Relationships: The branchiostegals would enable this group to be derived from the Pholidophoridae. It may be noted that the Archaeomaenidae and Oligopleuridae have cycloid scales while the Pleuropholidae, Pholidophoridae, Liguellidae, and Majokiidae have rhombic scales. Berg places this family in Pholidophoriformes. Miss Rayner believes the family slightly off the main Pholidophorus-Leptolepis line of evolution. Bertin and Arambourg place the family in the Leptolepiformes because of the fusion of the infra and supraorbital canals, probable loss of rostrals, and reduction of parietals and premaxilleries. But these two sensory canals do not join in Leptolepidae.

References: Woodward (1895), Rayner (1948), Bertin and Arambourg (1958), Berg (1947), Woodward (1890).

GROUP III. TELEOSTEI

With interoperculum (or secondarily lost). Lateral gulars absent. Two hypohyals (or secondarily one or both lost).

MALACOPTERYGII

Branchiostegals 0-36, one or more often spathiform. Median gular only in primitive clupeiforms. Epihyal and ceratohyal separate (except Siluroidei and Beloniformes). Never spines on opercular bones. Seldom with acanthopterygian pattern of 4 external and 0-4 (5-7) ventral or internal.

The division of teleost fishes into malacopterygian and acanthopterygian on the basis of branchiostegals has recently received support by a study on the retractores arcuiim branchialium by Holstvoogd (1963). Holstvoogd

(1963 and in litt.) reports the malacopterygian groups studied, Clupeiformes, Mormyriformes, Cypriniformes, Notacanthiformes, Anguilliformes (and Polypteriformes) lack the muscle retractores arcus branchialium. On the other hand, the acanthopteryian groups studied possess this muscle: Gadiformes, Gasterosteiformes, Syngnathiformes, Ophidiiformes, Percopsiformes, Cyprinodontiformes, Mugiliformes, Perciformes, Pleuronectiformes, Gobiesociformes, Tetraodontiformes, Mastastembeliformes and Batrachiiformes. The Myctophiformes also possess this muscle; as is discussed later this order may be close to the lineage that gave rise to the acanthopterygians. The Beloniformes also possess this muscle; this is puzzling since they are usually considered malacopterygians. Except for the latter, conclusions from the muscle study and the study of branchiostegals are in complete agreement.

ORDER CLUPEIFORMES

Branchiostegals 2-36, with 0-1 interhyal, $\frac{1}{2}$-12 epihyal, 0-23 ceratohyal and 0-5 hypohyal, with 2-12 external and 0-11 ventral (or rarely internal). Median gular present only in Albuloidei and more primitive suborders. Operculars complete, without spines and usually entire (rarely crenualte). Interhyal, epihyal, ceratohyal and two hypohyals present (except interhyal and one hypohyal absent in Phractolaemidae). Lower Cretaceous to present. Fifteen suborders and 54 families, 15 of which are known only from fossils.

Gosline (1960) divided the Clupeiformes into two divisions, Clupei and Osteoglossi. The Osteoglossi, with the exception of Hiodontidae, are here removed to the Mormyriformes, as discussed under that order.

The Hiodontidae are placed in a new suborder within the Clupeiformes.

Although the Clupeiformes do show some relationship to the Pachycormiformes, there seems little doubt that their closest relationships are to the Pholidophoriformes. Besides the similar branchiostegals, several other characters are shared: two supramaxillaries, lower jaw without prearticular and coronoids, and without independent supraangular. Rayner (1948) considered the two groups very close. Gardiner (1960) was of the belief that the teleosts arose from the Pholidophoriformes.

Some authors have considered that the Elopoidei may belong in the Holostei (Saint-Seine, 1956, Nybelin, 1957), on the basis of such characters as the ethmoid commisure connecting the infraorbital canals and the possession of a gular. However, these characters may be regarded as primitive holdovers. The development of a second hypohyal and of intermuscular bones clearly distinguishes the members of the Clupeiformes from their predecessors. The only alternate solution would be placement of the Lycopteroidei, Leptolepoidei and Elopoidei together in their own order. But this has little merit as the Albuloidei still retain a vestige of a median gular. So rather than establish a poorly defined order on the basis of this receding character it appears preferable to establish an order on the sharply defined grounds of the two new characters.

† SUBORDER LYCOPTEROIDEI

† Lycopteridae

Branchiostegals: At least 6 or 8 to 10 spathiform. In *Lycoptera middendorffi* 10 with 3 epihyal and 7 ceratohyal.

Gular: A median gular present in *Lycoptera*, less than one half length of mandible.

Operculars: Operculum large and rectangular above small suboperculum and with interoperculum.

References: Woodward (1895), Berg (1948a).

† SUBORDER LEPTOLEPOIDEI

† Leptolepidae

Branchiostegals: In *Leptolepis* about 21 with 9 broad and imbricating on the epihyal and about 12 spaced and delicate ones on the ceratohyal.

Gular: *Leptolepis* with a median gular one half the length of the mandible.

Operculars: Complete and entire.

Hyoid arch: Ceratohyal with ordinary hourglass-shape but noteworthy for the extension of a supplementary delicate rod of bone between its extremities on the upper side and for its large central perforation; interhyal, epihyal and one large hypohyal present.

References: Woodward (1895), Berg (1947), (1948), Rayner (1937), Nybelin (1963).

SUBORDER ELOPOIDEI

Branchiostegals at least 16-36 with 5-13 epihyal and 10-23 ceratohyal, about 12 being slightly external and 20-23 being ventral, the upper ones spathiform the lower ones becoming slender. A well developed but narrow median gular 1/3 to ¾ the length of the mandible. Two hypohyals (except Leptolepidae has but one). Operculars complete and entire. Gill membrane separate. Five families, two living.

Jordan, Evermann and Clark (1930) include the elopid families and albulids in separate suborders. Berg (1947) places both in the Suborder Clupeoidei. Gosline (1960) places both in the Suborder Elopoidei (separate from the Clupeoidei) but recognizing two superfamilies, Elopoidae and Albuloidae. It is the author's opinion that Jordan, Evermann and Clark were correct in awarding subordinal status to the two groups. The two groups differ in numerous profound characters. The Albuloidei (Albulidae and Pterothrissidae) differ trenchantly from the Elopoidei (Alopidae and Megalopidae) in the following characters: 1-3 branchiostegals instead of 5-13 on the epihyal; gular plate rudimentary or absent versus well developed; one versus two supramaxillaries; pelvic rays 10-14 instead of 15-17; maxillaries toothless instead of toothed; subterminal instead of terminal or superior mouth; gill rakers tubercle-like instead of long and slender; only two pairs of uroneurals instead of 4; terminal vertebra with no neural arch and with a greatly expanded median crest behind it instead of with a neural arch and a small median crest; 7 hypurals instead of 8-9; one posterminal centrum instead of two (characters from Berg, 1947, Hollister, 1939, Gosline, 1961, Gregory, 1933). These differences show the albuloids are considerably advanced with respect to the elopoids. Ridewood (1904) came to a similar opinion after study of their skulls, "There is no doubt that the Elopidae are the most archaic of existing teleosteans and that the Albulidae are in few respects more highly specialized; but the study of the skull does not show any direct affinity between the two families". Nybelin (1960) although he discovered the rudimentary gular plate in *Albula* felt that "The detection of this plate naturally does not mean that *Albula vulpes* would have a closer relationship to the Elopidae and Megalopidae than what has so far been assumed, for it is clear from other facts *Elops*, *Megalops* and *Albula* all represent evolutionary lineages of their own". The two groups are therefore treated as separate suborders.

Elopidae († Raphiosauridae)

Branchiostegals: Vary from 16 to 36, in †*Laminospondylus transversus* 16 or more; in †*Rhacolepis* about 20; in †*Thrissopater* about 30; in †*Esocelops* at least 15; in †*Spaniodon* at least 15; in †*Osmeroides* 20 with 5 broad ones on the epihyal and 15 on the ceratohyal; in †*Pachyrhizodus* 9-10 on the epihyal; in *Elops* 24-36 with 12 epihyal and 20-23 ceratohyal, the upper 12 being slightly on the lateral face, the remainder on the ventral face of the arch; the upper ones being broad and expanded, the lower narrow and elongate.

Gular: In *Elops* elongate narrow median gular occupying about one third of the mandibles; no pit line apparent on it. In *Esocelops* gular at least $\frac{3}{4}$ of mandible. In *Osmeroides* long and narrow, its length slightly more than $\frac{1}{2}$ mandible.

Operculars: Complete, operculum large, interoperculum triangular and modern.

Hyoid arch: Consists of 2 hypohyals, ceratohyal, epihyal and interhyal in *Elops*.

References: Springer (1957), Woodward (1901), (1902-1912), Ridewood (1904), Fowler (1936), Weber and de Beaufort (1913), Regan (1909).

Material examined: 5 *Elops saurus*, BC55-321, Louisiana, alcoholic; USNM26218, Key West, skeleton.

Megalopidae

Branchiostegals: *Megalops* 23-27 with 13 epihyal and 10-12 ceratohyal. The range of counts in the two species *atlanticus* and *cyprinoides* are identical.

Gular: A narrow elongate diamond-shaped gular without trace of pit line. Its length slightly exceeds half the length of the mandible. Attached by a ligament to the back of the mandibular symphysis.

Operculars: Complete and entire; a narrow suboperculum forming half the posterior border of the gill cover behind the operculum; suboperculum narrow.

Hyoid arch: An interhyal, epihyal, ceratohyal and two hypohyals present.

Relationships: The number and arrangement of the branchiostegals on the hyoid arch is similar to that in *Elops*. The gular is somewhat longer in *Megalops* than *Elops* but other fossil elopids have an equally long if not longer gular. The branchiostegal series therefore do not offer support to retention of the Elopidae and Megalopidae in separate families. Some authors do not separate them.

References: Fowler (1936), Day (1875), Weber and de Beaufort (1913), Ridewood (1904).

Material examined: 1 *Megalops atlanticus*, USNM 179715, British Guiana, skeleton.

† Ganolytidae

Branchiostegals: No data available.

SUBORDER ALBULOIDEI

Branchiostegals (4) 6-16 with 2-3 epihyal and 10-12 ceratohyal, 11 external and 1 ventral. A rudimentary gular present or absent. Operculars complete and entire. Gill membranes separate. Interhyal, epihyal, ceratohyal and two hypohyals present. Two families.

Albulidae

Pl. VI

Branchiostegals: In †*Chanoides* probably about 4; in †*Ancylostylos* probably 6; *Albula* 10-16. *Albula vulpes* observed (10) 11-13 left and 10-11 right with 2 epihyal and 10 ceratohyal, 11 external and 1 ventral.

While (10) 11-13 branchiostegals were found in 14 specimens from the Pacific coast of America (Peru to Mexico), Day (1875), Misra (1953) and Weber and de Beaufort (1913) report 14-16 from India and the Indo-Australian Archipelago. This might suggest two species are involved. In *Albula vulpes* the upper branchiostegals are broadly spathiform becoming narrower ventrally; they are all decurved and have a median external ridge basally. The lowest ones may not contact the ceratohyal but may be free in the membrane.

Gular: Nybelin (1960) discovered the presence of a very slender median gular about ½ the length of the mandible in *Albula vulpes*. It is rudimentary compared to that of the elopoids. In 3 and 6 inch specimens only a threadlike trace was observed. The gular is contained in a gular fold which, curving anteriorly, joins the two mandibles. Its posterior border is crenulate.

Operculars: Opercular bones complete and entire, suboperculum V-shaped.

Hyoid arch: Consists of 2 hypohyals, ceratohyal, epihyal and interhyal.

References: Misra (1953); Weber and de Beaufort (1913); Ridewood (1904); Woodward (1901).

Material examined: 10 specimens of *Albula vulpes*, BC56-160, from Peru one of which was cleared and stained for detailed examination; 3 alcoholic specimens, BC59-687, from Panama, Panama; one alcoholic, BC56-162, from Talara, Peru; one alcoholic, BC60-14, Acapulco, Mexico.

Pterothrissidae

Branchiostegals: In †*Istieus* about 10; in *Pterothrissa gissu* 6.

Gular: *Pterothrissa* lacks a median gular plate.

Operculars: Complete and entire.

Relationships: Differences in the possession of gular plate, dorsal fin, dentition of the maxillary, etc. would certainly warrant their familial separation, although some authors have considered Pterothrissidae a subfamily of Albulidae.

References: Günther (1887), Woodward (1901), Tomiyama and Abe (1958).

Material examined: None.

SUBORDER CLUPEIODEI

Branchiostegals 5-20, with 1-5 epihyal and 0-11 ceratohyal, 2-10 external and 0-11 ventral. Gular absent. Operculars complete and entire. Gill membranes separate. Interhyal, epihyal, ceratohyal and two hypohyals in all families examined. Fourteen families, four of which are known only from fossils.

The branchiostegal rays of Alepocephaloidea tend to be long and slender while at least the upper branchiostegals of Clupeoidea are broad and one or more bears a clupeoid projection. The branchiostegals of Rosauridae are suggestive of the Alepocephaloidea.

Superfamily Alepocephaloidea

Alepocephalidae

Branchiostegals: Vary from 5-9, but 13 in *Leptochilichthys*, all slender and lath-or rod-shaped. In *Alepocephalus* 6, *Anamalopterichthys* 7, *Asquamiceps* 5, *Aleposomus* 6-7, *Bathytroctes* 7-8, *Bellocia* 6, *Conocara* 6, *Ericara* 6, *Grimatotroctes* 7, *Leptoderma* 7, *Leptochilichthys* 13, *Macromastax* 9, *Micrognathus* 7, *Mitchillina* 6, *Narcetes* 8, *Nemabathytroctes* 7, *Photostylus* 6, *Rouleina* 6, *Talismania* 6-8, *Tauredophidium* 8, and *Xenodermichthys* 6-7. *Talismania bifurcata* 7 with 4 epihyal and 3 ceratohyal, 4 external and 3 ventral, slender, elongate and distally slightly laminar.

Operculars: In *Alepocephalus* operculum crenulate, suboperculum and interoperculum entire. In the family the gill membranes separate, sometimes united and free from the isthmus.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals in *Talismania*.

Relationships: *Leptochilichthys* differs quite strongly from other alepocephalids in having 13 branchiostegals instead of 5-9.

References: Weber and de Beaufort (1913), Grey (1958), Fowler (1936), Parr (1937, 1951, 1952), Maul (1948), Beebe (1933), Garman (1899), Tucker (1954), Günther (1887), Misra (1953).

Material examined: *Bathytroctes rostratus*, alcoholic specimen, USNM 137754-9, Philippines; *Talismania bifurcata*, alcoholic specimen, BC62-159, California.

Searsiidae

Branchiostegals: Vary from 4 to 8. In *Persparsia* 7, *Pellisolus* 7, *Holtbyrnia* 7-8, *Searsia* 7-8, *Normichthys* 8, *Mirorictus* 4, *Platytroctes* 5-6, *Sagamichthys* 6, *Maulisia* 7-8, *Mentodus* 7-8, *Barbantus* 7-8.

Relationships: Parr (1951) separated this family from Alepocephalidae. It is very closely related to the Alepocephalidae, being distinguished only by the presence of the shoulder organ. The similarity of the branchiostegal counts would confirm the closeness of their relationship.

References: Parr (1951, 1960), Maul (1954, 1957), Tucker (1954).

Macristiidae

Branchiostegals: Long, slender, curved with about 8-10 in *Macristium*.

Operculars: Complete and entire. Gill membranes free.

Relationships: Regan first placed this fish in the family Scopelidae; later he modified his view making it a distinct family close to the Alepocephalidae. Berg followed the latter view but stated its position was uncertain. Marshall (1961) on the capture of a second young specimen suggested that Macristium was the survivor of the fossil ctenothrissid fishes.

This author is inclined to disagree with the latter opinion. While the number of branchiostegals in the Ctenothrissidae and Macristiidae are about the same, the form of the branchiostegals is not. While the upper two branchiostegals in Ctenothrissidae are broad and spathiform, in Macristiidae all of the branchiostegals on the contrary are narrow. Scales are absent in Macristiidae, present in Ctenothrissidae. As Marshall points out the Macristiidae lack supramaxillaries while there are two well developed ones in the Ctenothrissidae. The number of vertebrae differ by about 20. The similarities in fin pattern and mouth angle may be a result of similarity in habits; they are not strong subordinal characteristics. On the other hand the Macristiidae are similar to the Alepocephalidae in many of the listed characters. Structure of the upper jaw and teeth, the slender branchiostegals, and the absence of scales agree with the Alepocephalidae. In some Alepocephalidae the ventrals are almost thoracic and the dorsal is central in position, thus approaching the Macristiidae.

Material examined: None.

Superfamily Clupeoidea

Dussumieriidae

Pl. VI

Branchiostegals: Vary from 6 to 20. *Spratelloides*, *Jenkinsia* and *Gilchristella* with 6. *Gilchristella* with 2 epihyal and 4 ceratohyal, 4 external and 2 ventral, branchiostegals spathiform with clupeoid projections. *Dussumieria* with 12-20 with 3½ on the epihyal and 8-8½ on the ceratohyal, all on the external surface. *Etrumeus* with 13-15 bearing 4 on the epihyal and 9-10 on the ceratohyal, all on the external surface. †*Histiothrissa* with 15. In *Etrumeus* most of the upper branchiostegals are broad and spathiform and bear an anterior projection at the base.

Operculars: Opercular bones complete and entire. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals in *Etrumeus*, *Dussumiera* and *Gilchristella*. In *Dussumiera* the epihyal possess a foramen and it and the ceratohyal emit small prongs toward one another on their internal face.

Relationships: The more numerous branchiostegals of Dussumieriidae would seem to indicate that it arose off the primitive clupeid stock before the Clupeidae. Chapman (1948a) agrees with this and adds several other characters to confirm this view.

Spratelloides, Jenkinsia and Gilchristella differ from other dussumeriids by having only 6 branchiostegals instead of at least 14 or more. The number of branchiostegals would appear to associate these fish with the Clupeidae rather than the Dussumieriidae. Spratelloides further agrees with the Clupeidae and differs from the Dussumieridae in having two instead of only one supramaxillary. Histiothrissa has too many branchiostegals for the Clupeidae and too many supramaxillaries for the Dussumieriidae; Arambourg (1954) has erected a special subfamily for it in the Clupeidae.

References: Chapman (1948a), Ridewood (1904a), Misra (1953), Munro (1955), Schultz et al (1953), Weber and de Beaufort (1913), Whitehead (1962).

Material examined: Alizarin specimens of Gilchristella aestuarius, from South Africa, NMC62-141; Dussumieria acuta, alizarin specimen, NMC63-71-S, Singapore; Etrumeus teres, alizarin specimen, NMC 63-70-S, Nagasaki, Japan.

Engraulididae

Branchiostegals: Vary from 7-19, with 1-3 epihyal, 8½-11 ceratohyal and 4-10 external and 0-11 ventral. Anchoviella 11-13, Setipinna 11-19, Thrissocles 10-14, Scutengraulis 12-14, Anchoa 10-15, Coila 7-13, Stolephorus 11-13, Engraulis 9-14, Lycothrissa 7-12. In Anchoa compressa 10 with 1 epihyal and 9 ceratohyal, 10 external and one ventral, the uppermost broad and spathiform, the lower becoming narrower, all with a clupeoid projection. Engraulis encrasicholus 10 with 1 epihyal and 9 ceratohyal. Coilia nasus 11 with 2½ epihyal and 8½ ceratohyal. Anchoa *hepsetus* 15 with 3 epihyal, 11 ceratohyal and 1 hypohyal, 4 external and 11 ventral, the upper ones broad and spathiform, all with a clupeoid projection on the base.

Operculars: Opercular bones complete and entire. Gill membranes separate or joined and free from the isthmus.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals in *Anchoa*, *Engraulis*, *Coilia*.

Relationships: The form of the branchiostegals indicates the Engraulididae to be related to the Dussumieriidae.

References: Chapman (1944), Weber and de Beaufort (1913), Chevey (1932), Ridewood (1904a), Day (1875), Smitt (1895), Misra (1953), Inger and Kong (1962).

Material examined: *Anchoa hepsetus*, alizarin specimen, NMC62-73, North Carolina.

† Clupavidae

Branchiostegals: Fig. 1584 of Bertin and Arambourg (1958) shows *Clupavus* bears at least 4 spathiform branchiostegals.

Operculars: Opercular bones complete and entire.

Relationship: According to Bertin and Arambourg may be placed in the neighbourhood of the Dussumieriidae.

References: Bertin and Arambourg (1958).

† Pseudoberycidae

Branchiostegals: Information not available.

Operculars: Operculum and suboperculum entire.

Relationships: Allied to the Clupeidae according to Berg.

References: Woodward (1901), Berg (1947).

† Syllaemidae

Branchiostegals: In †*Syllaemus* there are 10 delicate branchiostegals rays on the ceratohyal.

Operculars: Complete and entire.

Relationship: According to Berg they are allied to the Clupeidae.

References: Woodward (1902-12), Berg (1947).

† Ichthyodectidae

Branchiostegals: No information available.

Relationships: According to Woodward (1901) the vertebral axis, fins and scales are as in *Chirocentrites*.

Chirocentridae

Branchiostegals: Vary from 6-8. *Chirocentrus* with 6-8, with 2-3 on the epihyal and 4-5 on the ceratohyal; the ones on the epihyal being on the external, those on the ceratohyal on the ventral face of the arch; the upper 2-3 spathiform, the lower scythe-shaped. *C. hypsoseloma* with

6 and C. dorab with 8. The uppermost with a clupeoid projection. †Platinx with 6-7, †Chirocentrites with about 20.

Operculars: Complete and entire. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals, ventral side of ceratohyal notched for reception of branchiostegals.

Relationships: The Chirocentridae differ from the Alepocephalidae and Searsiidae by the breadth of the upper branchiostegals which are narrow in the other two families. The fossil Chirocentrites with 20 branchiostegals differs trenchantly from Chirocentrus with only 6-8. In fact it might be suggested that it does not belong in this family. Bertin and Arambourg (1958) have placed Chirocentrites in the family †Ichthyodectidae. This placement cannot be evaluated from the point of view of branchiostegals since branchiostegals are unknown in the Ichthyodectidae.

References: Woodward (1901), Ridewood (1904a), Day (1875), Chevey (1932).

Material examined: Chirocentrus hypsoseloma, alcoholic specimen, BC58-32, from Malaya; Chirocentrus dorab, alcoholic specimen, USNM 47990, from Cochin China.

Dorosomatidae

Branchiostegals: Vary from 5-6. Dorosoma 5-6 with 1 epihyal and 4 ceratohyal, 3 on the external and 2 on the ventral face of the hyoid arch; the upper three branchiostegals broad and scimitar-like the lower two acinaciform. The upper 3 have clupeoid projections at the base.

Nematalosa 6 with 1½ epihyal and 4½ ceratohyal.

Operculars: Opercular bones complete and entire. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals.

Relationships: Relationship to the Clupeidae, Engraulididae and Dussumieridae is clearly shown by the possession of a clupeoid projection at the base of the upper branchiostegals.

References: Day (1875), Ridewood (1904a), Vladykov (1945).

Material examined: *Dorosoma cepedianum*, alizarin specimens, NMC60-521-A, from Lake St. Claire, Canada.

Clupeidae

Pl. VII

Branchiostegals: Vary from 6 to 10 with 1½ - 3 epihyal and 4-8 ceratohyal, 3 external and 4-7 ventral. In *Alosa* 7; *Sardinops* 7 with 1½ epihyal and 5½ ceratohyal; *Opisthonema* with 6, 2 epihyal and 4 ceratohyal; *Clupea harengus pallasii* with 8-9, 2 epihyal, 7-8 ceratohyal, 3 external and 6-7 ventral; *Corica*, *Clupeoides*, *Amblygaster*, *Pellona*, *Opisthopterus*, *Raconda* 6; *Harengula* 5-6; †*Scombroclupea*, †*Diplomystus* with about 10; *Alosa pseudoharengus* 7 with 2 epihyal and 5 ceratohyal, 3 being external and 4 being ventral, the ventral ones being inserted in notches. *Opisthopterus dovi* 6 with 2 epihyal and 4 ceratohyal, 3 external and 3 ventral. In these genera the upper three branchiostegals are usually wide and spathiform, the lower ones being slender. An anterior projection arises from at the base of at least the upper branchiostegal. †*Scombroclupea* according to Woodward's figure does not bear these projections.

Operculars: Opercular bones complete and entire. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals in *Clupea*, and *Hyperlophus*.

References: Ridewood (1904a), Schultz et al (1953), Fowler (1936), Day (1875), Chapman (1944b), Misra (1953), Woodward (1901, 1902-12).

Material examined: *Alosa pseudoharengus*, one alizarin specimen, NMC60-452-A, from Lake Ontario, Canada; *Clupea harengus pallasii*, 4 alizarin specimens, BC60-326, British Columbia, Canada; *Opisthopterus dovi*, alcoholic specimen, BC57-83, Bahia de Petacalco, Mexico.

Denticipitidae

Branchiostegals: 5 in *Denticeps clupeoides* with 1 epihyal and 4 ceratohyal, all external, the uppermost broad mesially, the central 3 slender, the lowest broad, with a clupeoid projection, and bearing denticles along its anterior edge (unlike any other clupeiform). †*Palaeodenticeps* with 4 or 5, the upper 3 spathiform.

Operculars: Complete and entire. In *Denticeps* operculum denticulate, suboperculum small and edentulate, interoperculum elongate and denticulate; gill membranes separate. In *Palaeodenticeps* suboperculum denticulate.

Hyoid arch: In *Denticeps* consists of interhyal, epihyal, ceratohyal and two hypohyals. The lower hypohyal large, the upper small and located between the upper corners of the lower hypohyal and ceratohyal.

Relationships: The keeled ventral scutes on the belly, the connection between the gas bladder and ear, and the clupeoid projection are all characters suggesting clupeoid relationship. The reduction of caudal rays to 16 from the normal clupeoid number of 17 may represent an adaptation to miniaturization.

References: Clausen (1959), Greenwood (1960).

Material examined: *Denticeps clupeoides*, 1 alizarin and 2 alcoholic specimens, uncatalogued NMC specimens from the Upper Yewa on the boundary between Nigeria and Dahomey, received through the kindness of Dr. Clausen; alcoholic specimen, USNM 195992, from Nigeria.

Bathylaconidae

Branchiostegals: 8-9 in *Bathylaco*, broad, curved, scythe-like with bases bearing anterior projections.

Operculars: Complete and entire except for the posterior border of the operculum which is crenulate. Gill membranes separate.

Relationships: Goode and Bean (1896) first placed *Bathylaco* in the Synodontidae of the Iniomi, probably largely on the basis of the elongate jaws and oblique opercular apparatus. Parr (1948) included it in the Isospondyli and regarded it as a possible intermediate between the Isospondyli and the Iniomi. Bertin and Arambourg (1958) placed it in a new suborder, Bathylaconoidei, intermediate between the Stomiatoidei and the Esocoidei.

The broadness of the branchiostegals differentiates the Bathlaconidae from the Myctophiformes and from any stomiatioid or esocoid. The comma-shaped preorbital photophore need not indicate relationship to the Stomiatioidei since a similar photophore has arisen independently in the Myctophiformes. The anterior projections on the bases of the branchiostegals in Parr's figure are suggestive of the clupeids and relatives. Amongst the clupeoids the engraulidids perhaps are the most similar with the narrow elongated tooth jaws, oblique suspensorium, and large anterior eyes. The Bathylaconidae are provisionally placed in the Clupeoidei. However, until specimens of *Bathylaco* are available for osteological study placement will be uncertain.

References: Goode and Bean (1896), Parr (1948), Bertin and Arambourg (1958), Jordan and Evermann (1896).

Material examined: None.

† SUBORDER TSELFATOIDEI

Branchiostegals 13-14, with about 4 epihyal and 9-10 ceratohyal, all apparently on the ventral edge of the hyoid arch. No gulars. Uppermost branchiostegals spathiform, lower ones slender. Operculum and suboperculum present and entire; interoperculum not known. Epihyal and ceratohyal known. A single fossil family.

The family Tselfatidae was found by Arambourg (1954) who placed it in the Beloniformes. Bertin and Arambourg (1958) erected a new suborder, Tselfatoidei, for its reception in the Beloniformes.

Several characters do not support this ordinal placement. The Tselfatidae has too many branched caudal rays (18 instead of 13), too many pelvic rays (7 instead of 6), the dorsal and anal are very long and high instead of small low and posterior, the parasphenoid is toothed, the epihyal and ceratohyal are not sutured together, and the mouth is bordered by both the premaxillary and maxillary. All of these characters preclude its placement in the Beloniformes.

The entrance of the maxillary into the gape would permit placement in Clupeiformes, Notacanthiformes, Mormyriformes, Cypriniformes or Anguilliformes. The numerous caudal rays, normal anterior vertebrae, toothed parasphenoid, presence of a supraorbital, and numerous distally spathiform branchiostegals preclude placement in any of these orders except the Clupeiformes. All of the characters of the Tselfatidae are readily accommodated in the Clupeiformes except the long pedicels of the premaxillaries. The premaxillaries are reported to have long pedicels which would indicate that they are probably protractile, a character normally acanthopterygian. The majority of characters of the Tselfatidae would appear to place them among the primitive Clupeiformes such as Albuloidei, Clupeoidei and Ctenothrissidae.

† Tselfatidae

Branchiostegals: *Tselfatia* with 13-14 slender branchiostegals which become spathiform dorsally. About 4 epihyal and 9-10 ceratohyal, distributed along the ventral edge of the hyoid arch.

Operculars: Operculum and suboperculum entire; interoperculum not known.

Hyoid arch: Only epihyal and ceratohyal known. Epihyal and ceratohyal not sutured together.

References: Arambourg (1954), Bertin and Arambourg (1958).

Material examined: None.

† SUBORDER CTENOTHRISSOIDEI

† Ctenothrissidae

Branchiostegals: Vary from 8 to 10 with 2 or 3 epihyal and 7 ceratohyal in *Ctenothrissa*. The upper branchiostegals are spathiform the lower ones become narrow and acinaciform. The uppermost branchiostegal has anterior projection at the base.

Operculars: Complete and entire.

Relationships: This group was first placed in the berycoids because of its anterior pelvics. Regan and Berg have grouped it close to the clupeoids. The jaw structure, number form and arrangement of the branchiostegals agrees with this grouping. Bertin and Arambourg (1958) have placed the Ctenothrissidae in the Bathyclupeiformes, apparently on superficial agreements in body form and fin arrangement. The author cannot agree with this arrangement. The Bathyclupeidae have fin spines, ventrals with I5 rays, only one supramaxillary, and a perciform number, form and arrangement of the branchiostegals. While on the other hand the Ctenothrissidae lack fin spines, have two well developed supramaxillaries and have malacopterygian branchiostegals. While it is possible that ctenothrissid-like ancestors could have given rise to the bathyclupeids, the two families definitely do not belong in the same order or to the same level of evolution. The Ctenothrissidae may be imagined to have arisen off primitive clupeoid stock, developed a shortened deepened body and with this change more anterior pelvic fins and an enlarged dorsal fin.

References: Woodward (1901, 1902-1912).

† SUBORDER SAURODONTOIDEI

† Saurodontidae

Branchiostegals: No information available.

Operculars: Complete and entire.

References: Newton (1878).

SUBORDER HIODONTOIDEI, New Suborder

Branchiostegals 7-10, with 2-2½ epihyal and 6-7 ceratohyal, 4-5 on the external and 4-5 on the ventral face of the hyoid arch. No gulars. Uppermost branchiostegals spathiform. Opercular bones complete and entire. Gill membranes separate. Two hypohyals. One living family.

Regan (1929) placed the Hiodontidae in a superfamily with the Notopteridae, with which it bears a superficial resemblance. Berg (1947) followed Regan but raised the superfamily to a suborder. Gosline (1960) placed the superfamilies Hiodontoidae, Notopteroidae and Osteoglossoidae all in his division Osteoglossi of the Clupeiformes. However, the Hiodontidae would seem to be well separated from these groups, as it is distinguished from them by the following trenchant characteristics: possession of two hypohyals instead of one; upper branchiostegals spathiform instead of acinaciform or virgaform; 8 hypurals instead of 4 or fewer; nasals small instead of large. All of these characters combine to show that the Hiodontidae is distinct from the notopterid-osteoglossid group, and is much more primitive. Its origin appears to lie with the albuloids or clupeoids. As in some clupeoids a duct from the gas bladder contacts the inner ear. It differs from clupeoids and albuloids however, in lacking oviducts, in having the parapophyses coosified with the centra, and 16 branched caudal rays. These characters justify its subordinal separation.[1]

Hiodontidae (Hyodontidae)

Pl. VII

Branchiostegals: Vary from 7-10 in *Hiodon* (including *Amphiodon*). In *Hiodon tergisus* 8-9 with 2 epihyal and 6-7 ceratohyal, 4 on the external and 4-5 on the ventral surface of the hyoid arch, the uppermost 2-3 branchiostegals spathiform and expand distally. In *Hiodon alosoides* 7-10, usually 9 with 2½ epihyal and 6½ ceratohyal, 5 on the external and 4 on the ventral face of the hyoid arch.

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[1] A pertinent paper has just been received in final typing, Greenwood (1963). He raises Gosline's Osteoglossi to ordinal level. The author agrees with the separation of the Osteoglossi (except Hiodontidae) from the Clupeiformes. But this author feels the Osteoglossi are sufficiently close to the Mormyriformes to be included in them, thus a new order is not necessitated. The Hiodontidae have numerous primitive characters which are lacking in the Mormyriformes (as here construed) but which may be found in the Clupeiformes that it is clear they should be placed with the latter: 2 hypohyals, spathiform branchiostegals, gular fold, 8 hypurals, 3-4 uroneurals, adipose eyelid, postterminal centra, etc. Similarities of the Hiodontidae to the Notopteridae may either represent parallelisms or be evidence of distant common ancestry.

Operculars: Complete and entire. Gill membranes separate, with gular fold.

Hyoid arch: Interhyal, epihyal, ceratohyal and two epihyals in *Hiodon tergisus*.

References: Ridewood (1904), (1905b), Jordan and Evermann (1896), Boulenger (1904).

Material examined: *Hiodon tergisus*, alizarin specimen, BC58-164 from Lake Winnipeg, Manitoba; specimen BC60-250 from Lake Winnipeg, Manitoba; two alizarin specimens, NMC59-334 from Lac St. Pierre, Quebec. *Hiodon alosoides*, 1 alizarin and 10 alcoholic specimens from Saskatchewan River, Manitoba.

SUBORDER GONORHYNCHOIDEI

Branchiostegals 4-5, with 4 epihyal and 0-1 ceratohyal, all external, the upper 2 spathiform. Opercular bones complete and entire. Gill membranes broadly joined to isthmus. Two hypurals. A single family.

Gosline (1960) united Berg's suborder Chanoidei, Phractolaemoidei, and Cromerioidei with the Gonorhynchoidei. At the same time he appeared uncertain that these groups belong together, "These five groups are so widely different that any relationship between them is difficult to comprehend. Yet the following similarities may be marshalled". He then lists gill membranes always attached to isthmus (yet in *Chanos* they are united and free), the mouth small and toothless or nearly so, supramaxillaries absent, the preopercular border free only below (*Chanos*), if at all, and several other characters. In his key he characterizes the suborder as having 3-4 branchiostegals, however, Gonorhynchidae have 4-5.

This author agrees with Gosline that the Phractolaemidae, Kneriidae and Cromeriidae belong in the same suborder. These families share 3 branchiostegals, about 5-9 pelvic rays, 34-45 vertebrae, absence of axillary appendages, absence of pharyngeal teeth, gill opening restricted, scales cycloid or absent, presence of a gas bladder, a similar caudal skeleton (Gosline) and are all small African freshwater fishes. The Chanidae share with these 45 vertebrae, absence of pharyngeal teeth, cycloid scales, a gas bladder, a similar caudal skeleton (Gosline), but they differ in having 4 branchiostegals, 11-12 pelvic rays, having axillary appendages, caudal fin flaps, gill membranes united and free from the isthmus and being Indo-Pacific in distribution. These differences are not too trenchant. Further, Audenaerde (1961) in his osteological study of Phractolaemus states that numerous osteological and anatomical characters suggest a close relationship of Phractolaemus and Chanos.

Gonorhynchidae shares only these characters: pharyngeal teeth absent, gill membranes joined to isthmus (but opening not restricted). It differs in having 10 pelvic rays, 54-56 vertebrae, possession of axillary appendages, ciliated scales, gas bladder absent, a different caudal skeleton (Gosline) as well as in peculiar characters such as a median rostral barbel, tongue-like and fringed flap-like structures on the roof of the mouth, rounded basi-branchial teeth, posterior side of fourth gill and back of branchial cavity papillose, peritoneum black, thick lips, a pseudo-occipital condyle (Gregory, 1933), and others. It dwells in the Indo-Pacific. The characters shared with Chanidae are a high number of pelvic rays, axillary appendages and number of branchiostegal rays (4 in Chanidae, 4-5 in Gonorhynchidae). But while the branchiostegal ray number is similar, as noted by Gosline, they differ in arrangement and form. In Gonorhynchidae there are 4 on the epihyal, in Chanidae only 2. Those in Gonorhynchidae lack clupeoid projections, while those of Chanidae possess clupeoid projections. The gill membranes differ and they differ in the peculiar characters listed above.

It is concluded that Phractolaemidae, Kneriidae, Chanidae and Cromeriidae belong in one suborder, the Gonorhynchidae require a separate suborder.

Gosline (1960) stated that the caudal skeleton of Gonorhynchus bore considerable resemblance to that of Dussumieria. The dussumieriids and alepocephalids are the only clupeoids with as many as 4 branchiostegals on the epihyal like Gonorhynchus. The albuloids would also form a possible ancestor in the last respect, and somewhat resemble Gonorhynchus in dentition.

Gonorhynchidae

Pl. VII

Branchiostegals: Vary from 4-5 in Gonorhynchus. The upper two branchiostegals broaden distally into a lamina and are more or less straight. A ridge strengthens each of the branchiostegals. 4 branchiostegals on the epihyal and 0-1 on the ceratohyal, all on the external face of the arch.

Operculars: Complete and entire. The operculum extends in a wedge down into the suboperculum. The suboperculum extends more than half way up the posterior border of the operculum. Gill openings wide, membranes attached to isthmus.

Hyoid arch: Consists of large interhyal, epihyal, ceratohyal and two hypohyals.

References: Hubbs (1920), Ridewood (1905a).

Material examined: Gonorhynchus gonorhynchus, alcoholic specimen, USNM 59920 from New South Wales, Australia; G. gonorhynchus, alcoholic specimen, BC56-278 from New Zealand; G. gonorhynchus, alizarin specimen, NMC62-140, from South Africa.

SUBORDER CHANOIDEI

Branchiostegals 3-4 with 2 epihyal and 2 ceratohyal, all external, spathiform, with clupeoid projections at least in Chanidae. Gular absent. Opercular bones complete and entire. Gill opening restricted or gill membrane united and free from isthmus (Chanidae). Two hypohyals (Chanidae) or one (Phractolaemidae). Four families.

The relationships of this suborder are discussed under the Gonorhynchoidei. This suborder appears to be distinguished by the absence of an interhyal. But this is not yet verified in the Kneriidae or Cromeriidae.

Chanidae

Pl. VI

Branchiostegals: In Chanos 4 branchiostegals on each side, all broad and spathiform but lower three tapering, bases broad with anterior clupeoid projection, 2 on epihyal, 2 on ceratohyal, all on external face of hyoid arch.

Operculars: Complete and entire. A straight border between the operculum and suboperculum. Gill membranes united and free from isthmus.

Hyoid arch: Consists of epihyal, ceratohyal and two hypohyals. Interhyal absent, epihyal connected to hyomandibular via ligament.

Relationships: The anterior projection on the base of the branchiostegal is similar to that in the clupeoids. The reflexed basicranium of Chanos is much like that of the Dussumieridae.

References: Hubbs (1920), Day (1875), Jordan and Evermann (1896), Weber and de Beaufort (1913), Ridewood (1904a).

Material examined: Chanos chanos, alizarin specimen, BC60-25, Mexico.

Kneriidae

Branchiostegals: In Kneria 3 branchiostegal rays.

Operculars: Complete and entire. Operculum rounded posteriorly, suboperculum wedge-shaped, interoperculum elongate and expanded up around posterior border of preoperculum. Gill opening restricted to small lateral slit.

References: Giltay (1934a), Hubbs (1920), Berg (1947).

Material examined: None.

Phractolaemidae

Branchiostegals: 3 slender in Phractolaemus.

Operculars: Complete and entire. The lower limb of the preoperculum is much expanded and covers the elongate interoperculum, operculum oval, suboperculum wedge-shaped. Gill opening restricted and reduced to a small slit on the side of the head.

Hyoid arch: Interhyal apparently absent, epihyal, ceratohyal and one hypohyal present.

Relationships: Like Mormyriformes this family has only one hypohyal. However, the opercular and caudal skeleton differ strongly indicating the loss of a hypohyal is only a parallelism.

References: Hubbs (1920), Audenaerde (1961), Ridewood (1905), Poll (1957), Boulenger (1904).

Material examined: None.

Cromeriidae

Branchiostegals: 3 curved scimitar-like branchiostegals which terminate in a point, in *Cromeria*.

Operculars: Complete and entire. Operculum an oval, suboperculum a broad wedge, interoperculum elongate broadening posteriorly. Gill opening restricted to a small opening on the lateral surface.

Relationships: The Cromeriidae, Phractolaemidae and Kneriidae are closely related. They share three branchiostegals, a laterally restricted gill opening, a wedge-shaped suboperculum, an elongate interoperculum which broadens posteriorly plus characters previously mentioned. Of the three the Cromeriidae are the most degenerate, having lost the scales, supraorbitals, suprapreopercular, etc.

References: Hubbs (1920), Gregory (1933).

Material examined: None.

SUBORDER STOMIATOIDEI

Branchiostegals 5-24 with 0-1 interhyal, 3-8 epihyal, 4-12 ceratohyal and 0-5 hypohyal, 3-12 external and 0-7 ventral. Gular absent. Opercular bones complete and entire. Gill membranes separate, united and free from isthmus or joined to isthmus. Ceratohyal elongate, except in Sternoptychidae. Two hypohyals. Nine families, one wholly fossil, are placed in the family. Two additional families, one fossil are provisionally included.

The Rosauridae and Protostomiatidae are only provisionally placed in this suborder. Their branchiostegal series do not confirm placement here.

The remaining families share characters with one another and appear to form a natural phylogenetic unit. They are characterized by possession of numerous branchiostegals; by expansion of the upper one or two branchiostegals (except in Idiacanthidae), the remainder being slender; by the branchiostegals usually extending onto the lower hypohyal; by the deep and narrow operculum; by the reduced suboperculum and interoperculum; by the thin and poorly ossified opercular bones; and by the photophores on the branchiostegal membrane.

The high number of branchiostegals, elongate mouth, and deep operculum might lead one to conclude the stomiatoids were derived from the Engraulididae. However, the stomiatoids have a higher number of branchiostegals on the epihyal, making such a derivation unlikely. The high number of epihyal branchiostegals would be commensurate with derivation from the elopoids. This contention is supported by Regan (1923b) who found striking agreement in the skulls of Photichthys and Elops.

The unusual feeding mechanism of Chauliodontidae and Malacosteidae is described and illustrated by Tchernavin (1948), (1953) and Günther and Deckert (1959).

Gonostomatidae (incl. Maurolicidae)

Branchiostegals: Vary from 7-21. In Agyripnus 8-10, Bonapartia 11-16, Cyclothone 10-14; Danaphos 9-10, Diplophos 11-14, Gonostoma 10-14, Ichthyococcus 11-12, Margrethia 13, Maurolicus 9-10, Neophus 7-8, Photichthys 20-21, Pollichthys 11-12, Sonoda 8, Triplophus 11-14, Valencienellus 9-10, Vinciguerria 10-12, Woodsia 17, Yarella 13-16. In Vinciguerria lucetia 12 on both sides, with 4 epihyal, 7 ceratohyal and 1 hypohyal, all external, the upper 2 broad and scimitar-like, the lower ones becoming progressively more rod-like. Photophores occur on the branchiostegal membranes of all genera.

Operculars: Complete and entire. Operculum elongate and vertical, suboperculum and interoperculum reduced to small lamina. Gill openings wide, gill membranes separate.

Hyoid arch: Consists of Vinciguerria of interhyal, epihyal, long ceratohyal and two hypohyals. Arch connected to jaws by a membrane.

Relationships: The maurolicine and related genera, sometimes separated as a distinct family, have 7-10 branchiostegals, while the remainder have 10-21. This would support subfamilial recognition of the two groups.

References: Grey (1960).

Material examined: *Vinciguerria lucetia*, alizarin specimen, NMC61-195, from 900 miles west of Lower California.

Sternoptychidae

Pl. VII

Branchiostegals: Vary from 5 to 11. In *Argyropelecus* 9, *Polyipnus* 9-11, and *Sternoptyx* 5. *Argyropelecus* sp. with 10 branchiostegals, 3 epihyal and 7 ceratohyal, 3 on external and 7 on the ventral face of the arch; the uppermost is a rounded triangle, the next two lathe-like but expanding distally, the remainder rod-like. In *Sternoptyx* the upper branchiostegal is expanded and wing-like. The branchiostegal membranes bear photophores, 6 in *Polyipnus* and *Argyropelecus* and 3 in *Sternoptyx*.

Operculars: Complete and entire. Bones thin, laminar and take little alizarin stain. Opercular narrow and vertical, suboperculum and interoperculum small. Gill membranes free from isthmus or attached, sometimes united and free from isthmus.

Hyoid arch: Interhyal, long epihyal and ceratohyal, and 2 hypohyals present. The ceratohyal is bent in the middle with the apex upwards in *Argyropelecus*. Arch connected to jaws by a membrane.

References: Schultz (1961), Weber and de Beaufort (1913), Fowler (1936), Garman (1899), Jordan and Evermann (1896), Gregory (1933), Misra (1953).

Material examined: *Argyropelecus* sp., alizarin specimen, NMC61-184, from 400 miles off California.

Stomiatidae

Branchiostegals: Vary from 14-19. In *Stomias* 14-19, *Stomioides* 15.

Operculars: Complete and entire, gill membranes separate.

Hyoid arch: A membrane connects the lower jaw with the hyoid arch.

Relationships: Parr (1927) believed that the stomiatids deserved separation from the other two groups of stomiatoids, the gonostomatid group and the melanostomiatid group. This division is not reflected in the branchiostegal series.

References: Parr (1927), (1933), Weber and de Beaufort (1913), Maul (1956a), Regan and Trewavas (1930), Regan (1923).

Material examined: None.

Chauliodontidae

Branchiostegals: Vary from 15 to 21 in the genus *Chauliodus*. In *Chauliodus macouni* 20 branchiostegals with 5 epihyal, 11 ceratohyal and 4 hypohyal, the uppermost expanded, the remainder lathe-like.

Operculars: Complete and entire. Operculum narrow and vertical, suboperculum and interoperculum small. Gill membranes free.

Hyoid arch: Interhyal, long epihyal and ceratohyal, two hypohyals. The hyoid arch and tongue are free from the jaws at the sides, being attached to the symphysis only by an elastic ligament. The resulting freedom enables the jaws to be shot forward and upward, enabling prey to be more readily caught. Tchernavin (1948, 1953) reports on this interesting feeding mechanism.

References: Morrow (1961), Garman (1899).

Material examined: Chauliodus macouni, alizarin specimen, NMC61-192, from 200 miles off Washington.

Astronesthidae

Branchiostegals: In Astronesthes 14-24.

Operculars: Complete and entire.

References: Fowler (1936), Gibbs and Aron (1960), Maul (1956a), Weber and de Beaufort (1913).

Material examined: None.

Malacosteidae

Branchiostegals: Vary from 8-18. In Malacosteus 8 short rod-like branchiostegals; in Aristostomias 18 with one on the interhyal, 5 on the epihyal and 12 on the ceratohyal, the upper two expanded slightly and lath-like, the remainder rod-like. Photophores on the branchiostegal membrane.

Operculars: Complete and entire. Operculum narrow and vertical, interoperculum and suboperculum small and covered by the preoperculum which extends back because of the prolongation of the jaw. Gill membranes separate, not joined to jaws.

Hyoid arch: The hyoid arch is not connected to the front or sides of the mandible except by the long slender protractor hyoidei so that the mandible is completely free, hence the name loosejaws applied to the family. Hyoid arch consists of interhyal, long epihyal and ceratohyal and 2 hypohyals in Aristostomias and Malacosteus.

References: Günther, K. and Deckert (1959), Weber and de Beaufort (1913), Fowler (1936), Regan and Trewavas (1930).

Material examined: Aristostomias scintillans, alizarin specimen, NMC61-182 from 50 miles west southwest of Cape Flattery, Washington.

Melanostomiatidae

Pl. VI

Branchiostegals: Vary from 10-22 with 0-1 interhyal, 3-8 epihyal, 4-10 ceratohyal and 0-5 ceratohyal. In Tactostoma 13 with 5 epihyal, 6 ceratohyal and 2 hypohyal; in Bathophilus flemingi 10 with 3 epihyal, 7 ceratohyal and 0 hypohyal, 3 external and 7 ventral; Bathophilus metallicus 12 with 3 epihyal, 9 ceratohyal and 0 hypohyal; Chirostomias pliopterus 22 with 8 epihyal, 10 ceratohyal, and 4 hypohyal; Leptostomias bermudensis 19 with 6 epihyal, 8 ceratohyal and 5 hypohyal; Echiostoma tanneri 15 with 6 epihyal, 4 ceratohyal and 5 hypohyal; Melanostomias spilorhynchus 13 with 4 epihyal, 5 ceratohyal and 4 hypohyal; Photonectes *dinema* 15 with 5 epihyal, 6½ ceratohyal and 3½ hypohyal; *P. margarita* 13 with 4 epihyal, 7 ceratohyal and 2 hypohyal; *Flagellostomias boureei* 16 with 4 epihyal, 8 ceratohyal and 4 hypohyal; *Grammatostomias flagellibarba* 13 with 5½ epihyal, 6½ ceratohyal and 1 hypohyal; *Eustomias fissibarbis* 16 with 5 epihyal, 8 ceratohyal and 3 hypohyal. In *Bathophilus flemingi* the upper branchiostegal expands into a lamina distally, the rest are lath-like; in *Tactostoma macropus* the upper one is expanded into an elongate triangle, the rest are styliform. In *Flagellostomias* and *Photonectes* the upper branchiostegal was branched, probably as a result of fusion of branchiostegals.

Operculars: Complete and entire. Operculum elongate and vertical, suboperculum and interoperculum small.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals in *Bathophilus*, *Melanostomias*, *Photonectes* and *Tactostoma*. Arch attached to mandibles by membrane.

References: Günther (1887), Parr (1933), Beebe and Crane (1939), Regan and Trewavas (1930).

Material examined: *Bathophilus flemingi*, alizarin specimen, NMC61-80, off northern California; *Tactostoma macropus*, alizarin specimen, NMC61-182, 50 miles west southwest of Cape Flattery, Washington.

Idiacanthidae

Branchiostegals: Vary from 12 to 18 in *Idiacanthus*. In *Idiacanthus fasciola* 17 with 5 epihyal, 7 ceratohyal and 5 hypohyal, all long and slender, the upper most not expanded unlike the preceding stomiatoid families.

Operculars: Complete and entire. Operculum elongate and vertical, others small.

Hyoid arch: Consists of interhyal, long epihyal and ceratohyal and two hypohyals (basihyal of Beebe). Arch attached to mandibles by membrane.

Relationship: According to Beebe, closely related to the Melanostomiatidae. Differs from other stomiatoids in the lack of an expanded upper branchiostegal.

References: Beebe (1934), Garman (1899), Günther (1887), Weber and de Beaufort (1913), Regan and Trewavas (1930).

Material examined: None.

† Tomognathidae

Branchiostegals: At least 7 in *Tomognathus mordax*, the dorsal one spathiform, the remainder slender, with about 4-5 on the epihyal.

Operculars: Complete and entire. Operculum deep and narrow.

Relationship: The deep operculum, only the uppermost of the branchiostegals spathiform, and the high number, 4-5 of the branchiostegals on the epihyal suggest that this family is correctly placed in the Stomiatoidei.

References: Woodward (1902-1912), (1936).

† Protostomidae, *incertae cedis*

Branchiostegals: Vary from 10-24. In *Protostomias* about 24, short, slender branchiostegals; in *Pronotacanthus* 10 slender branchiostegals with 4 epihyal and 6 ceratohyal.

Operculars: Complete and entire in *Prostomias*; the operculum subtriangular with the suboperculum curving up around posteriorly, the interoperculum a small triangle. Operculum not deep and narrow in *Pronotacanthus*.

Hyoid arch: At least a long epihyal and short ceratohyal in *Pronotacanthus*.

Relationships: Arambourg (1954) removed *Pronotacanthus* from the Notacanthidae and placed it in the Stomiatoidei. The operculum and jaw apparatus of *Pronotacanthus* or *Prostomias* does not agree with that in other stomiatoids where the operculum is deep and narrow and the jaws and gape long making the suspensorium vertical. The arrangement of the branchiostegals, terminal mouth and absence of a "spinous" dorsal in *Pronotacanthus* exclude it from the Notacanthiformes.

References: Arambourg (1954), Woodward (1901).

Rosauridae, *incertae cedis*

Branchiostegals: In *Rosaura rotunda* 10 long slender branchiostegals which taper distally; about 4 epihyal and 6 ceratohyal;the uppermost is bent into an S-shape. Known only from a postlarval specimen of 8.4 mm. Branchiostegals extend out behind at right angle to the jaws, the rays continuing beyond the branchiostegal membrane.

Operculars: Entire. Operculum a vertically suspended oval, suboperculum and elongate oval. Interoperculum not yet developed or absent.

Hyoid arch: At this stage consists only of an interhyal and a ceratohyal element which has not yet divided into epihyal and hypohyal.

Relationships: Tucker (1954) considered the Rosauridae was most likely related to the stomiatoids, although its affinities were difficult to trace. Unlike the stomiatoids the branchiostegals in Rosauridae project backwards horizontally, while in the stomatoids they are between the jaws pointing towards the isthmus. Usually the upper branchiostegal of the stomiatoids is enlarged; in Rosauridae it is not enlarged. In these features of the branchiostegals *Rosaura* more resembles the alepocephalids. While the operculum of stomiatoids is elongate, forming most of the gill cover, it is quite reduced in Rosauridae and is no larger than the suboperculum. Because of the juvenile stage of the specimen it is difficult to come to conclusions on the relationships of Rosauridae until more material is obtained. It is hence provisionally left, *incertae cedis*, in the Stomiatoidei.

References: Tucker (1954).

Material examined: None.

† SUBORDER ENCHODONTOIDEI

† Enchodontidae

Branchiostegals: Vary from about 9-16. In *Halec* 9-15; *Enchodus* 12-16; *Eurypholis* about 15 slender attenuate branchiostegals, the upper apparently not spathiform; *Pantopholis* 14 narrow branchiostegals. Gular absent.

Operculars: Complete and entire in *Halec* and *Rharbichthys*, preoperculum obscures interoperculum in *Eurypholis*. In *Eurypholis* the suboperculum forms half, in *Rharbichthys* more than half of the posterior border of the gill cover.

Relationships: Gregory (1933) placed this family in the Iniomi. Berg (1947) includes it in the Clupeiformes. The slenderness of the upper branchiostegals and the great portion of the posterior border of the gill cover taken up by the suboperculum are tendencies towards the iniomous condition. But the failure of the branchiostegals to curve behind the gill cover and the inclusion of the toothed maxillaries in the gape place the Enchodontidae in the Clupeiformes.

References: Woodward (1901), (1902-12), Davis (1887).

SUBORDER SALMONOIDEI

Branchiostegals 2-19 with $\frac{1}{2}$-4 on the epihyal, 0-7 on the ceratohyal, 2-6 on the external and 0-6 on the ventral surface of the hyoid arch. At least the upper branchiostegals spathiform. Gular absent. Opercular bones complete and entire (except operculum crenulate in *Bathylagus*, *Aplochiton*, and some Argentinoidea. Gill membranes separate or sometimes united and free from the isthmus. Two hypohyals present. Ten living families plus one known only from fossils.

The Salmonoidei break down into three natural groups, the anadromous or freshwater Salmonoidea with 7-19 branchiostegals, the litophilus, anadromous or freshwater Osmeroidea with 3-10 branchiostegals and the offshore marine Argentinoidea with 2-6 branchiostegals. The Salmonoidea further have two upturned postterminal vertebral centra while the other two superfamilies have not more than one (Gosline, 1960). The branchiostegals and caudal structure both indicate that the Salmonoidea is the most primitive of the three groups. Further indications are that the Salmonoidea, but not the others, possess an opisthotic and a supramaxilla.

The families here included in the Argentinoidea have been treated as a separate suborder Opisthoproctoidei Chapman (1942, 1948). At the other extreme Hubbs (1953) has suggested synonymizing the Macropinnidae, Dolichopterygidae, Bathylagidae, Microstomidae, Xenophthalmichthyidae, Opisthoproctidae and presumably Winteriidae with the Argentinidae. An intermediate path has been followed here, recognizing the affinities of the groups under a superfamily and yet retaining the distinctions of most of the groups by familial status.

Superfamily Salmonoidea

Following the study of Norden (1961), Thymallidae and Coregonidae are synonymized with Salmonidae.

Salmonidae

Branchiostegals: Vary from 7-19 with 4 epihyal and 7 ceratohyal, 5 external and 6 ventral. In Oncorhynchus 10-20, Salmo 9-12, Salvelinus 8-14. Brachymystax 10-13, Hucho 10-14, Stenodus 8-12, Coregonus 7-10, Prosopium 7-9, Thymallus 8-12. In Salmo clarkii 11 with 4 epihyal and 7 ceratohyal, 5 external and 6 ventral, upper 4 broad and laminar, next 5 broad in the middle but narrowing at the ends, last 2 slender. In Thymallus arcticus 9-10 with 3 epihyal and 6-7 ceratohyal. In a single sample of 50 Oncorhynchus nerka, seven were found with 11 branchiostegals, nineteen with 12 and twenty four with 13.

Operculars: Complete and entire.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals in Salmo, Salvelinus and Thymallus. In Salmo and Thymallus epihyal about 2/3 the length of ceratohyal.

Relationships: It may be stated that the number of branchiostegals does not give support to the recognition of the families Coregonidae and Thymallidae. The subgenus Cristivomer has 12-14 branchiostegals while the subgenus Salvelinus has 9-12. While not giving basis for generic status of Cristivomer, because of overlap, it does again, like other characters, point to the divergence of Cristivomer from the other species of the genus. Norden (1961) considers that the Salmonidae are the most primitive subfamily. The high number of branchiostegals are in agreement with this opinion. The branchiostegal number would favour Oncorhynchus as being a primitive genus in the subfamily but Norden (1961) considers it the most advanced. Branchiostegals indicate Stenodus to be the most primitive of the whitefishes, an indication in accord with its well developed teeth.

References: Clemens and Wilby (1949), Berg (1949), Kimsey and Fisk (1960), Vladykov (1954), Miller (1950), Dymond (1943), Koelz (1929), Holt (1960), Kennedy (1943), Jordan and Evermann (1896), Norden (1961), Rounsefell (1962), Hikita (1962).

Material examined: *Salmo clarkii*, alizarin specimen, BC54-29, British Columbia; *Oncorhynchus nerka*, 50 alcoholic specimens BC61-694, British Columbia; *Salvelinus namaycush*, skeletal specimens, NM62-160-S, Ottawa fish market and NMC60-100 from Northwest Territories.

† Thaumaturidae

Branchiostegals: More than 5 in *Thaumaturus*.

Operculars: Complete and entire.

Hyoid arch: At least ceratohyal and epihyal present.

Relationships: Generally associated with the Salmonidae. The known number of branchiostegals is lower than in the Salmonidae. However, the series may be incomplete. Norden (1961) suggests from the caudal vertebra of *Thaumaturus* that it is allied to Argentinidae or Osmeridae which would agree with the known number of branchiostegals.

References: Voigt (1934).

Superfamily Osmeroidea

Gosline (1960) includes the Osmeridae, Plecoglossidae, Salangidae, Aplochitonidae, Retropinnidae and Galaxiidae in this superfamily. He further separated them into two groups with the first three families below in a northern hemisphere group and the last three families in a southern hemisphere group.

Osmeridae

Pl. VI, VII

Branchiostegals: Vary from 6-10. Hypomesus 6-8, Mallotus 8-10, Osmerus 6-8, Spirinchus 7-8, Allosmerus 6-7 and Thaleichthys 6-8. In Mallotus villosus 9 with 4 epihyal and 5 ceratohyal, 5 external and 4 on internal face of hyoid arch, the uppermost spathiform, the lowest virgaform. In Osmerus eperlanus mordax 7 with 4 epihyal and 3 ceratohyal, 4 on the external and 3 on the ventral face of the hyoid arch, the uppermost broad and spathiform becoming progressively narrow ventrally. In both of these species there is a slight anterior projection at the base of the branchiostegal, reminiscent of the clupeoids. The upper branchiostegal is only slightly curved in the family.

Operculars: Complete and entire. Gill membranes separate.

Hyoid arch: An interhyal, epihyal, ceratohyal and two hypohyals in Thaleichthys, Mallotus and Osmerus. The epihyal large, nearly as long as the ceratohyal in these genera.

References: McAllister (1963), Chapman (1941a).

Material examined: Osmerus eperlanus mordax, alizarin specimen, NMC62-110, Great Lakes, Canada; Mallotus villosus, alizarin specimen, NMC60-47, Yukon, Canada; also material listed in McAllister (1963).

Plecoglossidae

Branchiostegals: 5-6 branchiostegals in *Plecoglossus* with $2\frac{1}{2}$ on the epihyal and $3\frac{1}{2}$ on the ceratohyal, 3 on the external face and 3 on the ventral face of the hyoid arch. The upper three are broad, spathiform and crescentic, the lower three narrow.

Operculars: Complete and entire. Interoperculum small, covered by the ventral arm of the preopercle. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal about $\frac{3}{4}$ length of ceratohyal.

Relationships: The number and arrangement of the branchiostegals agree with the Osmeridae although there are generally more branchiostegals in the Osmeridae. The upper branchiostegal in Osmeridae is only very slightly curved whilst in the Plecoglossidae it is distinctly crescentic. Further, the interoperculum is normally exposed in Osmeridae whereas in the Plecoglossidae it is hidden by the preopercle.

References: Chapman (1941), Okada (1960).

Material examined: None.

Salangidae

Branchiostegals: 4 in *Salangichthys* and in family.

Operculars: Complete and entire, the interoperculum well developed. Gill membranes free from isthmus.

Relationships: In the reduced number of branchiostegals, lack of scales, and neotenous condition the Salangidae differ from the other northern Osmeroidea.

References: Gosline (1960), Okada (1960), Hubbs (1920), Wakiya and Takahasi (1937).

Retropinnidae

Branchiostegals: 5-6 in Retropinna. Upper branchiostegal broad and spathiform.

Operculars: Complete and entire.

References: Stokell (1941).

Material examined: Retropinna osmeroides, 2 alcoholic specimens, BC56-296. Ashley River, New Zealand.

Galaxiidae

Pl. VI, VII

Branchiostegals: Vary from 5-9. Galaxias with 5-9, Neochanna with 6-7. In Galaxias maculatus 5 with 2 epihyal and 3 ceratohyal, 3 on the external and 2 on the ventral face of the hyoid arch, the upper three spathiform. G. attenuatus 8 with 3 on the external face of the epihyal and 5 on the ventral ceratohyal, upper 3 spathiform. In Neochanna apoda 6 with 2 epihyal and 4 ceratohyal, 3 on the external and 3 on the ventral face of the hyoid arch, the upper 3 broad laminar, spathiform, the lower 3 slender. Galaxias indicus with 9. The upper spathiform branchiostegals haspate in form.

Operculars: Entire and complete. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. The epihyal is about one half as long as the ceratohyal.

References: Gregory (1933), Misra (1953), Stokell (1949).

Material examined: *Galaxias maculatus*, alizarin specimen, SU 22679 from Mayne Harbor, Patagonia; *Neochanna apoda*, alizarin specimen, BC56-288 from Wairarapa district, New Zealand, *Galaxias attenuatus*, alizarin specimen, NMC62-244, Hinds River, New Zealand.

Aplochitonidae (Haplochitonidae)

Branchiostegals: Varies from 3-6. In *Aplochiton zebra* 3 with ½ epihyal and 2½ ceratohyal, 2 on external face and 1 on ventral face of the hyoid arch, all broad spathiform, straight; in *Lovettia* 6.

Operculars: Complete and entire except for the border of the operculum which is crenulate in *Aplochiton*.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal about 2/5 of length of ceratohyal.

References: Chapman (1944a), Hubbs (1920), Gosline (1960).

Material examined: None.

Superfamily Argentinoidea

The classification of Cohen (1957) is followed for this group.

Argentinidae (incl. Microstomidae and Xenophthalmichthyidae).

Branchiostegals: Vary from 3-7. In *Argentina* 5-7, *Glossanodon* 4-5, *Nansenia* 3-4, *Microstoma* 3-4, *Xenophthalmichthys* 3. In *Argentina sphyraena* 7 with 2 epihyal and 5 ceratohyal, 3 on the external face and 4 on the ventral edge of the hyoid arch, the upper 3 broadly spathiform, the rest slender. In *Xenophthalmichthys danae*, 3 spathiform branchiostegals on the external face of the arch.

Operculars: Complete in *Argentina*, *Xenophthalmichthys* and *Nansenia*. Opercle and subopercle crenulate in *Nansenia*, entire in the others. Gill membranes separate (Argentininae) or broadly united and free from isthmus (Microstomatinae).

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals in *Argentina*, and *Nansenia*.

Relationships: According to the number of branchiostegals this family, and particularly the Argentininae, would be the most primitive of the superfamily. It is the only family of the superfamily with a postcleithrum and has the most numerous pelvic rays. This would confirm the indication given by the branchiostegals. Cohen (1957) has already stated this position.

References: Cohen (1957, 1958a, 1958b), Chapman (1942, 1942a, 1948), Bertelsen (1958), Jensen (1948), McAllister (1961), Regan (1925a), Bertin and Arambourg (1958).

Material examined: Argentina silus, 4 alcoholic specimens, NMC62-79, southwest of Sable Island, Nova Scotia.

Bathylagidae

Branchiostegals: Constantly number 2. Leuroglossus 2, Bathylagus 2. Two external epihyal; in B. pacificus they are broad, the breadth exceeding 1/3 the length; those in glacialis slender, the breadth less than 1/10 the length. Cohen (1957) indicates Beebe was in error in giving a count of 3-4 for Bathylagus and that he has never seen a single branchiostegal as reported by Hubbs (1920). But Hubbs was not in error, he stated only there was a single large branchiostegal and did not imply there was not a further slender one below.

Operculars: Complete and entire in Bathylagus pacificus and B. glacialis except that there are two slots in the posterior border of the operculum. In pacificus there is a groove which probably represents the point of fusion of the slots noted in glacialis. Gill membranes united and free from the isthmus.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals in Bathylagus. Beebe mislabels the hypohyals as basihyal.

References: Beebe (1933), Chapman (1943), Cohen (1957), (1958c), McAllister (1961), Bolin (1938).

Material examined: Bathylagus milleri, alizarin specimen, NMC61-183, from 100 miles off north end of Vancouver Island, British Columbia.

Opisthoproctidae (Dolichopterygidae, Winteriidae, Macropinnidae)

Branchiostegals: Vary from 2-4. *Rhynchohyalus* 4, *Macropinna* 3, *Dolichopteryx* 2, *Bathylychnops* 2, *Opisthoproctus* 2. In *Macropinna* 3 spathiform branchiostegals on the external surface of the ventral unossified epihyal.

Operculars: Complete and entire in *Macropinna*; interoperculum expanded, broadly displaced anteriorly away from the suboperculum but connected to it by a ligament; gill membranes united and free from isthmus.

Hyoid arch: In *Macropinna* consists of interhyal, epihyal, ceratohyal and two hypohyals. The epihyal is ossified only on its dorsal edge.

Relationships: The branchiostegals of *Dolichopteryx* definitely agree with their placement in the Opisthoproctidae rather than in the Alepocephaloidae (in which group they had been placed).

SUBORDER ESOCOIDEI

Branchiostegals 4-20 with 1-8 epihyal and 3-10 ceratohyal, 3-8 on the external and 1-10 on the ventral face of the arch. Branchiostegals acinaciform to spathiform. Gulars absent. Opercular bones complete and entire. Gill membranes separate. Hyoid arch complete with two hypohyals. Four families, one no longer living.

The number of branchiostegals would indicate the Esocidae (and †Palaeoesocidae) to be more primitive than the Umbridae and Dalliidae. But according to Gosline (1960) the caudal skeleton of *Umbra* seems more primitive than that of *Esox*. Other characters were therefore examined in Chapman (1934) in an attempt to determine which family was most primitive. In checking the characters: number of pelvic rays, caudal rays and actinosts; the presence of a postcleithrum, myodome, inframandibular, suborbitals, nasal, septomaxillary, and basisphenoid; presence of ribs on anterior vertebrae and reduction of the preorbital; the Esocidae were found most primitive, followed by the Umbridae and lastly the Dalliidae. In this case most characters are in agreement with the number of branchiostegals (and not the caudal skeleton) in demonstrating the Esocidae to be more primitive. Dallia on the other hand has one more branchiostegal ray than does the Umbridae, in disagreement with the indications by the other characters. However, the Dallidae and Umbridae are less different from one another than from the Esocidae. In the intermediate range of branchiostegals (7 or over) the difference of only one branchiostegal when there is overlap is not very significant. Further, evolution may act at different rates in different organs, so that while the branchiostegals in the Dalliidae remained in a slightly more primitive condition than in the Umbridae, other characters continued advancement (advance in this case being degeneration). The number of branchiostegals in the Palaeoesocidae is about the same as in the Esocidae. Palaeoesox further agrees with the Esocidae and differs from the Dalliidae and Umbridae in that suborbitals and nasals are present, thus confirming the placement on the basis of the branchiostegals.

The Esocidae and Palaeoesocidae on one hand and the Dalliidae and Umbridae on the other hand are divergent in the number of branchiostegals (10-20 as opposed to 4-8), and in the suborbitals, nasals, inframandibulars, etc. Therefore it seems unwise to place the Palaeoesocidae in the Umbroidea, and they are here placed provisionally in the Esocoidea.

It may be noted that the subopercle in Novumbra and particularly Dallia parallels the condition in the Myctophiformes where it sweeps up behind the operculum forming its posterior border. Similarly the presence of branchiostegals on the internal face of the ceratohyal is an iniomous condition.

The numerous branchiostegals with many on the epihyal and the double hypohyals suggest that the esocoids are descended from the elopoids or primitive clupeoids, perhaps not greatly distant from the stock that gave rise to the stomiatoids. Frost (1926) notes the sagitta of Esox resembles that of Megalops, but is more highly specialized.

Superfamily Esocoidea

Esocidae

Branchiostegals: Varies from 10 to 20 in Esox with 5-8 epihyal and 7-10 ceratohyal, 5-8 on the external face and 7-10 on the internal or ventral face of the hyoid arch. All of the rays are acinaciform. Crossman (1960) presents large samples showing variability within the species.

Operculars: Opercular bones complete and entire, although the posterior edges of the operculum and suboperculum may be weakly crenulate. Opercular-subopercular border straight, suboperculum not extending up behind operculum. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. The epihyal is about 2/3 the length of the ceratohyal. Two small prongs extend towards the hypohyals from the upper anterior end of the ceratohyal.

References: Crossman (1960), Berg (1949).

Material examined: *Esox masquinongy*, alizarin specimen, NMC60-219, Ontario.

† Palaeoesocidae

Branchiostegals: 13 branchiostegals in *Palaeoesox fritzschi* with 6 on the epihyal and 7 on the ceratohyal, 6 being on the external face of the epihyal and 7 on the inner face of the ceratohyal. Branchiostegals acinaciform.

Operculars: Complete and entire. Suboperculum extending diagonally up behind one third of the posterior border of the operculum.

Hyoid arch: At least ceratohyal and epihyal present.

Relationships: In shape, number and distribution of the branchiostegals Palaeoesocidae agree with the Esocidae and differ from the other two families.

References: Voigt (1934).

Material examined: None.

Superfamily Umbroidea

Umbridae

Pl. VI

Branchiostegals: Vary from 4-7. In *Umbra limi* 4-5 with 1 epihyal and 3-4 ceratohyal, 3 external and 1-2 ventral. The upper 2 are crescentic, the lower ones are slender. In *Novumbra hubbsi* 6-7 with 2-3 on the epihyal and 4-5 on the ceratohyal, 4-5 external and 2 ventral.

Operculars: Complete and entire. In *Umbra* suboperculum only extending slightly up the posterior margin of the operculum, in *Novumbra*, extending about half way up the posterior margin. In both the operculum extends wedge-like into the hollow of the boomerang-shaped suboperculum. Gill membranes separate.

Hyoid arch: Interhyal, epihyal, ceratohyal and two hypohyals in *Umbra* and *Novumbra*. In *Umbra* the dorsal edge of the ceratohyal sends two prongs towards the hypohyals, the epihyal is about 2/5 the length of the ceratohyal.

References: Chapman (1934), Dineen and Stokely (1954), Berg (1949).

Material examined: *Umbra limi*, 5 alizarin specimens, NMC60-486-A, from Bruce Co., Ontario; 5 alizarin specimens, NMC62-135 from Ottawa, Ontario; 5 specimens, BC59-199, Silver Lake, Ontario.

Superfamily Dallioidea

Dalliidae

Branchiostegals: Vary from 7-8 in *Dallia*, with 3 epihyal and 5 ceratohyal, 5 on the external and 3 on the internal face of the arch. All acinaciform as in Esocidae.

Operculars: Complete and entire. Suboperculum extends up behind about 4/5 of the posterior border of the operculum. The operculum extends down between the two wings of the suboperculum. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, dumbell-shaped ceratohyal and 2 hypohyals. Dorsal edge of anterior end of the ceratohyal sends 2 prongs towards the hypohyals. The epihyal is about 1/3 the length of the ceratohyal.

References: Berg (1949), Chapman (1934)

Material examined: *Dallia pectoralis*, 2 alizarin specimens, NMC62-244, from tributary to Tokotna River, Alaska.

ORDER MYCTOPHIFORMES (CETUNCULI, MIRIPINNATI)

Branchiostegals 6-26, with 2-9 on the epihyal, 3-14 on the ceratohyal, 0-2 on the hypohyal, slender and attenuate. Gular absent. Two hypohyals, ceratohyal, epihyal and interhyal present. Ceratohyal and epihyal not sutured. Opercular bones complete and entire, never with spines. Gill membranes separate. Upper Cretaceous to present. Seventeen living and 4 fossil families making a total of 21. These are grouped in four sub-orders.

The high number of branchiostegal rays and high number of branchiostegals on the epihyal, the presence of two supramaxillaries, two postterminal centra, two hypohyals, a high number of pelvic rays, the presence of 17 branched caudal rays and 3 epurals in the primitive members of the family indicate that the Myctophiformes must have arisen from an ancestor at least as primitive as the Clupeoidei or (Ctenothrissoidei) and perhaps from the Elopoidei. If the Aulopidae, as stated by some authors, have fulcral scales above the caudal then they must be derived from a group at least as primitive as the Elopoidei. The Myctophiformes thus form a branch, about equivalent and parallel to the Clupeiformes. Certain of the order possess a branchiostegal pattern which is similar to the acanthopterygian pattern (Myctophidae, Neoscopelidae, Alepisauroidei).

Marshall (1955) has arranged the myctophiform fishes in two suborders, the Myctophoidei and the Alepisauroidei. This arrangement agrees fairly well with what is known with the branchiostegal series. It must be admitted that data are lacking for certain of the families, most of which are deepsea forms, rare in collections. However, the following characterizations may be made at the present: Myctophoidei: subopercle and branchiostegals curl up around behind operculum exluding much of its posterior border (except Myctophidae and Neoscopelidae); branchiostegals either all on the ventral or all on the external face of the hyoid arch (except Myctophidae and Neoscopelidae); branchiostegals 7-26. Alepisauroidei: suboperculum and branchiostegals do not curl up around posterior border of operculum, the posterior branchiostegals on the external, the anterior branchiostegals on the internal face of the hyoid arch, branchiostegals 6-9. That a gas bladder, an orbitosphenoid, 2 instead of 1 post-terminal centra may be found in some of the Myctophoidei but not in the Alepisauroidei confirms the indication of the number of branchiostegals that the Myctophoidei are more primitive. The branchiostegals series also confirm the distinctness of the two suborders.

The whalefishes, comprising the three families or subfamilies, the Cetomimidae, Rondeletiidae and Barbourisiidae have been accorded different ordinal placement. Goode and Bean (1896) placed them in the Iniomi (= Myctophiformes), Jordan (1923) in the Cetunculi, Parr (1929, 1945), distributed them among the Xenoberyces (Rondeletiidae) and Iniomi (Cetomimidae, Barbourisiidae), Bertin and Arambourg (1958) in the Stephanoberyciformes, Berg (1947) the Cetomimidae in the Myctophiformes and the Rondeletiidae in the Stephanoberyciformes. Harry (1952) suggested relationship between the whalefishes and the Saccopharyngiformes. There has also been disagreement on the status of the whalefish families, Parr (1929, 1945) and Harry (1952) granting them familial status while Myers (1946) considered Barbourisiidae a subfamily of Cetomimidae. The latest author (Harry, 1952) is followed in according the three groups familial status.

Unequivocal evidence for placement of these families is slight. Cetomimidae and Barbourisiidae possess non-protractile premaxillaries, a condition most common in malacopterygians. The Barbourisiidae further has abdominal pelvics, a condition most common in malacopterygians. The Rondeletiidae also have abdominal pelvic fins. But Parr (1929) implies that rondeletiids have a protractile mouth, an acanthopterygian character. The short length of the ascending process of the premaxilla figured by Parr (1929) certainly does not suggest great protractility. The branchiostegal arrangement of the Rondeletiidae distinctly differs from that of the Beryciformes. In <u>Rondeletia</u> there are four external and four internal branchiostegals with 4 epihyal. This arrangement is typical of alepisauroid Myctophiformes but unknown in the Beryciformes (including Xenoberyces) where 4 external and 4 ventral with 2 (3) epihyal is the typical pattern. Unfortunately information is not available on branchiostegal arrangement of the Cetomimidae and Barbourisiidae. In summary then the abdominal position of the pelvics of the Rondeletiidae and Barbourisiidae, the non-protractile jaws of the Cetomimidae and Barbourisiidae and the branchiostegal pattern of the Rondeletiidae would seem to be characters in harmony with placement in the malacopterygians.

The protractility of the jaws in the Rondeletiidae is the only character in disharmony with this placement. The branchiostegals, bordering of the jaws solely by the premaxillaries, presence of a supramaxillary, and the 14-17 branched caudal rays of the whalefishes associate them with the Myctophiformes, particularly the Alepisauroidei. The whalefishes are here considered as a suborder of the Myctophiformes. (A possibility remains that they are degenerate Beryciformes). The reduction of the Cetunculi to subordinal status in the Berg system of classification requires the coining of a replacement name which is here established as Barbourisioidei, nomen novum.

Bertin and Arambourg (1958) have already reduced the order Miripinnati to subordinal level. Their action is followed here. The curving of the suboperculum and branchiostegals up behind the operculum recalls the myctophoid condition. The relationship of branchiostegals to the hyoid arch, with the lower ones apparently failing to insert on the inner face, resembles the myctophoids rather than the alepisauroids. However, this placement is only provisional. The slightly protrusible jaws (see fig. 12 of Mirapinna of Bertelsen and Marshall) in a microphagus fish suggest they are derived from a form with normally protrusible jaws. The fact that the jugular pelvics are unique amongst living pelagic teleosts suggests that the jugular pelvics were not developed as an adaption to pelagic life, but were retained from an ancestor with jugular pelvics. If these suggestions are valid then the Miripinnati should, judging from their numerous caudal and pelvic rays, absence of fin spines, and numerous branchiostegals be placed among the primitive acanthopterygians near the Ophidiiformes, Ateleopiformes and Gadiformes, with a derivation from a beryciform-like ancestor. They are provisionally left in the present position pending further research.

The families Myctophidae and Neoscopelidae differ from all others in the order in the possession: 2 branchiostegals on the epihyal (all others having (3) 3½-9), of a swim bladder (Bertelsen and Marshall, 1956) and of well developed photophores. In their possession of branchiostegals on the internal face of the hyoid arch and in the failure of the branchiostegals and suboperculum to sweep highly behind the operculum they differ from such myctophoids as Aulopidae, Harpodontidae and Synodontidae and agree with the Alepisauroidei. According to Frost (1926) the myctophid sagitta differs from those of other myctophoids. Their branchiostegal number lies between the Myctophoidei and Alepisauroidei. The three characters of the two families, unique to the order, would seem to require suprafamilial or subordinal recognition. This change is left, however, until the order is compartmentalized as a whole.

SUBORDER MYCTOPHOIDEI

Aulopidae

Branchiostegals: Vary from (9)13-16 with 7-8 epihyal and 6-8 ceratohyal. In *Aulopus japonicus* 13-15 long, slender, acinaciform branchiostegals which turn up around the posterior margin of the gill cover with 7 epihyal and 6-8 ceratohyal. *A. filamentosus* 15 with 8 epihyal and 7 ceratohyal. In †*Sardinoides* about 9.

Operculars: In *Aulopus* the opercular bones are complete and entire. The suboperculum sweeps scimitar-like up around the posterior and dorsal border of the operculum, forming the posterior edge of the gill cover.

In *Sardinoides* the suboperculum excludes most of the posterior border of the operculum.

References: Marshall (1955), Fowler (1936), Mead (1958), Bertelsen and Marshall (1956).

Material examined: *Aulopus japonicus*, alcoholic specimen, USNM 51439, Japan; *Aulopus* sp., alcoholic specimen, U. S. N. M. 135382, northwest Pacific.

† Cheirothrissidae (Chirothrissidae)

Branchiostegals: In †*Cheirothrix* from at least 5 to 9, curved in semicircle up behind gill cover.

Operculars: Complete and entire. Suboperculum curls around behind operculum.

Relationships: The shape and arrangement of the branchiostegals and the suboperculum would place this family in the Myctophoidei.

References: Woodward (1901), Davis (1887).

Chlorophthalmidae

Branchiostegals: Vary from 7-10 with 3-4 epihyal and 4-5 ceratohyal. In *Chlorophthalmus nigripinnis*, *C. chalybeius*, *C. albatrossis*, *C. acutifrons*, and *C. oblongus* 8 with 3½ - 4 epihyal and 4 - 4½ ceratohyal, all along the ventral edge of the arch, or with the upper ones slightly on the external and lower ones slightly on the internal face of the arch. All acinaciform in shape and curl up behind the suboperculum, some reaching the posterior notch in the suboperculum. A figure of 7 is also given for C. nigripinnis with 4 epihyal and 3 ceratohyal. In Chlorophthalmus agassizii 8-10, in C. productus 8 and C. corniger 8. Bathysauropsis gracilis with 8-10 with 3 epihyal and 5 ceratohyal. Branchiostegal counts might suggest that C. agassizii belongs in Bathysauropsis, but Misra and Bertelsen and Marshall give the count for agassizii as 8, so Günther's count of 10 may be in error.

Operculars: Opercular bones complete. Suboperculum large, S-shaped, curving up behind operculum and excluding 2/3 to all of the posterior border of the operculum. A stained specimen of Chlorophthalmus nigripinnis shows the dorsal edge of the operculum to be fimbriate and the dorsal tip of the suboperculum to give off slender threads of bone which reach the dorsal edge of the gill cover. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals in several species of Chlorophthalmus.

References: Okada and Sano (1960), Misra (1953), Garman (1899), Günther (1887), Jordan and Evermann (1896), Weber and de Beaufort (1913), Bertelsen and Marshall (1956).

Material examined: Chlorophthalmus nigripinnis, alizarin specimen, NMC62-245 from New Zealand.

Notosudidae

Branchiostegals: Vary from 9-10 with 4 epihyal and 6 ceratohyal. In *Notosudis argenteus* 10, *Luciosudis* 10, *Scopelosaurus* 9, *Luciosudis* sp. 10 with 4 epihyal and 6 ceratohyal.

Relationships: Marshall (1955) tentatively places *Scopelosaurus* in the Notosudidae.

References: Maul (1954), Weber and de Beaufort (1913), Bertelsen and Marshall (1956).

Material examined: None.

† Dercetidae

Branchiostegals: A few slender branchiostegals according to Woodward. In *Benthesikyme* (*Leptotrachelus*) at least 7.

Operculars: Complete in *Rhycodercetis*, *Benthosikyme*.

Relationships: *Rhynchodercetis* bears considerable resemblance to the nemichthyid-serrivomerid eels.

References: Woodward (1901).

Material examined: None.

Bathypteroidae

Branchiostegals: Vary from 11-14 with 4-5 epihyal and 7-8 ceratohyal. In *Bathypterois* 11-14, in *Benthosaurus* 11. *Bathypterois bigelowi*, *B. regis* and *B. filiferus* 11, 4 on the epihyal and 7 on the ceratohyal. Branchiostegals curve up around behind gill cover. *Bathypterois guentheri*

12 with 4 epihyal and 8 ceratohyal. B. atricolor and B. quadrifilis 12 with 5 epihyal and 7 ceratohyal.

Operculars: Complete. Gill membranes free from isthmus.

References: Mead (1958a), Fowler (1936), Jordan and Evermann (1896), Misra (1953), Günther (1887), Garman (1899), Bertelsen and Marshall (1956).

Material examined: None.

Ipnopidae

Branchiostegals: Vary from 10-17 with 3-4 epihyal and 7 ceratohyal. In Ipnops 10-12, Bathymicrops 11, in Bathytyphlops 15-17. Ipnops murrayi with 10 (other authors 12), 3 on the epihyal and 7 on the ceratohyal. Bathymicrops regis 11 with 4 epihyal and 7 ceratohyal. Ipnops agassizi 10. Branchiostegals swing up more than halfway behind gill cover.

Operculars: In Ipnops complete, suboperculum excludes posterior border of the operculum. Gill membranes separate.

References: Jordan and Evermann (1896), Weber and de Beaufort (1913), Mead (1958a), Garman (1899), Bertelsen and Marshall (1956).

Material examined: Ipnops murrayi, alcoholic specimen, USNM 101371, Gulf of Mexico at 24° N, 84° W.

Harpadontidae

Branchiostegals: Vary from 11-26, with 14 epihyal and 9 ceratohyal. In Harpodon 17-26, in Bathysaurus 11-12. In Harpadon at least, the branchiostegals curve up around behind the gill cover. In *Harpadon nehereus* there are 23 with 14 epihyal and 9 ceratohyal.

Operculars: Complete. Gill membranes separate in both genera.

Hyoid arch: Interhyal, and a long epihyal and ceratohyal present.

Relationships: The marked difference in the number of branchiostegals might suggest *Bathysaurus* is wrongly placed in this family.

References: Marshall (1955), Günther (1887), Jordan and Evermann (1896), Weber and de Beaufort (1913), Alcock (1891), Misra (1953), Bertelsen and Marshall (1956).

Material examined: *Harpadon nehereus*, alcoholic specimen, NMC63-290, Singapore.

Synodontidae

Pl. VIII, IX

Branchiostegals: Vary from 12-18 with 6-8 epihyal and 9-10 ceratohyal, all ventral. In *Synodus* 12-18, in *Trachinocephalus* 16, in *Saurida* 12-16. In *Synodus foetens* 17 with 8 epihyal and 9 ceratohyal, all elongate acinaciform branchiostegals inserting along the ventral edge of the arch and curling up behind the gill cover. In *Synodus scituliceps* 17 with 8 epihyal and 9 ceratohyal, all inserting on the ventral edge of arch and curving up behind the gill cover. In *Synodus lucioceps* 18 with 8 epihyal and 10 ceratohyal, in *Saurida unosquamis* 16 with 6 epihyal and 10 ceratohyal.

Operculars: Complete and entire. In *Synodus* the tip of the suboperculum curves up behind the operculum; gill membranes connected far forward and free from isthmus.

Hyoid arch: Interhyal, epihyal, ceratohyal and two hypohyals in *Synodus*.

References: Weber and de Beaufort (1913), Matsubara and Iwai (1951), Misra (1953), Marshall (1955), Garman (1899), Fowler (1936), Day (1875), Meek and Hildebrand (1923), Jordan and Evermann (1896), Bertelsen and Marshall (1956).

Material examined: *Synodus scituliceps*, alizarin specimen, U. B. C. specimen, Yavaros near Topolobampo, Mexico; *Synodus foetens*, alizarin specimen, from North Carolina, NMC62-73.

Myctophidae

Pl. VIII, IX

Branchiostegals: Vary from 8-10(12) with 2 epihyal, 5-6 ceratohyal and 1-2 hypohyal, 4 external and 5 internal. *Myctophum* 8-12, *Tarletobeania* 8-10(11), *Scopelopsis* 10, *Lampadena* 9-10, *Lampanyctus* 9, *Electrona* 8, *Benthosema* 7, *Dactylopogon* 12. In *Tarletobeania crenularis* 9 with 2 epihyal, 5 ceratohyal, and 2 hypohyal, 4 external and 5 internal; *Diaphus theta* 9 with 2 epihyal, 6 ceratohyal and 1 hypohyal, 4 external and 5 internal. *Electrona antarctica* and *E. carlsbergi* with 2 epihyal and 6 ceratohyal; *Benthosema glaciale* 7 with 2 epihyal, 6 ceratohyal and 1 hypohyal; *Myctophum humbolti* 8 with 2 epihyal, 5 ceratohyal and 1 hypohyal; *Lampanyctus crocodilus* and *Lampadena braueri* 9 with 2 epihyal, 5 ceratohyal and 2 hypohyal; *Lampadena nitida* and *Scopelopsis multipunctata*

10 with 2 epihyal, 6 ceratohyal and 2 hypohyal. Branchiostegals do not curve up around the posterior border of the gill cover, acinaciform. In 50 *Tarletobeania crenularis* ten were found with 8 branchiostegals, thirty four with 9, five with 10 and one with 11.

Operculars: Complete and entire. Suboperculum does not exclude the posterior border of the operculum, although it does angle upward slightly. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals in *Tarletobeania* and *Diaphus*. Photophores are borne by the outer face of the hyoid arch, e.g. in *Myctophum evermanni* 3 with one on the lower epihyal, one on the middle of the ceratohyal and one above the hypohyal.

Relationships: The high number of branchiostegals in †*Dactylopogon* exceeds that of most other myctophids.

References: Bertelsen and Marshall (1956), Fowler (1936), Garman (1899), Woodward (1901), Smitt (1895), Maul (1946), Weber and de Beaufort (1913), Fraser-Brunner (1949).

Material examined: *Tarletobeania taylori*, alizarin specimen, NMC60-308-S, off British Columbia or Washington; *Tarletobeania taylori*, alizarin specimen, BC58-324, off British Columbia or Alaska; 50 alcoholic specimens, BC60-170, off British Columbia; *Diaphus theta*, alizarin specimen, NMC60-308, off British Columbia.

Neoscopelidae

Branchiostegals: Vary from 8-10(11) with 2 epihyal, 4-5 ceratohyal and 0 epihyal. In *Solivomer* 10(11), *Neoscopelus* 8-9, *Scopelengys* 8. In *Solivomer arenidens* 28 specimens with 10 and one with 11 branchiostegals. Bertelsen and Marshall report *Neoscopelus macrolepudotus* 9 with 4 epihyal and 5 ceratohyal and *Scopelengys tristis* 8 with 4 epihyal and 4 ceratohyal. But a specimen of the latter examined by the author had 2 epihyal branchiostegals and 6 ceratohyal, 4 external and 4 internal on both sides. As 2 epihyal were found on both sides of the specimen and as only 2 were found in the closely related family Myctophidae the counts of 4 on the epihyal must be discounted until verified.

Operculars: Complete and entire. Suboperculum only partially excluded posterior border of operculum. Gill membranes separate.

Relationships: Some authors include the Neoscopelidae as a subfamily of the Myctophidae (Fraser-Brunner, Miller). Marshall (1955) is followed in recognizing it as distinct. The Myctophidae examined have branchiostegals on the hypohyal while Neoscopelidae examined do not.

References: Miller (1947), Marshall (1955), Weber and de Beaufort (1913), Misra (1953), Maul (1946), Fraser-Brunner (1949).

Material examined: *Scopelengys tristis*, alcoholic specimen, BC62-150, Baja California, Mexico.

† Ichthyotringidae, new name

Branchiostegals: In *Ichthyotringa* (as *Rhinellus*) Woodward reports 9, Davis 5 acinaciform.

Operculars: In Davis' figure the suboperculum appears to curve up around the posterior edge of the operculum. If this is correct then the Ichthyotringidae are properly placed in the Myctophoidei, but examination of the specimen is necessary to confirm this.

Relationships: The generic name *Rhinellus* Agassiz 1840 proposed for this fish group is preoccupied by the amphibian genus *Rhinellus* Bonaparte 1831 (the latter proposed for *Rhinella* Fitzinger 1826). In 1878 Cope proposed a new name *Ichthyotringa* for a related fossil. Authors (e.g. Romer, 1955 and White and Moy-Thomas, 1941) now consider *Ichthyotringa* Cope congeneric with *Rhinellus* Agassiz. The family name Rhinellidae used for this group must thus be replaced by Ichthyotringidae *nomen novum*, which has as its type-genus *Ichthyotringa* Cope (article 39 of Int. Code Zool. Nomencl.).

The elongate beak-like jaws of this group would appear to distinguish it from all other members of the suborder, indeed of the order. The apparent condition of the suboperculum, as noted above, would favour its inclusion in the Myctophoidei, rather than the Alepisauroidei.

References: Cope (1878), Woodward (1901), Davis (1887).

Material examined: None.

SUBORDER ALEPISAUROIDEI

Scopelarchidae

Branchiostegals: Vary from 6-8, usually 8 with 4 epihyal and 4 ceratohyal. In *Scopelarchus* 8, *Neoscopelarchoides* 8, *Promacheon* 6. *Scopelarchus anale* 8 with 4 on the outer surface of the epihyal and 4 on the internal surface of the ceratohyal. The upper branchiostegal somewhat apart from the others, and slightly expanded. *Scopelarchus guentheri* 8 with 4 epihyal and 4 ceratohyal; *Neoscopelarchoides dubius* and *N. elongatus* 8 with 4 epihyal and 4 ceratohyal.

Operculars: Opercular bones complete and entire in *Scopelarchus* (incl. *Scopelarchoides*). Interoperculum small.

Hyoid arch: Stated to be "normal".

References: Parr (1929), Weber and de Beaufort (1913), Bertelsen and Marshall (1956).

Material examined: None.

Evermannellidae

Branchiostegals: *Evermannella* with 8. *Evermannella indica* and *E. balbo* 8 with 4 on the epihyal and 4 on the ceratohyal.

Operculars: Complete and entire in *Evermannella*; interoperculum small.

Hyoid arch: Stated to be "normal".

References: Parr (1929), Günther (1887), Weber and de Beaufort (1913), Misra (1953), Bertelsen and Marshall (1956).

Material examined: None.

Paralepididae (Sudidae)

Branchiostegals: Vary from 6-9, with 3-4 epihyal and 4-5 ceratohyal. In *Sudis* 7-9, *Paralepis* 7-8, *Notolepis* 6-8, *Lestidium* 6-9, *Macroparalepis* 7-8, *Stemonosudis* 7. *Sudis hyalina* 7 with 3 epihyal and 4 ceratohyal. *Lestidium speciosum* 8 arranged in 3 separate groups: 2 very slender thread-like ones from the posterior corner of the outer epihyal, 2 from the outer surface of border between the epihyal and ceratohyal and 4 from the inner surface of the ceratohyal; *Lestidium intermedium* 6, upper 2 missing. *Lestidium ringens* 8 with 4 on the external surface of the epihyal and 4 on the internal surface of the ceratohyal, with a gap between the second and third, the 4th and fifth, and the fifth and sixth; all acinaciform. *Paralepis coregonoides borealis* and *P. brevis* 7 with 3 epihyal and 4 ceratohyal, all acinaciform. †*Holosteus* about 13.

Operculars: Complete and entire.

Hyoid arch: Interhyal, epihyal, ceratohyal and two hypohyals in *Lestidium ringens*, *Paralepis coregonoides borealis*.

Relationships: The gaps between certain of the branchiostegals appear to be characteristic of this family. †*Holosteus* has more branchiostegals than any other member known in the family, and may not belong in it; it further differs in its edentulous upper jaw. There are certain similarities to the Beloniformes and what is known of the branchiostegals does not disagree with this allocation.

References: Parr (1929), Fowler (1936), Harry (1951, 1953), Jordan and Evermann (1896), Maul (1945, 1962), Misra (1953), Danilchenko (1960).

Material examined: *Lestidium* sp., alcoholic specimen, BC55-36, Montega Bay, Jamaica; *Paralepis coregonoides borealis*, alcoholic specimen, NMC62-147, off Newfoundland; *Lestidium ringens*, alizarin specimen, NMC61-181, off Washington State.

Anotopteridae

Branchiostegals: Vary from 7-9 in *Anotopterus*, with 4 epihyal and 3-5 ceratohyal. Hubbs, Mead and Wilimovsky report 7 rays in six specimens, Abe 8 rays and Bertelsen and Marshall 9 rays. Hubbs et al consider previous counts of 6 to have missed the small anterior ray; with this the author concurs. The five large upper rays are attached to the outer face of the arch, the lower ones to the internal; all are slender and acinaciform.

Operculars: Complete and entire; gill membranes separate.

Hyoid arch: Interhyal, long epihyal and ceratohyal present (hypohyals not examined).

References: Hubbs, Mead and Wilimovsky (1953), Abe (1952), Bertelsen and Marshall (1956), Maul (1946), Kobayashi and Ueno (1956).

Material examined: *Anotopterus pharao*, alcoholic specimen, BC58-403, weathership Stonetown, North Pacific.

Alepisauridae

Branchiostegals: Vary from 7-8 with 4 epihyal and 3-4 ceratohyal. In *Alepisaurus* 7-8. *Alepisaurus aesculapius* 7 with 4 on the outer face of the ceratohyal. A gap exists between the ones on the epihyal and ceratohyal. All acinaciform. In *Alepisaurus ferox* 8 with 4 epihyal and 4 ceratohyal. Counts of 5 are regarded with doubt.

Operculars: Complete and entire.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal about equal in length to ceratohyal.

References: Bertelsen and Marshall (1956), Fowler (1936), Jensen (1948), Jordan and Evermann (1896).

Material examined: *Alepisaurus aesculapius*, skull at University of Columbia.

Omosudidae

Branchiostegals; *Omosudis* with 8. In *Omosudis lowei* 8, with 4 on the outer surface of the epihyal and 4 on the inner surface of the ceratohyal.

Operculars: Complete and entire, reduced in size except the suboperculum. Suboperculum with straight horizontal border between it and the operculum.

Hyoid arch: At least epihyal and ceratohyal present.

References: Parr (1929), Fowler (1936), Günther (1887), Jordan and Evermann (1896), Bertelsen and Marshall (1956).

Material examined: None.

SUBORDER BARBOURISIOIDEI, NEW (ORDER CETUNCULI)

Reasons are given above for not considering this group a distinct order, and for considering its derivation from the Alepisauroidei. Considering the diversity of forms included in the Clupeiformes, inclusion of the Barbourisioidei in the Myctophiformes does not unduly expand its definition. Reduction of the Cetunculi to subordinal status in the Berg system of nomenclature requires the coining of a replacement name. The most primitive, least specialized family is selected. The six instead of five or no pelvic rays, 17 caudal instead of 15 rays, four rather than fewer gills and of spiny skin instead of naked, would seem to indicate that the Barbourisiidae were the most primitive family. On a similar basis the Cetomimidae appear to be the most advanced and degenerate. Following Harry (1952) the three families are provisionally regarded as distinct, although it has been suggested they be reduced to subfamilies.

Barbourisiidae

Branchiostegals: 7 soft branchiostegal rays in Barbourisia rufa. These apparently turn up into the emargination between the operculum and suboperculum. The body, including the branchiostegal membranes, is covered by extremely close-set minute spines giving a velvety touch.

Operculars: Apparently complete and entire. An emargination exists between the operculars and suboperculum. This may be similar to the notch found in the suboperculum of Myctophoidei which gives the suboperculum an S-shape. Gill membranes separate.

References: Parr (1945), Abe and Maruyama (1963).

Material examined: None.

Rondeletiidae

Branchiostegals: In *Rondeletia bicolor* 7-8 with 4 on the outer epihyal and 4 from the inner surface of the ceratohyal.

Operculars: Complete and entire, operculum covering only dorsal edge of wing-shaped suboperculum. Suboperculum extending up behind lower half of operculum and sends a short projection up in front of the lower tip of the operculum. Gill membranes separate.

Hyoid arch: At least interhyal, epihyal and ceratohyal present.

References: Goode and Bean (1896), Parr (1929), Abe and Hotta (1963).

Material examined: None.

Cetomimidae

Branchiostegals: Vary from 8-9. *Ditropichthys storeri* 8, with 4 epihyal and 4 ceratohyal. *Cetostoma regani* 8, *Cetomimus gilli* 9.

Operculars: In *Cetostoma regani* complete and entire, suboperculum extending up under posterior portion of operculum so that the edge of the suboperculum is exposed. Suboperculum thus forming $\frac{3}{4}$ of edge of gill cover. Lower portion of suboperculum under interoperculum. Gill membranes separate.

Hyoid arch: Said to be strongly developed in *Cetostoma*.

References: Parr (1929), Bertelsen and Marshall (1956), Goode and Bean (1896).

Material examined: None.

SUBORDER MIRIPINNATOIDEI

Bertin and Arambourg (1958) reduced the order Miripinnati to a suborder. Their action is provisionally followed here.

Mirapinnidae

Branchiostegals: In *Mirapinna esau* 8 with 4 on the outer surface of the epihyal and 4 on the ceratohyal, all acinaciform. The upper branchiostegals curve parallel with the suboperculum up behind the operculum.

Operculars: In *Miripinna* complete and entire, the suboperculum elongate and extending up behind the operculum so that its tip is dorsal to the operculum. Interoperculum elongate. Gill membranes separate.

Hyoid arch: At least interhyal, epihyal and ceratohyal present.

References: Bertelsen and Marshall (1956).

Material examined: None.

Eutaeniophoridae (Taeniophoridae)

Pl. VIII

Branchiostegals: Vary from 7-9 with 3-5 epihyal and 4 ceratohyal. In *Eutaeniophorus festivus* 8-9 with 4 epihyal and 4 ceratohyal in sixteen specimens and 5 epihyal and 4 ceratohyal in five specimens. In *Parataeniophorus gulosus* 7-9 with 4 epihyal and 4 ceratohyal in eleven specimens, 5 epihyal and 4 ceratohyal in one specimen and 3 epihyal and 4 ceratohyal in one specimen, those on the epihyal being on its external face; in *P. brevis* 8 with 4 epihyal and 4 ceratohyal. Branchiostegals in all forms acinaciform and curve up behind operculum.

Operculars: In *Eutaeniophorus* complete and entire, the suboperculum extends up behind the operculum occluding most of its posterior border. Interoperculum elongate. Gill membranes separate.

Hyoid arch: In *Eutaeniophorus* consists of interhyal, epihyal, ceratohyal and two hypohyals.

References: Bertelsen and Marshall (1956), Bertelsen and Marshall (1958).

ORDER NOTACANTHIFORMES (HALOSAURIFORMES)

Branchiostegals 6-23 with 4-7 on the epihyal and 2-7 on the ceratohyal, all erupting from the external face of the hyoid arch; all acinaciform; gulars absent; opercular bones without spines and complete (except the Halosauridae lack a suboperculum); hyoid arch complete, with two hypohyals. Epihyal and ceratohyal not sutured. Gill membranes separate. Upper Cretaceous to present. Three families.

Regan (1929) places the three families in the same order, Berg (1947) placed the Halosauridae in a separate order, but most authors, Bertin and Arambourg (1958), and Bailey (1960) have not followed this action. The results of this study support the latter authors opinion. The families share numerous fairly straight (internal characters not known for Lipogenyidae) acinaciform branchiostegals erupting from the external face of the hyoid arch, needle-like teeth (absent in Lipogenyidae), numerous pelvic rays (7-11) some of which may change into spines, pelvics abdominal and close or fused, elongate anal fin, physoclistic gas bladder, maxillary spine (not all Halosauridae), a peculiar interoperculum with a projection extending back to the suboperculum, suboperculum with wing extending up in front of the operculum, small cycloid scales, elongate snout with inferior mouth, etc. The peculiar spines of the Notacanthidae and Lipogenyidae can be regarded as independently evolved and not derived from those in the acanthopterygian fishes.

Confirming the primitive nature of these fishes, that they are malacopterygian in nature, and that the spines must be an independent development are the following characters: the numerous branchiostegal rays on the lateral face of the hyoid arch (not in the 4 + 2-7 pattern), the numerous pelvic rays, the failure of the premaxillary to exclude the maxillary in Halosauridae, the lack of suturing between the epihyal and ceratohyal, inner pelvic radial of ispondylous type (Gosline 1961) and the cycloid scales. It is evident then that the Notacanthiformes are soft rayed fishes. Further, their characters permit them to be derived only from the primitive Clupeiformes. The most likely ancestral group in the Clupeiformes appear to be the elopoid ancestors of the Albuloidei. The Albuloidei have numerous branchiostegals on the external surface of the hyoid arch, 2 hypohyals, one supramaxillary, 10-14 pelvic rays, inferior mouth with toothless maxillary, needle-like teeth, long snout, perforated premaxillary, and membraneous cavernous suborbitals (absent in Notacanthidae), all pointing to the derivation of the Notacanthiformes from the elopoid ancestors of the Albulidae. According to Frost (1926) the sagitta of _Halsaurus_ is of the elopine type. The cartilaginous shelf from the ceratohyal the branchiostegals rest on in _Aldrovandia affinis_ may represent the bony shelf seen in _Albula_.

The more numerous branchiostegals, absence of fin spines, mouth bordered by premaxillary and maxillary, and presence of supramaxillary indicate the Halosauridae are the most primitive family in the group. However, they do have some specializations such as a ventral lateral line (which is doubtless associated with the secondary function of the lateral line, bearing photophores) and apparent absence of a suboperculum. The Lipogenyidae are little known and are apparently represented by only one specimen. They are characterized by the presence of several rays in the short dorsal fin, absence of teeth and the separation of the two rami of the lower jaw. While the latter might possibly be a teratological condition, the condition of the dorsal fin is both distinctive and intermediate between the other two families. While the dorsal fin is intermediate, most of the characters are close t to the Notacanthidae.

Halosauridae

Pl. VIII

Branchiostegals: Vary from 9-23, with 4-5 on the epihyal and 5-7 on the ceratohyal, all on the external face of the hyoid arch, all acinaciform. In Halosaurus 11-23, Aldrovandia 9-12, in †Echidinocephalus about 12. In Aldrovandia affinis (as Halosauropsis) 10 with 5 epihyal and 5 ceratohyal, all acinaciform, the upper ones with a small, thin blade on either side of the base, the lowest three rest on the external surface of a cartilaginous shelf projecting down from the lower side of the middle of the ceratohyal. In Aldrovandia macrochir 11 with 4 epihyal and 7 ceratohyal, on the external face of the arch and virgaform. In Halosaurus oweni 11 with 5 epihyal and 6 ceratohyal all on the external face of the arch, all acinaciform (Günther reports 14 for this species; it may be that branchiostegals were lost from the skeletal specimen here examined; alternately this specimen may be misidentified.

Operculars: In Aldrovandia affinis operculum entire, interoperculum reduced and consisting of a small section under the preoperculum with an extension backward to the operculum. The suboperculum apparently absent; its place taken by the enlarged backwardly extending preoperculum.

Günther has interpreted what is here believed to be the preoperculum as the suboperculum in Aldrovandia macrochir. This point should be verified on stained or skeletal material. Gill membranes separate.

Hyoid arch: In Aldrovandia macrochir, A. affinis and Halasaurus oweni consists of interhyal, epihyal, ceratohyal. The number of hypohyals is unknown. Epihyal ½ to 2/3 of the length of the ceratohyal. Ceratohyal dumbbell-shaped.

Relationships: The generic classification above follows Norman (MS). The branchiostegals would seem to affirm this generic separation. There are 12-23 in Halosaurus and 9-12 in Aldrovandia (assuming the count of 11 for Halosaurus oweni is incorrect). That Halosaurus lacks prominent lateral ridges on the head and has unenlarged lateral line scales would seem to indicate it is more primitive than Aldrovandia. This is in agreement with the higher number of branchiostegals in the genus Halosaurus. The Cretaceous Echidnocephalus is very similar in branchiostegals and other characters to present day Halosaurus. In Woodward (1901) the Enchelurus syriacus specimen P9168 and E. anglicus specimen P4249 may be halosaurids but Enchelurus syriacus P5998 appears from the conformation of its suboperculum and skull to be a primitive anguilliform or myctophiform precursor of the anguilliforms.

References: Goode and Bean (1896), Weber and de Beaufort (1922), Garman (1899), Günther (1887), Jordan and Evermann (1896), Woodward (1897).

Material examined: Aldrovandia (as Halosauropsis) affinis, alcoholic specimen, arch and branchiostegals dissected out and stained, SU 23199, Albatross station 4971; Aldrovandia (as Halosaurus) macrochir, skeletal specimen, USNM 26949, 36° 34' N, 73° 48' W; Halosaurus oweni, skeletal specimen, USNM 26711, 39° 29' N, 71° 46' W.

Lipogenyidae

Branchiostegals: Unknown.

Operculars: Unknown. Gill membranes separate.

Relationships: See above ordinal discussion. Only one specimen seems to be known.

References: Goode and Bean (1896), Jordan and Evermann (1896).

Material examined: None.

Notacanthidae

Pl. VIII

Branchiostegals: Vary from 6-13. In Notacanthus (8)9-13, Polyacanthonotus 9, and Macdonaldia 6. In Notacanthus phasganorus 9 with 4 epihyal and 5 ceratohyal, all on the external surface of the arch, all slender acinaciform (both in skeletal and alizarin specimen). In Günther's figure of Notacanthus sexspinis there appear to be 9 with 7 epihyal and 2 ceratohyal; this arrangement should be checked.

Operculars: In Notacanthus complete and without spines. The operculum and suboperculum divide distally into projections resembling branched fin rays. The rays branch two to four times. The suboperculum sends an arm up in front of the operculum, but not behind. The interoperculum is peculiar, the main body being a striated plate below the horizontal arm of the preoperculum. This striated plate sends back a strut which seats on the outside surface of the anterior end of the suboperculum. It is the similarity of this peculiar interoperculum in Halosauridae and Notacanthidae that forces one to believe that they have a close common ancestry, as a similar interoperculum is not found in any other groups. The dissection of the operculum and suboperculum into rays may serve to help reduce density and to reduce energy consumption during development. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. The ends of the hyoid bones are cartilaginous. The portions that are ossified are only weakly ossified judging by the weak absorption of alizarin. The ceratohyal is dumbbell-shaped. The epihyal is about $\frac{1}{4}$ the length of the ceratohyal (shorter than in Halosaurus).

Relationships: Pronotacanthus has been removed and placed in the †Prostomidae by Arambourg (1954).

References: Günther (1887), Maul (1955), Fowler (1936), Jordan and Evermann (1896), Tucker and Jones (1951), Garman (1899).

Material examined: Notacanthus phasganorus, one skeletal and one alizarin specimen, NMC62-133, from off Newfoundland, at 43° 32' 00" N, 48° 48' 00" W.

ORDER GIGANTURIFORMES

Branchiostegals, gulars, interhyal, epihyal, ceratohyal and hypohyals absent. Opercular bones complete and entire, without spines. Suboperculum larger than operculum. A single family in recent oceans.

Relationships: Regan (1925) derived the giganturids from the synodontids, and considered that they may have been a specialized offshoot from a line that lead to the Lyomeri. Fowler (1936) considered Stylephorus and Gigantura related. Walters (1961) came to a conclusion similar to Regan's, that the Giganturoidea may be a specialized offshoot of a line that led from a sub-myctophiform group such as the esocoids towards the synondontoid myctophiforms, and that this line later may have given rise to the Cetunculi and perhaps eventually to the Lyomeri.

In a comparison of about 30 characters in the lower orders, the Giganturidae were found closest to the Notacanthiformes, Saccopharyngiformes, Anguilliformes and Beloniformes, and of these four closest to the Anguilliformes and especially the Saccopharyngiformes. However, the similarities between these groups are mainly based on the absence of characters, a unsound method of basing phylogeny. It is unlikely that the Anguilliformes were ancestral to the Giganturiformes, although they may have had a common ancestor.

The hyoid arch is much reduced in the Saccopharyngiformes (Orton 1963), and essentially absent in the Giganturiformes. Further, the Saccopharyngiformes agree with the Giganturiformes in more characters than any other order. The Giganturiformes are more primitive and less degenerate than the Saccopharyngiformes in possessing opercular bones and a developed caudal fin, and a more normal body and fin arrangement. This author agrees therefore that there is a possibility of the same stock that gave rise to the Giganturiformes might have given rise to the Saccopharyngiformes.

In conclusion one can only say that the great degeneration that has taken place in the Giganturidae makes it difficult to judge its derivation. But that it is a soft-rayed fish and that it will be traced eventually to either the Clupeiformes or Myctophiformes seems most plausable. It is unfortunate that the caudal osteology is as yet undescribed. Judging from the fairly numerous caudal rays the caudal skeleton cannot be too reduced and might well hold the secret of its progenitors. The same holds for its axial skeleton.

The opercular bones are peculiar. The heavy down-bent operculum with its posterior suboperculum resembles that in Anguilliformes and Synbranchiformes and hence may well be a case of parallel evolution, since all have somewhat restricted gills and hence the need of a solid opercular bone onto which to insert strong pumping muscles. The posterior position of the suboperculum also shows some similarity to the Myctophoidei. The posterior interoperculum is also unusual. Doubtless it was backwardly displaced during evolution of the enormous posterior extension of the jaws.

Giganturidae

Branchiostegals: Absent.

Operculars: Complete and entire, without spines. In Gigantura operculum small, shaped like a downcurved petal, suboperculum a large triangle, interoperculum a small triangle located immediately below, instead of anterior to the suboperculum. Because of the oblique suspensorium the anterior 2/3 of the operculum is in front of the suboperculum. Gill opening restricted slightly in Bathyleptus, considerably in Gigantura.

Hyoid arch: Absent (except for hyomandibular).

References: Walters (1961), Regan (1925).

Material examined: None.

ORDER SACCOPHARYNGIFORMES (MONOGNATHIFORMES)

Branchiostegals, gular, operculars and hyoid arch (except hyomandibular) absent in the adult. But a cartilaginous operculum an interhyal and ceratohyal cartilage present in larvae. Gill openings restricted, latero-ventral or ventral and longitudinal instead of vertical. The gills are small and hoop-like, circling the small pharyngeal slits. Three families. Fossils unknown.

Because of the absence of the branchiostegal series and hyoid arch little may be said, from their point of view, of the ancestry of the Saccopharyngiformes. But the presence of an interhyal and operculum, newly discovered in the larvae (Orton, 1963) enables one to discount, in agreement with Berg (1948), Tchernavin's views (1947, 1947a) that this order does not belong in the teleostomes. Comparison of Orton's figures with de Beer's (1937) of Anguilla show the opercular element to be similar, but to appear earlier; the hyoid arch to be of different conformation, but to be delayed in formation of a hypohyal.

Various suggestions have been made as to the derivation of this order, such as from the Anguilliformes, Synbranchformes, Myctophiformes, Gadiformes and Syngnathiformes. Harry (1952) has recently indicated possible relationship to the whalefishes some of which share a curious spongy luminous tissue around the first dorsal and anal fin rays and anus. There are also similarities to the Giganturiformes (see discussions under that order). The leptocephalous larvae of Saccopharyngiformes indicate possible relationship to the elopoids, albuloids and anguilliforms. Orton (1963) believe that they "show significant developmental resemblances to the eels".

Saccopharyngidae

Branchiostegals: Apparently absent.

Operculars: Apparently absent in adults. Operculum in larvae ascribed to this family.

Hyoid arch: Apparently absent in adults. Cartilaginous interhyal and ceratohyal in larvae ascribed to this family.

References: Tchernavin (1947), (1947a), Bertin (1934), Orton (1963).

Material examined: None.

Eurypharyngidae

Branchiostegals: Apparently absent.

Operculars: Apparently absent in adults and larvae.

Hyoid arch: Apparently absent in adults. A cartilaginous interhyal and epihyal in larvae ascribed to this family.

References: Tchernavin (1947), (1947a), Bertin (1934), Orton (1963).

Material examined: None.

Monognathidae

Branchiostegals: Apparently absent.

Operculars: Apparently absent in adults.

Hyoid arch: Apparently absent in adults.

References: Bertin (1937), Bertin and Arambourg (1958).

ORDER MORMYRIFORMES

Branchiostegals 3-17 with 0-5 epihyal and 1-8 ceratohyal, 4-8 on the external and 0-5 on the ventral face of the hyoid arch, acinaciform or virgaform, sometimes slightly laminar. Gular absent. Operculum present and entire or crenulate; suboperculum, if present, entire; interoperculum, if present, entire. One hypohyal (the upper, except perhaps *Arapaima*) or none. Ceratohyal, epihyal and interhyal usually present (latter may not be ossified or may be absent). Gill membranes joined to isthmus, joined together and free from isthmus, and in one family separate. Seven recent plus one wholly fossil family. Upper Cretaceous to present.

Berg (1947) placed the osteoglossid families in the Clupeiformes, the mormyrid families in the Mormyriformes. Gregory (1933) placed these two groups in adjacent superfamilies in the Clupeiformes, as did Regan (1929). Gosline (1960) placed the osteoglossid families in their own division, Osteoglossi, separating them from all other clupeiform fishes, which he placed in the division Clupei.

The basic similarities in the branchial skeleton of the osteglossid and mormyrid-type families suggested that they belonged in the same group. That they differed in these characters from the Clupeiformes further suggested that the osteoglossid and mormyrid families be placed together in the same order, Mormyriformes. The Mormyriformes (used from here on in the expanded sense including the notopteroid, osteoglossoid and mormyroid families which are dealt with below) thus differ in having only one or no hypohyals while all Clupeiformes investigated (except the peculiar Phractolaemidae) have two hypohyals. The branchiostegals of Mormyriformes tend to be rectilinear and slender whilst at least the upper ones of Clupeiformes are usually broad and laminar. Gosline (1960) has indicated that the families here placed in Mormyriformes are peculiar in having a single postterminal centrum, the other postterminal centrum being fused with a hypural in such a way that the resultant element is horizontal. They have fewer (16 or less), than the usual number of branched caudal rays in the Clupeiformes, (17). Other common characters of the osteoglossid and mormyrid families are absence of a basisphenoid (except Notopteridae) and supramaxillary, usual presence of an orbitosphenoid, parapophyses coosified with centra, tendency towards fusion of the premaxillaries, meeting of the parietals; and a rigidly enclosed nasal capsule (Gosline, 1961) without diverticula and no supraorbital bone, the place of the latter being taken by a canal-bearing antorbital(?)

that fuses with the frontal. The notopterids and mormyrids share a peculiar ceratohyal shelf on which branchiostegals insert.

The Hiodontidae were included by Gosline (1960) in his division Osteoglossi. As shown under that family, they differ trenchantly from the Mormyriformes (as here construed) and should be placed in the Clupeiformes, in their own suborder.

The presence of the maxillaries in the gape, the presence of an orbitosphenoid in at least some of the members, the soft-rayed abdominal pelvics, cycloid scales, intramuscular bones and mesocoracoid indicate a clupeiform derivation for the Mormyriformes. Several shared features suggest a common ancestry with the albuloids. The characters mentioned above however, demonstrate the Mormyriformes to be at least as well separated from the Clupeiformes as the Myctophiformes.

Berg (1947) considered the Mormyriformes to include the Mormyridae and Gymnarchidae, excluding the osteoglossoids and notopteroids. He considered this order one of the best characterized, evidently on the basis of the well developed cerebellum. But the cerebellum is differently developed even in these two families. Significantly Svetovidov (1953, P. 392) did not consider the brain a useful taxonomic character at the ordinal level, "Therefore, not one of the structural features of the brain, with a *possible* exception of the cerebellum in the Mormyriformes, can be considered typical of any systematic group of fish--family, order". (Italics mine). Neither are the electric organs (with which the large cerebellum may be associated), considered of ordinal value - e.g. Electrophorinae, Malapteruridae. It is, therefore, with little hesitation that the limits of the Mormyriformes are changed, especially since several individual morphological characters, particularly the hyoid arch and caudal skeleton, point in the same direction.

SUBORDER OSTEOGLOSSOIDEI (PANTODONTOIDEI)

The Osteoglossidae and Arapaimidae appear to be more primitive, having a subopercle, a roof to the posttemporal groove, and a 10-17 branchiostegals, whereas the Pantodontidae and Heterotidae lack a suboperculum and a roof to the posttemporal groove and have only 7-11 branchiostegals. The four families are united by a unique character: the entopterygoid articulates with the lateral peg of the parasphenoid in a manner unknown in other fishes (Ridewood, 1905). The completeness of the opercular apparatus suggests that the fossil Plethodidae might be related to the Osteoglossidae and Arapaimidae although the small number of branchiostegals disagree with this allocation. Greenwood and Thompson (1960) lump the following families under Osteoglossidae.

The reduction of branchiostegals in the Heterotidae might be attributed to the presence of a respiratory organ on the 4th branchial arch.

Osteoglossidae

Branchiostegals: Branchiostegals vary from 10-17. In †*Dapedoglossus* at least 10; in † *Brychaetus* at least 15; *Osteoglossum* 10-11; *Scleropages* 13-17. In *Osteoglossum bicirrhosum* 11 with 3 epihyal and 8 ceratohyal, 8 on external and 3 on ventral face of hyoid arch, the upper 3 spathiform, the lower ones becoming virgaform.

Operculars: Complete, posterior borders crenulate. Suboperculum very small. Gill membranes united, free from isthmus.

Hyoid arch: Consist of one hypohyal (the upper), ceratohyal, epihyal; interhyal not described.

Relationships: Poll (1957) includes the Heterotidae in this family. However, the Heterotidae are distinguished by the possession of an epibranchial organ, and fewer branchiostegals, 7-9, instead of 10-17.

References: Ridewood (1905), Poll (1957), Woodward (1901), Norman (MS), Weber and de Beaufort (1913).

Material examined: *Osteoglossum bicirrhosum* alcoholic specimen, BC60-162, South America.

Arapaimidae

Branchiostegals: In *Arapaima gigas* 10-11, with 5 epihyal and 5-6 ceratohyal. The upper ones are larger, slightly expanded and lamellate, the lower ones more slender and rodlike. Several other authors (in Ridewood, 1905) place the number at 16.

Operculars: Complete and entire. Suboperculum very small, interoperculum hidden by expanded preoperculum.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and one hypohyal, probably the equivalent of the lower according to Ridewood. If this is so, then it differs from the other osteoglossoid families (which possess only the upper hypohyal), and the Arapaimidae would not belong in the suborder.

References: Ridewood (1905).

Material examined: None

† Plethodidae

Branchiostegals: About 6 in *Anogmius*.

Operculars: Complete and entire. Opercular subtriangular and heavy, preopercular expanded ventrally and may have covered the interoperculum.

References: Woodward (1899, 1901, 1902-12).

Material examined: None.

Pantodontidae

Branchiostegals: In *Pantodon buchholzi* 9-11, virgaform and almost straight.

Operculars: Operculum entire, interoperculum and suboperculum absent. Gill membranes separate.

Hyoid arch: A large ossified interhyal and a small upper hypohyal reported, other elements presumably present.

References: Ridewood (1905), Boulenger (1909), Berg (1947).

Material examined: None.

Heterotidae

Branchiostegals: In Heterotidae 7-9. Heterotis niloticus 8 with $3\frac{1}{2}$ epihyal and $4\frac{1}{2}$ ceratohyal. Of the epihyal branchiostegals the dorsal one lies halfway up the outer face of the epihyal and the lower two on the lower edge of the epihyal, the next one on the epihyal-ceratohyal border. The upper three are spathiform, the lower 5 are virgaform.

Operculars: Operculum large and entire, interoperculum entire. Suboperculum not observed by Ridewood but definitely reported by Valenciennes as a very small bone (in Ridewood). Greenwood and Thompson report a suboperculum. An epibranchial respiratory organ is borne by the 4th arch.

Hyoid arch: Epihyal, ceratohyal and a small upper hypohyal known.

References: Ridewood (1905), Poll (1957), Greenwood and Thompson (1960).

Material examined: None.

SUBORDER NOTOPTEROIDEI

Notopteridae

Branchiostegals: Vary from 3-9. In Notopterus 6-9, in Xenomystus 3. In Notopterus notopterus and N. chitla 8 with none on the epihyal and 8 on the ceratohyal, 5 on the lateral and 3 on the ventral face of the hyoid arch, all acinaciform in shape, the uppermost large, the others small; branchiostegals 2-5 rest on a small shelf emitted by the upper ceratohyal.

Operculars: In Notopterus suboperculum absent. Operculum crenulate, interoperculum entire. Gill membranes united and free from isthmus. Branchial respiration complemented by an accessory epibranchial organ of respiration and probably also by the very large gas bladder with many anterior and posterior ramnifications. The lack of dependence on aquatic respiration has probably lead to the degeneration of the sub-operculum and towards the reduction in number of branchiostegals. The degeneration in the hyoid arch may be attributed to the same factor.

Hyoid arch: In Notopterus interhyal (cartilaginous or very slightly ossified), epihyal, ceratohyal, and one hypohyal. Probably it is the lower of the two hypohyals which is lacking. The lower side of the ceratohyal sends down a wedge shaped shelf. On this shelf insert the 4 branchiostegals below the uppermost branchiostegal. This shelf is probably homologous with that in mormyrids.

References: Weber and de Beaufort (1913), Misra (1953), Ridewood (1903, 1905b), Hubbs (1920), Day (1875), Poll (1957), Boulenger (1904), Munshi (1960), Khanna (1961).

Material examined: Notopterus notopterus, alizarin specimen, BC55-412, from Pakistan.

SUBORDER MORMYROIDEI

Superfamily Gymnarchoidea, new superfamily

Gymnarchidae

Branchiostegals: 4 branchiostegals, the upper 3 on the epihyal and the lower on the ceratohyal. The count of 7 by Hyrtl (in Ridewood) is apparently erroneous as all other authors give 4 (he may have had a mormyrid).

Operculars: Complete and entire. The operculum hangs downward from the opercular process of the hyomandibular, instead of swinging out laterally as in other fishes. Suboperculum hidden under the operculum. Gill membranes joined to the isthmus and forming a free fold over it.

Hyoid arch: Epihyal and ceratohyal present. The epihyal is longer and larger than in the Mormyridae. Hypohyals are absent. Ridewood does not mention an interhyal.

Taxonomy: The definition of the superfamily Gymnarchoidea follows Berg's (1947) definition of the suborder Gymnarchoidei.

References: Ridewood (1905b), Gregory (1933).

Material examined: None.

Superfamily Mormyroidea

Mormyridae

Pl. VI, IX

Branchiostegals: Vary from 6-8, with 4-5 epihyal and 2-3 ceratohyal, usually all on the external face of the hyoid arch, (one may lose contact with arch). In *Mormyrops deliciosa* 7 with 2 free near the epihyal, 3 epihyal, 2 ceratohyal, the anterior 4 virgaform, the upper ones slightly expanded at the ends; *Petrocephalus catostomus* 8 with $4\frac{1}{2}$ epihyal and $3\frac{1}{2}$ ceratohyal, all lateral, uppermost laminar with central ridge, next spathiform, rest rectilinear acinaciform. *Petrocephlus bane* 8 with 2 free near the epihyal, 2 epihyal, 4 ceratohyal, the anterior 4 on the outer ceratohyal; *Isichthys henryi* 6 virgaform; *Gnathonemus moori* 7 with 4 epihyal and 3 ceratohyal, 6 on the external face and 1 on the ventral face of the arch, the branchiostegals rest on a thick flat shelf which projects ventrally from the epihyal and ceratohyal, the uppermost slightly spathiform, the lower ones virgaform.

Operculars: Complete and entire. In *Gnathonemus moori* operculum large, suboperculum reduced to a slender rod, interoperculum a small plate; in *Mormyrops deliciosa* operculum large, suboperculum an elongate triangular plate under the operculum, interoperculum and elongate bone; *Petrocephalus bane* with large operculum covering a small operculum with a small quadrangular interoperculum. Gill openings restricted.

Hyoid arch: In *Mormyrops deliciosa* hypohyals absent, in *Petrocephalus bane*, and *P. catostomus* one hypohyal present, the upper one; the other hyoid bones present in all examined, except that an interhyal is unknown.

References: Ridewood (1905b), Gregory (1933), Boulenger (1904).

Material examined: *Isichthys henryi*, alcoholic specimen, USNM 114767, Liberia; *Gnathonemus moori*, alcoholic specimen, hyoid arch and branchiostegals alizarin-treated, SU 15699, Cameroons; *Petrocephalus catostomus*, alizarin specimen, NMC63-6645, Angola.

ORDER CYPRINIFORMES

Branchiostegals 3-20, with 1-3 epihyal and 2-7 ceratohyal, 2-4 on the external and 1-15 on the ventral (or internal) face of the hyoid arch. Branchiostegals spathiform or at least laminar distally. Gular absent. Opercular bones complete, entire, without spines (except the siluroids which lack the suboperculum). Hypohyals two (but apparently one in Amphiliidae and Chacidae), rest of arch complete. Epihyal and ceratohyal separate or sutured. Gill membranes separate, united to one another and free from or joined to isthmus. Thirty-eight families, all living except one fossil *incertae cedis* family. Known from the Tertiary, questionably from the Cretaceous, to the present.

The presence of up to 20 spathiform branchiostegals, jaws bordered by premaxillary and maxillary (except in siluroids), presence of an orbitosphenoid and opisthotic, absence of true spines, up to 17 branched caudal rays, up to 17 rays in the abdominal pelvics, cycloid scales and usually 2 hypohyals and physostomus gas bladder all suggest the Cypriniformes belong in the Malacopterygii and together limit derivation from the Clupeiformes.[1] Of the Clupeiformes, the Clupeoidei is the only suborder with the necessary qualifications for an ancestral group.

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[1] Bertmar (1959,1961) indicates embryological characters of Characidae which he believes similar to or more primitive than *Amia*. However rib, scale, hyoid and caudal skeletal characters would strongly argue against his interpretation. Also (1961), he later considered the accessory branchial organs of Characidae to be homologous with those of *Dorosoma* and *Chanos* (both clupeiforms).

Clupeoid projections on the branchiostegals are shared by both groups. Gosline (1961) states that the caudal skeleton of Brycon bears a striking resemblance to that of the round herring, Dussummieria. The Dussumieriidae are the only family with a sufficient number of branchiostegals to be ancestral to the Cypriniformes (the Engraulididae also have a sufficient number but they are precluded as ancestors by their specialized jaws). But the Dussummieriidae are not suggested to be directly ancestral.

The Cypriniformes are here divided into two suborders, the Cyprinoidei and the Siluroidei. The Cyprinoidei are characterized by 3-5 usually broad branchiostegals; the presence of parietals, symplectic, suboperculum and metapterygoid; the parapophyses not co-ossified with the centra; and the epihyals and ceratohyals are not ankylosed. The Siluroidei have 3-20 slender branchiostegals; lack parietals, symplectic, suboperculum and metapterygoid; the parapophyses are co-ossified with the centra, epihyals and ceratohyals are ankylosed. From these characters it may be seen that the Cyprinoidei are in general more primitive and less modified than the Siluroidei. Curiously the branchiostegals have evolved in opposite directions in the two suborders. In the Cyprinoidei they have remained broad and laminar but become reduced in number, while in the Siluroidei the branchiostegals have remained numerous but become slender in form, expanding only distally into lamina. The suturing of the epihyal and ceratohyal parallels that in the acanthopterygian fishes. It follows a general tendency of bones to become sutured in the catfishes, for example the suturing of the two cleithra to one another.

SUBORDER CYPRINOIDEI

Branchiostegals 3-5, at least upper ones spathiform, with 1 epihyal and 2-3 ceratohyal, 2 external and 1-2 ventral or internal. Epihyal, ceratohyal and hypohyals not sutured. Opercular bones complete. Three superfamilies.

The Cyprinoidea are the most modified of the superfamilies; they have the lower pharyngeal bones enlarged and falciform, unlike the other two families. They doubtless arose from the Characoidea. From the Characoidea also arose the Gymnotoidea which lack dorsal and ventral fins, have an elongate anal fin and an anterior vent. The Characoidea are the most primitive family, have the most numerous branchiostegals, normal fins, most primitive Weberian apparatus (Alexander, 1962) and other characters (see Weitzman, 1962). Regan (1911b) revised this group. Weitzman (1962) is followed in uniting the Hemiodontidae, Gasteropelecidae, Citharinidae, Xiphostomatidae and Anostomidae with the Characidae.

Superfamily Characoidea

Characidae (Characinidae)

Pl. VIII, IX

Branchiostegals: Vary from 3-5 with 1 epihyal and 3 ceratohyal, 2 external and 2 ventral, spathiform with clupeoid projections. In Alestes 4, Anoptichthys 3-4, Anostomus 4, Astyanax 4, Brycon 4, Bryconaethiops 4, Carnegiella 4, Catroprion 4, Citharinus 4, Creagrutus 4, Cynodon 5, Distichodus 3-4, Gasteropelecus 4, Hemiodus 4-5, Hydrocyon 4, Hystricodon 4, Ichthyoborus 4, Myletes 5, Parodon 4, Piabucina 4, Pseudochalceus 4, Rhytiodus 4, Sarcodaces 4, Scissor 4, Serrasalmo 4, Tetragonopterus 4, Thoracocharax 5, Xenocharax 3, Xiphorhamphus 4, Xiphostoma (validity of certain of preceding genera not established). Astyanax fasciatus 4 with 1 epihyal and 3 ceratohyal, 2 external and 2 ventral, the anterior 2 fitting into notches in the ceratohyal, all broadly spathiform, the lower three with clupeoid projections. In Brycon meeki 4 with 1 epihyal and 3 ceratohyal, 2 external and 2 ventral, the anterior 3 with clupeoid projections and all broadly spathiform. Anostomus anostomus with 4 spathiform branchiostegals.

Operculars: Complete and usually entire in members of family investigated. But in Corynopoma the operculum of the male is elongated into a style which extends back under the dorsal and bears a circular flap of skin; in the female it is pointed and reaches just above the base of the pelvic fin. Gill membranes separate or joined to isthmus.

Hyoid arch: In Astyanax and Brycon interhyal, epihyal, ceratohyal and two hypohyals present.

References: Weitzman (1960, 1960a, 1960b, 1962), Schultz (1944), Günther (1864), Myers (1949), Boulenger (1901), Eigenmann (1917-1929), Hubbs (1920), Gregory and Conrad (1938), Gregory (1933), Regan (1911b).

Material examined: Astyanax fasciatus, alizarin specimen, NMC59-117, Honduras. Alcoholic specimens of the following: Anostomus anostomus, BC59-307, Vancouver Public Aquarium; Anoptichthys jordani, BC57-62, La Cueva Chica, Pajal, Mexico; Anoptichthys sp., BC57-61, Sabinos, Mexico;

Astyanax fasciatus mexicanus, BC57-417, Gonzales, Mexico.

Superfamily Gymnotoidea

Eigenman and Allen (1942) are followed in uniting the families Rhamphichthyidae, Sternarchidae and Electrophoridae, recognized by some authors, with the Gymnotidae.

Gymnotidae

Branchiostegals: 4 in all genera examined, Steatogenys, Sternarchus, Gymnotus and Electrophorus. Steatogenys elegans 4 with the upper 3 broad, the lowest slender. In Gymnotus carapo 4 broad rounded spathiform branchiostegals. In Electrophorus electricus 4 with 2 external and 2 ventral, the upper 2 broad and the lower 2 slender.

Operculars: Complete and entire in Steatogenys, Gymnotus, Sternopygus, Rhamphichthys, and Electrophorus. Gill opening restricted in Sternarchus, Steatogenys and Electrophorus.

References: Ellis (1913), Regan (1911b), Günther (1864), Gregory (1933).

Material examined: Steatogenys elegans, alcoholic specimen, BC62-559, aquarium specimen (British Guiana ?). Gymnotus carapo, alcoholic specimen, USNM 179564, Rio Urubu, Brazil. Electrophorus electricus, alcoholic specimen, BC58-392, Vancouver Public Aquarium.

Superfamily Cyprinoidea

Catostomidae

Pl. IX

Branchiostegals: 3 spathiform (except sometimes anteriormost) branchiostegals in all examined; with 1 epihyal and 2 ceratohyal, 2 external and 1 internal or ventral. Three found in *Carpiodes*, *Catostomus*, *Chasmistes*, *Cycleptus*, *Erimyzon*, *Hypentelium*, *Ictiobus*, *Megastomatobus*, *Minytrema*, *Moxostoma*, *Myxocyprinus*, *Pantosteus*, *Placopharynx*, *Thoburnia* and *Xyrauchen*. In *Catostomus commersonii* 3 with 1 epihyal and 2 external and 1 internal, branchiostegals spathiform with anterior clupeoid projections at base.

Operculars: Complete and entire. Gill membranes joined to isthmus.

Hyoid arch: In *Catostomus* consists of interhyal, epihyal, ceratohyal and two hypohyals.

Relationships: Nelson is able to divide the family into 4 groups on the basis of the shape of the bones of the opercular series.

References: Nelson (1949).

Material examined: *Catostomus commersonii*, alizarin specimens, NMC60-527A & S, Nanticok, Ontario.

Cyprinidae

Pl. VIII, IX

Branchiostegals: Constantly 3 (although abnormally 4), with 1 epihyal and 2 ceratohyal, and two external face and 1 internal or ventral. Three branchiostegals found in *Abramis*, *Alburnus*, *Aspius*, *Bliccopsis*, *Carassius*, *Cyprinus*, *Gila*, *Gobio*, *Gobiotia*, *Hampala*, *Hypothalmichthys*, *Labeo*, *Leptobarbus*, *Leucaspius*, *Leuciscus*, *Mylocheilus*, *Notemigonus*, *Notropis*, *Phoxinus*, *Pelecus*, *Ptychocheilus*, *Scardinius*, *Spirlinus*, *Tinca*, *Thynnichthys*, *Vimba* and numerous Indian genera (see Day). In *Cyprinus carpio* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 spathiform with clupeoid projections on the anterior 2; in *Notemigonus crysoleucas* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 ventral, all spathiform and with clupeoid projections on the base; in *Gobiotia ichangensis* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 ventral; in *Gila* 3 with 1 epihyal and 2 ceratohyal; in *Mylocheilus caurinum* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 ventral, all spathiform but the anteriormost with a clupeoid projection; *Ptychocheilus oregonense* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 internal, all spathiform, the posterior 2 with clupeoid projections; *Notropis bifrenatus* 3 with 1 epihyal and 2 ceratohyal, all spathiform with clupeoid projections. In a sample of 50 specimens of *Richardsonius balteatus* all had 3 branchiostegals.

Operculars: Complete and entire. Gill openings wide to narrow, membrane joined to isthmus, except Hypothalmichthyinae where they are united and free from the isthmus.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and 2 hypohyals in *Cyprinus*, *Notemigonus*, *Gila*, *Hypothalmichthys* and *Notropis*.

References: Harrington (1955), Uyeno (1961), Chevey (1932), Weber and de Beaufort (1916), Boulenger (1901), Nikolsky (1954), Bertin and Arambourg (1958), Day (1875), Smitt (1895), Hubbs (1920).

Material examined: *Cyprinus carpio*, skeleton, NMC61-220-S, Rideau Canal, Ontario; *Notemigonus crysoleucas*, alizarin specimen, NMC59-292, Caribou River, Nova Scotia, *Gobiotia ichangensis*, alcoholic specimen, BC53-164, China; *Mylocheilus caurinum*, alizarin specimen, BC54-433, British Columbia, Canada; *Ptychocheilus oregonense*, skull, Inst. Fish., University of British Columbia, from British Columbia; *Hypothalmichthys moritrix*, alcoholic specimen, BC59-653, Japan; *Richardsonius balteatus*, 50 alcoholic specimens, BC58-447, British Columbia.

Gyrinocheilidae

Branchiostegals: *Gyrinocheilus aymonieri* 3 with 0 epihyal and 3 ceratohyal, 2 external and 1 ventral.

Operculars: This family is distinguished from other cyprinoids by the possession of both an exhalent and inhalent gill opening. The inhalent opening is an oval aperture above the operculum, separated by a membrane from the exhalent opening. The latter is the normal gill opening behind the gill cover. As the inhalent opening is small the respiratory movements are of necessity rapid; 230-230 per minute. The habit of clinging with and or feeding on algae with the small suctorial rasping mouth may have lead to the development of another means of drawing water into the buccal cavity and over the gills. *Astroblepus*, a catfish with suctorial lips, is known to inhale water at the top of the gill opening and exhale at the bottom whilst using the mouth as a holdfast.

References: Smith (1945), Bertin and Arambourg (1958).

Material examined: *Gyrinocheilus aymonieri*, alcoholic specimen, uncatalogued, University of British Columbia, material from Malaya.

Cobitidae

Pl. IX

Branchiostegals: Constantly 3 with 1 epihyal and 2 ceratohyal, 2 on external and 1 ventral face. In *Cobitis* and *Botia* 3 and in numerous Indian forms (see Day). *Cobitis taenia* 3 with 1 epihyal and 2 ceratohyal, 2 external and 1 ventral, slender but expanding into a lamina distally.

Operculars: Complete and entire, elements smaller in *Cobitis* than in Cyprinidae. Gill openings restricted to sides.

Hyoid arch: In *Cobitis* consists of interhyal, epihyal, ceratohyal and 2 hypohyals.

References: Day (1875), Smitt (1895), Weber and de Beaufort (1916).

Material examined: *Cobitis taenia*, alizarin specimen, NMC59-249, Tisa River, Ukraine.

Homalopteridae

Branchiostegals: 3 in all forms examined. In *Homaloptera zollingeri* 3 spathiform; in *Bhavania* 3 with 2 epihyal and 1 ceratohyal; in *Hemimyzon abbreviata* 3 with the lowest expanded and spathiform, becoming more slender dorsally.

Operculars: Complete and entire. In Bhavania the posterodorsal tip of the operculum terminates in a point but apparently does not project as a spine. Interoperculum and to a certain extent the suboperculum reduced in size. Gill opening restricted to side of head.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals in Bhavania.

References: Weber and de Beaufort (1916), Ramaswami (1948).

Material examined: Alcoholic specimens of Hemimyzon abbreviata, BC53-178, and Homaloptera zollingeri, BC58-32, from Malaya.

Gastromyzonidae

Branchiostegals: In Gastromyzon 3 with 2 on the epihyal and 1 on the ceratohyal.

Operculars: Complete and entire.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals.

References: Ramaswami (1948).

Material examined: None.

SUBORDER SILUROIDEI

Branchiostegals 3-20, the distal portion of the upper branchiostegals spathiform with 1-3 epihyal and 2-13 ceratohyal and none or occasionally one on the external face and all or all but one on the ventral or internal face of the hyoid arch, the branchiostegals on the ceratohyal with a forked base, epihyal and ceratohyal usually and ceratohyal and hypohyal often sutured together, operculum and interoperculum present, the interoperculum forked for reception of the operculum, suboperculum absent. Twenty-eight families.

The best revision of the catfishes is still Regan (1911). There are two main populations of catfishes, the Old World ones (Eurasia and Africa), the South American ones, (also the North American Ictaluridae and the 3 marine families and derivates, Ariidae, Doiichthyidae and Plotosidae). The Old World catfishes appear more primitive than the South American catfishes, having more branchiostegals 4-20 as opposed to 3-17, more pelvic rays 6-14 as opposed to (0)5-10 (16), more barbels (2)4-8 as opposed to 2-6. The Bagridae and then the Siluridae are the most primitive of the Old World catfishes. The Ictaluridae clearly belong to the Old World catfishes with 8-13 branchiostegals 8-9 pelvic rays and 8 barbels. The author agrees with Regan that the Ictaluridae are very close to the Bagridae. The Plotosidae are close to the primitive bagrid stock, the Ariidae could be derived from the Bagridae or possibly the Schilbeidae or Pimelodidae. The Doiichthyidae are apparently derived from the Ariidae (Darlington, 1957). Of the South American catfishes the Pimelodidae appear to be the most primitive. Regan, Berg and Myers consider the Diplomystidae the most primitive of the catfishes, its maxillary being toothed and its 5th vertebrae not being suturally connected to the 4th, unlike all other catfishes. However, it is conceivable that the dentition on the maxillary is secondary; it is notable that other families such as the Chacidae, Pygiidae and Loricariidae have maxillaries of equal development. The loss of the suture between the 4th and 5th vertebrae may well be secondary rather than primitive. It is notable that the Diplomystidae have relatively few branchiostegals (7-8), pelvic rays (6) and barbels (2) which would indicate that the family is rather advanced. The Diplomystidae is therefore considered a moderately advanced family in the Suborder and is considered derivable from the Pimelodidae or its relatives. The South American freshwater catfishes, according to a survey of 8 characters, are derivable from the Ictaluridae or the Bagridae. It may be noted that the upper branchiostegals sweep up into the space vacated by the suboperculum.

Bagridae (Olyridae)

Branchiostegals: Vary from 6-13. In Macrones 8-13, Bagrichthys 7, Bagroides 7-8, Leiocassis 6-11, Mystus 9-13, Rita 8, Bagrus 12, Chrysichthys 9, Clarotes 9, Pseudobagrus 8, Olyra 6 ?, Liobagrus 12. In Mystusaor 11, with 1 epihyal and 10 ceratohyal.

Operculars: Operculum and interoperculum present. Gill membranes separate or united and free from isthmus.

Hyoid arch: In Rita consists of interhyal, two hypohyals, epihyal and ceratohyal, the last two sutured together.

References: Jayaram (1953), Inger and Kong (1962), Weber and de Beaufort (1913), Günther (1864), Day (1875), Hubbs (1920), Munshi (1960), Khanna (1961).

Material examined: *Mystus bleekeri*, alcoholic specimen, BC55-402, Tatta, Pakistan; *Leiobagrus marginatus*, alcoholic specimen BC53-168, Szechwan, China.

Siluridae

Pl. VIII

Branchiostegals: Vary from 8-20. In *Hemisilurus* 10-12, *Ceratoglanis* 10-11, *Belodontichthys* 13-15, *Silurichthys* 9, *Silurus* 12-15, *Wallago* 15-20, *Hito* 12-14, *Kryptopterus* (*Cryptopterus*) 8-17. In *Silurus glanis* 16 with 3 epihyal and 13 ceratohyal, 1 on the external the rest on the ventral surface of the arch, the uppermost spathiform, the rest acinaciform.

Operculars: Operculum and interoperculum present. Gill membranes separate in *Silurus* and in *Kryptopterus*.

Hyoid arch: In *Silurus* consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal not sutured together, although two prongs from the ceratohyal reach towards the epihyal; similar in *Wallago* but epihyal and ceratohyal are sutured together.

References: Haig (1951), Weber and de Beaufort (1913), Tomoda (1961), Smitt (1895), Inger and Kong (1962), Khanna (1961).

Material examined: Kryptopterus macrocephalus, alcoholic specimen, BC58-32, Malaya; Silurus glanis, alizarin specimen, NMC59-290 & S, Ukraine.

Schilbeidae

Branchiostegals: Vary from 7-10. In Helicophagus 9, Schilbe 8-10, Eutropius 9-10, Siluranodon 9, Schilbichthys 7, Lais 8-9, Pseudotropius 9-10, Neotropius 9.

Operculars: Operculum and interoperculum present.

References: Günther (1864), Kulkarni (1952), Weber and de Beaufort (1913).

Material examined: None.

Clariidae (Saccobranchidae, Heteropneustidae)

Branchiostegals: Vary from 7-15. In Tanganikallabes 15, Clariallabes 9-15, Gymnallabes 10, Channallabes 8-10, Dollichallabes 10, Vegitglanis 9, Horaglanis 11, Prophagorus 10, Heteropneustes (Saccobranchus) 7-8, Clarias 7-9, Heterobranchus 7-9.

Operculars: Operculum and interoperculum present.

References: Menon (1951), Gregory (1933), Weber and de Beaufort (1913), Hubbs (1920).

Material examined: Heteropneustes fossilis, alizarin specimen, NMC62-206-S, from India; Clarias macrocephalus, alcoholic specimen, BC59-532, from Cambodia.

Amblycipitidae (Amblycepitidae, Akysidae)

Branchiostegals: In Acrochordonichthys 6, Akysis 6.

Operculars: Gill membranes joined to isthmus.

References: Weber and de Beaufort (1913), Günther (1864).

Material examined: None.

Cranoglanididae

Branchiostegals: 8 branchiostegals in Cranoglanis sinensis.

Operculars: No data available, but gill membranes free from isthmus.

Relationship: May be close to Bagridae, but closer to Pangasidae (Myers).

References: Myers (1931), Peters (1880).

Material examined: None.

Sissoridae

Branchiostegals: Vary from 4-12. In Bagarius 12, in Glyptosternum 8-9, Gagata 5-7, Euchiloglanis 6, Erethistes 6, Sisor 4. In Euchiloglanis davidi 6 with 3 epihyal and 3 ceratohyal.

Operculars: Gill membranes separate or joined to isthmus.

References: Hora (1942), Weber and de Beaufort (1913), Günther (1864).

Material examined: Euchiloglanis davidi, alcoholic specimen, BC53-117, Sichang, China.

Pangasiidae

Branchiostegals: Vary from 7-11. In *Pangassius* 7-11.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal sutured together.

References: Günther (1864), Chevey (1932), Weber and de Beaufort (1913), Inger and Kong (1962), Khanna (1961).

Material examined: None.

Amphiliidae

Pl. VIII

Branchiostegals: 9 in *Amphilus grandis*, the upper two slightly expanded distally. *A. platychir* 9 with 2 epihyal and 7 ceratohyal, 4 posterior on the ventral and 5 anterior on the internal face of the hyoid arch, all acinaciform.

Operculars: Gill membranes separate. Operculum and suboperculum present.

Hyoid arch: Consists of interhyal; epihyal which is sutured to the ceratohyal and one hypohyal (the two hypohyals apparently fused).

References: Günther (1864).

Material examined: *Amphilus grandis*, alcoholic specimen, USNM 72922, Nairobi River, Africa; *A. platychir*, alizarin specimen, NMC63-67 & S, Northern Rhodesia.

Mochocidae (Synodontidae)

Pl. VIII

Branchiostegals: Vary from 5-7. In Mochocus 5, in Synodontis 6-7. In Mochocus niloticus upper two expanded distally. Synodontis woosnami 7 with 2½ epihyal and 4½ ceratohyal, 3 on the external and 3 on the internal face of the hyoid arch, all acinaciform.

Operculars: Gill membranes attached to isthmus in Mochocus and Synodontis. In Synodontis operculum and interoperculum present and entire. Gill opening internally restricted.

Hyoid arch: Consists of interhyal, epihyal which is sutured to the ceratohyal, and 2 hypohyals.

References: Regan (1911), Boulenger (1911), Günther (1864).

Material examined: Mochocus niloticus, alcoholic specimen, USNM 61297, Egypt. Synodontis woosnami, alizarin specimen, NMC63-68 & S, Northern Rhodesia.

Malapteruridae

Branchiostegals: 6 in Malapterurus electricus, the upper two stout and curved.

Operculars: Gill opening restricted.

References: Günther (1864).

Material examined: Malapterurus electricus, alcoholic specimen, USNM 118779, from Liberia.

Chacidae

Branchiostegals: 8 in *Chaca chaca* with 2 on the epihyal and 6 on the ceratohyal, all on the ventral face of the arch, the upper two stout. (But according to Weber and de Beaufort only 6 branchiostegals).

Operculars: Operculum and interoperculum present. Gill membranes joined to isthmus.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and apparently only one hypohyal (or two hypohyals very closely sutured). Epihyal and ceratohyal sutured together. Posterior ventral surface of ceratohyal flattened.

References: Weber and de Beaufort (1913), Günther (1864).

Material examined: *Chaca chaca*, alizarin specimen, NMC62-205 & S, India.

Plotosidae

Branchiostegals: Vary from 7-13. In *Paraplotosus* 9-11, *Plotosus* 11-13, *Cnidoglanis* 7, *Oloplotusus* 10 or 12 (?), *Porochilus* 7, *Copidoglanis* 8-10. In *Plotosus anguillaris* 11 with 1 epihyal and 10 ceratohyal, all on the ventral surface of the arch, the upper 2 spathiform distally.

Operculars: Operculum and interoperculum present. Gill membranes separate, or joined to isthmus.

Hyoid arch: In *Plotosus* consists of interhyal, epihyal, ceratohyal and two hypohyals, the three latter sutured together.

References: Weber and de Beaufort (1913), Günther (1864).

Material examined: Plotosus anguillaris, alizarin specimen, NMC62-204 & S, from India.

Ariidae

Pl. IX

Branchiostegals: Vary from 5-9 (12), with 1-1½ epihyal, 4-4½ ceratohyal, all ventral. In Arius 5-7 (8-9), Ketengus 5, Tetranesodon 6, Nedystoma 6, Hemipimelodus 5-8 (12), Osteogeneiosus 5, Batracocephalus 5, Cathorops 6, Aelurichthys 6. In Galeichthys felis 5 with 1 epihyal and 4 ceratohyal, all ventral, the upper 2 spathiform, the lower acinaciform. In Cathorops gulosa 6 with 1½ epihyal and 4½ ceratohyal.

Operculars: Operculum and interoperculum present. Gill membranes united and free from isthmus, or joined to isthmus.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and 2 hypohyals in Galeichthys and Cathorops, all but the interhyal being sutured together.

References: Weber and de Beaufort (1913), Günther (1864), Day (1875), Hubbs (1920), Chevey (1932).

Material examined: Galeichthys felis, alizarin specimen, NMC62-74 & S, North Carolina: Cathorops gulosa, alizarin preparation, BC59-670, Panama.

Doiichthyidae

Branchiostegals: In *Doiichthys novaeguineae* 6.

Operculars: Gill membranes separate.

References: Weber and de Beaufort (1913).

Material examined: None.

Ictaluridae

Pl. VIII

Branchiostegals: Vary from 8-13, with 2 epihyal and 7-8 ceratohyal, all ventral. In *Pylodictis* 12-13, *Noturus* 9, *Satan* 10-11, *Trogloglanis* 9, *Prietella* 9, *Ictalurus* 8-9. In *Ictalurus nebulosus* 2 epihyal and 7 ceratohyal, all ventral, upper two spathiform, rest acinaciform.

Operculars: Operculum and interoperculum present. Gill membranes separate in *Ictalurus*.

Hyoid arch: Interhyal, epihyal, ceratohyal and two hypohyals present. Epihyal, ceratohyal and hypohyals sutured together.

References: Suttkus (1961), Taylor (1955), Hubbs (1920), Jordan and Evermann (1896).

Material examined: *Ictalurus nebulosus*, skeletal specimen, NMC61-218-S, Ottawa, Canada; *I. nebulosus*, alizarin specimen, BC59-601, Dewdney Slough, British Columbia; *I. nebulosus*, alizarin specimen, NMC61-528-A, 3 miles west of Selkirk, Ontario, Canada; *I. punctatus*, skeletal specimen, NMC61-2176, Ottawa, Canada; *Noturus gyrinus*, alcoholic specimen, BC55-482, Virginia.

Diplomystidae

Branchiostegals: In *Diplomystes* 8.

Operculars: Gill membranes separate.

References: Eigenmann and Eigenmann (1890), Günther (1864).

Material examined: None.

Doradidae (Auchenipteridae)

Branchiostegals: Vary from 6-7. In *Auchenipterus* 6-7, *Trachelyopterus* 6, and *Doras* 7.

Operculars: Operculum and interoperculum present. Gill openings restricted to sides.

References: Günther (1864), Eigenmann (1925).

Material examined: None.

Ageniosidae

Branchiostegals: In *Ageniosus* 11.

Operculars: Gill membranes joined to isthmus.

References: Günther (1864).

Material examined: None.

Pimelodidae

Branchiostegals: Vary from 6-17. In *Pseudoplatystoma* 14-15, *Sorubim* 15-16, *Platystoma* 11-17, *Hemisorubim* 10-11, *Platystomichthys* 9, *Sciades* 9, *Pimelodus* 6-9, *Callophysus* 7-8, *Heptapterus* 8-9, *Rhambdia* 6. In *Rhambdia guatemalensis* 6 with 1 epihyal and 5 ceratohyal, and 11 ventral, upper 2 expanded.

Operculars: Operculum and interoperculum present. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal, and 2 hypohyals in *Rhambdia*; not sutured together.

References: Eigenmann and Allen (1942), Günther (1864), Regan (1911c).

Material examined: *Rhambdia guatemalensis*, alizarin specimen NMC62-7086, Yucatan.

Helogenidae

Branchiostegals: In *Helogenes marmoratus* 13.

Operculars: Gill membranes separate.

References: Günther (1864), Regan (1911c).

Material examined: None.

Hypophthalmidae

Branchiostegals: In *Hypophthalmus* 13-15, long slender virgaform.

Operculars: Gill membranes separate.

References: Günther (1864), Regan (1911c).

Material examined: *Hypophthalmus edentatus*, alcoholic specimen, USNM 86285, Peru.

Cetopsidae

Branchiostegals: In *Cetopsis* 8.

Operculars: Gill openings restricted.

References: Günther (1864), Regan (1911c).

Material examined: None.

Pygiidae (Trichomycteridae)

Branchiostegals: Vary from 7-8 (12). In *Nematogenys* 12, *Pygidium* (= *Trichomycterus*, *Thrycomycterus*) 7-8, *Eremophilus* 8. In *Pygidium punctulatus* 3rd branchiostegal expanded distally.

Operculars: Operculum and interoperculum present. Family, except *Nematogenys*, characterized by presence of several prickles on the operculum and interoperculum. Gill membranes joined to isthmus, or united and free from isthmus or separate.

Relationships: *Nematogenys* differs in more numerous branchiostegals and absence of prickling on the operculars, etc. from other genera. Eigenmann

(1918) awarded it subfamilial recognition and considered it more primitive than the other genera, then in 1926 (not seen) raised it to familial level. The latter position is more in accord with the more numerous branchiostegals. Alternately it might be possible that the genus belongs in some other family. The opercular spines are used in working forward into small openings under rocks and up waterfalls and may also function in branchial parasitism.

References: Ferreira and Soriano (1960), Günther (1864), Regan (1911c), Eigenmann (1918).

Material examined: *Pygidium punctulatus*, alcoholic specimen, USNM 88674, Peru.

Aspredinidae (Bunocephalidae)

Branchiostegals: 5 in *Bunocephalus* and *Aspredo*.

Operculars: Operculum reduced, scarcely larger than a branchiostegal ray, attached anteriorly to the interoperculum. Gill opening restricted.

Taxonomy: Myers (1960a) is followed in uniting the Bunocephalidae with the Aspredinidae.

References: Günther (1864), Regan (1911c), Myers (1960).

Material examined: None.

Callichthyidae

Branchiostegals: Vary from 3-4. In *Hoplosternum* 3, *Callichthys* 4, *Corydoras* 3. In *Corydoras aeneus* 3 with 1 epihyal and 2 ceratohyal, all ventral, upper one spathiform.

Operculars: Operculum and interoperculum present. Gill opening restricted.

Hyoid arch: In *Corydoras* consists of interhyal, epihyal, ceratohyal and two hypohyals. Hyoid bones not ankylosed together. Top of ceratohyal flattened, in lateral view ceratohyal broad posteriorly, narrowing anteriorly.

References: Günther (1864).

Material examined: *Corydoras aeneus*, alizarin specimen, NMC62-134-S, aquarium specimen; *Hoplosternum littorale*, alcoholic specimen, BC59-307, aquarium specimen.

Loricariidae

Branchiostegals: Regan gives the number of branchiostegals as 4 in the family description.

Operculars: Operculum and interoperculum present. Prickles may be present on the interoperculum and operculum of certain members of the Plecostominae. Gill opening restricted.

Relationships: The low numbers of branchiostegals and the prickly operculars may indicate relationship of this family to Callichthyidae.

According to Gosline (1947) it is probably the most specialized catfish family.

References: Regan (1904), Günther (1864), Jordan and Evermann (1896).

Material examined: None.

Astroblepidae (Argiidae)

Branchiostegals: In *Astroblepus* (=*Arges*, *Stygogenes*) 4.

Operculars: Gill membranes joined to isthmus. Said to take water in through an orifice at the top of the gill opening. As it has sucker-like lips this method of inhaling water is doubtless an adaption similar to that in the Gyrinocheilidae.

References: Günther (1864), Gosline (1947).

Material examined: None.

ORDER ANGUILLIFORMES

Branchiostegals 6-22, with 4-12 epihyal and 0-4 ceratohyal, all on the external face of the hyoid arch, usually filiform or virgaform, occasionally upper ones expanded distally, curving up around behind and often to above the upper border of the gill cover; jugiostegalia sometimes present; opercular bones usually complete, lacking spines, and entire or rarely crenulate (but interoperculum absent in Moringuidae and suboperculum and interoperculum absent in some Nemichthyidae). Suboperculum usually crescentic, curving up around behind operculum; operculum usually shaped like a short-handled spoon and curved downwards;

gill membranes joined to isthmus, opening restricted; interhyal absent (in adults) and sometimes the single hypohyal absent. Epihyal and ceratohyal present, usually slender, the epihyal forked at the dorsal tip, the epihyal and posterior ceratohyal not greatly expanded. Upper Cretaceous to present. Twenty-four families of which three are known only from fossils.

This order is well characterized by the peculiarities of the branchiostegal series, the spoon-shaped operculum bordered posteriorly and often dorsally by the curved suboperculum and by the slender upcurled branchiostegals. These striking characters enable recognition of a fossil anguilliform misplaced amongst the Halosauridae. There is little doubt that all forms investigated belong to the Anguilliformes and that it is a monophyletic group. Regan (1912b) and Trewavas (1932) are the main studies on this group. Gosline (1952) reports on four families, while Asano (1962) reviews the Japanese Congridae.

The peculiarities of the branchiostegal series are doubtless related to the pharyngial-type respiration, the expanded gill cavity and the reduced gill opening. With the adherence of the gill membranes to the isthmus the hyoid arch no longer pivots with gill cover movements. Hence the interhyal is not longer required and is lost. Similarly the hypohyals at the bottom of the arch are reduced to one, or are absent and the epihyal and ceratohyal become very slender. (However the epihyal and ceratohyal are still stout in the fossil families). The branchiostegals no longer impell a moving gill membrane (as in most fishes) and become reduced to reinforcing rods. The branchiostegal membrane here forms a muscular pulsing wall along which peristaltic waves pass and which draw water through the gills and out the gill opening. The mouth need not close during this process.

The origin of the eels is not yet settled. Woodward (1901) held that they were derived from the ganoids. Regan (1912b) concluded that they must be descended from clupeoid fishes. Gregory (1933) thought it not impossible that the eels might stand as a specialized offshoot from near the base of the Iniomi.

The fact that the maxillary enters the gape, together with the physostomus gas bladder indicate that the eels were derived from the Clupeiformes rather than the Myctophiformes. The leptocephalus larvae of the eels would be in agreement with this derivation.

However the strong resemblance between the suboperculum and branchiostegals of the Anguilliformes and the Myctophoidei (in both the suboperculum and branchiostegals curve around the operculum and the branchiostegals are long, slender and curved) do offer some support to the hypothesis of anguilliform derivation from the myctophiforms. The anguillavid Enchelurus syriacus is not unlike the synodontids. Perhaps the best solution to these alternatives is derivation from an elopoid line ancestral to the myctophiforms.

Eel classification is in a confused state. This is only partly due to the absence of knowledge of structures for classifying the different groups. A fairly sound basic framework of internal morphology is present. But many eels have been classified purely on the basis of external appearance and hence may be misplaced.

The branchiostegal series and related bones offer several characters to assist in the classification of the eels. Among these are the number of branchiostegals, whether the upper branchiostegal is expanded into a crescent, the arrangement of the branchiostegals on the hyoid bones, whether the branchiostegal base projects beyond the hyoid arch, the shape of the suboperculum (wedge-shaped or arc-shaped), the presence of the interoperculum, the fusion of the hyoid bones (some authors may have missed the unusual diagonal overlap of the epihyal and ceratohyal found in at least some of the eels), and the presence of a hypohyal. The upper bone of the hyoid arch appears to be the epihyal, the lower ceratohyal and a hypohyal may be present in some. The author has not discovered a bone definitely identifiable as an interhyal in adult eels. But an interhyal is known in larvae of *Anguilla* (de Beer, 1937) and of *Serrivomer* (Bauchot, 1959).

The living eels are generally divided into three groups, the anguillid, congrid and nemichthyid eels. The first two are distinguished by whether the frontal are ankylosed or united by suture. A further group may be distinguished within the congrid-type eels, those in which certain branchiostegals are free from the arch, overlap on the midventral line and are more numerous (17-51 total as opposed to 22 or fewer). They are known in Echelidae, Ophichthidae and apparently in Neenchelidae. These were termed jugostegelia by Parr (1930), who believed that they were not homologous with branchiostegals. But the fact that some branchiostegals in other families may be free from the arch (e.g. a free branchiostegal occurs in *Nessorhamphus*) and the close morphological similarity of jugostegelia and branchiostegals leads one to believe they are homologous. Nevertheless it is useful to retain the term for those secondarily multiplied, overlapping and free branchiostegals found in certain anguilliforms. The jugostegelia probably function in supporting the walls of the elongated branchial cavity.

† Anguillavidae

Branchiostegals: In *Anguillavis quadripinnis* at least 12, in *A. bathshebae* at least 15 slender virgaform branchiostegals. Some of the upper ones broaden out and curl upwards at their hinder ends. In *Enchelurus syriacus* at least 8 slender branchiostegals which curl up behind the suboperculum.

Operculars: The opercular bones appear to resemble those of *Anguilla* but only impressions remain. In *Enchelurus syriacus* the suboperculum is a narrow band which curls around parallel to the operculum ventrally and posteriorly.

Hyoid arch: Relatively stout and well developed, at least epihyal and ceratohyal present.

Relationships: The genus *Enchelurus* has been placed in the Halosauridae by Woodward (1901) and Romer (1955), probably because of the presence of pelvic fins which are absent in living eels. However, several characteristics strongly suggest that the *Enchelurus* belong amongst the primitive anguilliforms: the high number of vertebrae (about 100), the reduced caudal skeleton, pectoral girdle narrow and separated from the skull, the suboperculum and interoperculum curling around behind operculum, the slender virgaform branchiostegals, orbitosphenoid present, anterior neural arches laminar. Neither the terminal mouth, suboperculum nor the branchiostegals agree with the Halosauridae. Of the anguilliforms the presence of pelvic fins indicates that *Enchelurus* should be placed in the Anguillavidae.

A further comment may be made on Woodward (1901). His material of *Enchelurus syriacus* appears to be composed of two species. The holotype (P5998) has at most 20 dorsal rays, while a second specimen (P9168) appears to have at least 52 rays. The latter specimen and *E. anglicus* appear to be closer to *Anguillavis* in the length of their dorsals. *E. syriacus* (P5998) would appear to be the most primitive of eels, in its short dorsal fin. The author disagrees with Regan that *Anguillavis quadripinnis* is a dercetid. The shortness of its dorsal does not remove it from the eels since *Enchelurus* may have an even shorter dorsal, while the rows of bony lateral plates appear merely to be the normal lateral line scales of anguilliforms.

References: Woodward (1901), Hay (1903), Regan (1912b), Romer (1955).

Material examined: None.

† Urenchelyidae

Branchiostegals: In *Urenchelys* about 11 slender branchiostegals; these tend to curve up around the operculum.

Operculum: Complete and entire, suboperculum curves up behind operculum.

References: Woodward (1901), Hay (1903).

Material examined: None.

† Mylomyridae

Branchiostegals: Only four branchiostegals remain in the specimen, these are slender and virgaform, some probably missing.

Operculars: Only a fragment of the operculum remains in the specimen.

References: Woodward (1910).

Material examined: None.

Anguillidae

Pl. X

Branchiostegals: Vary from (8) 9-12 (13, 14). In *Anguilla rostrata* 11 with 9 on the epihyal and 2 on the ceratohyal, all on the external face, all filiform and curving up around to the postero-dorsal corner of the operculum. The upper portion of the uppermost branchiostegal expanded and scythe-like. Branchiostegals of two sides do not overlap.

Operculars: Complete and entire. Operculum paddle-shaped, suboperculum a narrow band curling parallel ventrally and posteriorly about the operculum, interoperculum a large broad triangle. Gill openings lateral and restricted.

Hyoid arch: Interhyal and hypohyal absent. Ceratohyal sends a prong over the dorsal edge of the epihyal; a short gap between their lower edges.

References: Day (1875), Smitt (1895), Ege (1939).

Material examined: Anguilla rostrata, alizarin specimen, NMC60-221, Magdalen Island, Quebec.

Muraenidae

Pl. IX, X

Branchiostegals: 9 in Muraena lentiginosa and Gymnothorax dovii. In the latter the lower 3 of the branchiostegals insert on the epihyal, the rest are free. In Muraena lentiginosa the branchiostegals turn around parallel with or past the upper end of the epihyal; none insert upon the arch. Branchiostegals slender and filiform, curve up around behind to above the posterodorsal edge of operculum; those of the two sides do not overlap.

Operculars: Complete and entire. Operculum cleaver-shaped with its lower edge continuous with hind edge. Suboperculum rectangular, situated anterior to the operculum and not sending an arm around it as in other anguilliforms. Interoperculum small and approximately square. Gill openings lateral and restricted.

Hyoid arch: Consists of very narrow epihyal and ceratohyal. Epihyal angulated and slightly forked at its dorsal end.

References: Gregory (1933), Regan (1912b).

Material examined: Muraena lentiginosa, alizarin specimen, BC59-241, Las Tres Marias, Mexico; Gymnothorax dovii, alizarin specimen, NMC59-141, Maria Magdalena Island, Las Tres Marias Islands, Mexico.

Myrocongridae

Branchiostegals: No data available.

Operculars: No data available. Gill opening lateral and restricted.

Relationships: Apparently only one specimen known. According to Regan as closely related to the Anguillidae as to the Muraenidae.

References: Günther (1870), Regan (1912b).

Material examined: None.

Xenocongridae (Chlopsidae, Chilorhinidae)

Branchiostegals: Vary from 12-21. In *Kaupichthys* 14-15, *Chilorhinus* 15-21, *Chlopsis* 12. In *Kaupichthys diodontus* 15 and, according to the figure, all on the epihyal (labelled as ceratohyal). In *Chilorhinus suensoni* 15-21, usually 17-19. Branchiostegals slender and circle around to postero-dorsal corner of operculum. Rays of sides do not overlap.

Operculars: Complete and entire. In *Chilorhinus brocki* operculum square, suboperculum with small rectangular portion in front of operculum and a narrow arc encircling the posterior operculum; interoperculum roughly rectangular. In *Kaupichthys* suboperculum crescentic and below the paddle-shaped operculum; interoperculum triangular. Gill opening restricted and lateral.

Hyoid arch: Consists of long angulate epihyal and short ceratohyal in *Kaupichthys*; in *Chilorhinus* ceratohyal and epihyal short and stout.

References: Gosline (1950, 1951, 1952), Böhlke (1956), Garman (1899).

Material examined: None.

Dysomminidae

Branchiostegals: In *Dysommina rugosa* about 16.

Operculars: Operculum elongate and low, other bones not mentioned. Gill opening restricted and ventrolateral.

Relationships: According to Böhlke and Hubbs close to Heterenchelidae, Moringuidae and Xenocongridae.

References: Böhlke and Hubbs (1951).

Material examined: None.

Heterenchelidae

Branchiostegals: In *Heterenchelys microphthalmus* 14 long slender branchiostegals, none expanded. Curve up around behind operculum to its postero-dorsal border; those of the two sides not overlapping.

Operculars: Complete and entire. Operculum wing-shaped (*not* paddle-shaped), tapering in its posterior portion; suboperculum elongate and oval, curving under the operculum but not reaching behind its posterior borders; interoperculum a triangle. Gill openings restricted, ventrolateral.

References: Regan (1912b).

Material examined: None.

Moringuidae (Anguillichthyidae)

Branchiostegals: In *Stilbiscus bahamensis* 10 slender branchiostegals which curve up behind the operculum, the uppermost expanded distally with posterior border crenulate. From Trewavas' figure apparently 4 on the epihyal and 6 on the long ceratohyal. Those of the two sides do not overlap. In *Moringua macrochir* 9 filiform branchiostegals.

Operculars: Operculum triangular, suboperculum a straight thin wedge extending up the angled postero-ventral border of the operculum; interoperculum said to be absent. Gill openings restricted, ventrolateral.

Hyoid arch: Epihyal apparently shorter than the ceratohyal; hypohyal absent.

References: Trewavas (1932), Gosline and Strasburg (1956).

Material examined: *Moringua macrochir*, alizarin specimen, NMC63-120-S, Hawaii.

Synaphobranchidae

Branchiostegals: Vary from 13-19. In *Synaphobranchus* 13-15 attached to the external face of the epihyal and ceratohyal and (contrary to Gill) curving up behind the opercular bones. In *Diastobranchus capensis* 18-19 slender curving up around the opercular bones, the upper four being expanded distally. Those of the two sides not overlapping.

Operculars: Complete and entire. Gill openings restricted, in *Synaphobranchus* ventral, longitudinal and almost confluent, in

Diastobranchus ventrolateral and oblique.

Hyoid arch: Epihyal and ceratohyal present.

References: Castle (1961), Gill (1891), Jordan and Evermann (1896).

Material examined: None.

Ilyophidae

Branchiostegals: In *Ilyophis brunneus* 14-15, non-overlapping, sweeping up around the operculars, the upper expanded.

Operculars: At least operculum and suboperculum present. Gill openings restricted, ventral, longitudinal and separated from one another.

References: Gilbert (1891), Jordan and Evermann (1898).

Material examined: *Ilyophis brunneus*, alcoholic specimen, USNM 185665, Florida.

Simenchelyidae

Branchiostegals: 8-10 in *Simenchelys parasiticus*, slender, elongate, curving up around operculars. Distal extremities of upper 4-5 expanded.

Operculars: Complete and entire. Operculum falciform, paralleled by the suboperculum, interoperculum widening upwards. Gill openings restricted, inferior, longitudinal and moderately separated.

Relationships: The expansion of the upper branchiostegals and the ventral gill slits would appear to relate the Synaphobranchidae, Ilyophidae and Simenchelyidae. Gosline (1952) has indicated the

Simenchelyidae belong in the group with ankylosed frontals.

References: Gill (1891b), Castle (1961), Gosline (1952).

Material examined: None.

Congridae

P. IX, X

Branchiostegals: Vary from 8-17, with 5-8 epihyal and 1-4 ceratohyal, all on the external face of the arc. In Taeniconger 10, Nystactichthys 7, Gorgasia 8, Conger 8-10, Uroconger 9-17, Chiloconger 9, Congrosoma 13, Xenomystax 11-12, Ariosoma 8-17, Xenoconger 11 or 12, Anago 9, Alloconger 9-11, Congriscus 9, Rhynochocymba 8-9, Rhynchoconger 8, Promyllantor 9, Japonoconger 9, Congrina 8. In Conger myriaster 9 with 5 epihyal and 4 ceratohyal all on external face of arch, upper three slightly broader. Taeniconger sp. 10 with 8 epihyal and 2 ceratohyal, all on external face of arch, upper 2 expanded distally, remainder filiform. Gorgasia punctata 8 with 7 epihyal and 1 ceratohyal, all on external face of arch, the two tips of the medial branchiostegals of each side meet but do not overlap, curve up around behind operculum. Ariosoma prorigera 12 which curve up around dorsal edge of operculum. Nystactichthys 7 with 5 epihyal and 2 ceratohyal. In none examined do the branchiostegals of the two sides overlap.

Operculars: Complete and entire or crenulate. In Gorgasia operculum paddle-shaped, suboperculum a semicircle below and behind the operculum, interoperculum an elongate triangle larger than or equal to the operculum. In Conger niger operculum crescentic paralleled by narrow suboperculum, interoperculum a large elongate triangle. *Taeniconger sp.* operculum cleaver-shaped, suboperculum sickle-shaped, expanding dorsally behind operculum, interoperculum a long large triangle. In *Japonoconger*, *Promyllantor* and *Congrina* posterior border of operculum crenulate. In *Uroconger lepturus* posterior edge of dorsal tip of suboperculum crenulate. Gill openings ventrolateral, restricted.

Hyoid arch: In *Taeniconger* consists of ceratohyal which sends a dorsal prong over the epihyal and a triangular hypohyal; all bones stout. In *Conger* the stout ceratohyal sends a dorsal prong over the epihyal. In *Nystactichthys* consists of epihyal, ceratohyal and hypohyal.

References: Garman (1899), Asano (1962), Gilbert (1891), Smitt (1895), Day (1875), Böhlke (1957, 1958), Jordan and Evermann (1896), Trewavas (1932), Myers and Wade (1941), Regan (1912b), Gosline (1952).

Material examined: *Taeniconger sp.*, alizarin specimen, NMC62-226-S, Ceralbo Island, Mexico; *Ariosoma prorigera*, alcoholic specimen, BC61-169, Mazatlan, Mexico; *Gorgasia punctata*, alizarin specimen, NMC62-211 & S, Petacalco Bay, Guerrero, Mexico.

Muraenesocidae

Branchiostegals: Vary from 8-22. In *Muraenesox* 16-22, in *Hoplunnis* 8. In *Muraenesox coniceps* 16 virgaform which curve up around operculum, in *Hoplunnis sp.* 8 virgaform branchiostegals which curve up behind the operculars, the upper one of which is expanded. Those of the two sides do not overlap.

Operculars: Complete and entire. In *Muraenesox* and *Hoplunnis* operculum paddle-shaped, suboperculum narrow and curves up around behind operculum, interoperculum triangular. Gill opening ventrolateral, restricted.

Relationships: The disparity in branchiostegal count between the 2 genera is noteworthy.

References: Day (1875), Trewavas (1932), Regan (1912b).

Material examined: *Hoplunnis sp.*, alcoholic dissected specimen, BC61-169, Mazatlan, Mexico. *Muraenesox coniceps*, alcoholic dissected specimen, BC59-665, off Rio Pasigo, Panama.

Derichthidae

Branchiostegals: 7 in *Derichthys serpentinus* all arising from the external face of the fused epihyal-ceratohyal, with swollen bases, slender and curving up behind the operculars, upper ones not expanded. Those of the two sides do not overlap.

Operculars: Complete and entire. Operculum a slender crescent paralleled by a very narrow suboperculum; an elongate, non-triangular, large interoperculum. Gill openings ventrolateral, restricted.

Hyoid arch: A single stout element formed by fusion of the epihyal and ceratohyal.

Taxonomy: Note removal of Gorgasia and Benthenchelys to the Congridae.

References: Beebe (1935), Trewavas (1932), Gosline (1952).

Material examined: None.

Nessorhamphidae

Branchiostegals: 6-7 slender filiform branchiostegals in Nessorhamphus ingolfianus. These curve up around to above the middle of the operculum. The upper and lowest fail to insert on the hyoid arch in Trewavas' specimen, falling slightly short of it, but in Beebe's specimen the lowest does reach the arch. The epihyal and ceratohyal are fused; a hint of the fusion point indicates one branchiostegal on what would be the ceratohyal portion, the remainder on the epihyal portion. Those of the two sides do not overlap.

Operculars: Complete and entire. Operculum paddle-shaped, suboperculum a slender ray which encircles the operculum to its dorso-posterior corner, interoperculum an elongate, slender, non-triangular bone.

Hyoid arch: Epihyal and ceratohyal fused to form a single bone, a trace of separation in one specimen between the anteriormost and adjacent branchiostegal.

References: Beebe (1935), Trewavas (1932).

Material examined: None.

Nettastomidae

Branchiostegals: 7 branchiostegals in *Nettastoma* sp., slender, curve up around operculum to its dorsoposterior corner. Those of the two sides do not overlap.

Operculars: At least oval operculum and narrow curved suboperculum present. Gill opening lateroventral, restricted.

References: Goode and Bean (1896).

Material examined: *Nettastoma* sp., alcoholic specimen, USNM 157939, from south of Great Bahamas Islands.

Neenchelidae

Branchiostegals: In *Neenchelys* 25 filiform branchiostegals which curve up around operculum. Only 5 insert on the hyoid arch (*ergo* 5 branchiostegals + 20 jugostegelia). Those of the two sides apparently overlap.

Operculars: No data available. Gill openings restricted, ventrolateral.

References: Weber and de Beaufort (1916), Bertin and Arambourg (1958).

Material examined: None.

Ophichthidae (Echelidae, Macrocephenchelyidae)

Branchiostegals: Vary from 17-51 filiform branchiostegals (including 4-46 jugostegelia) which overlap those of the other side. In *Brachysomophis* 18, *Caecula* 17, *Chlevastes* 25, *Cirrhimuraena* 24, *Cryptopterenchelys* 22, *Leiuranus* 28, *Myrichthys* 32, *Myrophis* 41-51, Muraenichthys 26-30, Phyllophichthys numerous overlapping, Pisodonophis 29-31. In Myrichthys 28 plus 4 jugostegelia which lie slightly behind the arch. In Myrophis 5 plus 36-46 jugostegelia which overlap. Leptenchelys described as with overlapping jugostegelia. In Muraenichthys cookei 6 branchiostegals + 24 jugostegelia which overlap those of the opposite side.

Operculars: Complete and entire. In Brachysomopsis, Leiuranus and Cirrhimuraena operculum a triangle with apex anteriormost; interoperculum and suboperculum elongate triangles with apex uppermost; the suboperculum in contrast with the others not sending a narrow arc-shaped process around the operculum. In Myrophis operculum oval, in Muraenichthys diamond-shaped, in Echelus paddle-shaped; in all of these the suboperculum encircling the operculum ventrally and posteriorly with a narrow band; interoperculum triangular.

Hyoid arch: Epihyal and ceratohyal fused (according to fig. in Gosline, 1951).

Taxonomy: Gosline (1952) is followed in uniting Echelidae with Ophichthidae.

References: Gosline (1951, 1952), Day (1875), Garman (1899), Myers and Wade (1941), Parr (1930).

Material examined: Muraenichthys cookei, alizarin specimen, NMC63-120-S, Hawaii.

Dysommidae

Branchiostegals: None externally apparent in thick skin - no data available.

Operculars: Gill openings restricted, ventrolateral.

Relationships: Bertin and Arambourg (1958) lump this family with Ilyophidae.

References: Alcock (1889), Tomiyama and Abe (1958), Trewavas (1932), Böhlke (1949), Barnard (1927), Matsubara (1936).

Material examined: None.

Serrivomeridae

Branchiostegals: Vary from 7-8 with 1 ceratohyal and 6-7 epihyal, elongate slender branchiostegals with bases broadened and ends curling up around to posterodorsal corner of operculum. In *Serrivomer samoensis* 7 with 6 epihyal and 1 ceratohyal, the 3 central rays with broadened bases and tips extending beyond hyoid arch. *Serrivomer brevidentatus* 8 with 7 epihyal and 1 ceratohyal only the second and third with tips extending beyond the hyoid arch, the rest inserting on the external face of the arch. *Serrivomer sector* 7 with 6 epihyal and 1 ceratohyal, only the tip of the third branchiostegal projecting beyond the arch, the upper two without flattened bases, all but the third inserting on the external face of the arch. *Platuronides danae* and *P. acutus* 8 with 7 epihyal and 1 ceratohyal, the tips of the second and third extend beyond the hyoid arch. The body of the branchiostegals is filiform, the tips tend to curve up around the operculum and the branchiostegals of the two sides fail to overlap in all species examined.

Operculars: Complete and entire in *Serrivomer* and *Platuronides*. The slender bone lying parallel and dorsal to the hyoid arch (labelled second hypohyal by Beebe) appears to be the interoperculum. Its dorsal position and overlap with the ceratohyal and epihyal is inconsistent with its identification as a hypohyal. Further, a second hypohyal is not found in other more primitive Anguilliformes. Operculum in *Serrivomer* crescentic, suboperculum boomerang-shaped, bordering the anterior and ventral (*not* posterior) edges of the operculum. Gill openings ventral, diagonal and confluent at their lowest point.

Hyoid arch: In adult *Serrivomer* and *Platuronides* a fairly stout ceratohyal and angulated epihyal present; interhyal and hypohyals unknown. Bauchot (1959) indicates an interhyal in larval *Serrivomer* and a single cartilage the precursor of the epihyal and ceratohyal. Lacking prong from ceratohyal extending over the dorsal side of the epihyal.

References: Bauchot (1959), Garman (1899), Beebe and Crane (1936, 1937), Castle (1961), Beebe (1935), Trewavas (1932).

Material examined: *Serrivomer sector*, alcoholic specimen, BC62-163, Guadalupe Island, Mexico.

Nemichthyidae (Avocettinidae)

Branchiostegals: Vary from 7-15, with 7-12 on the epihyal and 0 on the ceratohyal, all inserting on the external face of the hyoid arch, sometimes the tips of the rays extending over beyond the arch. In *Nemichthys* 8-12, *Avocettina* 7-12, *Labichthys* 8-9, *Nematoprora* 9. *Avocettina gilli* 7 with 7 epihyal and 0 ceratohyal, all filiform and inserting on the external face of the hyoid arch, and curving around in an arc up behind the operculum. *Labichthys carinatus* 8 with 8 on the external face of the epihyal and 0 on the ceratohyal, the lower ones with the bases extending beyond the arch. *Avocettina* sp. 12 with 12 epihyal and 0 ceratohyal, all inserting on the external face of the arch.

Operculars: In *Avocettina gilli* operculum and suboperculum trumpet-shaped and not curving around the operculum. Castle's "interoperculum" appears to be the preoperculum (the interoperculum is not illustrated). In *Nematoprora* operculum trumpet-shaped, interoperculum and suboperculum said to be absent.

Hyoid arch: Epihyal and ceratohyal present in *Avocettina* and *Labichthys*.

Relationships: Nemichthyidae lack a branchiostegal on the ceratohyal unlike the Serrivomeridae.

References: Beene and Crane (1937a), Castle (1961), Garman (1899), Bertin and Arambourg (1958), Trewavas (1932), Berg (1947).

Material examined: *Nemichthys scolopaceus*, alcoholic specimen, BC62-162, off Point Loma, California.

Cyemidae

Branchiostegals: Absent.

Operculars: Operculum suturally united with hyomandibular, interoperculum vestigial, suboperculum apparently absent.

References: Berg (1947), Bertin and Arambourg (1958).

Material examined: None.

Avocettinopsidae

Branchiostegals: 8-10 in *Avocettinops*, all on the external face of the epihyal, the bases of the lower two projecting over to the other side, slender and curved upwards. A pair of long slender elements, one on either side of the midline commencing opposite the anterior end of the ceratohyal may represent branchiostegals, but more likely is a split urohyal (partially split in *Avocettina*).

Operculars: Only operculum and suboperculum present.

Hyoid arch: Consists of epihyal, ceratohyal and a hypohyal (equal, respectively, ceratohyal, hypohyal and glossohyal of Bertin and Arambourg). Epihyal and ceratohyal non-overlapping.

References: Bertin and Arambourg (1958), Böhlke and Cliff (1956), Norman (1939).

Material examined: None.

ORDER BELONIFORMES

Branchiostegals (9) 10-15, with 2-4 on the epihyal, 7-9 ceratohyal, and 0-3 hypohyal (Bertelsen and Marshall give 7-12 for the ceratohyal; they apparently included the hypohyal branchiostegals as on the ceratohyal), all except 1 or 2 anteriormost branchiostegals which are free insert on the external face of the arch, and are acinaciform (but laminar). One hypohyal (the ventral), ceratohyal and epihyal present, the upper hypohyal and the interhyal being absent. Ceratohyal and epihyal sutured. Opercular bones complete, entire and without spines; operculum often with a slight notch on anteroventral border; the suboperculum v-shaped with an arm in front and behind the operculum, the latter arm forming about 2/3 of the posterior border of the gill cover. Gill membranes separate. Eocene to present. Four living families plus two fossil families questionably associated with this order.

This order is clearly identifiable by the 10-15 branchiostegals on the external face of the hyoid arch, the presence of only a single hypohyal (lower) and the absence of an interhyal. The five living families form a natural group. The two fossil families are provisionally left in this order. Knowledge of their anatomy is sparse and hence placement is difficult. The Tselfatoidei, placed in this order by Bertin and Arambourg (1958), have been shown to belong amongst the Clupeiformes.

Regan (1912a) considered this order derived from the malacopterygous physostomes but that it showed certain resemblances to the Cyprinodontiformes. Hubbs (1920) considered the branchiostegals wholly similar to those in typical Clupeiformes, an opinion later affirmed by Regan (1929). The otoliths of Beloniformes, according to Frost (1926), retain elopine and clupeoid features in details of the sagitta, while some species show resemblances to the forms of the orders Percopsiformes and Anguilliformes; they differed considerably from those of the Cyprinodontiformes. Gregory (1933) believed the facts justified Regan's placement ahead of the Microcyprini. Gosline (1961) indicated that the Beloniformes have the myctophiform type of inner pelvic radial organization. Freihofer (1963) stated the ramus lateralis accessories resembled that of Atherinidae. Holtsvoogd (1963) stated that the Beloniformes have a retractores arcuum branchialum like the acanthopterygians, unlike the malacopterygians.

The lack of spines, cycloid scales, abdominal pelvics with 6 soft rays, numerous laminar branchiostegals most of which are on the external face of the hyoid arch and lack of dorsal and ventral nasal sacs (Burne, 1909) are all characters commensurate with placement amongst the malacopterygians. The lack of supramaxillaries, orbitosphenoid, opisthotic, intermuscular bones, interhyal, pelvic splint and mesocoracoid; the physoclistic gas bladder and upper jaw bordered by premaxillary alone, the thirteen branched caudal rays, and reduced caudal skeleton; and the sutured epihyal and ceratohyal are all characters indicating a high level of advancement within the malacopterygians. The upper jaw bordered solely by the premaxillary and the structure of the pelvics would both favour the derivation of the Beloniformes on a common line with the Myctophiformes from a clupeiform ancestor.

The peculiar hyoid arch lacking an interhyal and upper hypohyal and with epihyal and ceratohyal sutured may be regarded as adaptions to supporting an elongate lower jaw. Parallel adaptions occur in other orders. In the long-jawed Lepisosteidae the epihyal and ceratohyal tend to fuse and the interhyal is obsolescent. In the long-snouted Syngnathiformes the hyoid bones strongly suture to form a single element. Thus the arch in the Beloniformes may be regarded as an adaption by the ancestral forms (retained in forms with jaws shortened) to carrying long jaws, rather than as a sign of relationship to the acanthopterygians. However, it might be possible that the Beloniformes branched off the line still close to the clupeiforms and myctophiforms which gave rise to the beryciforms and which had already developed a sutured epihyal and ceratohyal. The possession of the retractores arcuum branchialum is in line with this thesis.

† Rogeniidae, *incertae cedis*

Branchiostegals: No data available.

References: Jordan (1923).

† Forficidae, *incertae cedis*

Branchiostegals: No data available.

References: Jordan (1923).

Suborder Scomberesocoidei

Belonidae

Branchiostegals: Vary from 9-15, with 3 epihyal, 8 ceratohyal and 0-1 hypohyal. In Belone (including Tylosurus and Ablennes) 9-15. Belone houtuyni (formerly marinus) 11-12 with 3 epihyal, 8 ceratohyal and 0-1 hypohyal, all on the external face of the arch except perhaps the lowest which may lie free. All laminar acinaciform, bend half way up behind the gill cover. The bases of those inserting on the ceratohyal are expanded into an oval.

Operculars: Complete and entire. In Belone operculum with small notch on anteroventral border, suboperculum V-shaped with longer posterior arm extending 2/3 up posterior border of operculum, interoperculum elongate and hidden by lower arm of preoperculum. Gill membranes separate.

Hyoid arch: In Belone interoperculum and dorsal hypohyal absent, epihyal and ceratohyal sutured and of even width. Hypohyal set into the lower part of the hypohyal.

References: Day (1875), Smitt (1892), Weber and de Beaufort (1922), Mees (1962).

Material examined: Belone houttuyni, alizarin specimen, NMC 62-127 & S, Florida; alizarin specimen, NMC62-73 & S, North Carolina.

Scomberesocidae

Branchiostegals: Vary from 14-15. In Cololabis 14-15, Scomberesox 14. Cololabis saira 14-15 with 3-4 epihyal, 8-9 ceratohyal and 2-3 hypohyal, all on the external face of the hyoid arch, although the anteriormost may lie free in the gill membrane. Branchiostegals almost rectilinear, do not curve up behind gill cover, upper ones broad, laminar, pointed, lower ones attenuate.

Operculars: Complete and entire. In Cololabis operculum triangular with slight notch on anteroventral border, suboperculum v-shaped with posterior arm longer and reaching $\frac{3}{4}$ of way up posterior border of operculum, interoperculum largely hidden by preoperculum. Gill membranes separate.

Hyoid arch: Interhyals and upper hypohyal absent in Cololabis, epihyal and ceratohyal sutured, hypohyal inserted into ventral margin of ceratohyal.

References: Smitt (1892), Chapman (1943a).

Material examined: Cololabis saira, alizarin specimen, BC60-194, off Queen Charlotte Islands, British Columbia; alizarin specimen, NMC60-312, 620 miles west of Vancouver Island, British Columbia.

SUBORDER EXOCOETOIDEI

Hemirhamphidae (Evolantiidae?)

Branchiostegals: Vary from 10-14 with 3 epihyal, 9 ceratohyal and 1 hypohyal. In Hyporhamphus 13, Hemirhamphus 10-14, Fodiator 10-12, *Zenarchopterus* 10-11, *Euleptorhamphus* 10. In *Hyporhamphus unifasciatus* 13 with 3 epihyal, 9 ceratohyal and 1 hypohyal, all external except the anteriormost which is free, all laminar acinaciform, curving to about half way up the gill cover. Bases of branchiostegals only slightly expanded. In a sample of 34 *Fodiator acutus* from a single collection the following variation was encountered: 10 (9 specimens), 11 (20) and 12 (5).

Operculars: Complete and entire, operculum with small notch on antero-ventral border, suboperculum v-shaped with posterior arm longer and ascending 2/3 of way up posterior border of operculum, interoperculum elongate, triangular and hidden by the preoperculum. Gill membranes separate.

Hyoid arch: Interhyal and upper hypohyal absent, epihyal and ceratohyal sutured, hypohyal projects into ventral margin of the ceratohyal.

References: Day (1875), Chevey (1932), Hubbs (1920), Smith, J.L.B. (1955), Weber and de Beaufort (1922).

Material examined: *Hyporhamphus unifasciatus*, alizarin specimen, NMC62-246, San Lucas, Mexico. *Fodiator acutus*, 34 alcoholic specimens, BC61-116, Acapulco, Mexico.

Exocoetidae (Oxyporhamphidae)

Branchiostegals: Vary from 10-13 with 2 epihyal, 7-8 ceratohyal and 0-3 hypohyal, all being on the external face of the hyoid arch except for the anterior 0-3 which lie free in the gill membrane. In *Oxyporhamphus* 10, *Exocoetus* 10-11, *Fodiator* 11, *Cypselurus* 11-13, *Progonicthys* 10-12. In *Cypselurus furcatus* 11 with 2 epihyal, 7 ceratohyal and 3 hypohyal, all on the external face of the arch except the anterior 3 which lie free in the gill membrane, all laminar acinaciform. *Cypselurus californicus* 10 with 2 epihyal and 8 ceratohyal, all laminar acinaciform (anteriormost ray missing?). *Fodiator acutus* 11 with 2 epihyal, 7 ceratohyal and 2 hypohyal, all on the external face of the arch except for the anterior 2 which lie free in the gill membrane, all laminar acinaciform and curve half way up behind the gill cover.

Operculars: Complete and entire, in *Fodiator* and *Halocypelsus* operculum triangular and lacking a ventral notch in the anteroventral border, suboperculum v-shaped with posterior arm longest and ascending at least half way up the posterior edge of the operculum, interoperculum triangular and mostly hidden by the preoperculum. Gill membranes separate.

Hyoid arch: Interhyal and lower hypohyal absent, epihyal and ceratohyal joined by interdigiting prongs, hypohyal set into the ventral border of the ceratohyal.

Taxonomy: Parin (1963) includes the Oxyporhamphidae in the Exocoetidae.

References: Day (1875), Smitt (1892), Abe (1953, 1954b), Brunn (1935), Parin (1960).

Material examined: Cypselurus californicus, skeletal specimen, USNM 26907, California; Cypselurus furcatus, alizarin specimen, BC59-529, Gulf of Mexico, U.S.A.; Fodiator acutus, alizarin specimen, NMC58-197, Mexico.

ACANTHOPTERYGII

Branchiostegals 1-11, nearly always acinaciform. Gulars absent. Epihyal and ceratohyal usually sutured. Not infrequently, spines on opercular bones. Almost always with 4 external branchiostegals and 0-4 (5-7) ventral or internal.

Arambourg (1954) named a new species of Upper Cretaceous fossil, Omosoma simum. He placed it in the Stromateidae while Romer (1955) included it in Polymixiidae. If the reported following characters are true of it, then it has significance in the origin of the acanthopterygians. It is more primitive than known acanthopterygians in possession of intermuscular bones, 12 branchiostegals, mouth bordered half by premaxillaries and half by maxillaries, and 20 branched caudal rays. Yet the presence of spines in the dorsal and anal fins, thoracic ventrals with 5 rays, and vertebrae 10 + 15-16 indicate its pertinence to the acanthopterygians. These characters, if true, probably justify the creation of a new family for it, but more importantly qualify it as a link between the malacopterygians and acanthopterygians.

ORDER BERYCIFORMES

Branchiostegals (5?) 7-9 with 2 (3) epihyal (Bertelsen and Marshall report 1-3) and 2-7 ceratohyal (and 3 or 4 hypohyal in Polymixiidae), 4 external and 4 ventral, all acinaciform, relatively broad, sometimes with an anterior prolongation of the base of some of the upper branchiostegals. Two hypohyals, a short ceratohyal usually with a foramen, a short epihyal and interhyal. Epihyal and ceratohyal separate, not ankylosed together (but see note below about ancestors). Opercular bones complete, with or without spines. Suboperculum and interoperculum may have series of small spines. Gill membranes separate. Upper Cretaceous to present. Fourteen families included, two of which are known only from fossils.

According to Katayama (1960), Ostracoberyx, which Berg (1947) includes as the Ostracoberycidae in the Beryciformes, belongs in the Serranidae; Katayama is followed. Regan (1911) revised the order.

According to Regan (1929) this order is directly intermediate between the clupeoids and the Perciformes. Frost (1927) found the sagitta of Holocentridae was similar in general form to that of Elops, but that the sulcus was distinctly percoid. According to Gosline (1961) the caudal skeletons of the basal berycoids are nearer the basal clupeiform type (Albula) than is that of Clupea. Gosline (1963a) derives the beryciforms from the myctophiforms. The berycoids have the iniomous expansion of the inner pelvic radial.

The author agrees with Regan that these fishes are intermediate in some characters between the malacopterygian and acanthopterygian fishes, although definitely belonging in the acanthopterygian group. The following characters of the beryciforms are primitive: 1-2 supramaxillaries; orbitosphenoid usually present; 16-17 branched caudal rays; numerous pelvic rays; a postterminal centrum in primitive families; fairly numerous branchiostegal rays 7-9. On the other hand, most acanthopterygian characters are present: the form and arrangement of the branchiostegals is acanthopterygian; the upper jaw is bordered by the premaxillary alone; there are ctenoid scales and true fin spines; the gas bladder is physoclistic; there is a subocular shelf; premaxillaries are protrusable; there may be an opercular spine. These characters indicate definite acanthopterygian placement.

The next question to ask is whether the beryciforms arose from the Myctophiformes or the Clupeiformes. The shape and disposition of the branchiostegals, the shape of the inner pelvic ray, the position of the pelvic fins, the bordering of the upper jaw by the premaxillary alone, absence of a mesocoracoid, physoclistic gas bladder tend to favor the Myctophiformes and exclude the Clupeiformes. The presence of an orbitosphenoid in the Beryciforms slightly favors the Clupeiforms as does the caudal skeleton (Gosline, 1961). Perhaps the best resolution is derivation of the Beryciforms and Myctophiformes on a common line from primitive clupeiforms (such as elopoids, tselfatoids, ctenothrissoids or clupeoids).

Regan (1911) created a new order for the families Melamphaidae and Stephanoberycidae which he thought were derived from the berycoids but differed from them in the toothless palate, absence of a subocular shelf, triangular shape of the single supramaxillary and in the absence of an orbitosphenoid. (The Anoplogasteridae and possibly the Gibberichthyidae might also now be considered related to this group). However, later (1929) he withdrew this order and provisionally included them amongst the Berycomorphi. The latter action has been followed by Berg but not by Bertin and Arambourg (1958). The branchiostegal number and pattern would indicate that these families are related to the Beryciformes. The possession of a perforated ceratohyal by the Melamphaidae would also indicate that they belong with other Beryciformes. Since the characters by which this group of families differ are chiefly ones of degeneration, perhaps due to a bathypelagic existence, and there is good evidence of beryciform affinity, it might seem preferable to include them within the Beryciformes, perhaps as a suborder. (However, data are lacking on the Gibberichthyidae).

In the Beryciformes examined a suture is lacking between the epihyal and the ceratohyal. However, the suture known in both the Zeiformes and Perciformes, both of which are descended from the Beryciformes or their close ancestors. It therefore might be supposed that the immediate ancestors of the Beryciformes, from which these three orders descended, possessed an epiceratohyal suture. The suture would then have been secondarily lost in the Beryciformes, as they have become lost in some representatives of other acanthopterygian orders. See also comment on the fossil Pycnosterinx under the Polymixiidae.

Reasons have already been discussed for removal of the Barbourisioidei from the Beryciformes to the Myctophiformes. The Trachyberycidae, formerly included in the Beryciformes, are probably bramids (Mead and Maul, 1958).

† Berycopsidae

Branchiostegals: At least 5 in *Berycopsis*.

Operculars: Complete and apparently entire.

Hyoid arch: Ceratohyal apparently not perforated.

References: Woodward (1901), (1902-12).

† Dinopterygidae

Branchiostegals: No data available.

References: Woodward (1901).

Berycidae

Branchiostegals: 8-9 in † *Hoplopteryx*; 8 sometimes 7 or 9 in *Beryx*. *Beryx splendens* 7 with 2 on the epihyal and 5 on the ceratohyal. In † *Hoplopteryx simus* 6 insert on the ceratohyal. Branchiostegals, curved, fairly broad, acinaciform.

Operculars: Complete and entire, operculum with blunt projection on † *Hoplopteryx* and *Beryx*. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and 2 hypohyals in † *Hoplopteryx* and *Beryx*; the ceratohyal is perforated by an oval foramen.

References: Abe (1959), Günther (1887), Jordan and Evermann (1896), Smitt (1892), Maul (1954), Starks (1904a), Woodward (1901), (1902-12).

Material examined: None.

Holocentridae (Myripristidae)

Fig. 3

Branchiostegals: Usually 8, rarely 7. In Holocentrus 8; Myripristis 8, exceptionally 7. Holocentrus suborbitalis 8, with 2 epihyal and 6 ceratohyal, 4 on the external face and 4 on the ventral face of the hyoid arch, all acinaciform, upper 4 with slightly enlarged bases. Holocentrus ascensionis 8 with 2 epihyal and 6 ceratohyal.

Operculars: Holocentrus with opercular bones complete and serrate, operculum with 1 or more strong spines. Myripristis opercular bones complete and serrate, opercle usually with spine. Gill membranes separate.

Hyoid arch: In Holocentrus consists of an interhyal, a broad epihyal and ceratohyal and two hypohyals. Epihyal and ceratohyal separate. Groove on outer face of epihyal and ceratohyal. Ceratohyal imperforate.

References: Fowler (1936), Day (1875), Starks (1904a), Hubbs (1920), Meek and Hildebrand (1923), Weber and de Beaufort (1929).

Material examined: Holocentrus suborbitalis, alizarin specimen, BC60-17, from Acapulco, Mexico.

Trachichthyidae (Korsogasteridae)

P. X

Branchiostegals: Constantly 8. In Aipichthys 8, Hoplostethus (incl. Leiogaster) 8, Gephyroberyx 8, Korsogaster 8, Trachichthys 8. Hoplostethus intermedius 8 with 2 epihyal and 6 ceratohyal, 4 external and 4 ventral, all acinaciform, the uppermost with an oval elongate base, the next three with slightly enlarged bases. Hoplostethus japonicus 8 with 2 epihyal and 4 ceratohyal.

Operculars: In Hoplostethus a small opercular spine, rest of opercle smooth, suboperculum entire, interoperculum spinulose. Gill membranes separate.

Hyoid arch: Consists in Hoplostethus of interhyal, broad epihyal and ceratohyal and two hypohyals; ceratohyal with central oval foramen.

References: Woodward (1902-12), Fowler (1936), Parr (1933a), Garman (1899), Jordan and Evermann (1896), Starks (1904a), Maul (1954), Weber and de Beaufort (1929).

Material examined: Hoplostethus intermedius, alizarin specimen, NMC62-245, New Zealand.

Diretmidae

Branchiostegals: In Diretmus argenteus 7-9.

Operculars: In Diretmus opercular without spine, opercular bones apparently complete and entire judging from figures.

References: Johnson (1863), Fowler (1936), Koefoed (1953), Maul (1949), Abe (1953a).

Material examined: None.

Caristiidae (Elephanoridae)

Branchiostegals: In Platyberyx (5?) 7, Caristius 7. Maul gives a count of 7 for Platyberyx opalescens, a number which would appear normal for the family; but Koefoed and Fowler give a count of 5. Whether the latter authors have missed two rays in their counts (which seems most likely to the author) or whether some specimens actually have 5 rays is not certain.

Operculars: Opercular bones apparently complete and entire in Platyberyx.

References: Koefoed (1953), Maul (1949), Fowler (1936).

Material examined: None.

Anomalopidae

Branchiostegals: 8 in Anomalops and Photoblepharon.

Operculars: Judging by figures, complete and entire.

References: Weber and de Beaufort (1929), Bertin and Arambourg (1958).

Material examined: None.

Monocentridae

Pl. X

Branchiostegals: Monocentris japonicus 8 with 2 epihyal and 6 ceratohyal, 4 external and 4 ventral, all acinaciform, the lower 3 but one spinulose with 3-7 spinules on centre of ventral side.

Operculars: Opercular bones complete and spinulose, operculum with blunt outer spine in *Monocentris*.

Hyoid arch: Consists of large interhyal, ceratohyal, epihyal and two hypohyals; the ceratohyal with an oval perforation.

References: Starks (1904a).

Material examined: *Monocentris japonicus*, alizarin specimen, NMC62-142 & S, South Africa.

Polymixiidae

Branchiostegals: *Polymixia* with either 7 or 8 (counting barbel splints), the posterior 4 being regular acinaciform branchiostegals with 1½ on the epihyal and 2½ on the ceratohyal, these 4 being on the external face of the hyoid arch and having slightly enlarged bases. An attenuate barbel arises from the posterior corner of the lower hypohyal. Around the base of this barbel are three small curved splints which support it. These splints according to Starks (1904a) are homologous with branchiostegals. This theory explains why *Polymixia* apparently has only 4 branchiostegals although all other beryciforms have 7 or 8. There is a further possibility that the barbel itself represents a modified branchiostegal, although its form does not suggest this.

Operculars: Complete, entire and lacking spines. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal separate. Ceratohyal imperforate.

Relationships: Because the Mullidae also have hyoid barbels and a branchiostegal count of four, authors have suggested that the two families are related. However, Starks (1904a) has pointed out that the barbel structure is basically different. Since other structures do not support the nearness of the families, the Mullidae should not be placed in the Beryciformes. *Pycnosterinx*, which has been placed in the Polymixiidae by Romer, has from at least 5 branchiostegals to 11. Since 11 branchiostegals is more than is possessed any other genus in the order (sometimes up to 9) it would be worthwhile investigating whether this genus really belongs in the order.

References: Starks (1904a), Davis (1887), Fowler (1936), Lachner (1955), Jordan and Evermann (1896).

Material examined: None.

Melamphaidae

Pl. X

Branchiostegals: 8 in the genera *Melamphaës*, *Scopelogadus*, *Scopeloberyx* and *Poromitra*, 7 in the genus *Sio*. In *Melamphaës lugubris* 8 with 2 epihyal and 6 ceratohyal, 4 on the external and 4 on the ventral face of the arch, upper 2 crescentic, the rest acinaciform.

Operculars: Complete and entire except for the operculum which is crenulate. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and 2 hypohyals. Epihyal and ceratohyal separate. Ceratohyal with an oval foramen.

References: Garman (1899), Günther (1887), Weber and de Beaufort (1929), Moss (1962).

Material examined: *Melamphaës lugubris*, alizarin specimen, NMC61-187, Pacific Ocean at 47½° N, 146½° W.

Anoplogasteridae (Caulolepidae)

Branchiostegals: *Anoplogaster* (= *Caulolepis*) 8. *A. cornuta* 8 with 3 epihyal and 5 ceratohyal, 4 external and 4 ventral, all acinaciform.

Operculars: Operculum with two blunt spines. Gill membranes united and free from isthmus.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and 2 hypohyals.

References: Fowler (1936), Maul (1954), Günther (1887).

Material examined: *Anoplogaster cornutus*, alcoholic specimen, BC62-164, south of Guadalupe Island, Mexico.

Stephanoberycidae

Branchiostegals: *Stephanoberyx* 7, *Malacosarcus* 8. According to Hubbs *Stephanoberyx* has the standard acanthopterygian pattern.

Operculars: Complete and spinulose. Gill membranes separate.

References: Goode and Bean (1896), Günther (1887), Hubbs (1920), Jordan and Evermann (1896).

Material examined: None.

Gibberichthyidae

Branchiostegals: No data available.

Operculars: Complete and entire except operculum with a broad flat spine. Gill opening wide according to figure.

References: Parr (1933a).

Material examined: None.

ORDER LAMPRIDIFORMES

Branchiostegals 5-7 with 0-3 epihyal and 3-5 ceratohyal, 4-6 external and 0-2 ventral; opercular bones complete, entire and without spines; gill openings separate or narrowly joined to isthmus; interhyal, epihyal, ceratohyal and one to two hypohyals present; the upper hypohyal, if present, above the anterior end of the ceratohyal; epihyal and ceratohyal united by suture (although their borders may be serrate). Oligocene to present. Six families.

Boulenger (1904) considered the Lamprididae close to the Gasterosteidae. Regan (1907a) considered the Allotriognathi derivable from the Beryciformes. In Velifer (Frost, 1927) the principal otolith is fairly generalized and resembles that of the berycoid Polymixia. Gosline (1961) stated the caudal skeleton of Velifer set it to one side of the lineage leading to percoids. Gosline (1963a) questionably derives the lampridiforms from a myctophiform lineage. The absence of opercular spines, up to 17 branched caudal rays, the numerous soft pelvic rays and the presence of an orbitosphenoid all indicate this order to be more primitive than other acanthopterygian orders except the Beryciformes. The insertion of all the branchiostegals on the external face of the hyoid arch in the Regalecidae and Stylephoridae is probably a secondary condition. The ceratohyal foramen in Stylephoridae is evidence for placement among primitive acanthopterygians.

SUBORDER VELIFEROIDEI

Veliferidae

Branchiostegals: 6 placed very close together in Velifer and Metavelifer. Counts of 4, are probably erroneous, as indicated by Walters.

Operculars: Complete and entire, no spines. Gill membranes narrowly joined to isthmus.

References: Walters (1960), Gregory (1933), Regan (1907, 1907a).

Material examined: None.

SUBORDER LAMPRIDOIDEI

Lamprididae (Lampridae)

Branchiostegals: 6-7 acinaciform in Lampris.

Operculars: Complete and entire, no spines.

References: Jordan and Evermann (1896), Smitt (1892), Gregory (1933), Regan (1907a).

Material examined: None.

SUBORDER TRACHIPTEROIDEI (TRACHYPTEROIDEI)

Lophotidae

Branchiostegals: 6 in *Eumecichthys*.

References: Abe (1954).

Material examined: None.

Trachipteridae (Trachypteridae)

Branchiostegals: *Trachipterus* with 6, perhaps rarely 7, with 3 epihyal and 3 ceratohyal, 4 on the external and 2 on the ventral face of the arch, all slender acinaciform, hidden by elongate interoperculum.

Operculars: Complete and entire, without spines, thin, papery, striated. Gill membranes separate.

Hyoid arch: Interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal separate. Dorsal hypohyal lies above the anterior end of the ceratohyal. Cartilage lies between the lower hypohyal, ceratohyal and epihyal. Arch short and wide.

References: Hubbs (1920), Jordan and Evermann (1896), Smitt (1892), Weber and de Beaufort (1929).

Material examined: *Trachipterus rexsalmonorum*, alizarin specimen, SU 36830, Monterey, California.

Regalecidae

Pl. X

Branchiostegals: 6 with 1 epihyal and 5 ceratohyal. In Regalecus argenteus all, unusually for an acanthopterygian, an the external face of the hyoid arch and slender acinaciform.

Operculars: Complete, entire and without spines.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal with opposing edges serrate (reminent of suture?) and separated by cartilage. Upper hypohyal extends over the dorsal edge of the anterior end of the ceratohyal. Lower hypohyal separated from its neighbours by cartilage.

References: Parker (1890), Hubbs (1920), Day (1958), Smitt (1892), Benham and Dunbar (1906).

Material examined: None.

SUBORDER STYLEPHOROIDEI

Stylephoridae

Pl. X

Branchiostegals: In Stylephorus 5 all on the external face of the ceratohyal, with their bases on the dorsal edge of the ceratohyal and their tips pointing upwards. This position, on the upper edge of the ceratohyal is unique.

Operculars: Complete and entire, without spines.

Hyoid arch: Consists of an anterior subrectangular epihyal, a rectangular ceratohyal with a ventral beryciform foramen, and a single posterior, triangular hypohyal.

The unique placement of the branchiostegals deserves some discussion. Starks (1908) considered the hyoid elements were in their normal position with the hypohyal anteriormost and the epihyal posteriormost. If this interpretation is true then the branchiostegals must have migrated across the anterior face, from the lower to the upper edge and turned through 180°. Also the first branchiostegal became smaller than the last (contrary to the usual condition).

However, another interpretation of the hyoid elements is possible. The hyoid arch is normally close to vertical in this order. If the lower end of the arch moved posteriorly the normally dorsoanterior edge of the arch would become ventral and the branchiostegals would lie on the upper side. An impetus for such a movement of the arch is conceivable. The lower jaw in this suborder is enormously elongate. It is possible that during evolution of this elongate jaw the prolongation carried the lower end of the arch posteriorly and inverted it. Support for this theory lies in the shape of the ceratohyal in this suborder, concave above and concave below, and in the ventral position of the ceratohyal foramen. These conditions are the inverse of the normal. This theory also explains the odd dorsal position and size sequence of the branchiostegals. Evidence therefore favours interpretation of the arch as rotated forward. Thus Starks' epihyal is the hypohyal, and his hypohyal is the epihyal. A similar inverted position of the arch is found in stomiatoids when the lower jaw is thrown forward.

References: Starks (1908), Fowler (1936), Hubbs (1920).

Material examined: None.

ORDER ZEIFORMES

Branchiostegals (5) 6-8, with 0-1 (4) epihyal and 2-8 ceratohyal, 4 on the external and 3-4 on the ventral face of the hyoid arch, all acinaciform. Two hypohyals, a ceratohyal, epihyal and interhyal present. Suture between the epihyal and ceratohyal. Ceratohyal with a foramen (foramen may lack upper border and open dorsally). Opercular bones complete and without spines; interoperculum may be spinulose. Gill membranes separate. Palaeocene to present. Seven families, one known only from fossils.

Zeoids have been considered closely related to the chaetodonts (Starks, 1898, 1902). However, several characters show the zeoids to be more primitive and not closely related to the chaetodonts: the high number of branchiostegals; high number of vertebrae; high number of pelvic rays. Further the zeoids, unlike the chaetodonts, lack a subocular shelf, and so could not have given rise to them. The number and pattern of the branchiostegal rays and the perforated ceratohyal agree on the other hand with the Beryciformes. There is also agreement in the number of vertebrae, otoliths (Frost, 1927), pelvic rays and other characters. Since the number of supramaxillaries, caudal rays, range of pelvic rays, and range of branchiostegals is lower than in the Beryciformes and since the subocular shelf is present in the Beryciformes, the Zeiformes must be derived from the Beryciformes (or their close relatives), rather than vice versa. Gosline (1961, 1963a) indicates the Zeiformes arising from the Beryciformes, Fig. 4, and Regan (1910) had already evinced this opinion. The perforated ceratohyal is an important new character in relating these two groups.

The branchiostegal arrangement in the Caproidae is said to be 4 epihyal and 2 ceratohyal (Starks, 1902) and this differs considerably from that in other Zeiformes where it is 0-1 epihyal and 6-8 ceratohyal. This arrangement deserves checking.

Various specialized or degenerate characters such as only 13 branched caudal rays, indicate that the Zeiformes are not ancestral to the perciform assemblage, an ancestry which must be left to the Beryciformes.

Classification of this order follows Myers (1960).

Zeidae

Pl. XI

Branchiostegals: Vary from 7-8. In *Zeus* 7 (8) (Starks stated 8 in text but figures only 7; other authors and my own observations show 7); *Cyttus* 7-8; *Capromimus* 7; *Parazen* 7. *Zeus faber* 7 with 0 epihyal and 7 ceratohyal, 4 external and 3 ventral, all acinaciform, the 2nd to 5th have an anterior basal projection. *Capromimus abbreviatus* 7 with 1 epihyal and 6 ceratohyal, 4 on the external and 3 on the ventral face of the hyoid arch, all acinaciform. *Cyttus novaezeelandis* 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 ventral, all acinaciform.

Operculars: In *Zeus* complete and entire, without spines, v-shaped suboperculum occluding posterior border of operculum, interoperculum very long and nearly vertical in position.

Hyoid arch: In Zeus and Capromimus consists of interhyal, deep epihyal and ceratohyal, and two hypohyals. The epihyal and ceratohyal with interdigitating prongs (incipient suture) extending towards one another, but not in contact, in Zeus. Zeus with oval foramen in centre of ceratohyal; Capromimus with large foramen lacking dorsal border. In both, the fifth and sixth branchiostegals insert in notches on the lower border of the ceratohyal.

References: Fowler (1936), Mead (1957), Starks (1898), Myers (1960).

Material examined: Zeus faber, alizarin specimen, NMC62-144 & S, South Africa; alcoholic specimen, BC57-58, England; Cyttus novaezeelandicus, alcoholic specimen, BC56-269, Cook Strait, New Zealand.

Zeniontidae

Branchiostegals: Zenion 8, Cyttula 7.

References: Weber and de Beaufort (1929), Jordan and Evermann (1898).

Material examined: None.

Macrurocyttidae

Branchiostegals: At least 5 judging from Fowler's figure.

Operculars: Complete and entire, gill opening moderate, extends forward to below eye.

References: Fowler (1934), Myers (1960).

Material examined: None.

Oreosomatidae

Pl. XI, XII

Branchiostegals: In Allocyttus 7, Neocyttus 7, Xenocyttus 7, Oreosoma 7. Neocyttus gibbosus 7 with 1 epihyal and 6 ceratohyal, 4 upper external, next 2 ventral and lowest external, all acinaciform, lowest two but one fitting into notches on lower side of ceratohyal.

Operculars: In Neocyttus complete and entire except for interoperculum which is spinulose, operculum an elongate triangle with its posterior border occluded by the v-shaped suboperculum, suboperculum with rectangular projection extending ventroposteriorly.

Hyoid arch: In Neocyttus consists of interhyal, deep epihyal and ceratohyal and 2 hypohyals. Epihyal and ceratohyal separate, without prongs. Ceratohyal with large foramen, lacking dorsal border. The 5th and 6th branchiostegals insert in notches on the lower border of the ceratohyal.

References: Johnson and Hajny (1952), Abe (1957a), Jordan and Evermann (1898).

Material examined: Neocyttus gibbosus, alizarin specimen, NMC62-245 & S, 25 miles off Tauranga, New Zealand.

Grammicolepidae

Branchiostegals: 7 in *Grammicolepis* and *Xenolepidichthys*, all on the ceratohyal with 4 on the external and 3 on the ventral face of the arch.

Operculars: Complete; rugose border on upper operculum of *Grammicolepis*, others entire.

References: Goode and Bean (1896), Myers (1937).

Material examined: None.

Caproidae (Antigoniidae)

Branchiostegals: Varies from 5-6. *Antigonia* 6, *Capros* 5, *Crassispinus* 6. *Antigonia rubescens* 6 with 4 epihyal and 2 ceratohyal.

Operculars: In *Antigonia* opercular bones complete and entire, interoperculum elongate and horizontal.

Hyoid arch: In *Antigonia* consists of interhyal, deep epihyal, ceratohyal and two hypohyals. The ceratohyal is pierced by a large foramen near its upper edge.

References: Starks (1902), Fowler (1936), Maul (1948), Goode and Bean (1896), Berry (1959a).

Material examined: None.

† Palaeocentronotidae

Branchiostegals: In †*Palaeocentronotos boeggildi* 6 acinaciform present.

Operculars: Small operculum and slender interoperculum known.

Reference: Kuhne (1941).

Material examined: None.

ORDER BATHYCLUPEIFORMES

Branchiostegals 7, with 2-2½ epihyal and 4½-5 ceratohyal, 4 on the external and 3 on the ventral face of the hyoid arch, all acinaciform. Interhyal, epihyal and ceratohyal present; number of hypohyals unknown. From external dissection epihyal and ceratohyal separate, not sutured together. Opercular bones complete and entire. Gill membranes separate. Fossils not known. A single family.

The placement of this family has varied. Its discoverer preferred it to the Clupeidae, but Boulenger and Weber (from Berg, 1947) placed it in the Pempheridae. Regan (1913) placed it in the Suborder Percoidea, division Perciformes. Berg (1947) placed them amongst the malacopterygians between the Clupeiformes and the Myctophiformes, but more recently Gosline (1961) and Smith and Bailey (1962) agreed that it should be placed in the order Perciformes.

Several definitive characters indicate that *Bathyclupea* is an acanthopterygian fish: the spines in the fins, the protrusable jaws, pelvic rays I5, the suborbital shelf (Smith and Bailey (1962), and the 4 external and 3 ventral branchiostegal rays which are acinaciform in shape. Other characters confirming this placement are the jugular pelvics and low number of branched caudals (15). The cycloid scales may be a result of secondary loss of ctenii. A most significant character is the physostomous gas bladder. No other acanthopterygian fish is known to be physostomous. If this character is not a secondary development it means that the Bathyclupeidae are not evolved from living iniomous families, all of which (Marshall, 1960) lack open gas bladders. One must thus either derive them from ancestral iniomous fishes supposedly having an open gas bladder, or from the Clupeiformes branching off before the physoclistous Beryciformes. However, should the physostomous condition prove to be secondary, there would seem to be no reason not to include them amongst the primitive acanthopterygians.

At any rate most characters indicate that the Bathyclupeiformes belong among the acanthopterygian fishes, probably amongst the more primitive and it is here that they are provisionally placed.

Bathyclupeidae

Branchiostegals: 7 in the single genus *Bathyclupea*. In *Bathyclupea argentea* 7 with 2½ epihyal and 4½ ceratohyal, 4 on the external and 3 on the ventral face of the hyoid arch; all acinaciform. *Bathyclupea hoskynii* 7 with 2 epihyal and 5 ceratohyal, 4 on the external and 3 on the ventral face of the hyoid arch, all acinaciform; pattern identical in *Bathyclupea schroederi*.

Operculars: Complete and entire in *B. argentea*; operculum without a spine but with a strip of striae across the upper portion. Gill membranes separate.

Hyoid arch: Interhyal, epihyal, and ceratohyal present; hypohyal(s) not investigated.

References: Jordan and Evermann (1896), Weber and de Beaufort (1931), Regan (1913), Alcock (1891), Misra (1953), Dick (1962).

Material examined: *Bathyclupea schroederi*, alcoholic specimen, USNM 185676, Honduras; *Bathyclupea hoskynii*, alcoholic specimen, USNM 109491, Gulf of Aden; *Bathyclupea argentea*, alcoholic specimen, USNM 186317, off Trinidad.

ORDER SYNGNATHIFORMES

Branchiostegals 1-5 with 0-4 epihyal and 0-3 epihyal, 1-4 external and 0-1 interhyal slender acinaciform or filiform branchiostegals. Interhyal (except *Fistularia*), epihyal, ceratohyal and one or two hypohyals present. Epihyal and ceratohyal usually sutured together; arch modified in different fashion in each group. Branchiostegals often inserting under a lateral ridge on the ceratohyal. Lower hypohyal large, v-shaped and usually receiving a wedge-shaped projection from the ceratohyal. Opercular bones complete and entire, without spines. Gill membranes separate or joined to the isthmus. Lower Oligocene to present. Six living families.

The Gasterosteiformes and Syngnathiformes have been variously associated in one order or in two adjacent orders by many authors such as Boulenger (1904), Berg (1947), Starks (1902a), and Bailey (1960) under such names as the Thoracostei, Catosteomi, Hemibranchii, Gasterosteiformes and Syngnathiformes. Regan (1929) included them all in the Solenichthyes except for the Gasterosteidae and Aulorhynchidae which he placed in the Scleroparei. Bertin and Arambourg (1958) expanded Berg's classification and placed them in three adjacent orders, Gasterosteiformes, Aulostomiformes and Syngnathiformes. Gosline (1963a) questionably derives the Syngnathiformes and Gasterosteiformes from the Percopsiformes. Jungerson (1908, 1910), Starks (1902a) and Gregory (1933) have studied aspects of their osteology.

The Gasterosteiformes and Syngnathiformes have some obvious similarities such as a long snout with a small and vertical mouth and the pelvic fins which are abdominal or subthoracic. However, there are many fundamental differences between the groups. Gosline (1961) states that the syngnathiform jaws differ widely from the gasterosteiform jaws. Although the snouts are elongate in the two groups they are roofed differently, the frontals roofing the snout in the Gasterosteiformes, but not in the Syngnathiformes. The soft pelvic rays number 1-4 in the Gasterosteiformes and 3-6 in the Syngnathiformes (or absent in Syngnathidae). The Gasterosteiformes possess ribs and parietals, unlike the Syngnathiformes. The construction of the hyoid arch is normal in Gasterosteiformes but considerably modified in the Syngnathiformes. The hyoid arch does not project through the isthmus forming a knob in the Gasterosteiformes as it usually does in the Syngnathiformes. The Gasterosteiformes have a keel on the caudal peduncle and the Syngnathiformes do not. The pelvics lie under the middle of the pectoral fin in the Gasterosteiformes, but behind this point in the Syngnathiformes. The dorsal and anal fin rays are branched in the

Gasterosteiformes and unbranched in the Syngnathiformes. The Gasterosteiformes are further united by these breeding characteristics: building a nest of vegetation cemented together with kidney secretions; guarding the nest; developing red pelvic fin membranes in the breeding male of several of the genera.

The Gasterosteiformes are derivable from the Perciformes. The numerous pelvic fin rays and dorsal spines and other characters necessitate derivation of the Syngnathiformes from the Beryciformes or the Zeiformes.

Judging from the pelvic and dorsal fins and the number of branchiostegals, the Macrorhamphosidae and Solenostomidae appear to be most primitive and the syngnathids the most advanced. The families are all quite highly specialized in their own directions, however, and none can easily be envisioned as ancestral to the others. Some of the Zeiformes such as Antigonia or Capromimus would appear to be close to the ancestors of the Syngnathiformes.

Solenostomidae

Pl. XI

Branchiostegals: One branched filiform branchiostegal which curves up behind the operculum. This branchiostegal appears to have resulted from the fusion of two branchiostegals, one rising from the epihyal and one from the lower surface of the ceratohyal. Basally they are closely approximated and presumably fused, then for a short distance they are joined by a bony membrane. While the filiform shape of the branchiostegals is imilar to that of Syngnathidae their insertion is different. Although the upper branchiostegal in Aulostomus and Fistularia is also branched, in their case it appears to be a result of one branchiostegal splitting rather than two fusing; the shape also differs from that of Solenostoma in that they are distinctly acinaciform.

Operculars: Complete and entire. Operculum somewhat fan-shaped with 3 crests on the outer face. Suboperculum filiform forming a hemicircle below the operculum; interoperculum a thin lamina under the preoperculum. The branchial cavities of the two sides communicate through a large oval foramen below the branchial skeleton (otherwise only in some Pleuronectiformes). Gill membranes separate.

Hyoid arch: Consists of an interhyal, epihyal, ceratohyal and two hypohyals. The interhyal is wedge-shaped with the broad end angled up and slightly enlarged. Its position is unusual lying on the external face of the epihyal and ceratohyal. Neither the epihyal or the ceratohyal sends prongs towards one another although the end of the ceratohyal is notched as if to receive a prong. The epihyal is only a fifth of the length of the ceratohyal. The two hypohyals send a wing posteriorly which extends nearly half way along the mesial surface of the ceratohyal. The lower hypohyal just anteriorly beyond the ceratohyal, the upper one lies above the anterior end of the ceratohyal. The specialized hyoid arch of the Solenostomidae is quite unlike the specialized hyoid arch of the other three families.

References: Jungerson (1910), Weber and de Beaufort (1922).

Material examined: None.

Macrorhamphosidae

Branchiostegals: Vary from 4-5. In Centriscops lilliei 5 with 4 close together on the upper end of the ceratohyal, the fifth free in the membrane, all slender and acinaciform.

Operculars: Complete and entire, gill openings wide.

Hyoid arch: In Centriscops consists of a small oval interhyal imbedded in the reduced epihyal, a large triangular ceratohyal which extends into the large v-shaped lower hypohyal and an upper hypohyal which lies above the posterior half of the ceratohyal. The elements are so closely adjoined that they are very difficult to discern.

References: Weber and de Beaufort (1922), Fowler (1936), Jordan and Evermann (1896).

Material examined: Centriscops lilliei, Cook Strait, New Zealand, BC56-272, hyoid arch and branchiostegals of one side dissected out, cleared and stained with alizarin.

Centriscidae (Amphisilidae)

Pl. XI

Branchiostegals: Vary from 3-5. In Centriscus scutatus 4 slender acinaciform branchiostegals, curve up around to middle of gill cover.

Operculars: Complete and entire. Gill membranes joined to isthmus.

Hyoid arch: Consists of round interhyal imbedded in upper end of arch, a small ventral epihyal, a large ceratohyal which sends a triangular prong into the large v-shaped lower hypohyal and a small upper hypohyal above the end of the ceratohyal.

References: Day (1875), Jungerson (1910), Chevey (1932), Weber and de Beaufort (1922), Danilchenko (1960).

Material examined: *Centriscus scutatus*, alcoholic specimen, BC59-574, Bangkok.

Fistulariidae

Pl. XI

Branchiostegals: 5 in *Fistularia petimba* with 2-3 epihyal and 2-3 ceratohyal, all on the external face except the lowest which is on the internal face of the hyoid arch. All acinaciform and almost rectilinear. The uppermost forks once close to the expanded base. This is interpreted as the division of a single branchiostegal (rather than a fusion of two) because there is no trace of fusion in the base and because there is the normal acanthopterygian complement of four on the external face of the hyoid arch, if a fusion had taken place one would expect only three branchiostegals on the external face. Several authors give a count of 5-7 for this family. However, those authors who have made anatomical studies and the observations of this author are in agreement that the number is 5.

Operculars: Complete and entire, without spines. Operculum oval except for the anterior border where it is invaded by the corner of the suboperculum. Gill membranes separate.

Hyoid arch: In Fistularia epihyal sends a long wedge into the v-shaped ceratohyal, lower hypohyal with projection onto dorsomesial face of ceratohyal, upper hypohyal small and lying above lower hypohyal. Jungerson considered the absence of an interhyal as due to its fusion with the epihyal. Examination of the end of the epihyal in his figures would lead me to deduce rather that the interhyal has been lost and the epihyal has elongated to make up for its absence.

References: Jungerson (1910), Fowler (1936), Day (1875), Meek and Hildebrand (1923), Jordan and Evermann (1896), Weber and de Beaufort (1922).

Material examined: Fistularia sp., skeletal specimen, USNM 26094, West Indies; Fistularia petimba, 1 alizarin plus two alcoholic specimens, BC57-79, Acapulco, Mexico.

Aulostomidae

Pl. XI

Branchiostegals: 4 in Aulostomus maculatus and chinensis. A. coloratum 4 all on the outer face of the epihyal, the uppermost stoutest and terminally divided into filaments.

Hyoid arch: In Aulostumus maculatus interhyal triangular with broad end uppermost epihyal sending a broad wedge into the v-shaped ceratohyal. Lower hypohyal sending a projection along the lower face of the ceratohyal. Upper hypohyal lying above and behind anterior end of the lower hypohyal.

References: Jungerson (1910), Fowler (1936), Jordan and Evermann (1896), Weber and de Beaufort (1922), Wheeler (1955).

Material examined: *Aulostomus chinensis*, alcoholic specimen, BC54-87, Hawaii.

Syngnathidae

Pl. XI

Branchiostegals: Vary from 1-3. In *Syngnathus* 2-3, *Siphostoma* 2, *Hippocampus* 2, *Phyllopteryx* 2 and *Nerophis* 1. In *Syngnathus fuscus* two filiform ones emerge from the external face of the ceratohyal from under a small lateral projection and curl up around to the posterodorsal corner of the operculum (much as in Anguilliformes). The single branchiostegal of *Nerophis* is branched; probably it represents two branchiostegals fused basally. In *Hippocampus hilonis* 2 emerge from the external face of the ceratohyal. In *Siphostoma typhle* 2 filiform branchiostegals emerge from under a projection on the lateral face of the ceratohyal.

Operculars: Complete and entire. Operculum oval shaped in *Syngnathus*; suboperculum a small crescentic lamina on lower side of operculum, terminates in a thread; interoperculum elongate.

Hyoid arch: In *Syngnathus* and *Siphostoma* interhyal a round knob imbedded in the epihyal. Ceratohyal large with a small ventrally directed ridge terminating in a projection which hangs over the base of the branchiostegals; extends as a wedge into the lower v-shaped hypohyal. Upper hypohyal (absent in *Nerophis*) present in *Siphostoma*, *Hippocampus* and *Syngnathus* and situated behind and above the anterior end of the hypohyal. Through comparison with Centriscops the author was able to see that the interhyal of Jungerson (1910) consisted of the interhyal imbedded in the epihyal. Thus the enigma of the apparent absence of an epihyal in Syngnathidae was solved. The hyoid arch makes a characteristic bulge on the underside of the head.

References: Jungerson (1910), Weber and de Beaufort (1922), Smitt (1895).

Material examined: Hippocampus hilonis, alizarin specimen, BC59-307, Vancouver Public Aquarium; Syngnathus fusca, alizarin specimen, NMC61-172, Halifax, Nova Scotia; S. griseolineata, alizarin specimen, NMC61-98-S, Point Gravina, Alaska.

ORDER OPHIDIIFORMES, NEW ORDER

Branchiostegals (5) 6-9 (10), with 2 epihyal and 5-6 ceratohyal, 4 on the external and 3-4 on the ventral face of the hyoid arch, all acinaciform, the middle ones often with anterior projections at the base. Interhyal, epihyal, ceratohyal and two hypohyals present. The epihyal and the ceratohyal may be sutured together. Ceratohyal without foramen. Opercular bones complete, opercular spines 1-3. Gill membranes separate, narrowly attached to isthmus, or somewhat united and free from the isthmus. Five families. Fossils from the Palaeocene or Eocene to recent. Fig. 2 shows the percopsid projection.

Gill (1884) included the Gadiformes, Ophidiiformes, Ateleopiformes, Zoarcidae and several other percoids and blennioids in his order

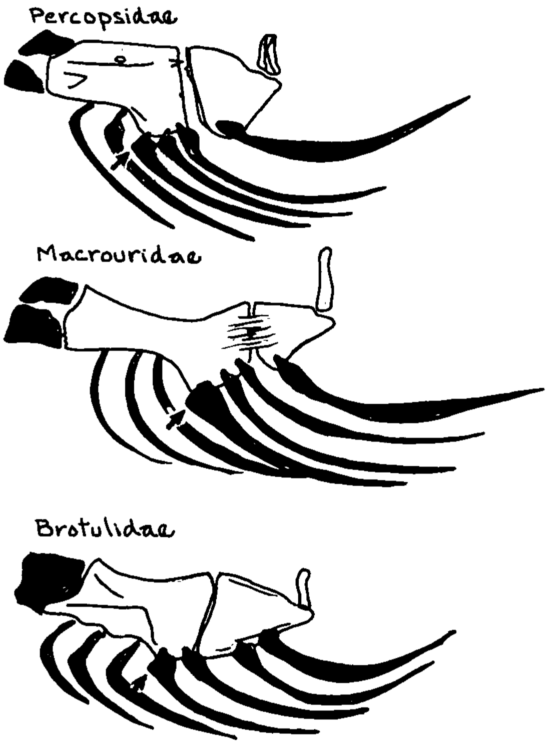

Fig. 2. Percopsid projections (arrow) in a percopsiform, gadiform and ophidiiform (top to bottom).

Jugulares. According to Garman (1899) the families Zoarcidae, Ophidiidae and Brotulidae are closely related to the Gadidae and Macrouridae and belong in the order Acanthini. Hubbs (1920) considered the Ophidiidae members of the Acanthopterygii. Goodrich (1909) considered the ophidicids allied to the Zoarcidae while Boulenger (1910) considered ophidioids as degraded blenniids, not related to the cods. Gregory (1933) felt that evidence was insufficient to set aside the many signs of relationship between the anacanths and the blennies and ophidiids. Jordan put the ophidioids in his Jugulares, far from the cods. Regan (1912) placed them as the division Ophidiiformes in the suborder Blennioidea, while Berg (1947) placed them in their own suborder following the Blennioidei. Gosline (1953) indicated Dinematichthys had a typically percoid caudal skeleton with 15 branched rays and (1961) that the basic pattern of the caudal skeleton of Beryciformes, Zeiformes and Perciformes is similar. Rosen (1962) has suggested that the Ophidioidei, Gadiformes, Percopsiformes and Amblyopsiformes form a phylectic assemblage. Gosline (1963a) believed that there is a close relationship between the percopsiforms and the amblyopsoids and that the percopsiforms share a common ancestry with the gadiforms. Freihofer (1963) considered the patterns of the ramus lateralis accessorius in Gadiformes, Ophidiidae, Brotulidae and Zoarcidae to be basically alike, but unlike those of (other) blennioids.

The number, arrangement and form of the branchiostegals of the Ophidiiformes, the suturing of the epihyal and ceratohyal, the opercular spines of some genera, the protrusible upper jaw, and the caudal skeleton are all definite evidence that they are acanthopterygian fishes.

Several features differentiate the Ophidiiformes from the Perciformes. The Ophidiiformes have a higher range of branchiostegals, usually 7-9, whereas the Perciformes usually have 5-7. The Ophidiiformes lack spiny rays in the fins; of the Perciformes only the Ophicephalidae lack spires in the fins. This assemblage of characters indicates that the Ophidiiformes are distinct from the Perciformes. The high number of branchiostegals in the Ophidiiformes and the close relation of the Ophidiiformes to the Gadiformes indicates that the Ophidiiformes are more primitive than the Perciformes.

The Ateleopiformes and Gadiformes are close to the Ophidiiformes (as will be shown below). Yet neither of these two orders can have given rise to the Ophidiiformes. The Ateleopiformes are very degenerate, lacking such structures as the basisphenoid, pterosphenoid, epiotic, opisthotic, gas bladder and scales which are present in the Ophidiiformes. The Gadiformes differ from the Ophidiiformes in having more numerous pelvic rays, first two vertebrae long and with sessile epipleurals, front of anterior centrum concave (instead of convex), lack of supramaxillary bone, pelvic bones posterior to clavicular symphysis, lack of opercular spines, possession of mental barbel and two or three dorsal fins. Thus the Gadiformes are distinct from the Ophidiiformes and cannot be immediately ancestral to them. This leaves only the Beryciformes as possible ancestors to the Ophidiiformes; the form of the branchiostegal bases would agree with this derivation, as well as branchiostegal number and arrangement. (see next paragraph for sources of above data).

The Ophidiiformes do show many characters in common with the Ateleopiformes and Gadiformes as the following list shows (many not yet verifiable for the Ateleopiformes): Large otoliths, males often sound producing and parapophyses broadened for gas bladder support; percopsid projection on fourth branchiostegal; vertical fin rays more numerous than one per vertebra (unlike Blennioidei); absence of orbitosphenoid and basisphenoid; fin spines absent (except possibly a single dorsal spine in some); pelvics thoracic to mental with one ray elongate and probably sensory; olfactory nerves not passing through orbits (except Gadoidei); scales cycloid (except macrouroids); opisthotic separates exoccipital and prootic; lower arm of operculum invades suboperculum obliquely and suboperculum forms much of the border of the gill cover; upper jaw at least slightly protractile; branchiostegals usually 7-9; two hypohyals; hyomandibular broad; a supramaxillary (except Gadiformes); vertebrae numerous (about 45-89); caudal skeleton reduced and simplified to one or two plates (data from Clothier, 1950; Hotta 1961; Regan 1903; Gosline, 1953; Berg, 1947; Gregory, 1933).

From the above data it may be seen that the Ophidiiformes form a distinct order, yet show affinities to the Ateleopiformes and Gadiformes (and ancestrally to the Beryciformes). Rosen (1962) has indicated that the Percopsiformes (including his Amblyopsiformes) also show affinities to this assemblage. Of the above characters they share the lack of orbitsphenoid and basisphenoid; pelvics thoracic; opisthotic separates exoccipital and prootic (see Rosen's figures); hyomandibular broad; suboperculum forms most of posterior border of gill cover; two hypohyals; caudal fin reduced. They differ in having fewer vertebrae (27-36); in having a more normal caudal fin with up to 17 branched rays; a ceratohyal foramen; a short anal fin; and in lacking a protrusable upper jaw. It is concluded that they are related to the Ophidiiformes, Gadiformes and Ateleopiformes but separated from them at an early stage.

For the sake of completeness another group with possible affinities may be mentioned here. The Gobioidei have the opisthotics (when present) between the exoccipitals and prootics (Gosline, 1955, Regan, 1911d); the operculum primitively bears two close spines (e.g. Kraemeria, Typhlichthys); the caudal skeletons of Ptereleotris and Amblyopsis are similar in having two hypural plates with a small splint above and below and in having a plate-like ossicle in front of the upper splint (the goby differs in fusion of upper hypural with the adjacent centrum); an interspace between the preoperculum and symplectic of gobioids and percopsiforms (Gosline, 1955, Rosen, 1962); a broad parasphenoid and hyomandibular and similar gill rakers in Eleotris and Percopsiformes; the rows of neuromasts on the head are similar to those of percopsiformes (although gobies examined lack the sublabial row), the branchiostegal number and arrangement is similar to Percopsiformes. The gobioids differ from the percopsiforms in lack of parietal bones, the broad junction of the gill membranes with the isthmus, the lack of a beryciform foramen in the ceratohyal, and the lack of a frenum. This suggestion of relationship is preliminary and requires further investigation to determine if the similarities are parallelisms or denote relationship. For the moment the Gobioidei are left in the Perciformes.

There has recently been doubt cast upon the distinctness of the Brotulidae and the Ophidiidae. According to Norman their gill membranes are different but the number of branchiostegals is almost the same (Ophidiidae 7-9 (10), Brotulidae (5,6) 7-9). The families are here provisionally considered distinct.

Ophidiidae

Branchiostegals: Vary from 7-9 (10). *Brotuloides* 7, *Genypterus* 7, *Leopophidium* 7, *Ophidion* 7-10, *Otophidium* 7, *Parophidion* 7, *Raneya* 7, *Xylacyba* 8. *Genypterus capensis* 7 with 2 epihyal and 5 ceratohyal, 4 external and 3 ventral, all acinaciform, the middle 5 with anterior projections at the base. *Otophidium marginatum* 7, the upper scimitar-shaped, *Otophidium taylori* 7 with 2 epihyal and 5 ceratohyal, 4 external and 3 ventral, upper scimitar-shaped, broad mesially.

Operculars: Complete in the three species of *Otophidium* with single opercular spine, in *Genypterus* complete, operculum with single spine, upper tip of suboperculum frayed into 4 rays; suboperculum excludes most of posterior border of operculum in *Genypterus* and *Otophidium*. Gill membranes separate in *Otophidium*, joined to isthmus in *Ophidion novaculum*. In the entire family, gill membranes are nearly separate and narrowly attached to isthmus behind pelvics according to Norman (MS).

Hyoid arch: In *Genypterus* and *Otophidium* consists of interhyal, epihyal, ceratohyal and 2 hypohyals. The epihyal and ceratohyal sutured internally and externally. Ceratohyal foramen lacking.

References: Harry (1951a), Böhlke and Robins (1959), Robins (1961), Fowler (1936), Garman (1899), de Beaufort and Chapman (1951), Cohen (1961).

Material examined: Otophidium marginatum, alcoholic specimen, USNM 131497, Cape Hatteras, Florida; O. welshi, alcoholic specimen, USNM 102178, off Virginia Capes; O. taylori, alcoholic specimen, BC61-200, Santa Monica Bay, California; Genypterus capensis, alizarin specimen, NMC62-143 & S, South Africa.

Brotulidae

Pl. XIII

Branchiostegals: Vary from (5,6) 7-9. In Alcockia 8, Barathrites 6, Barathrodemus 8, Bassozetus 8, Bathronus 5, Brotula 8, Cattaetyx 8-9, Celema 8, Dicrolene 8, Dinematichthys 6-7, Diplocanthopoma 8, Echelybrotula 7, Eretichthys 8, Glyptophidium 8, Holomycteronus 8, Hypleuron 8, Lamprogrammus 8, Leucicorus 8, Mastigopterus 8, Monomeropus 8, Monomitopus 8, Neobythites 8, Oligopus 8, Parabrotula 5 or 6, Porogadus 8, Pseudonus 8, Pycnocraspedon 8, Sciadonus 7, Vulcanus 8, Xenobythites 8. Brotula multibarbata 8 with 2 epihyal and 6 ceratohyal, 4 on the external and 4 on the ventral face of the hyoid arch, all acinaciform. Ogilbia sp. 7 with 2 epihyal and 5 ceratohyal, 4 on the external and 3 in notches on the ventral face, all acinaciform, the middle 5 with anterior projections at the base.

Operculars: Complete in Ogilbia; the opercular with 3 spinules on the upper arm, the lower arm invading the suboperculum which forms most of the border of the gill cover. Similar in Dicrolene but upper arm of operculum narrow and terminating in a single pungent spine. Petrotyx, Eutyx and Pseudobythites without opercular spines, Microbrotula and Diploacanthopoma with a spine. Gill membranes usually separate in the family (Norman, MS).

Hyoid arch: In Ogilbia consists of interhyal, epihyal, ceratohyal and 2 hypohyals. The latter nearly sutured together; no ceratohyal foramen. In Dicrolene (Gregory, 1933, Fig. 256) ceratohyal bowed downward.

References: Fowler (1936), Günther (1887), Norman (MS), Garman (1899), de Beaufort and Chapmen (1951), Gosline (1953).

Material examined: Brotula multibarbata, alcoholic specimen, USNM 167354, Gilbert Islands; Ogilbia sp. alizarin specimen, NMC62-217 & S, Las Tres Marias Islands, Mexico.

Pyramodontidae

Branchiostegals: 7 in Pyramodon. Snyderidia 7 with 2 epihyal and 5 ceratohyal.

Operculars: In Pyramodon operculum with two inconspicuous diverging ridges ending in a spine-like tip. Gill membranes separate in Pyramodon and Snyderidia.

References: Smith, J.L.B. (1955), de Beaufort and Chapman (1951), Gosline (1960a).

Material examined: None.

Carapidae (Fierasferidae)

Branchiostegals: Vary from 6-7. Carapus 7, Onuxodon 7, Echiodon 7, Encheliophis 6-7.

Operculars: In Encheliophis complete, an opercular spine. In Carapus complete, operculum v-shaped, the lower arm invading the suboperculum which forms most of the posterior border. Gill membranes nearly separate in Encheliophis. Gill membranes somewhat united, free from isthmus in family (Norman, MS).

References: Bonham (1960), Fowler (1936), de Beaufort and Chapman (1951), Arnold (1956), Smitt (1895), Smith, J.L.B. (1955a).

Material examined: Encheliophis (Jordanicus) gracilis, alcoholic specimen, USNM 65884, Tahiti.

ORDER ATELEOPIFORMES

Branchiostegals 7-9, with 3-4 epihyal and 4 ceratohyal, 4 on the external face and 3 on the ventral face of the hyoid arch, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present and separated by cartilage. Epihyal and ceratohyal not sutured. Ceratohyal without foramen. Opercular bones complete and entire. A single family. Fossils unknown.

Goode and Bean (1896) and Boulenger (1904) placed the Ateleopidae next to the Ophidiidae. Radcliffe (1913) placed the Ateleopiformes in the macrouroids. Regan (1929) put the Ateleopidae in a separate suborder under the Iniomi; Bertin and Arambourg (1958) placed them next to the Miripinnatoidei and Myctophoidei in the Clupeiformes. Berg (1947) placed them in their own order, Ateleopiformes following the Myctophiformes. Bertelsen and Marshall (1958) considered the Miripinnati were very close to the Ateleopidae. Walters (1962, unpublished paper presented at ASIH meetings) considered them related to the Miripinnatoidei. Bertelsen and Marshall (1956) suggested that the Miripinnati were closer to the Chondrobrachii (=Ateleopiformes) than any other pre-berycomorph order considered.

The bordering of the upper jaw solely by the premaxilla separates the Ateleopidae from the Clupeiformes and lower orders. A protrusable upper jaw is very rarely found in malacopterygian fishes (being found only in the miripinnatoids, which may also belong in the Acanthopterygii). The Ateleopidae have jugular pelvics, a character unknown in the malacopterygians (except in the Miripinnatoidei). The arrangement and form of the branchiostegals are acanthopterygian, the number primitive acanthopterygian. These three strong characters would therefore place the Ateleopidae amongst the acanthopterygians. Doubtless the absence of spines has been partly responsible for the allocation amongst malacopterygians. However, the long first dorsal ray of a specimen of _Ijimaia antillarum_ (under a microscope but without dissection or staining) appeared to lack annulae and appeared to be a flexible spine (even should it prove not to be the absence of fin spines need not preclude it from the acanthopterygians). The lack of an acanthopterygian suture between the epihyal and ceratohyal is probably related to the reduction of ossification in this deep-sea group.

Relationship to the Miripinnatoidei has been suggested. They have 17 principal caudal rays and 4-10 pelvic rays whereas the Ateleopidae have 14 or fewer caudal rays (14 in Ijimaia and 10 in Ateleopus) and 1-3 pelvic rays. However, until the insertion of the lower branchiostegal rays or other indicative characters of Miripinnatoidei are ascertained it appears advisable to provisionally leave them where they have been placed.

To what group of acanthopterygians are the Ateleopidae related? The presence of a supramaxillary restricts derivation to the Perciformes or sub-Perciformes. The only one of these groups having as many branchiostegals are the Ophidiiformes and the Beryciformes. The number of pelvic rays, caudal rays and vertebrae, the position of the pelvics and absence of a basisphenoid in the Ateleopidae all agree with the Ophidiiformes rather than the Beryciformes. Derivation of the Ateleopidae from the Ophidiiformes appears to be indicated. Differences between the two orders are mainly those of reduction. The ateleopids have only one pelvic radial and lack scales, opisthotics, pterosphenoids and epiotics found in Ophidiiformes. The shorter dorsal of the Ateleopidae is difficult to interpret, may represent the retention of a more primitive condition or a secondary shortening. Further resemblances between the Ateleopidae, ophidiiforms and gadiforms are discussed under the Ophidiiformes.

Ateleopidae

Pl. VIII

Branchiostegals: Vary from 7-9. In Ateleopus natalensis 7 with 3 epihyal and 4 ceratohyal, 4 on the external and 3 on the ventral face of the hyoid arch, all acinaciform (the branchiostegals lying in the gap between the epihyal and ceratohyal are distributed in the formula as they would be if the epihyal and ceratohyal met). *A. indicus* 7-8 with 3-4 epihyal and 4 ceratohyal; *A. natalensis* 7 with 3 epihyal and 4 ceratohyal; *A. japonicus* 8 (9 specimens) or 9 (2 specimens). *Ijimia plicatella* 8 (2 specimens); *I. fowleri* 7 (1); *I. loppei* 7 (2); *I. antillarum* 7 (2) with 4 on external epihyal and 3 on ventral ceratohyal.

Operculars: In *Ateleopus natalensis* complete and entire; operculum triangular; suboperculum v-shaped lying below operculum and excluding its posterior border; interoperculum a long narrow lamina from mandible to suboperculum; gill membranes separate (as in all genera).

Hyoid arch: In *Ateleopus natalensis* consists of interhyal, epihyal, ceratohyal and two hypohyals. The hypohyals are separated by cartilage. There is a gap between the epihyal and ceratohyal.

References: Rivero (1935), Günther (1887), Weber and de Beaufort (1929), Alcock (1891), Misra (1953), Bertelsen and Marshall (1956).

Material examined: *Ateleopus natalensis*, hyoid arch and rays dissected out, SU 31358, Durham, Natal. *Ijimaia antillarum*, alcoholic specimen, USNM 157993, south of Mobile, Alabama.

ORDER GADIFORMES (MACROURIFORMES)

Branchiostegals (5) 6-8 with 0-1 epihyal and 5-8 ceratohyal, 4 on the external and 3-4 on the ventral face of the hyoid arch, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present. Epihyal and ceratohyal usually connected on their internal face by a suture (not in Moridae), the hypohyals and ceratohyal separate. Ceratohyal without foramen. Opercular bones complete and entire. Gill membranes united and free from or joined to isthmus. Three suborders with 6 families. Lower Tertiary (Palaeocene) to present.

Berg (1947) regarded the Gadiformes as a lowly organized order derived from forms allied to the Pachycormidae, probably at the end of the Cretaceous. Regan (1910) considered the cods much more generalized than the ophidioids, near which they have been placed by some authors, and that they were perhaps derived from some generalized myctophoid stock such as the Aulopidae. Hubbs (1920) regarded Corphaenoides as having a typically acanthopterygian branchiostegal apparatus. Gregory (1933) believed many features suggest relationship to various percomorphs and considered the opercular region differed most widely from the Aulopus type. According to Gosline (1961) the protrusible upper jaw of Gadiformes and Macrouriformes seem essentially of perciform type. The retractores arcuum branchialium reported in Gadiformes by Holstvoogd (1963) is an acanthopterygian character.

The double hypohyal, sutured epihyal and ceratohyal and acinaciform branchiostegals argue against Berg's derivation of the Gadiformes from the Pachycormiformes and suggest derivation from higher forms. The number, arrangement and form of the branchiostegals are those of primitive acanthopterygians and the suture between the epihyal and ceratohyal strengthens acanthopterygian placement. Other characters agreeing with this position are the protrusable upper jaw, the dorsal fin spine in the macrouroids, the anterior pelvics and the bordering of the upper jaw solely by the premaxillary, physoclistic gas bladder, retractores arcuum branchialium, absence of intermuscular bones and absence of an orbitosphenoid.

Two characters have offered difficulty in the placement of the Gadiformes, the numerous pelvic rays (5-17) and the absence of fin spines (except the first dorsal ray of macrouroids and possibly the first dorsal ray of Merluccius). However, none of the malacopterygii or holostei have as many as 17 pelvic rays (except Cypriniformes which cannot of course be ancestral). Therefore, the pelvic ray count of up to 17 is not a primitive condition but represents a secondary multiplication (as in some Pleuronectiformes where they have secondarily multiplied to 13 rays). However, a sufficient number of the more primitive members do have a pelvic count of seven to suggest that this is close to the original number of the order. This number would suggest that the Gadiformes are more primitive than the Perciformes. The lack of pelvic spines need not prevent placement in the Acanthopterygii. In some Pleuronectiformes and in the Ophicephalidae the pelvic spines have been lost. It is therefore not necessary to regard these two characters as a bar to placement among the acanthopterygians.

The pelvic ray count of 7 and the branchiostegal number of 5-8 suggest derivation from the Beryciformes or Zeiformes. Osteological characters of the Gadiformes make a derivation from the Beryciformes more likely. As is discussed under the Ophidiiformes it is likely that the Gadiformes and Ophidiiformes arose from a single offshoot of the Beryciformes.

SUBORDER GADOIDEI

Moridae

Pl. XII

Branchiostegals: Vary from (6)7(8). In *Laemonema* 7, *Physiculus* 7, *Gadella* 7, *Mora* 7, *Halogyreus* 7, *Brosmiculus* 6, *Lepidion* 7(8), *Antimora* 7, *Tripterophycis* 7, *Gargilius* 7. Günther (1887) reported *Melanonus* with 5 but Koefoed (1953), Gregory (1933), Maul (1952) and Beebe (1932) all report 7 so it seems likely Günther was in error or had an abnormal specimen. *Antimora rostrata* 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 ventral, all acinaciform; the 4th branchiostegal with peropsid projection.

Operculars: In *Antimora* complete, operculum subtriangular, the posterior border concave, the upper posterior corner with a weak spine; suboperculum with posterior border dividing into rays and forming most of the edge of the gill cover.

Hyoid arch: In *Antimora* consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal separated by cartilage.

References: Beebe (1932), Günther (1887), Böhlke and Mead (1951), Weber and de Beaufort (1929), Koefoed (1953), Maul (1952), Garman (1899), Fowler (1936).

Material examined: *Antimora rostrata*, alizarin specimen, NMC62-118 & S, Grand Banks, Newfoundland.

Bregmacerotidae

Branchiostegals: 7 in Auchenoceros and Bregmaceros. Auchenoceros punctatus 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 ventral, all acinaciform.

Operculars: In Auchenoceros gill membranes separate, in Bregmaceros united and free.

Hyoid arch: In Auchenoceros consists of interhyal, epihyal, ceratohyal and two hypohyals. Ceratohyal bent downwards as in some ophidiiforms. Epihyal and ceratohyal sutured together.

References: Day (1875), Garman (1899), Weber and de Beaufort (1929).

Material examined: Auchenoceros punctatus, alizarin stained dissection, BC56-281, Otago, New Zealand.

Gadidae (Ranicepitidae)

Pl. XII, XVI

Branchiostegals: Varies from (6)7(8). In Lota 7(8), †Palaeogadus 7, Gadiculus 7, Gaidropsarus 7, Gadus 7, Pollachius 7, Merluccius 7, Molva 7, Melanogrammus 7, Phycis 7, Onus (6)7, Raniceps 7, Brosmius 7. Lota lota 7 with 0 epihyal and 7 ceratohyal, 4 external, the next on the internal and the anterior 2 on the ventral face of the hyoid arch, all acinaciform. Raniceps 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 internal. Merluccius productus 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 internal, all acinaciform, number 3 and 4 with anteriorly directed projections at the base. The fourth branchiostegal with percopsid projection.

Operculars: Complete and entire in *Lota lota* though there is a suggestion of a spine on the operculum. Gill membranes separate or united and free in the family.

Hyoid arch: In *Lota* consists of interhyal, epihyal, ceratohyal and two hypohyals, the epihyal and ceratohyal sutured internally, the hypohyals not sutured. In *Merluccius* the epihyal and ceratohyal sutured internally, the ceratohyal angled downwards as in ophidiforms.

References: Danilchenko (1960), Gill (1891a), Fowler (1936), Jordan and Evermann (1898), Maul (1952), Smitt (1892), Berg (1949).

Material examined: *Lota lota*, alizarin specimen, NMC60-453 & S, Aklavik, Northwest Territories; skeletal specimen, uncatalogued BC specimen from Squanga Lake, Yukon. *Merluccius productus*, skeletal specimen, BC collection, California.

SUBORDER MURAENOLEPIDOIDEI

Muraenolepidae

Branchiostegals: In *Muraenolepis marmorata* 5, the second one with an anterior basal process directed downwards.

Operculars: Operculum rounded, without point. Gill membranes united and free.

References: Günther (1880).

Material examined: None.

SUBORDER MACROUROIDEI

Macrouridae (Macruridae)

Pl. XII

Branchiostegals: Vary from 6-7(8). In Bathygadus 6-7, Coryphaenoides 6, Nezumia 7, Coelorinchus 6, Malacocephalus 7, Phalacromarurus 6-7, Mataeocephalus (6)7, Hymenocephalus 7, Ventrifossa (6)7, Lionurus 7, Macruroplus 7, Cetonurus 7, Macrourus 6-7(8), Trachyrinchus 7, Macruronus 7, Steindachneria 7, Oxygadus 6, Grenurus 7, Cariburus 6, Trachonurus 7, Cynomacrurus 6, Odontomacrurus 6, Echinomacrurus 7. Macrourus bairdii 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 ventral, all acinaciform, the fourth with an anterior prong at the base (the percopsid projection, see fig. 2).

Operculars: In Macrourus bairdii complete and entire, gill membranes united and free. In family gill membranes united and free from isthmus or joined to it.

Hyoid arch: In Macrourus consists of interhyal, epihyal, ceratohyal and two hypohyals. The epihyal and ceratohyal joined internally by a suture, the hypohyals separate except the lower one sends a broad prong on the internal face of the ceratohyal.

References: Maul (1951), (1952), Norman (MS), Weber and de Beaufort (1929), Smitt (1895), Fowler (1936), Koefoed (1953), Garman (1899), Parr (1946), Gilbert and Hubbs (1916).

Material examined: Macrourus bairdii, alizarin specimen, NMC62-115-S, Grand Banks, Newfoundland.

Macrouroididae

Branchiostegals: 7 in Squalogadus modificatus.

Operculars: Gill membranes united and free from isthmus in Squalogadus and joined to isthmus in Macrouroides.

References: Radcliffe (1913), Gilbert and Hubbs (1916).

Material examined: None.

ORDER PERCOPSIFORMES (AMBLYOPSIFORMES)

Branchiostegals 6 with 1 epihyal and 5 ceratohyal, 4 on the lateral face and 2 on the ventral face of the hyoid arch, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present. Epihyal and ceratohyal sutured or with vestiges of sutures. Ceratohyal with or without a foramen. Opercular bones complete; operculum with none, one or two spines. Gill membranes separate or joined far forward to isthmus. Eocene to present. Three families known.

According to Regan (1929) this is an isolated order without evident relationships except to the Isospondyli or primitive Iniomi. According to Hubbs (1920) they have six branchiostegals exactly as in the Acanthopteri. According to Gosline (1961) the caudal skeleton is specialized and similar to the Cyprinodontiformes' but the pelvic structure and antorbital bone indicate a "lower" teleostean condition, the ensemble of characters suggesting that they are an offshoot of a primitive scopeliform or protoscopeliform. Bailey (1960) suggests they are perhaps remotely related to the Beryciformes. Gosline (1963) considers the cyprinodontiforms are percopsiform derivatives and that the Percopsiformes share a common ancestry with the Gadiformes.

The branchiostegal number, form and arrangement, the suturing together of the epihyal and ceratohyal, the presence of spines in the fins, the ctenoid scales, the retractores arcuum branchialium, the presence of opercular spines in some members, all suggest that these are acanthopterygian fishes. The 16-17 branched caudal rays and numerous pelvic rays indicate that they are more primitive than the Perciformes and the Zeiformes but less primitive than the Beryciformes. The Beryciformes indeed form the logical ancestors of the Percopsiformes. Confirmatory evidence of this is furnished by a foramen in the ceratohyal of Percopsis, and the one or two opercular spines (in Amblyopsidae and Aphredoderus) and the lacrymal and preopercular spines of Aphredoderus. Rosen (1962) suggests affinity with the ophidioids and gadiforms; evidence for this is discussed under the Ophidiiformes. The evidence suggests origin on a common line, with perhaps the percopsiforms branching off earlier on the common line from the beryciformes. It was also pointed out under the Ophidiiformes that the gobioids may be related to the Percopsiformes.

Starks (1904) placed the Amblyopsidae together with the pikes and topminnows in his order Haplomi. Regan (1911a) separated off the pikes and placed the cyprinodonts and amblyopsids as separate suborders in a new order Microcyprini. This arrangement has been followed by Berg (1947). But differences had begun to accumulate between the two suborders since Regan erected them. Regan himself found several profound differences. Frost (1926) found the otoliths of Amblyopsis showed no resemblance to those of other cyprinodontiforms. Woods and Inger (1957) added further distinguishing characters whilst revising the Amblyopsidae. Bertin and Arambourg (1958) erected a new order for the reception of Amblyopsidae. Gosline (1961) found differences between amblyopsids and other cyprinodontiforms while at the same time indicated similarities in the caudal skeleton of amblyopsids and *Aphredoderus*. Gosline (1963a) reaffirmed the similarity between percopsiforms and amblyopsoids. Rosen (1962) studied carefully the relationships of Amblyopsidae and found that they had been misplaced in the Cyprinodontiformes and showed numerous osteological, myological and functional similarities to *Aphredoderus*. He provisionally assigned the Amblyopsidae to a separate order adjacent to the Percopsiformes.

Evidence was found in this study to support the views of Gosline and Rosen. The Amblyopsidae were found to have two hypohyals and opercular spines unlike cyprinodontiforms but like percopsiforms. The hypohyals are sutured to the ceratohyal unlike the Cyprinodontiformes but like the Percopsiformes. Further the sublabial, mandibular and cephalic rows of neuromasts in aphredoderids and percopsiforms show surprising resemblance (see and compare fine figures of Woods and Inger, 1957, and Moore and Burris, 1956). The first dorsal ray of a cleared and stained *Typhlichthys* appeared to be spinous, unlike the dorsal of Cyprinodontiformes but like that of Percopsiformes. In Amblyopsidae the opisthotic separates the exoccipital and prootic as in Percopsiformes. Rosen notes other similarities. These close similarities to the Percopsiformes plus differences shared with the Percopsiformes differentiating them from the related ophidiiforms, ateleopiforms and gadiforms indicate to the author that the Amblyopsidae belong in the order Percopsiformes.

The differences between the Amblyopsidae and other Percopsiformes appear no greater than those between Aphredoderidae and Percopsidae.

SUBORDER APHREDODEROIDEI

Aphredoderidae

Pl. XI, XII

Branchiostegals: 6 in *Aphredoderus sayanus* with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform, the uppermost fairly broad mesially, almost crescentic; the lower two fitting into notches on the lower side of the ceratohyal; without anterior projections at base.

Operculars: Complete and entire except operculum has a sharp spine, which is a continuation of its horizontal ridge; sometimes a small spine above it. Gill membranes joined fairly far forward to isthmus, almost separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal strongly sutured together, a suture also joining each hypohyal to the ceratohyal. Upper border of ceratohyal emarginated; over this evacuation projects a short arm from the posterior end of the ceratohyal (see fig. 2). This may be interpreted as a beryciform foramen the upper border of which has been lost, permitting it to open on the upper edge of the ceratohyal. This interpretation is strengthened by finding a small but normal beryciform foramen in Percopsidae and by the fact that the zeiform *Neocyttus* has similarily lost the dorsal border to its foramen (unlike *Zeus*).

References: Hubbs (1920), Jordan and Evermann (1896).

Material examined: Aphredoderus sayanus gibbosus, alizarin specimen, NMC62-72, North Branch of the Bad River, Michigan.

SUBORDER AMBLYOPSOIDEI

Amblyopsidae

Pl. XII

Branchiostegals: In Typhlichthys subterraneous 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform. Chologaster agassizi 6 with 4 external and 2 ventral.

Operculars: Complete. Typhlichthys with two weak spines, posterior border of suboperculum striated (according to Rosen, cartilaginous). Gill membranes narrowly joined to isthmus in family.

Hyoid arch: In Typhlichthys consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal sutured on dorsal internal face by two prongs. Hypohyals each send a prong towards the ceratohyal. No ceratohyal foramen.

References: Woods and Inger (1957), Jordan and Evermann (1896), Rosen (1962).

Material examined: Typhlichthys subterraneous, alizarin specimen, NMC58-5 & S, Mammoth Cave, Kentucky, August 1863; Chologaster agassizi, alcoholic specimen, NMC59-82, Kentucky.

SUBORDER PERCOPSOIDEI

Percopsidae

Pl. XI

Branchiostegals: 6(7) in *Percopsis omiscomaycus* with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform, the 4 lower ones with percopsid projections at the base, the uppermost fairly broad mesially. *Columbia transmontana* 6 with 4 external and 2 ventral. In 50 specimens of *Percopsis omiscomaycus*, 48 were found with 6 and 2 with 7 branchiostegals. Percopsid projections present (see fig. 2).

Operculars: Complete and entire, the suboperculum usurping more than half of the posterior border of the operculum. Gill membranes separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal separate or with 1-3 prongs extending towards one another. Prongs extending from lower hypohyal towards the ceratohyal, but not from the upper. A small beryciform foramen in the upper mesial ceratohyal, sometimes fused over. Upper hypohyal extends slightly over anterior end of the ceratohyal.

References: Hubbs (1920), Jordan and Evermann (1896).

Material examined: *Percopsis omiscomaycus*, alizarin specimen, NMC60-469-A, Lake Erie, Ontario; alizarin specimen, BC57-224, Fort Nelson, British Columbia; 50 alcoholic specimens, BC57-362, Alberta.

ORDER CYPRINODONTIFORMES

Branchiostegals 4-6(7) with 1 epihyal and 4-5 ceratohyal, 4 external and 1-2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and a single hypohyal (the lower) present. Epihyal and ceratohyal sutured dorsally. Ceratohyal without foramen. Opercular bones complete and entire, lacking spines, suboperculum often continuing dorsoposteriorly as a slender ray. Gill membranes separate or united and free from the isthmus. Seven families. Lower Oligocene to recent.

The Microcyprini were at one time placed in the malacopterygian group Haplomi with the pikes and galaxiids. Regan (1911a) then separated them from the pikes. Hubbs (1920) demonstrated the acanthopterygian pattern of the branchiostegals in the Cyprinodontiformes. Gregory (1933) considered the Microcyprini to be malacopterygian, and their acanthopterygian characters to have evolved through parallel evolution. Gosline (1961), Myers (1931) and Rosen (1962) discussed the protrusible upper jaw in Cyprinodontiformes. Gosline (1963) derives the Cyprinodontiformes (_sensu stricto_) from the Amblyopsoidei.

In several characters the Cyprinodontiformes resemble malacopterygians: lack of fin spines, scales usually cycloid, pelvics abdominal and without spines. In many of these characters plus the possession of a single ventral hypohyal and a highly placed pectoral the Cyprinodontiformes resemble the Beloniformes. They differ decidedly in the number and arrangement of the branchiostegals and in the presence of the interhyal. However, it seems possible that the high pectoral fins, tendency towards loss of protractility of the premaxillary are adaptions to living and feeding on the surface of the water, the fins used for maintaining the fish at the surface, and the premaxillary used for skimming the surface so that great protractility is no longer advantageous. If these suggestions are true then the characters are a result of parallel evolution and do not necessarily indicate relationship to the malacopterygians.

Characters indicating acanthopterygian relationship are the number, form and arrangement of the branchiostegals; the sutured epihyal-ceratohyal; the physoclistic gas bladder; the presence in some of protrusible premaxillaries and ctenoid scales (ctenoid in *Lamprichthys* and *Xenodexia*). The Cyprinodontiformes are therefore placed in the Acanthopterygii. The presence of 6 pelvic soft rays indicates placement in the sub-Perciformes. The removal of Amblyopsidae to the Percopsiformes is discussed under the latter and under Ophidiiformes.

Cyprinodontidae

Pl. XVI

Branchiostegals: Vary from 5-6(7). In *Fundulus* 5-6, *Jordanella* 5, *Oryzias* 6, *Panchax* 5, *Aplocheilus* 5, *Cyprinodon* 5-6, *Lebias* 5, *Lucania* 6, *Adinia* 5, *Empetrichthys* 5, *Zygonectes* 5(6), *Haplocheilus* 5-6, *Rivulus* 6, *Pterolebias* 6, *Cynolebias* 7, *Orestias* 5, *Simpsonichthys* 6, *Haplochilichthys* 5. *Oryzias latipes* 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform. *Fundulus diaphanus* 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform.

Operculars: In *Fundulus* complete and entire, dorsoposterior corner of suboperculum terminating in a slender ray. Gill membranes separate or united and free in the family.

Hyoid arch: In *Fundulus* interhyal, epihyal, ceratohyal and the lower hypohyal present. In it and *Oryzias* the epihyal and ceratohyal connected dorsally.

References: de Carvalho (1959), Weber and de Beaufort (1922), Garman (1895), Eigenmann and Allen (1942).

Material examined: *Oryzias latipes*, alizarin specimen, uncatalogued aquarium specimen of aquarium stock at Institute of Fisheries, University of British Columbia. *Fundulus diaphanus*, alizarin specimen, NMC62-77, Rideau River, Ontario.

Adrianichthyidae

Branchiostegals: 6-7 in *Xenopoecilus*, 5 in *Adrianichthys*.

Operculars: Gill membranes separate.

References: Weber and de Beaufort (1922).

Material examined: None.

Goodeidae

Pl. XII

Branchiostegals: Vary from 4-5. In *Goodea* 5, *Zoogeneticus* 4, *Characodon* 4, *Giardinichthys* 5, *Xenotoca* 5. In *Goodea* sp. 5, the upper two fairly broad. *Xenotoca variata* 5 with 1 epihyal and 4 ceratohyal, 4 on the external and 1 on the internal face of the hyoid arch, all acinaciform but upper ones broad mesially.

Operculars: Complete and entire in Xenotoca. Gill membranes united and free in Xenotoca, Giardinichthys and Goodea.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and the lower hypohyal in Xenotoca; epihyal and ceratohyal sutured together dorsally; hypohyal and ceratohyal separate.

References: Hubbs (1932), Garman (1895).

Material examined: Goodea sp., 2 alcoholic specimens, BC60-7, Chapala, Mexico; Xenotoca variata, alizarin specimen, NMC62-68, Rio de Aguas, Mexico.

Jenysiidae

Branchiostegals: In Jenynsia 5 branchiostegals, hidden under gill cover.

References: Myers (1931a), Garman (1895).

Material examined: Jenynsia lineata, alcoholic specimen, USNM 84469, Buenos Aires, Argentina.

Anablepidae

Pl. XII

Branchiostegals: 6 in Anableps. Anableps dovii 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform but uppermost broad mesially.

Operculars: In Anableps complete and entire, gill membranes united and free from isthmus.

Hyoid arch: Consists in *Anableps* of interhyal, epihyal, ceratohyal and the lower hypohyal. Epihyal and ceratohyal joined by a dorsal suture. Hypohyal sutured ventrally to the ceratohyal.

References: Garman (1895).

Material examined: *Anableps dovii*, alizarin specimen, NMC62-71, Honduras.

Poeciliidae (Tomeuridae)

Pl. XII

Branchiostegals: Vary from 5-6. In *Poecilopsis* 5, *Poecilia* 5-6, *Tomeurus* 5, *Gambusia* 6, *Mollienesia* 5-6, *Belonesox* 6, *Cnesterodon* 5, *Girardinus* (*Glaridodon* incl.) 5, *Xiphophorus* 5, *Pseudoxiphophorus* 6, *Heterandia* 5. In *Poeciliopsis viriosa* 5 with 1 epihyal and 4 ceratohyal, 4 external and 1 ventral, all acinaciform.

Operculars: Complete and entire in *Phallichthys*, *Carlhubbsia*, *Cnesterodon*, *Phalloceros*, *Lebistes*, *Belonesox* and *Poeciliopsis*. Gill membranes united and free in family, or separate (*Tomeurus*).

Hyoid arch: In *Poeciliopsis* consists of interhyal, epihyal, ceratohyal and the lower hypohyal; epihyal and ceratohyal sutured dorsally; hypohyal and ceratohyal separate.

References: Garman (1895), Meek (1904), Meek and Hildebrand (1916), Jordan and Evermann (1896), Gregory (1933), Rosen and Bailey (1959), Rosen and Kallman (1959).

Material examined: Poeciliopsis viriosa, alizarin specimen, NMC59-181 & S, Los Llanos, Mexico; Tomeurus gracilis, alcoholic specimen, USNM 92977, British Guiana.

Horaichthyidae

Branchiostegals: 4 in Horaichthys setnai.

Operculars: Gill membranes united and free from isthmus.

References: Kulkarni (1940).

Material examined: None.

ORDER PLEURONECTIFORMES

Branchiostegals 6-7(8), with 2-4 epihyal and 3½-5 ceratohyal, 4 external and 2-3 ventral (sometimes the anteriormost external), all acinaciform, the mesial branchiostegal of each side sometimes in contact. Interhyal, epihyal, ceratohyal and two hypohyals present. Epihyal and ceratohyal sutured together. Ceratohyal sometimes with beryciform foramen. Opercular bones complete, operculum sometimes frayed posteriorly into strands, suboperculum with slender postero-dorsal extension. Gill membranes separate or united and free from isthmus. Two suborders, seven families one of which is known only from fossils. Lower Eocene to recent.

Hubbs (1920) considered the branchiostegals of Solea as of the acanthopterygian type. According to Regan (1929) Psettodes is a typical percoid, aside from asymmetry, and might almost be placed in the Serranidae. In comparing flatfishes with Epinephelus, Gadus and Zeus Norman (1934) found the flatfishes closest to Epinephelus.

The author agrees with designating the pleuronectiform branchiostegals as acanthopterygian. Further the ceratohyal foramen and frequent presence of 7 branchiostegals would indicate derivation from a primitive perciform or from a beryciform. The low number of caudal rays of primitive Pleuronectiformes would favour derivation from perciform ancestors rather than beryciform ancestors, but the pelvic count of 5-6 (secondarily to 13), soft rays would favour beryciform derivation.

The torsion of the head in Pleuronectiformes has not notably influenced the branchiostegal series or hyoid arch. This is doubtless because the torsion of the cranium is mainly restricted to the orbital region. The jaws, gills and branchiostegals are much less affected. The sliding valve is a flap of skin underlying the bases of the gill membranes of certain pleuronectiform families.

The discovery that the anterior branchiostegal contacts its counterpart on the other side in the Soleoidea as well as the Pleuronectoidea makes the hypothesis of diphyletic origin of the Pleuronectiformes highly unlikely. A somewhat similar character is known only in the Synbranchidae where the anterior branchiostegal of one side crosses its counterpart. This feature probably functions to strengthen the weak and otherwise unsupported center section of the united gill membrane.

SUBORDER PSETTODOIDEI

Psettodidae

Branchiostegals: 7 in Psettodes.

Operculars: Complete and entire. Gill membranes separate, sliding valve well developed.

References: Hubbs (1945a), Smith, J.L.B. (1950), Day (1875).

Material examined: None.

✝ Joleaudichthyidae

Branchiostegals: No data available.

Operculars: Opercular present and spineless.

References: Chabanaud (1937).

Material examined: None.

SUBORDER PLEURONECTOIDEI

Superfamily Pleuronectoidea

Bothidae

Pl. XVI

Branchiostegals: Vary from 6-7. In Scophthalmus (= Rhombus) 7, Pseudorhombus 6-7, Bothus 6-7, Monolene 7, Platophrys 7, Lepidorhombus 7, Zeugopterus 7. Scophthalmus aquosus 7 with 2 epihyal and 5 ceratohyal, 4 on the external and 3 on the ventral face of the hyoid arch, all acinaciform. Paralichthys lethostigma 7 with medial one on each side touching the other distally. The medial branchiostegals of each side are separated in Scophthalmus, while in the Bothinae and Paralichthyinae the inner branchiostegals of each side meet posteriorly to form a V.

Operculars: In Scophthalmus and Paralichthys complete and entire, suboperculum with a ray emerging posteriorly from its dorsal corner. Gill membranes separate in Scophthalminae, united and free in the other subfamilies.

Hyoid arch: In *Scophthalmus* consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal sutured together. Lower hypohyal sends a prong into the ceratohyal. The ceratohyal with a foramen.

References: Day (1875), Hubbs (1945a), Garman (1899), Smitt (1892), Fowler (1936).

Material examined: *Scophthalmus aquosus*, alizarin specimen, NMC60-207, Magdalen Islands, Quebec; alcoholic specimen, BC55-491, Lower Chesapeake Bay, Virginia; *Paralichthys lethostigma*, alcoholic specimen, BC55-320, Louisiana.

Citharidae

Branchiostegals: 6 in *Lepidoblepheron ophthalmolepis*. The lowest ray of each side not in contact with the other.

Operculars: Complete and entire in *Citharoides*. Gill membranes separate in the family.

References: Hubbs (1945a), (1946), Smith (1950).

Material examined: None.

Pleuronectidae

Pl. XII

Branchiostegals: Vary from 7(8). In *Hippoglossus* 7, *Hippoglossoides* 7(8), *Limanda* 7, *Reinhardtius* 7, *Pleuronectes* 7, *Lepidopsetta* 7, *Lyopsetta* 7, *Microstomus* 7, *Psettichthys* 7, *Glyptocephalus* 7, *Platichthys* 7, *Psettichthys* 7. In *Lepidopsetta bilineata* 7 with 3 epihyal and 4 ceratohyal, 4 external and 3 ventral; *Lyopsetta exilis*, *Psettichthys melanostictus* and *Platichthys stellatus* 7 with $2\frac{1}{2}$ epihyal and $4\frac{1}{2}$ ceratohyal, 4 external and 3 ventral; in *Microstomus pacificus* and *Hippoglossoides elassodon* 7 with $3\frac{1}{2}$ epihyal and $3\frac{1}{2}$ ceratohyal, 4 external and 3 ventral; in *Glyptocephalus zachirus* 7 with 4 on the external epihyal and 3 on the ventral ceratohyal; in all species curved acinaciform and the seventh ray of each side closely approximated at the tip forming a V or a Y.

Operculars: Complete and entire in *Hippoglossus*, complete and entire in *Psettichthys* except opercular border frayed into two rays dorsally and suboperculum emitting a ray on its posterior corner. Gill membranes united and free, sliding valve well developed.

Hyoid arch: Complete in all examined with interhyal, epihyal, ceratohyal and two hypohyals, the epihyal and ceratohyal joined by a suture.

References: Hubbs (1945), Smitt (1892), Gregory (1933), Day (1875), Kobayashi and Ueno (1956).

Material examined: The following all alizarin specimens: *Psettichthys melanostictus*, NMC62-215 & S, Vancouver, British Columbia; *Lepidopsetta* *bilineata*, BC56-83, Saturna Island, British Columbia; *Lyopsetta exilis*, BC53-40-A, Vancouver, British Columbia; *Microstomus pacificus*, BC54-95, Vancouver, British Columbia; *Glyptocephalus zachirus*, BC54-95, Vancouver, British Columbia; *Hippoglossoides elassodon*, BC54-95, Vancouver, British Columbia; *Platichthys stellatus*, BC uncatalogued, from British Columbia.

Superfamily Soleoidea

Soleidae

Branchiostegals: Vary from 6-7(8). In *Achirus* 7, *Solea* 6-7, †*Turabuglossus* 7, †*Eobuglossus* 7, *Paraplagusia* 6, *Soleichthys* 6, *Synaptura* 6. The lowest branchiostegal of each side touches the other on its mesial portion (contrary to Schmidt in Norman, 1934).

Operculars: Complete and entire in *Achirus*, suboperculum with a slender posterior extension. Gill membranes united and free, no sliding membrane.

Hyoid arch: Consists in *Achirus* of interhyal, epihyal, ceratohyal and at least one hypohyal. Epihyal and ceratohyal sutured together.

References: Hubbs (1945a), Day (1875), Smitt (1892), Chabanaud (1937).

Material examined: *Achirus mazatlanus*, alizarin specimen, NMC62-67-S, Guaymas, Mexico.

Cynoglossidae

Branchiostegals: 6 in *Cynoglossus*. *Cynoglossus robustus* 6 acinaciform; the median rays of each side connected closely together (contrary to Schmidt in Norman, 1934).

Operculars: Complete in Cynoglossus, operculum V-shaped, suboperculum and interoperculum striated, suboperculum forming 5/6 of the posterior border of the gill cover. Gill membranes united and free.

References: Hubbs (1945a), Norman (1934), Day (1875).

Material examined: Cynoglossus robustus, alcoholic specimen, BC58-2, Malaya.

ORDER PERCIFORMES

(including Mugiliformes, Phallostethiformes, Polynemiformes, Ophicephaliformes, Thunniformes, Dactylopteriformes)

Branchiostegals (3)4-7(8), with 0-4 epihyal and 2-6 ceratohyal, 4 (very rarely 3) on the external and 0-4 on the ventral face of the hyoid arch, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals (one in the Phallostethidae, Mystinichthys and perhaps in Dactylopteridae). Epihyal and ceratohyal usually sutured together. Ceratohyal in primitive members with foramen. Opercular bones complete, operculum with 0-3 spines, suboperculum and interoperculum with (rarely 1-2, seldom more) or without spines. Gill membranes separate, joined to the isthmus or united and free from the isthmus. Includes 27 suborders, one of which is known only from fossils and 197 families 6 of which are known only from fossils. Upper Cretaceous to present.

The perciforms appear to be derived from the Berycomorphi according to Regan (1913). In this most authors including this one appear agreed. The form, number and arrangement of the branchiostegals and the suturing of the epihyal and ceratohyal of this order are typically acanthopterygian.

Linking the Perciformes to the Beryciformes are perforated ceratohyals found in some primitive Perciformes (e.g. Serranidae). Specializations such as reduced caudal fins do not permit other sub-perciform acanthopterygians to be ancestral to the Perciformes.

The Mugiliformes and Phallostethiformes are included in the Perciformes. Their pelvics appear to be secondarily subabdominal or abdominal. In all other characters including branchiostegals they agree with the Perciformes. The Scleroparei have also been ordinally separated from the Perciformes but differ only in that the second infraorbital is united with the preopercular. These differences appear neither so important or so constant as to warrent separation as orders.

Judging from the number of branchiostegals the gill membranes and the hyoid arch, the suborders Percoidei and Cottoidei appear to be most primitive, followed by the Carangoidei and Scombroidei.

Beacuse of the relative constancy of the branchiostegal series, almost always 5-7 in this order, descriptions are presented at the subordinal level rather than the family level. Any distinctive patterns in the suborder are noted. Families examined by the author are marked by an asterisk. The number of branchiostegals follow the family and the number of genera the counts are based on is separated by a comma, e.g. *Embiotocidae (5) 6, 2 (=one or more examples of Embiotocidae examined, branchiostegals 6, rarely 5 in one or more species from each of 2 genera).

SUBORDER PERCOIDEI

Branchiostegals (3,4)5-7(8) with ½-2 epihyal 4-5(6) on the ceratohyal, (3)4 external and (1)2-3(4) ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal usually sutured together. Ceratohyal with foramen or traces of foramen in the Serranidae, Centrarchidae, Branchiostegidae. Opercular bones complete, 0-3 opercular spines (about half of families with opercular spines), spines on suboperculum and interoperculum lacking (or rarely present -- Malacanthidae). Gill membranes separate or united, sometimes joined to isthmus. Three divisions including 52 families.

The three divisions (following Matsubara) appear to have some phylogenetic basis, judging by the branchiostegals, Division I having (4)5-7(8) branchiostegals with gill membranes separate or united, II having (3)5-6(7) branchiostegals with gill membranes separate, united or joined to isthmus and III having (3)5-6 branchiostegals and gill membranes joined to isthmus. Thus, division I would appear most primitive, III most advanced with II in between.

The following are the families included. An asterisk marks each family which has been examined by the author.

Division I: Acropomatidae (Acropomidae): 7,1; *Apogonidae (Cheilodipteridae) 6-8,3; *Arripidae 7, 1; *Branchiostegidae (Latilidae) 6,3; *Centrarchidae (5)6-7,8; *Cepolidae (Pl. XV) 6,1; Emmelichthyidae (Inermiidae) 6-7,1; Enoplosidae 7,1; Glaucosomidae 7,1; Henichthyidae 7,1; *Histiopteridae 7,1; *Kuhliidae (Duleidae) 6,1; *Lobotidae 6,2; *Malacanthidae 6,2; *Mullidae 4 (including barbel) ,3; *Nandidae 6,1; *Ostorhinchidae ((H) Oplegnathidae) 6-7,1; Pempheridae 6-7,2; *Percidae (Pl. XIV) 6-8,7;

Plesiopidae 5-6,3; Polycentridae 6,1; ☆Pomatomidae 7,1; ☆Priacanthidae 6,1; ☆Pristolepidae 6,1; Pseudochromidae 5?-6,1; Pseudogrammidae 6,1; Pseudoplesiopidae 6,1; ☆Scombropsidae 7,1; ☆Serrandiae (Ostracoberycidae) (Pl. XIII) 6-7,36; ☆Trichodontidae (Pl. XIV) 6,1.

Division II: Centropomidae 6-7,2; Coracinidae (Dichistiidae) 6,1; Gadopsidae 6,1; ☆Kyphosidae (Pl. XIV; Cyphosidae, Girellidae) 6-7,3; Lactariidae 7,1; ☆Leiognathidae (Pl. XIV; Gerridae) 5-6,3; Lethrinidae 6,2; ☆Lutjanidae (Lutianidae) 6-7,6; Maenidae (Centracanthidae) 6,3; ☆Nemipteridae 5-7,7; Pentapodidae 6,1; ☆Pomadasyidae (Banjosidae, Haemulidae, Gaterinidae) 6-7,7; Scorpididae 7,1; ☆Sciaenidae (Pl. XIV) 7(8),8; ☆Sillaginidae 6,1; ☆Sparidae (Pl. XIV) 5-6,13; ☆Theraponidae 6,1.

Division III: ☆Aplodactylidae (Haplodactylidae) 5-6,3; ☆Cheilodactylidae (Chilodactylidae) (3)5-6,6; Chironemidae 6,1; ☆Cirrhitidae 6,1;[1] Latridae 6,2.

In 50 specimens of the sciaenid, *Elattarchus archidium*, 49 were found with 7 branchiostegals and 1 with 8 (BC56-234, Paita, Peru).

One of the most distinctive families of this suborder is the Mullidae. These, unlike any other family in the group, have only 4 branchiostegals. Three of these are normally placed on the external face with 2 epihyal and 1 ceratohyal. The anteriormost is situated on the elongated anterior tip of the hyoid arch where it serves as the base of the hyoid barbel. This branchiostegal is short, stout and twisted basally; distally it is cartilaginous and flexible. Lo Bianco (1907) followed the development of the barbel showing how it moves anteriorly to its

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[1] Randall, J.E. 1963. Review of hawkfishes. Proc. U.S. Nat. Mus. 114: 389-451.

adult mental position. Starks (1904) figured the hyoid arch and branchiostegals of Mulloides and demonstrated that it is structurally different from that of the Polymixiidae and hence the outward similarity must be a product of parallel evolution rather than common ancestry. Another modification of branchiostegals was found in Priacanthus serrula where the branchiostegals were spinulose along their ventral edges; these small spines were lacking in Priacanthus tayenus.

References: Abe (1957), (1960), (1960a), Bertin and Arambourg (1958), Berry (1958), Berg (1949), Bailey (1959), de Beaufort (1940), Caldwell (1962), Chevey (1932), Day (1875), Dineen and Stokely (1956), Fowler (1936), (1959), Gregory (1933), Günther (1859, 1860, 1862, 1887), Green (1941), Hubbs (1920), Herre (1933), (1939), Jordan and Evermann (1896), (1898), Jordan and Fowler (1902), Johnson and Hajny (1957), Kimsey and Fisk (1960), Katayama (1960), Kuang-yu (1956), Meek and Hildebrand (1923), (1925), Meek (1904), Matsubara and Iwai (1958), McPhail (1961), Okada and Suzuki (1954), Robins and Starck (1961), Smitt (1892), Starks (1904), Scultz (1958), Schroeder (1930), Starck and Courtenay (1962), Smith, J.L.B. (1962), Weber and de Beaufort (1929, 1931, 1936), Whitley (1959), Woodward (1901), Woolcott (1957).

SUBORDER SCOMBROIDEI

Branchiostegals (5?)6-7(8) usually 7 with 2-3 epihyal and 4-5 ceratohyal, 4 external and 2-3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without foramen. Opercular bones complete, entire, without spines. Gill membranes separate (except in Luvaridae where joined to isthmus). Ten families, 4 of which are known only from fossils.

Blochiidae may not belong here. Romer (1955) placed it questionably in the Heteromi and Woodward (1942) considered it little different from *Coelorhynchus* and *Pelargorhynchus*.

The following families are included: ☆Scombridae (=Acanthocybiidae and Thunnidae) 7,7; †Palaeorhynchidae 7,1; Istiophoridae (Histiophoridae) 7,1; †Blochiidae - no data available; Xiphiidae 7,1; Gempylidae 7-8,6; †Euzaphlegidae (Zaphlegidae) and †Xiphiorhynchidae - no data available; ☆Trichiuridae 7-8,6; ☆Bramidae (Pteraclidae, Steinegeriidae) 7,4.

The Trichiuridae are peculiar in that the posterior border of their subopercular and opercular bones is fimbriate, the borders being smooth in the other families. The Trichiuridae differ from the Scombridae and Istiophoridae in that the ceratohyal sends a narrow rod under the posterior portion of the hypohyal.

References: Abe (1952, 1953a, 1961), Danilchenko (1960), David (1943), Day (1875), Fowler (1936, 1959), Garman (1899), Günther (1887), James (1961), Jordan (1919), Jordan and Evermann (1896), Khanna (1961), Matsubara and Iwai (1952), Okada and Suzuki (1956), Smitt (1892), Tucker (1956), Weber and de Beaufort (1931), White and Moy-Thomas (1941), Maul (1948, 1954).

SUBORDER CARANGIOIDEI

Branchiostegals 5-8 with 2 epihyal and 4-6 ceratohyal, 4 external and 2-4 ceratohyal, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal with foramen (Carangidae, Formionidae) or without (Rachycentridae). Opercular bones complete, entire and without spines. Gill membranes usually separate, sometimes united and free from or joined to isthmus. Seven families, one known only from fossils.

The following families are included: †Ioscionidae - no data available; ☆Carangidae (Pl. XIV; Nematistiidae) 7-8,8; ☆Coryphaenidae 8,1; ☆Formionidae 7,1; Luvaridae 5?-6,1; Menidae 7,1; ☆Rachycentridae 7,1.

The Carangidae is the most primitive family having more branchiostegals, the gill membranes separate and with a ceratohyal foramen, Luvaridae the most advanced having the fewest branchiostegals and the gill membranes joined to the isthmus.

References: Berry (1959), Bolin (1940), Day (1875), Fields (1962), Fowler (1936, 1959), Gregory and Conrad (1943), Hubbs (1920), Jordan and Evermann (1896), Meek and Hildebrand (1925), Merriman (1943), Weber and de Beaufort (1931), Woodward (1901), Smitt (1892).

SUBORDER MUGILOIDEI

Branchiostegals (5?)6-7 with 2-3 epihyal and 4 ceratohyal, 4 external and 2-3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without beryciform-type foramen. Opercular bones complete, without spines or at most a single weak spine. Gill membranes separate. Three families.

The mugiloids, polynemoids and phallostethoids are usually considered as forming a natural group. The group is sometimes excluded from the Perciformes as a separate order (Gosline, 1962). The present author and Freihofer (1963) place them amongst the lower Perciformes. The branchiostegals and hyoid arch give no characters to support separation from the Perciformes. According to Gosline (1962) the Sphyraenidae and Polynemidae retain more generalized features than the others while the Atherinidae have diverged the farthest; and the Phallostethidae appear to be derived from atherinid-like ancestors. The number of branchiostegals are in complete agreement with this arrangement. The Polynemidae and Sphyraenidae have the most branchiostegals -7. In the Mugilidae and Atherinidae they are reduced to 6, while the Phallostethidae have only 5. The Phallostethidae are also distinguished by a single hypohyal. The branchiostegals are thus in agreement with the evolutionary picture formed from the supramaxillaries, number of vertebrae, pharyngeal bones, etc.

The following families are included: *Sphyraenidae (Pl. XIII) 7,1; *Mugilidae (5)6,4; *Atherinidae (Pl. XIV) (5?)6,3.

References: Meek and Hildebrand (1923), Jordan and Evermann (1896), Weber and de Beaufort (1922), Williams (1959), Day (1875), Berg (1949), Smitt (1892), Hubbs (1920).

SUBORDER PHALLOSTETHOIDEI

Branchiostegals 5 with 1 epihyal and 4 ceratohyal, 4 external and 1 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and only one hypohyal present, the lower; epihyal and ceratohyal sutured together. Ceratohyal without foramen. Opercular bones complete, spineless but with point. Gill membranes separate. A single family.

The Cyprinodontiformes also have a single hypohyal, but this must be regarded as a parallelism, since the presence of advanced features such as spinous dorsal in the Phallostethidae do not indicate relationship. However, it is notable that a block of cartilage is found above the lower hypohyal and that the epihyal and ceratohyal are joined by a dorsal suture in both groups. It is possible that these features are adaptions to upturned jaws or losses involved in miniaturization. That it is the latter is suggested by the discovery of these features in the minute goby, Mystinichthys luzonensis.

A single family is included: *Phallostethidae (Neostethidae, Pl. XIII) 5,3.

References: Bailey, R.J. (1936), Myers (1928), Hubbs (1944).

SUBORDER POLYNEMOIDEI

Branchiostegals 7 with 1 epihyal and 6 ceratohyal, 4 external and 3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without foramen. Opercular bones complete, without spines (operculum and suboperculum fimbriate on posterior borders in Polydactylus). Gill membranes separate. A single family.

A single family included: *Polynemidae (Pl. XIV) 7,2.

References: Hubbs (1920), Day (1875), Jordan and Evermann (1896), Chevey (1932), Weber and de Beaufort (1922).

SUBORDER TRACHINOIDEI

Branchiostegals 6-7 with 1-2 epihyal and 4-6 ceratohyal, 4 external and 2-3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present (only examined in Bathymasteridae). Epihyal and ceratohyal sutured together (Opisthognathidae) or not (Bathymasteridae). Ceratohyal without foramen. Opercular bones complete with 0-2 spines on the operculum and none on the suboperculum and interoperculum. Gill membranes separate, united to each other and free from or joined to the isthmus. Twelve families plus one *incertae cedis* family provisionally placed here.

Regan (1913) in reviewing this group considered it an unsatisfactory and perhaps artifical assemblage. The characters considered here confirm the opinion, that it is not a uniform assemblage. Schultz (1941) united the Kraemeriidae (not followed) and the Limnichthyidae with the Trichonotidae (followed). Rofen (1958) considered the Kraemeriidae closest to *Trichonotus* (not followed). Gosline (1955) removed the Kraemeriidae to the Gobioidei (followed).

The following families are included: *Parapercidae (Mugiloididae, Pinguipediade) 6,2; *Pteropsaridae (Percophididae, Percophididae, Bembropsidae) 7,2; Trachinidae 6,1; Creediidae 7,1; *Hemerocoetidae 6-7, 1; *Trichonotidae (Limnichthyidae) 6-7,3; *Opistognathidae (Opisthognathidae) 6,1; Owstoniidae 6,1; *Bathymasteridae 6,1; Champsodontidae 6-7,1;

Chiasmodontidae 6-7,1; *Cheimarrichthyidae (Chimarrichthyidae) 6,1; Oxudercidae - incertae cedis, no data available.

References: Day (1875), de Beaufort and Chapman (1951), Regan (1913), Hubbs (1920), Okada and Suzuki (1952), Fowler (1936), Smitt (1892), Gregory (1933), Schultz (1941), Meek and Hildebrand (1928), Sato and Ueno (1953), Günther (1861), Myers (1935), (1939), Ogilby (1898), Gosline (1963), Ginsburg (1955).

SUBORDER ANABANTOIDEI (LUCIOCEPHALOIDEI)

Branchiostegals 5-6 with 0-2 epihyal and 4-5 ceratohyal, 4 external and 1-2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without foramen. Opercular bones complete with or without spines. Gill membranes separate or united and free from the isthmus. Five families.

Regan (1909), (1910) and Jordan (1923) included the Anabantidae, Luciocephalidae and Ophicephalidae in the Order Labyrinthici. In 1929, Regan considered that the Anabantidae with the Luciocephalidae and the Ophicephalidae belonged in two separate suborders of the Percomorphi. Berg (1947) raised the Ophicephalidae to ordinal level and included each of the other two families in their own suborder amongst the Perciformes. Liem (1963) supported the latter changes and recognized four anabantid families, naming two new ones and reviving another. Freihofer (1963) considers that these families are related and show percoid affinities.

This author considers that more recent authors have overemphasized differences and have failed to consider common characteristics in relating the above groups. Further luciocephalids and anabantids do not differ in

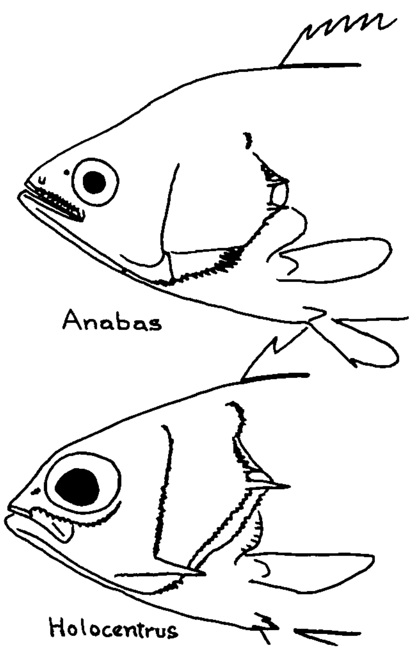

Fig. 3. Opercular spines in *Anabas* and *Holocentrus*. Note close similarity, although the suboperculum of *Holocentrum* differs in occluding posterior border of operculum.

two of the characters listed by Liem. The element called a median gular in Luciocephalus is actually a basihyal (=glossohyal) as shown by its attachment to the hypohyals and the basibranchials; this bone does differ from that found in many fishes in that it can be seen through the floor of the mouth and that the tip of the tongue is not free. These may be effects of the elongation of the lower jaw. Neither would one expect a median gular in a definitely acanthopterygian fish. Secondly the author has found that the Luciocephalidae do have a gas bladder although it is peculiarly divided into two chambers connected by a dorsal duct, one under the caudal vertebrae and one in the anterior portion of the body cavity. The other differences listed by Liem are, to the author's mind, indicative of the familial or suprafamilial level.

The three groups share some unusual characters. The Anabantidae, Luciocephalidae and Ophicephalidae share an epibranchial organ, a gas bladder which extends beyond the main portion of the body cavity posteriorly under the caudal vertebrae, and parasphenoid teeth. Further, the three groups share a special adaptation to breeding in poorly oxygenated water. The eggs float, and are usually guarded by one or more of the parents. It seems very improbable that such unusual characters could be found together in a group of families by chance, and thus these unusual characters must therefore be indicative of common origin.

A further suggestion will be made here but not developed. The anabantoids show surprising similarities in their skulls to the Hiodontidae (compare Liem, 1963, with Ridewood, 1905b), e.g. parasphenoid teeth, cranial foramina, and relations of the bones. The parasphenoid peg of osteoglossoids is reminiscent of that in anabantoids. Further, the anabantoids have up to 8 hypurals (Liem, 1963). These characters are unknown in other acanthopterygians and are found only in primitive malacopterygians. Yet the anabantoids and ophicephalids appear to have true spines (except ophicephaloids), protrusible upper jaw, suborbital shelf (Smith and Bailey, 1962) and acanthopterygian branchiostegals and hyoid arch. Further, the Anabantidae have a serrate operculum, suboperculum and interoperculum (as well as preopercular and lacrimal) and the operculum bears two long spines; this combination is known only in the Beryciformes (see fig. 3).

While the Anabantoidei have several characters more primitive than the Beryciformes they are in other respects more advanced and hence are not immediately ancestral to the Beryciformes. In several of their advanced characters, such as 5-6 branchiostegals, loss of orbitosphenoids and supramaxillaries, and fewer pelvic and caudal rays the Anabantoidei have paralleled the Perciformes. It is probably this parallelism which has lead to their misplacement.

The solution to this peculiar character combination would appear to be the derivation of the anabantoids and ophicephaloids from the line that gave rise to the berycoids, but branching off before the berycoids. (The relatively low number of branchiostegals in the anabantoids and ophicephaloids would then represent a reduction parallel to that in the Perciformes). The presence of parasphenoid teeth in primitive acanthopterygians may well indicate the pertinence of the Tselfatoidei to their ancestry. The two suborders are provisionally left here until this position can be verified. It also remains to be verified that the parasphenoid teeth and the 8 hypurals (of Anabantidae) are primitive and not secondary developments. The order Ophicephaliformes would be available for their reception.

Five families included: *Belontiidae 5-6,4; *Anabantidae 5-6,3; Osphronemidae 6,1; Helostomatidae 6,1; *Luciocephalidae 5,1.

References: Chevey (1932), Liem (1963), Poll (1957), Hubbs (1920), Day (1875), Berg (1947), Weber and de Beaufort (1922).

SUBORDER OPHICEPHALOIDEI (OPHIOCEPHALOIDEI)

Branchiostegals 5 with 2-3 epihyal and 2-3 ceratohyal, 4 external and 1 internal, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals strongly sutured to the ceratohyal. Ceratohyal without foramen. Opercular bones complete, spineless. Gill membranes united and free from the isthmus. A single family.

The common origin of this suborder with the Anabantoidei has been previously discussed. The ophiocephaloids differ from the anabantoids in that the branchiostegals have moved posteriorly on the hyoid arch, so that there are more on the epihyal. In this character, in the position of the hypohyals and in the strong suturing of the hyoid bones there are resemblances to the Synbranchiformes; but they differ strongly in the form of the opercular bones.

Taxonomy: As shown by Myers and Shapovalov (1931) Channa Scopoli 1777 has priority over its subjective synonym Ophicephalus Bloch 1794 (the earlier Channa Gronow 1763, Zoophyllacium, has been ruled not available as the principles of zoological nomenclature were not applied in that work - Opinion 267; Scopoli's 1777 work, Introd. Hist. Nat., has on the other hand been placed on the list of accepted works, Opinion 329).

(Ophiocephalus Hamilton 1882 is an unjustified emendation of Ophicephalus Bloch 1794). Thus Channa is the correct generic name for the snakeheads.

The first published family name is apparently Ophicephaloidei Bleeker 1859. It has priority over Channidae. With the termination corrected the proper family name therefore becomes Ophicephalidae. The suborder becomes Ophicephaloidei.

According to the Berg system of ordinal names the stem of the order is based on the family name. Should an ordinal name be required it would therefore be Ophicephaliformes.

A single family included: *Ophicephalidae (Ophiocephalidae, Channidae) 5,1.

References: Day (1875), Hubbs (1920), Poll (1957), Munshi (1960), Weber and de Beaufort (1922).

SUBORDER URANOSCOPOIDEI

Branchiostegals 6(7) with 1(2) epihyal and (4)5 ceratohyal, 4 external and 2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together or not. Ceratohyal foramen absent. Opercular bones complete, spineless, operculum and suboperculum frayed into rays (except Leptoscopidae). Gill membranes separate or united and free from the isthmus. Three families.

Starks (1923) considered the Uranoscopoidei related to the blennioid fishes. The Trichodontidae are similar to the uranoscopoids in having fringed lips and mesopterygoid reduced or absent. They further share lacrimal spines with the Uranoscopidae and dermal hyoid fringes with Dactyloscopidae. A detailed comparison would be valuable.

The following families included: ☆Leptoscopidae 6,1; ☆Uranoscopidae 6,7; ☆Dactyloscopidae 6,4.

References: Starks (1923), Hubbs (1920), Garman (1899), de Beaufort and Chapman (1951), Gregory (1933), Regan (1913), Day (1875), Fowler (1936), (1959), Miller and Briggs (1962), Jordan and Evermann (1898), Myers and Wade (1946).

SUBORDER STROMATIOIDEI

Branchiostegals 5-7 with 2 epihyal and 4-5 ceratohyal, 4 external and 2-3 ventral, all acinaciform. Epihyal and ceratohyal sutured together. Opercular bones complete, without spines. Gill membranes separate, united and free or joined to isthmus. Four families.

Arambourg (1954) includes the upper Cretaceous genus Omosoma in the Stromatioidei. It differs from the Stromatioidei and indeed all known Acanthopterygii in having 12 branchiostegals, intermuscular bones and 20 caudal rays, even though it has spines in its dorsal and anal fin, thoracic ventrals, a mouth bordered solely by the premaxillaries, and 10 + 15-16 vertebrae. This unusual combination of characters removes it from the Stromateidae and would seem to make it one of the precursors of the acanthopterygii, and a rather important in the evolution of teleosts.

The following families are included: ☆Nomeidae (Centrolophidae) 5-7,4; ☆Labracoglossidae 7,1; ☆Stromateidae (Pampidae) (Pl. XIII, XIV) (5)6(7),3; Tetragonuridae 5-6,1.

References: Abe (1953a, 1954, 1954a, 1955, 1959a), Grey (1955), Jordan and Evermann (1896), de Beaufort and Chapman (1951), Fowler (1936), Day (1875), Kobayashi (1961), Ueno (1954a).

SUBORDER CHAETODONTOIDEI

Branchiostegals 4-7 with 1-3 epihyal and 4-5 ceratohyal, 4 external and 0-3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal with foramen (Ephippidae) or without. Opercular bones complete, spineless. Gill membranes united and free from or joined to isthmus. Eight families.

The Zanclidae and Acanthuridae appear to be related to one another and differentiated from the other families in having only 4-5 branchiostegals. The Ephippidae (*Parapsettus*) are peculiar in that their lower two branchiostegals are buried in the muscle of the isthmus, the gill opening being restricted.

The following families are included: *Monodactylidae (Psettidae, Amphistiidae) 6-7,1; *Toxotidae (Pl. XIV) 7,1; Drepanidae (Drepanichthyidae) 6,1; *Ephippidae (Platacidae, Chaetodipteridae) 6-7,4; *Chaetodontidae (5?)6-7,3; Scatophagidae 6-7,1; *Zanclidae 4,1; Acanthuridae (Nasidae, Hepatidae) 4-5,2.

References: Day (1875), Fowler (1936,1959), Weber and de Beaufort (1936), Hubbs (1920), Chevey (1932), Jordan and Evermann (1898), Meek and Hildebrand (1928), Gregory (1933).

SUBORDER EMBIOTOCOIDEI

Branchiostegals (5) 6 with 2-2½ epihyal and 3½-4 ceratohyal, 4 external and 2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without foramen. Opercular bones complete, spineless. Gill membranes united and free from isthmus or slightly joined to it. A single family.

Family included: *Embiotocidae (Pl. XIV) (5)6,2.

<u>References</u>: Tarp (1952), Jordan and Evermann (1898), Hubbs (1920).

SUBORDER POMACENTROIDEI

Branchiostegals 5-6 with 1-3 epihyals and 3-4 ceratohyals, 4 external and 1-2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal foramen absent. Operculars complete, spineless. Gill membranes united and free from isthmus. Two families.

The following families included: *Cichlidae (Pl. XIV) 5-6,3; *Pomacentridae (4)5-6,10.

<u>References</u>: Travassos and Pinto (1959), Jordan and Evermann (1898), Meek (1904), Hubbs (1920), Kamohara (1960), Meek and Hildebrand (1925), Chevey (1932), Fowler (1959).

SUBORDER NOTOTHENOIDEI

Branchiostegals 5-7 with 2 epihyal and 4-5 ceratohyal, 4 external and 2-3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal not sutured together (Nototheniidae). Ceratohyal without foramen (only Nototheniidae examined). Opercular bones complete, operculum with 0-3 spines, suboperculum and interoperculum with 1 spine (Chaenichthyidae) or none. Gill membranes separate (Bovichthyidae) or united and free from the isthmus or joined to the isthmus (other families). Five families.

The following families are included: ☆Bovichtidae (Bovichthyidae) 7,1; ☆Nototheniidae (Pl. XV) (5)6-7,3; Harpagiferidae 5,1; Bathydraconidae[1] 7,3; Channichthyidae (Chaenichthyidae) 6,1.

References: Regan (1913a), Gregory (1933), Dollo (1904), DeWitt and Taylor (1960).

SUBORDER AMMODYTOIDEI

Branchiostegals (6)7(8) with 2 epihyal and 5 ceratohyal, 4 external and 3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal separate. Ceratohyal without foramen. Opercular bones complete, spineless, posterior ventral border of suboperculum dissected into rays. Gill membranes separate. Two families.

Two families included: ☆Ammodytidae (Bleekeridae) (Pl. XIII) (6) 7(8),2; Hypoptychidae 4,1.

References: Beebe and Tee-Van (1938), Hubbs (1920), Fowler (1936), Jordan and Evermann (1896), Smitt (1895), Gosline (1963).

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[1] Counts of 6 and 10 are in error for Bathydraco (DeWitt and Tyler, 1960).

SUBORDER CALLIONYMOIDEI

Branchiostegals 5-7, with 3-4 epihyal and 2-3 ceratohyal, 4 external and 2 ventral, all acinaciform or filiform. Interhyal, epihyal, ceratohyal and two hypohyals present. Opercular bones complete and entire (Callionymidae) or operculum and suboperculum with spine (Draconettidae). Gill membranes joined to isthmus. Two families.

In the Callionymidae the gill opening is restricted to a small foramen on the upper side of the head and the branchiostegals become filiform terminally. In the Draconettidae the gill opening is broader, extending to just above the pelvic base and the branchiostegals are acinaciform. It would appear that in the Callionymidae the branchiostegals lost the function of moving the gill membrane when it became broadly connected to the isthmus and lower side of the body and retained only the function of support. With only a supporting function the branchiostegals degenerated from an acinaciform to a filiform condition, much as they have in the eels.

Two families included: *Callionymidae 5-7,1; *Draconettidae 6,1.

<u>References</u>: Briggs and Berry (1959), Day (1875), Fowler (1936), Jordan and Evermann (1898), Smitt (1892), Garman (1899), Gregory (1933).

SUBORDER BLENNIOIDEI

Branchiostegals 4-7(8) with 1-2 epihyal and 3-5 ceratohyal, 4 external and 1-3 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together or not. Ceratohyal without foramen. Opercular bones complete, spineless (except the Congrogadidae may have an opercular spine). Gill membranes united and free from the isthmus or joined to the isthmus. Sixteen families, one of which is known only from fossils.

The following families included: ☆Tripterygiidae 6-7,1; /Pterygocephalidae 5,1; Clinidae[1] (Ophiclinidae, Ophioclinidae) (5)6(7), 11; Blenniidae (5)6(7),9; ☆Congrogadidae (Haliophidae) 4 or 6,5; Peronedyidae 4,1; ☆Zoarcidae (Pl. XV; Lycodapidae, Derepodichthyidae) (4)5-6(7),14; ☆Scytalinidae 6,1; ☆Anarhichadidae 6-7,3; ☆Stichaeidae (Lumpenidae, Xiphisteriidae, Cebedichthyidae) 6,2; ☆Zaproridae 6,1; ☆Pholididae 5-6(7),2; Ptilichthyidae 6,1; ☆Cryptacanthodidae 6,1; Xenocephalidae - no data available; Notograptidae - no data available.

Makushok (1958) gives a count of 3 branchiostegals for Ptilichthys, while Bean (1882) gives 5. Kobayashi (1961) and myself have found 6 (4 specimens examined).

References: Andriashev (1955), Barsukuv (1959), de Beaufort and Chapman (1951), Beebe and Tee-Van (1938), Berg (1949), Böhlke (1961), Borodin (1933), Chapman and Townsend (1938), Clemens and Wilby (1961), Day (1875), Fowler (1936), (1959), Garman (1899), Gosline (1963), Gregory (1933), Günther (1867), Hubbs (1920), Hubbs, Clark (1952), (1953), Jordan and Evermann (1898), Kobayashi (1961a), Makushok (1958, 1961, 1961a), McAllister and Krejsa (1961), Norman (MS), Ogilby (1898), Regan (1912), Smith, C.L. (1957), Smith, J.L.B. (1952), (1961), Smitt (1892), Stephens (1961), Ueno (1954).

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[1] Stephens (1963, U. Cal. Pub. Zool. 68: 1-133, 15 pl.) has recognized the Chaenopsinae as a family and revised them. They have 6 branchiostegals, gill membranes united and free.

SUBORDER SCHINDLERIOIDEI

Branchiostegals 5 with 2 epihyal and 3 ceratohyal, 3 external and 2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal present (hypohyals not present). Interhyal (cartilaginous) articulates with the head instead of the base of the hyomandibular; epihyal and ceratohyal ossified and sutured dorsally; ceratohyal without foramen. Operculum present, slender, spineless; interoperculum and suboperculum absent. A single family.

Gosline (1959) indicates this family is unique in its caudal skeleton and in the insertion of the hyoid arch. In fact, a similar condition is also found in the tiny goby, Mystichthys luzonensis. There is a cartilaginous interhyal present in our material, unlike Gosline's, and the epihyal and the ceratohyal are joined by a dorsal suture. The interhyal inserts on the head of the hyomandibular instead of as usual at the lower end of the hyomandibular. However, in developing embryos, such as Gasterosteus (de Beer, 1937, pl. 57, 4.2 mm stage), the interhyal inserts just below the head of the hyomandibular; by the 25 mm stage the interhyal has moved down towards the lower tip of the hyomandibular, the normal adult position, with the tip of the hyomandibular forming the symplectic. Thus the condition of the hyoid arch in Schindleriidae is not a new development but represents the retention of the larval condition, a retention not unexpected in such a neotenic fish. This retention agrees with Gosline's general statement that the "ossifications" that do occur in Schindleriidae are not of the adult fish type at all but are merely calcifications of normally larval structures. A further modification from the normal acanthopterygian condition is the possession of only 5 branchiostegal rays in which the uppermost (external) ray is lost. Normally only the ventral branchiostegals are lost leaving 4 branchiostegals on external face of the hyoid, instead of the only 3 found as in Schindleriidae.

A single family included: Schindleriidae (1).

References: Gosline (1959), de Beaufort and Chapman (1951), Giltay (1934).

Material examined: *Schindleria praematura*, 2 alizarin UBC specimens, Islas Revillagigedo at southeast end of Isla Clarion, Mexico, identified by Dr. Rosenblatt.

SUBORDER LABROIDEI

Branchiostegals 5-6 with 1 epihyal and 4 ceratohyal, 4 external and 1 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together or not. Ceratohyal without foramen. Opercular bones complete, spineless. Gill membranes united and free or joined to the isthmus. Three families.

The following families included: *Labridae 5-6,15; *Scaridae (Calliodontidae) 5,4; *Odacidae 5,1.

References: de Beaufort (1940), Fowler (1936, 1959), Meek and Hildebrand (1928), Jordan and Evermann (1898), Day (1875), Smitt (1892), Chevey (1932), Schultz (1958), Hubbs (1920).

SUBORDER GOBIOIDEI

Branchiostegals (3) 4-6 with 1-2 epihyal and 4 ceratohyal, 4 external and 2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal separate. Ceratohyal without foramen. Opercular bones complete and spineless (may be soft points). Gill membranes joined to the isthmus. Six families.

The Kraemeriidae have often been placed near the Trichonotidae. Gosline (1955) however moved them to the Gobioidei (along with the Microdesmidae). Rofen (1958) was lead to believe the genus Trichonotus is the closest relative of the Kraemeriidae. The present study favours Gosline's view. The branchiostegals number 5 in the Kraemeriidae with 1 on the epihyal; the gill membranes are joined to the isthmus. In all the Trachinoidei examined the branchiostegals are 6-7 with 2 on the epihyal and the gill membranes are seldom joined to the isthmus. On the other hand the branchiostegals in the Gobioidei are usually 5 (3-6) with 1-2 epihyal and the gill membranes are always joined to the isthmus. This is then evidence for placement of the Kraemeriidae in the Gobioidei. In the tiny goby (to 14 mm) Mystichthys luzonensis the interhyal inserts above the ventral end of the hyomandibular, as in the neotenic Schindleriidae, and only the lower hypohyal is ossified.

Some eleotrids are distinct in having branchiostegal spines. Belobranchus has a sharp spine directed upwards and forwards on the first or first and second branchiostegals while Valenciennea, Pteroculiops and Diaphoroculius have none or rarely one spine. The Trypaucheninae (Taenioididae) are peculiar in having a separate opening at the top of the operculum; this leads to a cavity separate from the gill cavity.

Gosline (1955) indicated that the distribution of the branchiostegals is peculiar in the Gobioidei. However, they appear to resemble the typical perciform pattern.

The following families are included: ☆Eleotridae 4-6,6; ☆Gobiidae (Pl. XV; Periophthalmidae) 3-5,16; Rhyacichthyidae 6; Taenioididae 5,1; Kraemeriidae 5,1; Microdesmidae (Cerdalidae, Pholidichthyidae, Gunnelichthyidae) (4)5-6,1.

References: Böhlke and Robins (1960), (1960a), (1961), Day (1875), Fowler (1936), Garman (1899), Gosline (1955), Günther (1861), Herre (1945), Hubbs (1920), Jordan and Evermann (1898), Koumans (1953), Matsubara and Iwai (1959), Myers and Wade (1946), Norman (MS), Rofen (1958), Te Winkel (1935).

SUBORDER KURTOIDEI

Branchiostegals 7 in *Kurtus indicus* with 4 lateral and 3 internal, 2 epihyal and 5 ceratohyal, all acinaciform. Operculars complete, spineless. Gill membranes separate.

A single family included: ☆Kurtidae 7,1.

References: de Beaufort and Chapman (1951), Day (1875), Boulenger (1904), Bertin and Arambourg (1958).

SUBORDER SIGANOIDEI

Branchiostegals 5 with 1½ epihyal and 3½ ceratohyal, 4 external and 1 ventral, all acinaciform. The lowest branchiostegal broad and buried in the isthmus (as Ephippidae). Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together. Ceratohyal without foramen. Opercular bones complete, spineless. Gill membranes joined to isthmus.

A single family included: ☆Siganidae 5,1.

References: Chevey (1932), Jordan and Fowler (1902a), Hubbs (1920), Day (1875).

† SUBORDER RHAMPHOSOIDEI

No data available on branchiostegals, operculars or hyoid arch. It has been placed with the hemibranchs (Eastman, 1914), in the Ammodytoidei (Romer, 1955) and its own suborder of the Perciformes (Berg, 1955).

A single family: Rhamphosidae (Ramphosidae) - no data (1).

SUBORDER COTTOIDEI

Branchiostegals (4) 5-7 (8) with 1-2 epihyal and 4-6 ceratohyal, 4 external and 1-3 (4) ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals; epihyal and ceratohyal sutured together or not. Ceratohyal without foramen. Opercular bones complete, 0-3 spines on operculum and 0-1 usually 0 on the operculum and suboperculum. Gill membranes separate, united and free from or joined to the isthmus. Twenty-one families.

The following families included: ☆Scorpaenidae (Pl. XIII) 6-7(8), 34; Synancejidae (6)7,4; Congiopodidae 5,1; Pataecidae 6,1; Gnathanacanthidae - no data; Aploactidae 5-6,1; Caracanthidae 4-5,1; ☆Anoplopomatidae 6,1; ☆Hexagrammidae (Pl. XV; Zaniolepidae) 6-7,1; Parabembridae - no data; Bembridae (Bembradidae) 7,1; ☆Platycephalidae 7,3; Hoplichthyidae - no data; ☆Cottidae (Rhamphocottidae) (5)6-7,14; Cottocomephoridae 6 (family); Comephoridae 6 (family); Normanichthyidae 5,1; ☆Psychrolutidae 7,1; ☆Cottunculidae 7,1; ☆Agonidae (Pl. XV) 6,2; ☆Triglidae (Pl. XV) 6-7,5; ☆Peristediidae 7,1.

References: Bolin (1952), Clark (1937), Day (1875), Fowler (1936), (1959), Freeman (1951), Garman (1899), Gill (1891d), Gregory (1933), Günther (1860), Hubbs (1920), Jordan and Evermann (1898), MacLeay (1881), Matsubara (1943), Matsubara and Hiyama (1932), Ruttenberg (1954), Schmidt (1928, 1950), Smith, J.L.B. (1950), Smitt (1892), Taranets (1941), Waite (1923), Watanabe (1960), Welander and Alverson (1954), Woodward (1901).

SUBORDER CYCLOPTEROIDEI

Branchiostegals 6 with 2 epihyal and 4 ceratohyal, 4 lateral and 2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal separate. Ceratohyal without foramen. Operculars complete, spineless. Gill opening restricted. Three families.

The following families included: *Cyclopteridae 6,1; *Liparidae (Pl. XV) 6,3; Eutelichthyidae 6,1.

References: Fowler (1936), Cohen (1960), Burke (1930), Garman (1899), Hubbs (1920), Smitt (1892), (1895), Tortonese (1959).

SUBORDER DACTYLOPTEROIDEI

Branchiostegals 6 with 3 epihyal and 3 ceratohyal, 4 external and 2 ventral, all acinaciform. Interhyal, epihyal, ceratohyal and only one hypohyal present (latter point should be checked); epihyal and ceratohyal separate. Ceratohyal without foramen. Opercular bones complete, small and spineless. Gill openings reduced. A single family.

This family differs from the Scleroparei in having as many as 3 branchiostegals on the epihyal, in the reduction in size of its opercular bones and having only a single hypohyal. The branchiostegals and related bones thus confirm its placement in a separate suborder.

A single family included: *Dactylopteridae (Pl. XIII) 6,1.

References: Gill (1891c), Day (1875), Hubbs (1920).

ORDER GASTEROSTEIFORMES

Branchiostegals 3-4 with 1 epihyal and 2-3 ceratohyal, all external, slender and acinaciform. Interhyal, epihyal, ceratohyal, and two hypohyals present. Interhyal small. Epihyal and ceratohyal joined by a dorsal suture which forms a strut. Opercular bones complete, entire, without spines. Gill membranes joined to isthmus or united and free from the isthmus. Eocene to present. Three families, one wholly fossil, plus one family provisionally included here.

The relationships of this group and the reasons for separation of it from the Syngnathiformes are discussed under the Syngnathiformes.

Aulorhynchidae

Pl. XVII

Branchiostegals: 4 branchiostegals in *Aulorhynchus flavidum* with 1 epihyal and 3 ceratohyal, all on the external face of the arch, all acinaciform, aside from a basal bend the rays are quite straight.

Operculars: Complete and entire; operculum leaf-shaped, pointed behind; suboperculum and interoperculum elongate. Gill membranes united and free from isthmus.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. Interhyal larger at lower end. Epihyal and ceratohyal joined by a suture which forms a stay on the mesial side of the arch. Ceratohyal elongate and swelling little posteriorly, unlike that of the Gasterosteidae. Lower hypohyal anteriormost; and sends a prong backward on the mesial face of the ceratohyal. Upper hypohyal above anterior end of the ceratohyal.

References: Bertin and Arambourg (1958), Jordan and Evermann (1896).

Material examined: Aulorhynchus flavidum, alizarin specimen, San Juan Bautista Island, southeast Alaska, NMC61-163-S; alizarin specimen, BC60-548, British Columbia.

Gasterosteidae

Pl. XVI, XVII

Branchiostegals: 3 in Gasterosteus, Spinachia, Culaea (=Eucalia), Apeltes, and Pungitius. In Gasterosteus aculeatus (freshwater type and marine type) 3 with 1 epihyal and 2 ceratohyal, all external, and all slender acinaciform, slightly bowed. Pungitius pungitius 3 with 1 epihyal and 2 ceratohyal, all external, slender acinaciform and slightly bowed.

Operculars: In Gasterosteus, Pungitius and Culaea complete and entire, posterior border of operculum not ending in a point; suboperculum sigmoid with upper curve of s extending up in front of operculum, the posterior curve attenuate and extending up behind the operculum (posterior curve in Pungitius fraying into two slender points). Gill membranes united and free from the isthmus (Culaea, Pungitius) or joined to isthmus (Gasterosteus, Apeltes).

Hyoid arch: In *Gasterosteus*, *Culaea* and *Pungitius* consists of interhyal, epihyal, ceratohyal and two hypohyals; interhyal ends equal or lower larger; epihyal and ceratohyal joined by a strut; posterior end of ceratohyal about twice width of anterior end; upper hypohyal lies above anterior end of ceratohyal; lower hypohyal anteriormost and sends a prong backward along the lower side of the ceratohyal.

References: Berg (1949), Bertin and Arambourg (1958), Jordan and Evermann (1896), Smitt (1895).

Material examined: *Gasterosteus aculeatus* (freshwater type), alizarin specimen at Institute of Fisheries, U.B.C., from Vancouver, British Columbia; *Gasterosteus aculeatus* (marine type), alizarin specimen, NMC59-441, Ungava Bay, Quebec; *Pungitius pungitius*, alizarin specimen, NMC61-228 & S, McConnell River, Northwest Territories; *Culaea inconstans*, alizarin specimen, NMC61-200, southern Saskatchewan.

† Protosyngnathidae

Branchiostegals: No data available.

Operculars: Operculum ovate.

Relationships: Woodward (1901) synonymizes *Protosyngnathus* with *Aulorhynchus*. Berg (1947) places it in its own family. The operculum looks most like that of *Aulorhynchus* rather than that of the syngnathoids, as figured by Günther.

References: Berg (1947), Woodward (1901), Günther (1876), Von der Mark (1876).

Indostomidae, *incertae cedis*

Branchiostegals: 5-6 Branchiostegals.

Operculars: Operculum with serrate radiating ridges; the margin of the operculum is emarginate between the points where these ridges meet the border. Gill membranes separate.

Relationships: Until the osteology of this family is better known its placement is uncertain. The number of branchiostegals and pelvic rays is higher than in Gasterosteidae and Aulorhynchidae. According to Bolin (1936) the majority of characters - body form, fins, teeth, lateral line system, anterior vertebrae and branchiostegals link it most closely to the Aulorhynchidae and Aulostomidae. The numerous pectoral rays agree more with the Syngnathiformes. The serrated radiating ridges on the operculum are unusual. The branched rays of the median fins agree rather with the Gasterosteiformes.

References: Berg (1947), Prashad and Mukerji (1929), Bolin (1936).

Material examined: None.

ORDER ICOSTEIFORMES

Branchiostegals 6-7 with 1-2 epihyal and 4-5 ceratohyal, 4 external and 2 ventral, all acinaciform. Operculars complete, striate with crenulated edges, without spines. Gill membranes separate. Interhyal, epihyal, ceratohyal and 2 hypohyals. Articulating surfaces of epihyal, ceratohyal and hypohyals cartilaginous. A single recent family.

According to Regan (1923a) there is nothing in their organization to prevent the assumption that they are specialized and degenerate perciforms. The author agrees with this opinion, the branchiostegal form and distribution, the spiny scales, premaxillary bordered upper jaw, 5 pelvic rays, physoclistic gas bladder all favour derivation from the perciforms. Such differences as lack of fin spines, non-protractible premaxillaries and abdominal pelvics can be regarded as secondary modifications.

Icosteidae

Branchiostegals: In *Icosteus aenigmaticus* 6-7 with 2 epihyal and 4 ceratohyal, 4 on external and 2 on ventral face of hyoid arch. In three specimens examined by the author and one reported by Abe (1954a) the branchiostegals have numbered 6, but Kobayashi and Ueno (1956) report 7 and Regan (1923) and Jordan and Evermann (1896) report 6-7.

Operculars: Complete, outer surface striated, border crenulate; without spines. Gill membranes narrowly joined to isthmus anteriorly, nearly separate.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal separated by their cartilaginous unsutured ends.

References: Abe (1954), Regan (1923a), Kobayashi and Ueno (1956), Jordan and Evermann (1896).

Material examined: *Icosteus aenigmaticus*, alcoholic specimen, BC53-99-A, Vancouver Island, British Columbia; alcoholic specimen, Hetta Inlet, near Cordova, Alaska, BC63-09, alcoholic specimen, USNM 49163, San Diego, California; alcoholic specimen, BC59-523, off Queen Charlotte Islands, British Columbia.

ORDER ECHENEIFORMES

Branchiostegals 8-11, with 2 epihyal and 6-9 ceratohyal, 4 on the external face and 4-7 on the internal face of the hyoid arch, acinaciform; opercular bones complete and entire (or opercular crenulate), without spines; suboperculum V-shaped, ascending behind and before operculum; gill membranes separate; interhyal, epihyal, ceratohyal and two hypohyals present, the lower hypohyal invading the lower edge of the ceratohyal; epihyal and ceratohyal sutured. Eocene or Oligocene to present. Two families, one wholly fossil, the other living.

According to Gill (1883) the Echeneidae approach the Gobioidea and Blennioidea and definitely are not related to the Scombridae and Carangidae which have the basis cranii double. Regan (1912d) concluded that they were basically percoid, that their fins were very similar to those of Pomatomidae, Carangidae and Rachycentridae and that the Echeneidae may have evolved from percoids of this type. Starks (1930) considered the shoulder girdle of Echeneidae to be considerably like some of the fishes of the family Scombridae, with the cleithrum turned back at the top and extending but little above the scapula. Gregory (1933) suggested they were derived from relatively primitive percoids such as the stromatioid Palinurichthys, the barrelfish, which lurks under logs.

The high number of branchiostegals (8-11), would seem to be best regarded as a secondary multiplication from the usual perciform number of 6 to 8, in the absence of other primitive acanthopterygians characters and in the presence of the standard perciform number of I5 ventral and 15 branched caudal rays. Derivation would then seem feasible from one of the primitive perciform suborders.

/ Opisthomyzonidae

Branchiostegals: Not visible in specimen of *Opisthomyzon*.

Operculars: Impression of an operculum visible.

References: Wettstein (1886), Gudger (1926).

Material examined: None.

Echeneidae

Pl. XI

Branchiostegals: Varies from 8-11 with 2 epihyal and 6-9 ceratohyal, 4 on external and 4-7 internal face, all acinaciform, curving up behind the suboperculum. *Remoropsis brachyptera* with 9, 2 epihyal and 7 ceratohyal, 4 external and 6 internal; *Rhombochirus osteochir* with 8 (3 specimens) with 2 epihyal and 6 ceratohyal, 4 external and 4 internal; *R. brachyptera* 9 (2 specimens); *Remilegia australis* 11 with 2 epihyal and 9 ceratohyal, 4 external and 7 internal; *Echeneis naucrates* 9; *Remora remora* 9 (3 specimens) with 2 epihyal and 7 ceratohyal, 4 external and 5 internal. Day (1875) apparently followed by Fowler (1936) reports 7 branchiostegals in *Echeneis*, *Remora*, *Remoropsis* and *Remorina*. Day apparently missed the smaller anterior branchiostegals in the thick skin so his counts are not recorded with the above counts made by dissection, on alizarin stained specimens or by careful examination. Hubbs (1920) also implied there were but 6 or 7 branchiostegals found in *Echeneis*. While it is quite possible or even probable that counts of 7 will be found, from present evidence such a count will not be usual.

Operculars: Complete and entire, without spines. In a specimen of *Remora remora* the ventral border of the operculum was crenulate, in *Echeneis naucrates* and *Remoropsis brachyptera* it was entire. Suboperculum crescentic, bordering the lower half of the hemicircular operculum, interoperculum elongate, anterior border notched. Gill membranes separate.

Hyoid arch: Small interhyal; epihyal; ceratohyal; and two hypohyals present. The epihyal and ceratohyal are joined by interdigitating prongs. The lower hypohyals sends a two pronged fork into the lower ceratohyal, the upper interhyal lies dorsolaterally to the anterior end of the ceratohyal.

References: Hubbs (1920), Strasburg (1957), Fowler (1936), Day (1875), Jordan and Evermann (1898).

Material examined: *Remoropsis brachyptera*, alizarin specimen and one alcoholic specimen, BC54-72, San Lucas, Baja California, Mexico; 2 alcoholic specimens, BC56-435, Galapagos; *Rhombochirus osteochir*, dissected specimen, BC57-171, Las Tres Marias Islands, Mexico; alcoholic specimen, BC59-266, Maria Magdalena Island, Mexico; *Remilegia australis*, alcoholic specimen, BC53-236, Goose Island Banks, British Columbia; *Echeneis naucrates*, alcoholic specimen, BC53-180, Columbia; *Remora remora*, skeletal specimen, USNM 265667, 39°N, 72°W: 2 uncatalogued NMC specimens, offing of southern Nova Scotia.

ORDER TETRAODONTIFORMES (TETRODONTIFORMES)

Branchiostegals (3)5-6 with 0-2 epihyal and 3½-6 ceratohyal, (3) 4 external and 1-2 ventral, lowest branchiostegal (except in Ostraciidae and Molidae) expanded, the rest acinaciform (except Molidae where they secondarily somewhat resemble the spathiform). Interhyal, epihyal, ceratohyal and two hypohyals present. Epihyal and ceratohyal sutured. Ceratohyal without foramen. Opercular bones complete, entire, lacking spines (except Chilomycterus). Gill openings restricted to sides of head. Four suborders with 11 families, 3 families of which are known only from fossils. Upper Cretaceous to recent.

Regan (1902) believed that there could be no question as to the close relationship of the less specialized forms of Plectognathi (=Tetraodontiformes) to the Acanthuridae, but considered that the Tetraodontiformes differed ordinally from that family. Hubbs (1920) correctly indicated that the branchiostegals of this group are of the acanthopterygian type. Gregory included the zanclids and teuthids (=acanthurids) in the order. Le Danois (1955), followed by Bertin and Arambourg (1958) removed the Canthigasteridae, Molidae, Tetraodontidae, Diodontidae and Ostraciidae from the order and placed them amongst the malacopterygians in the group Orbiculati. This change was made on the basis of the lack of spines in the fins (Tyler, 1962, pertinently points out that Triodon has spines), and a number of other characters such as feeble ossification of the skeleton (hardly true), medioparietal cranium (not restricted to malacopterygii) and dorsal and anal opposed to one another on posterior portion of the body (found in acanthopterygians such as Lophiiformes, Pegasiiformes, Echeneiformes, etc.). None of these necessitate placement in the malacopterygii. Most authors, e.g. Regan, Berg, Gregory, Hubbs, have considered them as acanthopterygian. Tyler (1963) succinctly scuttles Le Danois' classification.

The branchiostegal system is in agreement with Tyler's opinion. The number, form and arrangement of the branchiostegals and the epihyal-ceratohyal suture are definitely acanthopterygian. The curiously expanded lower branchiostegal is found in members of both of the two groups into which Le Danois divides the Tetraodontiformes. This indicates the artificiality of the division.

The branchiostegals undergo some interesting variations in this group. In the Ostraciidae there is a tendency towards expansion of the ends of the branchiostegals. In the Molidae the branchiostegals are expanded even more and resemble spathiform branchiostegals except that they are thick and nonlaminar. In the other families the lowest branchiostegals is expanded distally into an elongate triangle or fan. These expansions may be related to the small gill opening and to the stiffening of the wall of the branchial chamber by thick skin or bony plates. These two factors would probably necessitate a stronger branchial pumping mechanism than is usual. From this strong branchial pumping mechanism may have developed the peculiar inflating habit of some Tetraodontiformes. The puffing Tetraodontiformes belong to the suborders that have the lowest branchiostegal expanded. In the puffing families this branchiostegal is further expanded and strengthened and the upper edge is curled outwards. Tyler (1962) has neatly explained the function of this expanded branchiostegal by ascribing to it the function of the pump which inflates the distensable gut of the puffers. It is further notable that in the two puffer families there are only three gills, while in other Tetraodontiformes there are four gills. It is possible that with their better developed respiratory pump as many as four gills were no longer necessary.

SUBORDER BALISTOIDEI

† Eotriogonodontidae

Branchiostegals: No data available.

References: Woodward (1901).

† Spinacanthidae

Branchiostegals: No data available.

References: Woodward (1901).

† Trigonodontidae

Branchiostegals: No data available, known only from the front teeth.

References: Woodward (1901), Bauza (1948).

Triacanthidae (Triacanthodidae)

Branchiostegals: 6 in *Triacanthus oxycephalus* with 2 epihyal and 4 ceratohyal, 4 external and 2 ventral, the upper 3 acinaciform, the next two scimitar-like, the lowest very broad mesially with its greatest length equalling 1/3 of its length.

Operculars: In Triacanthus, Johnsoniana, Tydemania, Macrorhamphosodes the opercular bones complete, entire and spineless, the operculum vertically suspended and the interoperculum elongate and narrow anteriorly but broad at point of contact with the suboperculum. Gill opening restricted to side of head.

Hyoid arch: Epihyal and ceratohyal very short and deep.

References: Day (1875), Fraser-Brunner (1941), Gregory (1933).

Material examined: Triacanthus oxycephalus, alcoholic specimen, BC59-574, Thailand.

Monacanthidae (Aluteridae)

Pl. XVI

Branchiostegals: Vary from (3)5-6. Stephanclepis 6, Alutera 6, Osbeckia 6, Monacanthus 5, Psilocephalus 3. Monacanthus hispidus 5 with 1½ epihyal and 3½ ceratohyal, 4 external and 1 ventral, the lowest broad, laminar and scimitar-like, the rest acinaciform.

Operculars: Operculars complete and entire in Monacanthus and Alutera with interoperculum elongate and not reaching posteriorly past the epihyal, operculum vertically suspended. Gill openings restricted.

Hyoid arch: In Monacanthus consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal sutured together. Ventral hypohyal the anteriormost, the dorsal hypohyal partially over the anterior end of the ceratohyal.

References: Day (1875), Gregory (1933), Fraser-Brunner (1940).

Material examined: *Monacanthus hispidus*, alizarin specimen, BC59-529, Gulf of Mexico.

Balistidae

Branchiostegals: 6 in *Balistes*, *Xanthichthys* and *Abalistes*. *Balistes verres* 6 with 4 external epihyal and 2 ventral ceratohyal, the 4 upper close together, the lowest laminar and highly curved, while the upper ones are acinaciform.

Operculars: Complete and entire in *Balistes*; operculum vertically suspended, interoperculum elongate and not reaching posteriorly past the epihyal.

Hyoid arch: In Balistes consists of interhyal, epihyal, ceratohyal and two hypohyals; epihyal and ceratohyal sutured together, the upper hypohyal more posterior. Ceratohyal normally expanded posteriorly.

References: Day (1875), Gregory (1933), Fraser-Brunner (1935).

Material examined: *Balistes verres*, alcoholic specimen, BC60-467, Guerrero, Mexico.

SUBORDER TETRAODONTOIDEI (TETRODONTOIDEI)

Triodontidae

Branchiostegals: 6 in *Triodon bursarius*, the upper 4 close together on the external face, the lower 2 on the ventral face of the hyoid arch, all acinaciform except the lowest which is scimitar-shaped and laminar except the dorsal edge curves out somewhat (but not as much as in the tetraodontids and diodontids, according to Tyler, 1962).

Operculars: In Triodon complete and entire, interoperculum broad at point of contact with suboperculum, tapering anteriorly. Gill opening restricted.

References: Day (1875), Tayler (1962).

Material examined: None.

Tetraodontidae (Tetrodontidae, Canthigasteridae,
Colomesidae, Lagocephalidae,
Chonerhinidae).

Branchiostegals: Vary from 5-6. In Canthigaster 5-6, Sphaeroides 5, Tetraodon 5-6. Canthigaster punctatissima 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform except the lowest which is stout, expanded into a fan and curls outward on the upper edge.

Operculars: Complete and entire in Tetraodon, Sphaeroides and Canthigaster; interoperculum elongate with ventral projection mesially; operculum elongate, vertical with a pointed projection dorsally. Gill opening restricted.

Hyoid arch: In Canthigaster at least epihyal, ceratohyal and one hypohyal present; epihyal and ceratohyal strongly sutured together; ceratohyal with a large triangular ventral projection just anterior to the middle of its length.

References: Fowler (1936), Day (1875), Hubbs (1920), Fraser-Brunner (1943), Tyler (1962).

Material examined: *Canthigaster punctatissima*, alizarin specimen, BC60-119, Taboga Island, Panama.

Diodontidae

Branchiostegals: 6 in *Diodon* and *Chilomycterus*. In *Chilomycterus atinga* 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, all acinaciform except the last which is stout, fan-shaped and has upper edge elevated.

Operculars: Complete and entire in *Diodon* and *Chilomycterus* except suboperculum has an oblique projection pointing mesially. Gill opening restricted.

Hyoid arch: In *Chilomycterus* interhyal not seen, but epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal sutured together.

References: Fraser-Brunner (1943), Chevey (1932), Hubbs (1920), Tyler (1962).

Material examined: *Chilomycterus atinga*, alizarin specimen, NMC62-75 & S, North Carolina.

SUBORDER OSTRACIOIDEI

Ostraciidae (Aracanidae)

Branchiostegals: 6 in *Ostracion*, *Lactophrys* and *Rhineosomus*. *Rhineosomus triqueter* 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform, the lowest not expanded. *Lactophrys tricornis* 6 with 1 epihyal and 5 ceratohyal, 4 external and 2 ventral, upper 2 and the lowest normal acinaciform in shape, the middle 3 with rounded ends.

Operculars: In Rhineosomus operculars complete; suboperculum terminating dorsoposteriorly in a point; interoperculum secondarily approaching that of Pegasus, narrow and short, commencing on the epihyal, terminating on the lower hypohyal being joined to the jaw by a tendon; epihyal and ceratohyal with serrated ends which do not actually contact one another (5 inch specimen). Gill opening restricted.

Hyoid arch: Short and broad in Lactophrys and Rhineosomus. In Rhineosomus consists of interhyal, epihyal, ceratohyal and two hypohyals, the upper hypohyal posteriormost and partly overlying the end of the ceratohyal.

References: Day (1875), Hubbs (1920).

Material examined: Rhineosomus triqueter, alizarin specimen, NMC60-338, Barbados; Lactophrys tricornis, alizarin specimen, Sonda de Campeche, Mexico.

SUBORDER MOLOIDEI

Molidae

Branchiostegals: 6 in Mola; 5 in Ranzania laevis, the upper 2 rays being coalesced; Mola mola 6 with 2 epihyal and 4 ceratohyal, 4 external and 2 ventral, becoming broad distally but thick; the lowest being half as thick as wide.

Operculars: Complete but reduced. In Mola operculum small, suboperculum pointed posteriorly, interoperculum reduced to a splint, entirely embedded in the long ligament between the angular and the suboperculum

(Tyler, 1962). Gill opening restricted.

Hyoid arch: In Mola at least epihyal, ceratohyal and two hypohyals present, these all separated by a layer of cartilage and themselves being poorly ossified.

References: Fraser-Brunner (1951), Smitt (1895), Tyler (1962), Gregory (1933).

Material examined: Mola mola, alcoholic specimen, BC62-355, San Juan Harbor, British Columbia.

ORDER MASTACEMBELIFORMES (incl. CHAUDHURIIFORMES)

Branchiostegals 6 with 1-1½ epihyal and 4½-5 ceratohyal, 4 on the external, the fifth on the internal and the sixth on the ventral, all acinaciform. Interhyal, epihyal, ceratohyal and two hypohyals present. Epihyal and ceratohyal sutured. Opercular bones complete, entire, spineless, operculum suspended from above. Gill membranes separate or narrowly united and free; opening restricted from above, the opercular having no free edge. Fossils unknown. Two families.

Boulenger (1904) considered the Mastacembelidae were possibly derived from the Blenniidae. Regan (1912) considered that they were related to but more specialized than the Percomorphi, showing no particular affinity to any particular group of Percomorphous fishes. Job (1941) concluded that the larvae are percoid in appearance and possibly the Mastacembelidae may have originated from a percoid fish remotely allied to Nandidae. Freihofer (1963) considered the pattern of the ramus lateralis accessorius points to an affinity with the percoids.

The number, arrangement and form of the branchiostegals and the suturing of the epihyal and ceratohyal are typically acanthopterygian and there can be little doubt, as other characters attest, that the Mastacembeliformes are derived from the Perciformes. Regan (1919) and Anandale and Hora (1923) agree that the Chaudhuriidae are related to the Mastacembelidae. With this group of related families the author would like to associate the Synbranchidae. The Synbranchidae, Mastacembelidae and Chaudhuriidae share a similar number of branchiostegals and arrangement of the hypohyals, with hypohyal two perforated and dorsal to the end of the ceratohyal.

These three groups, Mastacembelidae, Chauduriidae and Synbranchiformes, also share the following characters: gill opening restricted from above (an unusual condition, gill openings generally are restricted from below); 70 or more vertebrae; 0-2 pelvic rays; scales cycloid or absent; gas bladder physoclistic or absent; air breathing (Chaudhuriidae not known); upper jaw non-protrusible; no opisthotic, supramaxillary, orbitosphenoid, subocular shelf; epiotic, sphenotic and parietals present; suborbitals reduced or absent; caudal reduced to 10 or fewer rays; dorsal and anal fins and body long. The dorsal restriction of the gill opening may be associated with retention of inhaled air bubbles.

Various authors have concluded that the Synbranchidae were related to the eels, apparently considering only their external appearance. Even Bertin and Arambourg (1958) retain them in adjacent orders. The condition of the branchiostegals and hyoid arch strongly contradicts this and indicates placement in the acanthopterygians.

The characters differentiating Mastacembelidae from Chaudhuriidae are few: Chaudhuriidae lack scales, fleshy tentacle on snout, fin spines, have a reduced shoulder girdle and fewer vertebrae (Annandale and Hora, 1923). The Mastacembelidae are now known, like the Chaudhuriidae, to possess a basisphenoid (Sufi, 1956). All may be regarded as degenerative changes. Whereas these differences certainly justify recognition of a family or possibly even suborder they do not appear to warrant ordinal recognition of the Chaudhuriidae. As there are no striking characters peculiar to the Chaudhuriidae, Bailey (1960) is followed in synomymizing the order Chaudhuriiformes with the Mastacembeliformes.

Mastacembelidae

Pl. XVI, XVII

Branchiostegals: 6 in Mastacembelus and Macrognathus. In Macrognathus aculeatus 6 with 1½ epihyal and 4½ ceratohyal, 4 external and 2 ventral, all slender acinaciform; M. armatus 6 with 1½ epihyal and 4½ ceratohyal, 4 external, the fifth on the internal and the sixth on the ventral face of the arch, all acinaciform; M. mellandi 6 with 1 epihyal and 5 ceratohyal, 4 external, fifth on the internal and the sixth on the ventral face of the hyoid arch, all acinaciform. The innermost branchiostegals of each side do not cross. Mastacembelus pancelas 6 with 4 on external and 2 on internal face of arch.

Operculars: In Mastacembelus complete, entire and spineless. The operculum cleaver-shaped, suspended from its anterodorsal corner. Gregory (1933) indicates the operculum and suboperculum as fusing posteriorly;

in all specimens examined by the author they were distinct. Gill membranes separate or narrowly united and free, so restricted from above that the operculum is bound to the body.

Hyoid arch: In Mastacembelus consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal joined by two or three suturing prongs. Hypohyal one anteriormost, sending small prong below ceratohyal. Hypohyal two perforated by a small foramen, with posterior two thirds lying above the end of the ceratohyal.

References: Sufi (1956), Gregory (1933), Day (1875), Job (1941), Khanna (1961), Regan (1912).

Material examined: Mastacembelus pancelas, BC55-64, India; Macrognathus armatus, alizarin specimen, NMC62-207-S, India; M. aculeatus, BC alizarin specimen, Malaya; M. mellandii, alizarin specimen, NMC63-69 & S, Northern Rhodesia.

Chaudhuriidae

In the stage of final typing the author was able to clear and stain a specimen of the rare genus Chaudhuria recently obtained through the kindness of Dr. A.G.K. Menon.

Branchiostegals: 6 in Chaudhuria caudata (both sides), with 1 epihyal and 5 ceratohyal, 4 external and 2 internal (the 5th inserted higher on the inner face than the 6th), all slender acinaciform.

Operculars: Gill membranes separate; opening restricted - extends to just above pectoral fin.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal not (yet) sutured (specimen may be too small for this to have developed). Hypohyal one anteriormost, sending a small prong below the ceratohyal. Hypohyal two lying half over the ceratohyal and half over hypohyal one and emitting a small dorsal projection.

References: Regan (1919), Anandale and Hora (1923).

Material examined: *Chaudhuria caudata*, NMC63-118-S, alizarin specimen, Inle Lake, South Shan States, Burma.

ORDER SYNBRANCHIFORMES (SYMBRANCHIFORMES)

Branchiostegals 5-6 with 2-3 epihyal and 3-4 ceratohyal, 4 on the external and 2 on the ventral face of the hyoid arch, acinaciform, rather stout, round in cross-section, needle-like and slightly curved; interhyal, epihyal, ceratohyal and two hypohyals present, the last four sutured together. Opercular bones complete and entire. Gill membranes united and free, the opening dorsally restricted, resulting in a single median ventral oval opening or slit. Fossils unknown. Three families.

SUBORDER ALABETOIDEI

Alabetidae

Branchiostegals: No data.

Operculars: Gill membranes united and free; dorsally restricted opening - producing effect of a single transverse ventral opening.

References: Regan (1912c).

SUBORDER SYNBRANCHOIDEI

Cuchiidae (Amphipnoidae)

Branchiostegals: 6 in *Cuchia cuchia*.

References: Day (1875).

Material examined: None.

Synbranchidae (Symbranchidae)

Pl. XVI, XVII

Branchiostegals: 6 in *Synbranchus* and *Monopterus*. *Synbranchus marmoratus* 6 with 2-2½ epihyal and 3½-4 ceratohyal, 4 on the external and 2 on the ventral face of the hyoid arch, acinaciform and soout; the anteriormost branchiostegal on the left crosses the anteriormost on the right hyoid arch; this may serve to strengthen the united gill membranes (a similar adaption in some Pleuronectiformes). *Monopterus javensis*, *M. bengalensis* and *M. albus* with 6, although according to Day (1875) *javensis* may have 5 or 6. *M. albus* 6 with 3 epihyal and 3 ceratohyal, 4 on the external and 2 on the ventral face of the hyoid arch, needle-shaped, round in cross-section and gently curved; the upper 4 are short and separated from the larger 2 below. *M. fluta* 5, needle-like, slightly curved, the anterior one longer and not crossing its counterpart of the other side.

Operculars: In *Synbranchus* complete and entire, operculum longer in the horizontal plane. In *Monopterus* complete and entire, operculum long in the vertical plane, paddle-shaped. *Synbranchus* with a short transverse oval gill opening on the ventral side of the head - the result of a dorsally restricted gill opening and the gill membranes united and free from the isthmus.

Hyoid arch: In *Synbranchus* interhyal, epihyal, ceratohyal and two hypohyals present; the epihyal and ceratohyal, the lower hypohyal and the ceratohyal firmly sutured together. In *Monopterus* epihyal and ceratohyal sutured together.

References: Hubbs (1920), Day (1875), Chevey (1932).

Material examined: *Synbranchus marmoratus*, alizarin specimen, NMC62-69 & S, Guatemala; alizarin preparation of arch and branchiostegals, SU 47046, Trinidad; *Monopterus albus*, skeleton, USNM 191144, Taiwan; *Monopterus fluta*, alcoholic specimen, BC58-572, Malaya.

ORDER LOPHIIFORMES

Branchiostegals (4) 5-6, with 0-1 (2) epihyal and 5-6 ceratohyal, 4 external and 1-2 internal or ventral, all acinaciform, stout and mesially round. Interhyal, epihyal, ceratohyal and one or two hypohyals present. Epihyal and ceratohyal sutured or not. Opercular bones complete, operculum typically Y-shaped, often with posterior spine. Gill opening restricted. Eocene to present. Sixteen families.

The relationship of this family is discussed under Gobiesociformes where it is shown that the Lophiiformes, Batrachoidiformes and Gobiesociformes are apparently closely related. It is likely that one of the Percoidei, or at least one of the Perciformes, gave rise to the Lophiiformes themselves.

SUBORDER LOPHIOIDEI

Lophiidae

Pl. XVI

Branchiostegals: 6 in *Lophius* and *Lophiomus*. In *Lophius piscatorius* 6 with 1 epihyal and 5 ceratohyal, 4 on the external and 2 on the internal face of the hyoid arch, all basally stout, mesially tending to be cylindrical and terminally attenuate acinaciform branchiostegals. *Chirolophius forbesii* 6 with 1 epihyal and 5 ceratohyal, 4 external and two ventral. In the deeper water forms there is a tendency for the second hypohyal, the brace between the epihyal and ceratohyal, and the spine on the suboperculum to be lost.

Operculars: In *Lophius* complete; the operculum Y-shaped with base inserting on the hyomandibular the anterior arm broad, the posterior arm attenuate; the suboperculum an elongate triangle with apex posteriormost, the lower anterior corner forming a spine and giving off a slender support along the anterior border of the operculum and off its external face a small spine, the lower border fimbriate; interoperculum giving off a small laterally directed spine. Gill membranes broadly joined to isthmus.

Hyoid arch: In *Lophius* consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal elongate, the first turned upwards at its posterior end; the two joined by interdigitating prongs dorsally. A small lower hypohyal. The larger dorsal hypohyal sends a curved lamina posteriorly along the upper and internal face of the ceratohyal, where it is received by a depression in the ceratohyal. Although this projection does not have the exact form of that found in the batrachoidids and gobiesocids it will be seen that a slight lateral rotation will complete a cylinder and bring it to lie on the external face as in those 2 groups. *Chirolophius* similar but upper hypohyal exposed on lateral surface.

References: Hubbs (1920), Garmann (1899), Jordan and Evermann (1898), Smitt (1892), Gregory (1933).

Material examined: *Lophius piscatorius*, alizarin specimen, NMC62-56, Emerald Bank of Nova Scotia; *Chirolophius forbesii*, alizarin specimen, BC59-247, Mazatlan, Mexico.

SUBORDER ANTENNARIOIDEI

Antennariidae

Branchiostegals: 6 in *Antennarius* and *Histrio*.

Operculars: Operculum Y-shaped with two arms broad, suboperculum and interoperculum are elongate entire laminae. Gill opening reduced to a pore situated below pectoral base, or far posterior (*Abantennarius*).

Hyoid arch: At least interhyal, epihyal, ceratohyal are known to exist.

References: Hubbs (1920), Day (1875), Jordan and Evermann (1898), Smitt (1892), Gregory (1933), Schultz (1957).

Material examined: None.

Chaunacidae

Branchiostegals: 6 in Chaunax coloratus with 0 epihyal and 6 ceratohyal, 4 on the external and 2 on the ventral face, all acinaciform.

Operculars: In Chaunax complete and entire, without spines. Gill opening behind pectoral fin.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and one apparently cartilaginous hypohyal (according to figure); epihyal and ceratohyal apparently separate.

References: Garman (1899).

Material examined: None.

Brachionichthyidae

Branchiostegals: No data available.

Operculars: Gill aperture restricted to small opening just above and behind axil.

References: Cuvier (1817), Günther (1861), Macleay (1881).

Material examined: None.

Ogocephalidae (Oncocephalidae)

Branchiostegals: Vary from 5-6. Ogocephalus 6, Zalieutes 6, Halieutaea 5-6, Dibranchus 6, Malthopsis 6. In Ogocephalus darwini 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, the uppermost enlarged, all acinaciform (Hubbs, 1958 in a lapsus calumni, reports the posterior 4 on the epihyal). In *Zalieutes elater* 6 with 0 epihyal and 6 ceratohyal, 4 on the external and 2 on the internal face of the hyoid arch, all acinaciform, the uppermost notably larger and angled more vertically. In *Malthopsis spinulosa* 6 with 4 on the external and 2 on the ventral face of the hyoid arch, the uppermost notably larger. In *Ogcocephalus vespertilio* 6 branchiostegals, the upper 4 external, the lower 2 ventral, the upper branchiostegal greatly enlarged.

Operculars: In *Malthopsis* operculum triangular with a posterior notch, rather than Y-shaped as in other lophiiforms. On its lower posterior corner there is an apparently separate knob with 6 spinules (according to Garman's figure), suboperculum sabre-shaped and entire, interoperculum may or may not be present, at least not shown by Garman. In *Halieutichthys* operculum forms a more normal lophiiform Y with upper arm attenuate, lower arm broad; anterior and posterior arms of suboperculum much enlarged and forming margin of disk; dorsal arm of suboperculum failing to border operculum posteriorly but passing behind operculum and contacting the supracleithrum; the latter radical organization might warrant subfamilial recognition. In *Ogcocephalus* operculum of normal Y-shape; suboperculum with anterior and posterior projections but the upper arm reaching up to the upper arm of the operculum; the interoperculum a lamina between the suboperculum and mandible; all bones entire and without spines; suboperculum forming part of border of disk. Gill opening reduced to pore above pectoral base.

Hyoid arch: In *Zalieutes* interhyal, epihyal, ceratohyal known to be present; the epihyal and ceratohyal sutured internally and externally.

References: Day (1875), Jordan and Evermann (1898), Hubbs (1920, 1958), Garman (1899).

Material examined: *Zalieutes elater*, alizarin specimen, BC59-247, Mazatlan, Mexico. *Ogcocephalus darwini*, alcoholic specimen, BC56-440, Tagus Cove, Albermale Island, Galapagos Islands.

SUBORDER CERATIOIDEI

Caulophrynidae

Branchiostegals: In *Caulophryne jordani* 6 with 0 epihyal and 6 ceratohyal, 4 external face and 2 ventral face, all acinaciform; the upper ones lie free between the epihyal and ceratohyal (the bones have not completed development in the larval skeleton portrayed but the above would seem the most likely resulting arrangement in the adult, although possibly one might end up on the epihyal). Epihyal and ceratohyal separate.

Operculars: In *Caulophryne* complete; operculum Y-shaped; suboperculum elongate and reaching up towards the upper arm on the operculum; interoperculum elongate and nearly vertical. Gill opening restricted.

Hyoid arch: In *Caulophryne* interhyal, epihyal, ceratohyal and one hypohyal known.

References: Bertelsen (1951).

Material examined: None.

Melanocetidae

Branchiostegals: In Melanocetus johnsoni with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform.

Operculars: Complete, suboperculum bears a small anteriorly directed spine; suboperculum reaches up towards upper arm of operculum. Gill opening restricted.

Hyoid arch: Interhyal, epihyal, ceratohyal figured. Epihyal and ceratohyal separate.

References: Bertelsen (1951).

Material examined: None.

Himantolophidae

Branchiostegals: In Himantolophus groenlandicus 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral or internal, all acinaciform.

Operculars: In Himantolophus complete, operculum Y-shaped, suboperculum elongate and reaching up towards upper arm of operculum, interoperculum very slender. Gill opening restricted.

Hyoid arch: Interhyal, epihyal and ceratohyal figured.

References: None.

Diceratiidae

Branchiostegals: In Diceratias bispinosus 6 with 0 or 1 on the epihyal and 5 or 6 on the ceratohyal, 4 external and 2 internal or ventral face, all acinaciform. Paroneirodes with 6.

Operculars: Operculum in Diceratias Y-shaped, suboperculum extending up to upper arm of operculum and anteroventrally directing a spine anteriorly, interoperculum elongate, narrow. Gill opening restricted.

Hyoid arch: In Diceratias consists of interhyal, epihyal, ceratohyal (the hypohyals not figured).

References: Bertelsen (1951), Maul (1962a).

Material examined: None.

Oneirodidae

Branchiostegals: 6 in Oneirodes, Lasiognathus, Thaumanichthys, and Chaenophryne. In Chaenophryne draco 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform. In Oneirodes eschrichti 6 with 0 epihyal and 6 ceratohyal, 4 on external and 2 on ventral or internal face, all acinaciform. Lasiognathus sp. 6 with 6 ceratohyal, 4 external and 2 ventral or internal. Thaumanichthys pagidostomus (?) 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform. Dolopichthys allector 6 with 0 epihyal and 6 ceratohyal, 4 on external and 2 on ventral face of hyoid arch, all acinaciform.

Operculars: Complete, subopercular spine absent, gill opening restricted. The shapes of the opercula and subopercula differ between genera. In Oneirodes operculum V-shaped with arms equally broad but upper one shorter; suboperculum an inverted comma in Microlophichthys operculum V-shaped with arms narrow and tapering, the upper one shorter; operculum an inverted comma. In Tyrannophryne operculum V-shaped with slender arms, upper shorter; suboperculum oval. In Leptacanthichthys operculum V-shaped with arms lomg and slender but upper arm shorter; suboperculum an inverted comma. In Ctenochirichthys operculum V-shaped with slender arms, the upper arm shorter; suboperculum elongate. In Dolopichthys operculum V-shaped with slender arms, the upper shorter; suboperculum teardrop-shaped. In Danaphryne upper arm of operculum reduced to a small point on the large cone-shaped lower arm; suboperculum an inverted comma. In Pentherichthys operculum V-shaped, upper arm broad and short, the lower long and slender; suboperculum an elongate teardrop. In Lophodolus operculum V-shaped with slender arms, the upper shorter or subtriangular with region between arms filled with osseus tissue; suboperculum an elongate teardrop. In Chaenophryne operculum subtriangular with lower wing longest; suboperculum teardrop-shaped. In Lasiognathus operculum V-shaped with arms subequal, suboperculum an elongate oval. In Thaumanichthys operculum mulitradiate with upper radii more incised than lower; suboperculum wing-shaped.

Hyoid arch: Consists of interhyal, epihyal and ceratohyal in Chaenophryne and Oneirodes; hypohyal(s) not portrayed; epihyal and ceratohyal separate. In Thaumanichthys interhyal, epihyal, ceratohyal and single hypohyal present; epihyal and ceratohyal separate.

References: Bertelsen (1951), Gregory (1933), Garman (1899), Maul (1961), (1962a).

Material examined: None.

Centrophrynidae

Branchiostegals: In *Centrophryne spinulosa* 6 with 0 or 1 epihyal and 5 or 6 ceratohyal, 4 external and 2 ventral, all acinaciform.

Operculars: Complete, suboperculum extending up to postero-dorsal corner of triangular operculum, interoperculum elongate; suboperculum with small antrorse spine. Gill opening restricted.

Hyoid arch: Consists of interhyal, epihyal, ceratohyal and a single hypohyal; epihyal and ceratohyal separate.

References: Bertelsen (1951).

Material examined: None.

Ceratiidae

Branchiostegals: 6 in *Ceratias* and *Cryptosaras*. In *Cryptosaras couesii* and *Ceratias holboelli* 6 with 0 epihyal and 6 ceratohyal, 4 external and 2 ventral, all acinaciform.

Operculars: In *Ceratias* complete and entire; *Cryptosaras* same but subopercular spine present. Gill opening restricted.

Hyoid arch: In *Cryptosaras* and *Ceratias* interhyal, epihyal, ceratohyal and two hypohyals present; epihyal and ceratohyal separate.

References: Bertelsen (1951).

Material examined: None.

Gigantactinidae

Branchiostegals: 6 in *Gigantactis* and *Rhynchactis*. In *Gigantactis* 6 with 0 or 1 epihyal and 5 or 6 ceratohyal, 4 external and 2 ventral face, all acinaciform.

Operculars: In *Gigantactis* operculum basically Y-shaped; suboperculum slender, comma-shaped reaching towards upper arm of operculum and spineless; interoperculum slender, elongate, and spineless. Gill opening restricted.

Hyoid arch: Consists of at least interhyal, epihyal and ceratohyal; epihyal and ceratohyal separate.

References: Bertelsen (1951).

Material examined: None.

Neoceratiidae

Branchiostegals: In *Neoceratias spinifer* 5-6 with epihyal and 4 ceratohyal, 4 external and 2 ventral or internal, all acinaciform.

Operculars: Operculum in *Neoceratias* Y-shaped with upper arm more slender, suboperculum slender, spineless and reaching up to upper arm of operculum, interoperculum short (males) to long (females). Gill opening restricted.

Hyoid arch: Consists of interhyal, epihyal and ceratohyal; epihyal and ceratohyal separate; hypohyals not portrayed.

References: Bertelsen (1951).

Material examined: None.

Linophrynidae

Branchiostegals: Usually 5, rarely 4. In *Photocorynus spiniceps*, *Edriolychnus schmidti*, *Linophryne macrophryne*, and *Borophryne apogon* 5, all on the ceratohyal, with 4 external and 1 ventral or internal, all acinaciform. In *Linophryne coronata* with 1 epihyal and 4 ceratohyal, 4 external and 1 ventral.

Operculars: Complete in *Photocorynus*, *Edriolychnus*, *Linophryne* and *Borophryne*. Operculum varying from Y-shaped to triangular (the region between the arms of the Y being filled in), suboperculum spineless, entire elongate and teardrop-shaped, interoperculum slender and elongate.

Hyoid arch: In *Photocorynus* and *Borophryne* consists of interhyal, separate epihyal and ceratohyal and a single hypohyal; similar in *Edriolychnus* and *Linophryne* except hypohyal not exhibited in figure. In *Linophryne coronata* the hyoid barbel appeared to be composed of the interhyoideus muscle and a nerve which issued from the hind end of the mandible.

References: Bertelsen (1951).

Material examined: *Linophryne coronata*, SIO-282-65A, from 27° 05'N, 138° 25' W to 27° 15.5' N, 137° 58' W.

ORDER BATRACHOIDIFORMES

Branchiostegals 6 with 2 epihyal and 4 ceratohyal, 4 external and two internal or ventral, all acinaciform, tending to be round in section mesially. Two hypohyals, the upper sending a cylindrical projection along the dorso-lateral face of the ceratohyal and with a foramen. Ceratohyal, epihyal and interhyal present. The ceratohyal and epihyal sutured. Opercular bones complete, opercular with one or two spines. Gill membranes broadly joined to isthmus. Pliocene to present. A single family.

The relationships of this family are discussed under Gobiesociformes - that they were derived from forms close to the Lophiiformes, and that the close ancestors of the Batrachoidiformes gave rise to the Gobiesocidae. Starks (1923) however, believed the batrachoids were allied to the uranoscopoids. The hyoid arch, branchiostegal rays and opercular bone give clear evidence of the Batrachoidiformes belonging in the Acanthopterygii.

Batrachoididae

Pl. XVI, XVII

Branchiostegals: 6 in Coryzichthys, Holobatrachus, Opsanus and Porichthys. In P. notatus (2 specimens) 6 with 2 epihyal and 4 ceratohyal, 4 upper ones external, the next one internal and the lowest one ventral, all acinaciform.

Operculars: In Porichthys complete, the operculum Y-shaped with the base inserting on the hyoid arch, the upper arm forming a posteriorly directed spine; the suboperculum being Y-shaped with the posterior arm dividing into filiaments, the interoperculum laminar. In Opsanus the operculum with a second spine between the arms of the Y, and the suboperculum being a triangle.

Hyoid arch: In Porichthys consists of interhyal, epihyal, ceratohyal and two hypohyals. Epihyal and ceratohyal sutured. The upper hypohyal sends a cylindrical projection along the dorsolateral face of the ceratohyal, which has a groove to receive it. A foramen is located in the upper corner of the upper ceratohyal. The anteriorly placed lower hypohyal sends one prong obliquely posteroventrally and a second smaller prong between the upper hypohyal and the end of the ceratohyal.

References: Fowler (1936), Meek and Hildebrand (1928), Day (1875), Smitt (1892), Jordan and Evermann (1898), Hubbs (1920).

Material examined: Porichthys notatus, alizarin specimen, BC53-302, Denman Island, British Columbia; alizarin specimen, NMC59-99, English Bay, British Columbia.

ORDER GOBIESOCIFORMES

Branchiostegals 5-7, usually 6 with 2 epihyal and 4 ceratohyal, 4 on the external face and 2 on the internal face of the hyoid arch, all stout and acinaciform. One hypohyal, ceratohyal, epihyal and interhyal present. Hypohyal sending a cylindrical extension along the dorsolateral face of the ceratohyal. Ceratohyal and epihyal separate. Opercular bones complete, posterior borders of operculum and suboperculum may be fimbriate and the latter may terminate in a spine. Gill membranes united and free from isthmus or joined to isthmus. There is a possible Miocene fossil.

A single family.

Among the various opinions expressed as to the origins of the Gobiesocidae, Boulenger (1904) has suggested the Callionymidae because of the position of the pelvic fins, Starks (1905) after a careful osteological study of it and related groups came up with "small results" although the families Batrachoididae and Callionymidae, particularly the first, did offer some slight indications of relationship. Regan (1929) offered only that they were related to the Percomorphi, Briggs (1955) stated they were most closely allied to the batrachoids, but said there was some resemblance to the Callionymoidei, Freihofer (1963) considered the pattern of the ramus lateralis accesorius basically like the pattern in Cottidae and Liparidae.

The branchiostegal number, shape and arrangement confirm that the Gobiesocidae are acanthopterygian. That the epihyal and ceratohyal are separate must be regarded as secondary. The stout and mesially cylindrical branchiostegals are similar to those in Batrachoidiformes and Lophiiformes, ordinarily acanthopterygian branchiostegals are flatter in cross-section. As in the Batrachoididae the fifth branchiostegal is more dorsally inserted on the mesial face and the branchiostegals increase in size downwards, except that the third is largest in Gobiesocidae and the fourth in Batrachoididae; the size then decreases downwards from the largest. A most striking similarity exists between the single hypohyal of the Gobiesocidae and the upper hypohyal of the Batrachoididae. In both, the body of the hypohyal is cylindrical and lies projecting outwards along the external face of the ceratohyal; the ceratohyal is slightly hollowed out to receive the hypohyal; between the posterior end of the hypohyal and the ceratohyal is a slight gap, then there is a socket on the ceratohyal to receive this end; the upper anterior end of the hypohyal has a projection and there is a small foramen on the anterior end of the hypohyal. This striking relationship of the hypohyal and ceratohyal and form of the hypohyal is not known in any other group. Although the Gobiesociformes have only one hypohyal the ventral anterior corner of it resembles the lower hypohyal of the Batrachoididae and it requires little imagination to consider that the single hypohyal of Gobiesocidae is the result of fusion between the two of Batrachoididae with the loss of the ventral anteriorly directed prong of the lower hypohyal of Batrachoididae. It remains to be seen whether embryology will provide evidence for the latter. In a 10 mm. s.l. specimen there was only one hypohyal with no sign of a fusion. Unfortunately Runyan, who studied the embryology of Gobiesox strumosus, (1961) does not dwell upon this point. The condition of the hyoid arch in the Lophiidae also resembles that of Gobiesocidae, but to a lessor extent.

Examination of the caudal skeleton of Gobiesox and Porichthys showed them to be very similar. Both have two hypural plates each bearing 6 fin rays. The lower hypural in each sends forward a projection on the lower side. The fin rays emit a small lateral projection where they contact the hypurals. In addition, the last neural and haemal arches are slightly expanded terminally instead of being attenuate.

Other characters the Gobiesocidae shares with the Batrachoididae are branchiostegals usually 6; gill membranes may be joined to the isthmus; number of gills reduced from 4; a similar vertebral range; ventral fin rays reduced; apparently only epipleural ribs present; the infraorbitals and spinous dorsal are reduced or absent; the posttemporal simple; without opisthotic, pterosphenoid or basisphenoid; pelvics anterior; dorsal reduced or absent; branched caudal rays 10 or less. These characters are also borne by the Lophiiformes except that in it, the pelvics have 5 soft rays and epipleurals are absent. At least the primitive Lophiiformes have similar hyoid arches, though less highly evolved. Thus the Lophiiformes can be judged to belong to this group of orders, although slightly more primitive. Although they are more primitive than the Batrachoidiformes and the Batrachoidiformes are more primitive than the Gobiesociformes neither is directly ancestral to the other, each group having its own specializations. But it seems likely that the Lophiiformes are closest to the ancestral form that the Batrachoidiformes arose fairly close to the branching off point of the Lophiiformes, and the Gobiesociformes fairly close to the branching off point of the Batrachoidiformes.

Gobiesocidae

Pl. XVI, XVII

Branchiostegals: Vary from 5-7. *Apletodon* 6, *Aspasmaminima* 6, *Aspasmichthys* 6, *Aspasmogaster* 6, *Chorisochismus* 6, *Conidens* 6, *Cochleoceps* 6, *Creocele* 6-7, *Dellicthys* 6, *Diplecogaster* 6, *Diplocrepis* 6, *Gastrocyathus* 6, *Gastroscyphus* 6, *Gobiesox* 6, *Gouania* 6, *Haplocylix* 6, *Lepadichthys* 6, *Liobranchia* apparently 6, *Opeatogenys* 5, *Parvicrepis* 5-6, *Pherallodus* 6, *Trachelochismus* 6-7. In *Gobiesox maeandricus* (five specimens) 6 with 2 epihyal and 4 ceratohyal, 4 external and 2 internal, all stout and acinaciform, the central portion of the branchiostegals is nearly round in cross-section, not flat; the posteriormost of the 2 internal branchiostegals is inserted higher up on the mesial face. In Gobiesox strumosus 6 with 4 external and two internal.

Operculars: In Gobiesox complete; operculum triangular with posterior border fimbriate; suboperculum triangular with posterodorsal border fimbriate, posterior and terminating in a spine; interoperculum small and laminar, situated at some distance anteriorly, lying over the epihyal. Gill membranes united and free from the isthmus, or joined to the isthmus. The operculum and suboperculum angle downwards and posteriorly (because of the backward extension of the preoperculum).

Hyoid arch: In Gobiesox consists of interhyal, epihyal, ceratohyal and one hypohyal. Epihyal subrectangular with interhyal parallel to its posterior face and pivoting on its posterior ventral corner, an unusual relationship. The epihyal and ceratohyal are separate. The ceratohyal is elongate, the expansion at its epihyal end occupying a very small space. The ceratohyal is grooved to receive the cylindrical portion of the hypohyal on its dorsolateral face. The anterior end of the hypohyal sends out a dorsal and ventral projection. From its appearance it seems likely the hypohyal is composed of a fusion of the lower small batrachoid hypohyal and larger upper one. A 10 mm. specimen did not show a separate lower hypohyal or a line of fusion.

References: Briggs (1955), Runyan (1961), Starks (1905).

Material examined: Gobiesox maeandricus, 2 alizarin specimens, NMC62-29, Ucluelet, British Columbia; alizarin specimen, NMC60-297, Roller Bay, British Columbia; alizarin specimen, BC59-291, Jordan River, British Columbia; skeletal specimen, USNM 26446, Monterey, California.

ORDER PEGASIFORMES

Branchiostegals 5 with 2-3 on the epihyal and 2-3 on the ceratohyal, 4 on the external and 1 on the internal surface, all elongate acinaciform, curve up around parallel to gill cover. Opercular bones complete and entire, operculum and suboperculum very small, interoperculum inserting on epihyal and resembling a large interhyal. Preoperculum forming a pseudogular. Gill opening restricted to small lateral pore. Interhyal, sutured epihyal and ceratohyal, and two hypohyals present. A single extant family.

The relationships of this extremely unusual-looking family are not clear. Jungerson (1915) considered them to be clearly acanthopterygian, and to represent at least a suborder of their own, but suggested that they might possibly be a strongly modified offshoot from the stem of the Scleroparei. However, he admitted they showed no close relationship with existing Scleroparei, and certainly not with forms such as Agonus or Aspidophoroides. Rendahl (1930) did not venture an opinion in his revision of the family. Regan in 1913 stated the rather striking similarities to some of the Scorpaenoidei did not indicate relationship and later (1929) that the systematic position was uncertain. Berg (1947) accorded them the most advanced position in his scheme of fishes but gave no opinion on their origin. The body armour suggests relationship to the syngnathids or agonids, the pectorals to the dactyloperids, according to Herald (1961).

The arrangement of the branchiostegals, the protrusible premaxillaries, and the spine in the ventral fin clearly indicate that this family is acanthopterygian. The unusual hyoid arch with the single hypohyal, pseudo-interhyal, the modified opercular bones and gill opening reduced to a pore confirm other indications that this family is highly distinctive. The branchiostegals show some resemblance to those of the lophioids. Several other characters are shared with that group: horizontal pectorals, restricted gill openings, few principal caudal rays, posttemporal fused to skull, 3 or fewer pectoral radials, protrusible upper jaw, lack of opisthotic and basisphenoid, and reduced infraorbital series. Externally there is some resemblance to the Ogcocephalidae. However, some of these characters may well represent parallelisms.

There are certain similarities to the Indostomidae. The number of branchiostegals (5-6) is similar, both have bony plates on the body, laterally spinous elongate nasals, ventrals reduced and subabdominal, upper jaw protrusible, pectoral rays unbranched, jaw teeth reduced or absent, posttemporal joined to skull, branchiostegals curved up behind operculum (according to figure of Indostomus in Prashad and Mukerji), and the anal lies below the soft dorsal. The number of rays in the soft dorsal and anal, the number of vertebrae and body plates are about the same. They differ in that the Pegasidae have the first seven vertebrae joined (this is probably to support the longer snout), the caudal rays of Pegasidae are fewer and unbranched (8 as opposed to 12), the gill membranes are joined to the isthmus in Pegasidae but separate in Indostomus, the Pegasidae lack a spinous dorsal (but the supports for one exist according to Jungerson), and the Indostomidae lack a pelvic spine (according to Bolin). In all of these characters, except the last, the Pegasidae are more advanced than the Indostomidae. None of the differences would appear to preclude the derivation of the Pegasiformes from the Indostomidae. The pelvic spine of the Indostomidae can be considered to have been lost. However, until the branchiostegals, hyoid arch, caudal skeleton and other characters of Indostomidae (and Pegasidae) are better known it seems advisable to leave Indostomidae where it is. The Pegasidae are marine Indo-Pacific while the Indostomidae are freshwater Burmese fish. A marine invasion during the Tertiary is known to have occured in the present range of the Indostomidae, however.

Another relationship is suggested by the peculiar opercular bones of Pegasidae. The operculum and suboperculum are very small and hidden in a fold of skin behind the preoperculum. The interoperculum does not contact the suboperculum but is connected posteriorly to the hyoid arch; both its ends are notched. These peculiar features are found elsewhere only in the Daclytoperidae. Other common characters would also suggest relationship: anterior vertebrae joined; similar number of vertebrae; nasals coalesced; 8 caudal rays; pectorals unbranched, elongate and horizontal, with the uppermost rays apparently forming the anterior border (whereas in the Triglidae the ventral rays form the anterior border); gill membranes joined to isthmus and opening constricted; and suborbitals attached to preoperculum. This possibility deserves further investigation.

Pegasidae

Pl. XVI

Branchiostegals: In Pegasus 5. Pegasus volitans 5 with 2 or 3 epihyal and 2 or 3 ceratohyal, 4 external and 1 internal, all acinaciform and very long attenuating to filiform distally, paralleling the edge of the pseudogular around behind to the gill opening.

Operculars: Complete and entire. Operculum V-shaped with the upper arm fanlike, suboperculum a triangle. Both bones very small and lying in a small flap of skin before the gill pore in a gap between the bony plates. Interoperculum a long splint, the posterior end notched and inserting on the epihyal, appearing at first glance to be the interhyal. Gill opening restricted to small pore on lateral surface of head.

Hyoid arch: Small interhyal inserting on internal face of epihyal, epihyal and ceratohyal stout and sutured strongly together, hypohyal sutured to anterior end of ceratohyal, hypohyal onto the whole length of the ventral face of the ceratohyal - the latter a unique relationship.

References: Jungerson (1915), Rendahl (1930).

Material examined: Pegasus volitans, alizarin preparation of arch and branchiostegals, SU 27700, Batanga, Luzon, Philippines; Pegasus volitans, alizarin specimen, NMC63-115-S, Takao, Formosa.

DISCUSSION OF RESULTS

Because of the length of the study it is useful to bring together, in an abbreviated form, the more important findings. Each finding is described in a short paragraph and reference is made to the pages where it is discussed in full detail. Discussion is presented under two headings, New Findings and Confirmed Findings. Data are summarized in table 1 and phylogenetic relationships are depicted in Pl. XVIII.

New Findings

The Hiodontidae and Notopteridae have been considered closely related by Berg (1947) and Gosline (1960) (see p. 151). The Hiodontidae differ trenchantly from the Notopteridae in lacking a caudal gas bladder caecum, in having 2 hypohyals, a much more primitive caudal skeleton, an adipose eyelid and gular fold, and in other characters. These indicate that the Hiodontidae are more primitive and are not closely related. A new suborder, Hiodontoidei, is erected for the reception of the Hiodontidae, and placedamongst the primitive Clupeiformes.

The Notopteridae, together with the Osteoglossidae, Pantodontidae, Heterotidae, and Arapaimidae differ from the Clupeiformes (in which group Berg (1947) and Gosline (1960) place them) and agree with the Mormyriformes in: the reduction of hypohyals, the pecular caudal skeleton, the non-spathiform upper branchiostegals, the rigidly enclosed nasal capsule without diverticula or suborbital bone, the posteriorly closed myodome, the downward process on the second hypobranchial (except Heterotidae), and other characters (p. 151, 216). It is concluded that these families require removal from the Clupeiformes and placement in the order Mormyriformes. In the light of the absence of a lateral parasphenoid peg, the low number of branchiostegals, and the presence of a basisphenoid and a lateral cranial foramen, the Notopteridae appear closer to the Gymnarchidae and Mormyridae than to the osteoglossoid families.

The recently named suborder, Tselfatoidei, had been placed in the Beloniformes (p. 148). However its separate epihyal and ceratohyal, mouth bordered both by premaxillary and maxillary, 18 branched caudal rays, 7 pelvic rays, and parasphenoid teeth all provide evidence for the conclusion that it should be placed in the Clupeiformes instead of in the Beloniformes.

The families Myctophidae and Neoscopelidae (p. 188) differ from all other Myctophiformes in the possession of only 2 epihyal branchiostegals, a gas bladder and well developed photophores. It is suggested that they require suprafamilial or subordinal separation from other Myctophiformes.

Current authors, Berg (1947) and Liem (1963), place the Anabantidae and Luciocephalidae in the Perciformes and the Ophicephalidae in a separate order (p. 356). Although Regan originally placed the three in their own order he later changed his mind and included them in the Perciformes. There is, however, good evidence for their close relationship to one another in the possession of the following peculiar characters: a caudal gas bladder caecum, an epibranchial respiratory organ, possession of parasphenoid teeth and a similar ramus lateralis accessorius.

The Cretaceous genus Omosoma (p. 280, 361) has been placed in the Beryciformes (Polymixiidae) and in the Perciformes (Stromateidae). However, its possession of as many as 12 branchiostegals, 20 caudal rays

\+ = present
0 = absent
\- = not known
s = spathiform
a = acinaciform
v = virgaform
f = filiform
S = separate
U = united and free
J = joined

ORDERS	MEDIAN GULARS	LATERAL GULARS (PAIRS)	NUMBER OF BRANCHIOSTEGALS	BRANCHIOSTEGALS ON INTERHYAL / EPIHYAL / CERATOHYAL / HYPOHYAL	BRANCHIOSTEGALS ON EXTERNAL FACE / VENTRAL OR INTERNAL FACE	BRANCHIOSTEGAL FORM	HYOID ELEMENTS PRESENT INTERHYAL / EPIHYAL / CERATOHYAL / HYPOHYALS	EPIHYAL-CERATOHYAL SUTURE	GILL MEMBRANES-SEPARATE UNITED OR JOINED	OPERCULARS PRESENT OPERCULUM / SUBOPERCULUM / INTEROPERCULUM / OPERCULAR SPINES
CROSSOPTERYGII										
Hoploptychiformes	-	1	10	- - - -	- -	s	- - - -	-	-	+ + 0 0
Osteolepiformes	0-1	1	4-8	- - - -	- -	s	- - - -	-	-	+ + 0 0
Coelacanthiformes	0-1	1	0	0 0 0 0	0 0	0	+ 0 + 1	0	S	+ + 0 0
DIPNEUSTI										
Dipteriformes	2	2	2-3	- - - -	- -	s	- - - -	-	-	+ + 0 0
Phaneropleuriformes	1	2	2	- - - -	- -	s	- - + -	-	-	+ + 0 0
Uronemiformes	-	-	-	- - - -	- -	-	- - + -	-	-	+ + 0 0
Ctenodontiformes	-	1	-	- - - -	- -	-	- - - -	-	-	+ + 0 0
Ceratodiformes	0	0	0	0 0 0 0	0 0	0	? 0 + 1	0	J	+ + 0 0
Lepidosireniformes	0	0	0	0 0 0 0	0 0	0	0 0 + 0	0	J	+ + 0 0
BRACHIOPTERYGII										
Polypteriformes	0	1	0	0 0 0 0	0 0	0	+ 0 + 1	0	S	+ + 0 0
ACTINOPTERYGII - CHONDROSTEI										
Palaeonisciformes	0-1(2)	0-1	4-23	- - - -	- -	s	+ 0 + 1	0	-	+ + 0 0
Tarrasiiformes	-	-	15	- - - -	- -	s	- - - -	-	-	+ + 0 0
Phanerhynchiformes	-	-	series	- - - -	- -	a	- - - -	-	-	+ + 0 0
Haplolepiformes	1	1	1-3	- - - -	- -	s	- - - -	-	-	+ + 0 0
Redfieldiiformes	0	0	0-1(2)	- - - -	- -	s	- - - -	-	-	+ + 0 0
Perleidiformes	1	1	7-12	- - - -	- -	s	+ 0 + -	0	-	+ + 0 0
Dorypteriformes	0	0	0	0 0 0 0	0 0	0	- - - -	-	-	? 0 0 0
Bobasatraniiformes	-	-	0-4	- - - -	- -	s	- - + -	-	-	+ 0 0 0
Pycnodontiformes	0	0	2-5	- - - -	- -	a	- - - -	-	-	+ 0 0 0
Ptycholepiformes	1	1	series	- - - -	- -	s	- - + -	-	-	+ + 0 0
Pholidopleuriformes	1	1	6-14	- - - -	- -	s	- - + 1	-	-	+ + 0 0
Cephaloxeniformes	-	-	-	- - - -	- -	-	- - - -	-	-	+ + 0 0
Aethodontiformes	1	-	-	- - - -	- -	-	- - - -	-	-	+ + 0 0
Luganoiformes	-	-	-	- - - -	- -	-	- - - -	-	-	+ + 0 0
Peltopleuriformes	-	-	6-7	- - - -	- -	s	- - - -	-	-	+ + 0 0
Platysiagiformes	-	-	13	- - - -	- -	s	- - - -	-	-	+ + 0 0
Chondrosteiformes	0	0	9-12	- - - -	- -	s	- - + 1	-	-	+ + 0 0
Saurichthyiformes	0	0	1-3	- - - -	- -	-	- - + 1	-	-	+ 0 0 0
Acipenseriformes	0	0	1	1 0 0 0	1 0	-	+ 0 + 1	0	UJ	+ +00 0
HOLOSTEI										
Ospiiformes	1-2	0	9-12	- - 8 2	10 0	s	- + + -	0	-	+ + + 0
Amiiformes	1	0	5-30	0/0-6/9-21/0	9-21 0	s	+ + + 1	0	S	+ + + 0
Lepisosteiformes	0	0	3	0/2 /1 /0	3 0	s	- + + 1	0	U	+ + 0 0
Aspidorhynchiformes	0	0	12-13	- - - -	- -	s	- + + -	0	-	+ + + 0
Pachycormiformes	1	0	30-50	- - - -	- -	s	- + + 1	0	-	+ + + 0
Pholidophoriformes	1	0	1?-18	- - - -	- -	s	- - - -	-	-	+ + + 0
TELEOSTEI - MALACOPTERYGII										
Clupeiformes	0-1	0	2-36	0/½-13/0-23/0-5		s(a)	+(0)+ + 2(1)	0	S(UJ)	+ + + 0
Myctophiformes	0	0	6-26	0/2-9/3-14/0-2		a	+ + + 2	0	S	+ + + 0
Mormyriformes	0	0	3-17	0/0-5/1-8/0	4-8 0-5	a	+ + + 0-1	0	JU(S)	+ +0 +0 0
Notacanthiformes	0	0	6-23	0/4-7/2-7/0	all 0	a	+ + + 2	0	S	+ +0 + 0
Giganturiformes	0	0	0	0 0 0 0	0 0	0	0 0 0 0	0	J	0 0 0 0
Saccopharyngiformes	0	0	0	0 0 0 0	0 0	0	0 0 0 0	0	J	0 0 0 0
Cypriniformes	0	0	3-20	0/1-3/2-14/0	2-4 1-15	as	+ + + 1-2	+0	JUS	+ +0 + 0
Anguilliformes(+4-46 jugostegalia)	0	0	6-22	0/4-12/0-15/0	0-10 0-15	f	0 + + 0-1	0	J	+ +(0)+(C) 0
Beloniformes	0	0	(9)10-15	0/2-4/7-9/0	all 0	a	0 + + 1	+	S	+ + + 0
ACANTHOPTERYGII										
Ophicephaliformes	0	0	5-6	0/1-2/4-5/0	4 1-2	a	+ + + 2	+0	SU	+ + + +0
Beryciformes	0	0	7-9	0/2(3)/2-7/0	4 4	a	+ + + 2	0	S	+ + + +0
Lampridiformes	0	0	5-7	0/0-3/3-5/0	4-6 0-2	a	+ + +1-2	0	SJ	+ + + 0
Zeiformes	0	0	(5)6-8	0/0-1(4)/2-8/0	4 3-4	a	+ + + 2	+0	S	+ + + 0
Ophidiiformes	0	0	(5)6-9(10)	0/2/5-6/0	4 3-4	a	+ + + 2	+	SUJ	+ + + +0
Gadiformes	0	0	(5)6-8	0/0-1/5-8/0	4 3-4	a	+ + + 2	+	SU	+ + + 0
Ateleopiformes	0	C	7-9	0/3-4/4/0	4 3	a	+ + + 2	0	S	+ + + 0
Syngnathiformes	0	0	1-5	0/0-4/0-3/0	1-4 0-1	af	+ + + 1-2	+0	SJ	+ + + 0
Percopsiformes	0	0	6	0/1/5/0	4 2	a	+ + + 2	+0	SJ	+ + + +0
Pleuronectiformes	0	0	6-7(8)	0/2-4/3½-5/0	4 2-3	a	+ + + 2	0	SU	+ + + 0
Bathyclupeiformes	0	0	7	0/2-2½/4½-5/0	4 3	a	+ + + -	-	S	+ + + 0
Cyprinodontiformes	0	0	4-6(7)	0/1/4-5/0	4 1-2	a	+ + + 1	+	SU	+ + + 0
Perciformes	0	0	(3)4-7(8)	0/0-4/2-6/0	(3)4 0-4	a	+ + + 2(1)	+0	SUJ	+ + + +0
Gasterosteiformes	0	0	3-4	0/1/2-3/0	3-4 0	a	+ + + 2	+	UJ	+ + + 0
Icosteiformes	0	0	6-7	0/1-2/4-5/0	4 2	a	+ + + 2	0	S	+ + + 0
Tetraodontiformes	0	0	(3)5-6	0/0-2/3½-6/0	4 1-2	a	+ + + 2	+0	J	+ + + 0
Echeneiformes	0	0	8-11	0/2/6-9/0	4 4-7	a	+ + + 2	+	S	+ + + 0
Mastacembeliformes	0	0	6	0/1-1½/4½-5/0	4 2	a	+ + + 2	+	SU	+ + + 0
Synbranchiformes	0	0	5-6	0/2-3/3-4/C	4 2	a	+ + + 2	+	U	+ + + 0
Lophiiformes	0	0	(4)5-6	0/0-1(2)/5-6/0	4 1-2	a	+ + + 2	+0	J	+ + + +0
Batrachoidiformes	0	0	6	0/2/4/0	4 2	a	+ + + 2	+	J	+ + + +0
Gobiesociformes	0	0	5-7	0/2/4/0	4 2	a	+ + + 1	0	UJ	+ + + 0
Pegasiformes	0	0	5	0/2-3/2-3/0	4 1	a	+ + + 2	+	J	+ + + 0

Table 1. Summary of data on branchiostegal series and hyoid arch in Teleostome fishes.

and intermuscular bones demonstrates it to be more primitive than known Beryciformes and to require at least a new family for its reception. It is highly significant in that although it is an acanthopterygian it possesses characters otherwise known only in the malacopterygians.

The gobioids, currently placed in the Perciformes, are suggested as possibly related to the Percopsiformes, judging by their lateralis system, their caudal skeleton and the position of the opisthotic (p. 315, 330, 369). They are provisionally left in the Perciformes.

The clupeoids and some derivatives were found to be characterized by the clupeoid projection on one or more branchiostegals (p. 10, 137); the percopsoids, ophidiiforms, and gadiforms by the percopsid projection on their 4th branchiostegal (p. 10, 311).

Confirmed Findings

The following findings are not new, but the confirmation of existing knowledge is often valuable. Some findings are, however, in opposition to current views (and in agreement with views expressed earlier).

The supraordinal groups (p. 69) Chondrostei, Holostei and Teleostei are redefined. The Chondrostei are characterized by the lack of an interoperculum, the Teleostei by 2 hypohyals, while the Holostei have an interoperculum and but a single hypohyal.

The elopoids and albuloids are each (p. 132) considered subordinally distinct, in disagreement with Berg (1947) but in agreement with Jordan (1896).

The gonorhynchoids are considered (p. 153) subordinally distinct from the chanoids in disagreement with Gosline (1960) but in partial agreement with Berg (1947) (but Berg's Phractolaemoidei is included in the Chanoidei).

The cypriniforms (p. 335), in agreement with Gosline (1961) are considered derived from a clupeoid, as evidenced by clupeoid projections in characids.

In essential agreement with Rosen and Freihofer, the ophidioids (p. 311), gadiforms, amblyopsids, and percopsiforms are considered to be related groups. The author differs somewhat from Rosen on the following three points. The ophidioids are considered, on the basis of branchiostegal number and form, reduction of pelvics, lack of mental barbel, characters of the anterior vertebrae, presence of large otoliths, opisthotic position, and other characters, to require a new order, Ophidiiformes. The amblyopsids on the other hand, are not considered to require ordinal separation from the Percopsiformes. Thirdly, the Ateleopiformes (p. 319) and possibly the Mirapinnatoidei (p. 187) appear associated with these orders. Data from the hyoid arch and branchiostegals suggest, in agreement with other authors, that the Lophiiformes, Batrachoidiforms and Gobiesociformes form a related group of orders (p. 409).

While the evolutionary tendency towards loss of branchiostegals (recognized by earlier authors) is verified, several apparent exceptions are pointed out (Pachycormiformes, Elopoidei, Anguilliformes, Echeneiformes).

ADAPTIVE EVOLUTION

In the previous section branchiostegals have been studied to determine what similarities or differences they indicate between different groups - phylogenetic evolution. Here they are studied to determine how they responded to changes without and within the fish - adaptive evolution.

A fish must adapt to changes without and within. Changes in one organ may necessitate changes in another organ. The effects of the development of aerial respiratory organs, elongation of the mandible, development of a filter feeding apparatus, of increase or decrease in size, of separate, united or joined gill membranes on the branchiostegal series are discussed below. Adaptive changes restricted to single groups have already been discussed in the phylogenetic section.

Accessory Respiratory Organs

In the warm, swampy waters of the world where there is little oxygen there frequently evolve accessory respiratory organs for breathing in air. Does partial or complete dependence on other means of respiration result in a reduction of the branchiostegal series? Table 2 below compares the number of branchiostegals and the condition of the gill membranes in forms with accessory respiratory organs and in the forms from which they were probably derived. The type of accessory respiratory organ is listed. Data on accessory respiratory organs is from Carter (1957), Poll (1957), Berg (1947), Bertin (1958).

Thirty families are listed. Most of the families have relatively few branchiostegals, nine or fewer (except Arapaimidae, Megalopidae and

Amiidae). It can be seen that certain of the families show a reduction in the number of branchiostegals from their ancestral form. Some families, notably the Notopteridae and Osteoglossidae, may lose their suboperculum. The gill membranes are most often united to one another and free from or joined to the isthmus, rather than primitively separate. That is, the gill aperture tends to be reduced. It thus appears in some cases that the assumption of other means of respiration may have resulted in a reduction in the number of branchiostegals and a reduction in the size of the gill opening. That a more marked effect from aerial respiration is not found might be ascribed to aquatic respiration still being important at some season or phase of life. It is possible that branchiostegals in *Arapaima* are not lost because of the method of feeding. Fontenele (1959) described *Arapaima* as feeding on loricariids by using a strong suction; this may be induced by abduction of the branchiostegals.

Table 2. Relation between aerial respiratory organs and branchiostegal number and gill membranes.

Group	Aerial Respiratory Organ	Branchiostegal number	Gill membrane	Branchiostegal Number of Progenitor
Ceratodidae	single dorsal lung	0	R	0-3
Lepidosirenidae	double ventral lung	0	R	0-3
Protopteridae	double ventral lung	0	R	0-3
Polypteridae	double ventral lung	0	R	1-3*
Lepisosteidae	cellular gas bladder	3	U	5*
Amiidae	cellular gas bladder	10-13	S	14*
Megalopidae	gas bladder	23-27	S	20-36
Chanidae	accessory branchial organ	4	U	5-20
Kneriidae	epibranchial organ	3	R	5-20
Phractolaemidae	alveolar gas bladder	3	R	5-20
Umbridae	vascularized gas bladder	4-7	S	7-20
Heterotidae	epibranchial organ	7-8	S	10-17
Arapaimidae	cellular gas bladder	16	S	10-17
Notopteridae	epibranchial organ and gas bladder	(3)6-9	U	10-17
Gymnarchidae	cellular gas bladder	4	U	6-8
Characidae (_Erythrinus_, _Lebiasina_)	vascular gas bladder	4	-	3-5
Electrophoridae	buccal papillae	4	R	3-5
Sternarchidae (_Hypopomus_)	modified gills	4	R	3-5

Table 2 (Cont'd)

Group	Aerial Respiratory Organ	Branchiostegal number	Gill membrane	Branchiostegal Number of Progenitor
Cobitidae (*Cobitis*, *Misgurnus*)	intestine	3	J	3
Doradidae	stomach or gut	7	R	3-15
Loricariidae (*Ancistrus*, *Plecostomus*)	stomach	4	J	3-15
Clariidae (*Heteropneustes*)	postbranchial diverticulum	7-8	S	7-15
Anabantidae (*sensu lato*)	suprabranchial organ	5-6	U	6-7
Luciocephalidae	pharyngial diverticulum	5	S	6-7
Ophicephalidae (=*Channidae*)	suprabranchial organ	5	U	6-7
Gobiidae (*Periophthalmidae*)	glandular and buccal and gill cavity	5	J	5-6
Cyprinodontidae (*Girardinus*, *Lebias*, *Orestias*)	branchial papillae	4-5	U	4-6
Mastacembelidae	mucus coated gills	6	U J	6-7
Cuchiidae (*Amphipnoidae*)	branchial diverticula	5-6	U	6
Synbranchidae	buccal cavity and intestine	5-6	U	6

S = gill membranes separate

U = gill membranes united and free from isthmus

J = gill membranes joined to isthmus

R = gill opening restricted

Filter Feeding Apparatus

Certain of the plankton feeders are filter-feeders. They pass relatively large volumes of water through a fine screen formed by the numerous elongate gill rakers emitted by the gill arch. The influence of this apparatus and manner of feeding on the extent of the gill opening and the number of branchiostegals is considered here.

Amongst the more well known of the plankton feeding fish are the clupeoids (Clupeidae, Engraulididae, Dorosomatidae, Dussumieriidae), the Polyodontidae, Salmonidae (certain *Oncorhynchus* and *Coregonus* species), and Myctophidae. All of these groups, except the Polydontidae, have the gill openings wide, the gill membranes separate and fairly numerous branchiostegals, 5 to 15. Although the gill membranes of the Polyodontidae are unsupported by branchiostegals and united and free from the isthmus, the gill openings are still very wide.

A natural experiment exists in the non-filter feeding families which develop a filter feeding species. From the benthic Cottidae have evolved the pelagic filterfeeding Comephoridae (or Comephorinae). While the gill membranes are united and free from or joined to the isthmus in Cottidae, they have become separate in Comephoridae (Taranetz, 1941, Nikolsky, 1954). The phytoplankton feeding Hypothalmichthyinae have the gill membranes united and free instead of joined to the isthmus as in most Cyprinidae (Nikolsky, 1954). However, in the phytoplankton feeding *Tilapia esculenta* the gill membranes do not appear to have been greatly modified; but it also feeds upon detritus. However, it may generally be said that the gill openings of filter feeders are wide with the gill membranes separate and free from the isthmus and that there are fairly numerous branchiostegals. These conditions may be considered an adaption to passing relatively large volumes of water through the gill rakers. It may be noted that the wide gill openings of filter-feeding teleostomes are paralleled by the wide gill slits of the planktonophagous elasmobranchs, Cetorhinus and Rhincodon.

Filter-feeding families are more common in the malacopterygii than in the acanthopterygii. A possible explanation is that usually the gill membranes are separate and there are more branchiostegals to support the long gill membranes in the Malacopterygii while frequently these conditions do not pertain in the Acanthopterygii. It is notable that the branchiostegals have not secondarily increased in filter feeding Acanthopterygii such as Comephorus and Tilapia.

Size

To determine how far body size influences the number of branchiostegals and gill membranes, giant and miniature fish are compared. The giant fish are defined as those 10 feet or more in length, miniature fish as those groups having many representatives 3 inches (7.5 cm.) long or less. The comparison is restricted to surface waters and to those fish lacking accessory respiratory organs. Fishes belonging in the giant category were found with the assistance of Norman and Fraser (1937), Smith, J.L.B. (1950) and Herald (1961). Istiophorid nomenclature follows Robins and de Sylva (1960). Species are listed under giant fish because only a few species are known over 10 feet, families under miniature fish because there is little information on fish of minimum size and the difficulty of establishing the adult size of small fishes.

Table 3. Number of branchiostegals and gill membrane attachment in some giant fishes (ten feet or longer).

Species	Maximum Size (feet)	Branchiostegal Number	Gill Membranes
Acipenseridae			
Huso huso	28	1	J
Acipenser transmontantus	20	1	J
Acipenser sturio	10	1	J
Polyodontidae			
Psephurus gladius	12	1	U
Chirocentridae			
Chirocentrus dorab	12	8	S
Siluridae			
Silurus glanis	13	15-16	S
Pimelodidae			
Brachyplatysoma filamentosum	15*	15-17	S
Muraenidae			
Thyrosoidea macrurus	10*	9	R
Serranidae			
Promicrops lanceolatus	12	7	S
Scombridae			
Thunnus thynnus	14	7	S
Isiophoridae			
Makaira indica	16	–	U
Tetrapterus angirostris	11*	7	U
Istiophorus orientalis	11	7	U
Istiophorus albicans	11	7	U
Xiphiidae			
Xiphias gladias	15	7	S
Scaridae			
Chlorurus gibbus	12	5	J
Labridae			
Cheilinus sp.	10	5	U

S = gill membrane restricted

U = gill membranes united and free from isthmus

J = gill membranes joined to isthmus

R = gill opening restricted

Table 4. Branchiostegal number and gill membrane attachment in miniature fish (groups having many species of 3 or less inches).

Group	Branchiostegal Number	Gill Membrane Attachment
Salangidae	4	J
Denticipitidae	5	S
Cromeriidae	3	-
Mirapinnatoidei	7-9	J
Characidae	3-5	S(J)
Astroblepidae	4	J
Callichthyidae	3-4	R
Homalopteridae	3	R
Solenostomidae	1-2	R
Amblyopsidae	6	J
Cyprinodontidae	4-6(7)	U(S)
Goodeidae	4-5	U
Phallostethidae	5	S
Apogonidae	(6)7(8)	S
Gobiidae	(3)4-6	J
Schindleriidae	5	S
Kraemeriidae	5	J
Dactyloscopidae	6	S
Tripterygiidae	6-7	U
Caracanthidae	4-5	R
Gasterosteidae	3	UJ
Gobiesocidae	5-6(7)	UJ
Pegasidae	5	R

It may be seen from tables 3 and 4 that the giant fishes have from 1-17 branchiostegals, 5-16 neglecting the Acipenseriformes, whereas the miniature fishes have from 1-9. Only in the Acipenseriformes of the giant fishes does the count descend below 5, while in 13 of the 24 miniature groups the count descends below 5. That is, miniature fishes tend to have fewer branchiostegals. Giant fishes tend to have more branchiostegals, but this tendancy is less marked. The relationship also holds if the size of fishes with over 20 branchiostegals is examined (see list under jaw length). These (neglecting, as above, the deep water stomiatid families, Gonostomatidae, Chauliodontidae and Astronesthidae which fail to reach a foot) attain medium to large sizes, 1-8 feet.

It may also be seen from.the above tables that miniature fishes more commonly have the gill membranes joined to the isthmus. The membranes are joined to the isthmus or the opening restricted in 12 of 23 miniature families but only in 5 of the 17 giant families.

Several factors may influence branchiostegal number and gill membrane attachment in small fishes. The increase in relative surface area of the body in small fishes may permit some respiration to be conducted through the skin. With less dependence on branchial respiration it is possible that branchiostegals would be lost and the gill opening be reduced. In this regard Te Winkel (1935) has found a reduction in gill area in very small fish. Another factor might be the supporting strength of the gill membrane itself. It is conceivable that as the size of the gill membrane decreases it become relatively stronger.

Te Winkel (1935), Hubbs (1944) and Myers (1958) have found parallel trends in other characters. Myers reported minute fishes often exhibited a reduced number of scales and fin rays, as well as other features. A reduced number of branchiostegals and reduction in gill opening can now be added to the list of morphological and physiological adaptions undergone in miniaturization.

Jaw Length

The length of the gill slit between the isthmus and the jaws is related to the length of the jaws. If the jaws extend further posteriorly then this portion of the slit may be longer. Since this slit must be covered by the branchiostegal-supported gill membrane a relationship might be expected between its length and the posterior extension of the jaws. The jaws may of course shorten or lengthen anteriorly without affecting the lower part of the gill slit.

Of the Clupeiformes the large-mouthed elopoids, dussumieriids, engraulidids, stomiatoids, salmonoids and esocids tend to have many branchiostegals, (5)7-36. The small-mouthed remaining clupeoid families, together with the albuloids, the gonorhynchoids, the remaining salmonoid families, and the dalliids and umbrids have 2-16. This would suggest that there is a positive correlation between length of jaws and number of branchiostegals in the Clupeiformes. The correlation is not, of course, perfect. In osmerids for example, the jaw does not extend back past the eye in the Hypomesinae where the branchiostegals number 6-10, whereas the jaw does extend past the eye in the Osmerinae where the branchiostegals number only 6-8 (McAllister, 1963).

It has been shown previously that the malacopterygians tend to have more branchiostegals, 0-36, than the acanthopterygians, 1-11. Samples of the marine fishes of British Columbia (figures in Clemens and Wilby, 1961) and the fishes of South Africa (black and white figures in Smith, J.L.B., 1950) show that malacopterygians tend to have longer jaws than acanthopterygians. A jaw was considered long if it passed a vertical from the posterior margin of the eye. Using this approximate method 52% of the 46 British Columbia malacopterygians have long jaws while only 11% of the 207 acanthopterygians have long jaws. Similarly, in the South African sample 61% of the 99 malacopterygians have long jaws while only 13% of the 343 acanthopterygians had long jaws. Myers (1958) has already indicated this in more general terms.

The above data would suggest that there is a correlation between the posterior extension of the jaw and the number of branchiostegals. This may further be tested by examining jaw length in families having over 20 branchiostegals. The following are families with branchiostegals more numerous than 20: †Caturidae, †Pachycormidae, †Palaeoniscidae, Megalopidae, Elopidae, Gonostomidae, Chauliodontidae, Astronesthidae, Harpadontidae, Halosauridae, Xenocongridae, Muraenesocidae, Neenchelidae, Echelidae and Ophichthyidae. In 13 out of 15 of these families the jaw extends slightly too greatly behind the eye, in only 2 (Megalopidae and Halosauridae) does the jaw fail to extend behind the posterior border of the eye. There thus appears to be a strong relationship between branchiostegal number and jaw length.

It would appear that the presence of many branchiostegals and hence a long gill membrane would permit the jaws to extend far posteriorly with a consequently long ventral gill slit. But, the presence of many branchiostegals does not necessitate that the jaws be long. Secondly, few branchiostegals and a short gill membrane would appear to limit in posterior extension of the jaws.

Gill Membrane Attachment

The branchiostegals support the gill membranes. Hence changes in the gill membrane might be expected to influence the number of branchiostegals. The gill membranes are longer when separate and shorter where united and free from the isthmus or joined to the isthmus. In the Clupeiformes the suborders with gill membranes usually separate have (4-6) 7-20 (21-36) branchiostegals, while the suborders with the gill membranes united and free from or joined to the isthmus have 3-5. In the salmonoid Clupeiformes both states are found. In those salmonoid families in which the gill membranes are separate the branchiostegals number 4-19, where they are not separate the branchiostegals number 2-4. The same relation is seen in the Siluroidei where families with gill membranes always separate have 7-20 branchiostegals while families with gill membranes not always separate have 3-12 branchiostegals. The perciform suborders with gill membranes always separate have 5-7(8) branchiostegals, with gill membranes not always separate (3) 4-7. Thus it may be concluded that fishes with the gill membranes separate tend to have more branchiostegals than those that lack separate gill membranes.

A further test of the relationship may be made by examining those families having more than 20 branchiostegals (see list under jaw length). The fossil families must be omitted since the condition of their gill membranes is uncertain. All of the non-anguilliform families with more than 20 branchiostegals have separate gill membranes. The relationship between number of branchiostegals and gill membrane attachment is thus further verified.

When the gill opening is restricted a further change may often be observed. The branchiostegals may attenuate to filiform condition. Filiform branchiostegals are found in Anguilliformes, Syngnathiformes and Pegasiformes. All of them have restricted gill openings. This relationship may be explained mechanistically. The gill membranes move less and support themselves more when broadly attached. Selection for strong supporting branchiostegals then decreases. Economic selection and selection for flexibility then favour slender, filiform branchiostegals. It cannot be said that all fishes with restricted gill openings have filiform branchiostegals, e.g. Melanostigma amongst others. However, it may be said that all fishes known with filiform branchiostegals have restricted gill openings.

Deep Sea

Life in the deepsea (below shelf and deeper, + 200 m.) does not appear to greatly influence the number of branchiostegals or elements of the hyoid arch. A possible exception being the Giganturiformes and the Saccopharyngiformes in which the adults lack the hyoid arch and branchiostegals.

The effect rather appears to be on the composition of the skeletal elements. The arch and branchiostegals in deepsea fishes are soft and flexible and take up alizarin stain slowly; signs of poor ossification. Not only are the bony sections poorly ossified but the ossifications of elements are often not complete, the ends of elements still being cartilaginous. Denton and Marshall (1958) and Marshall (1960) document the relationship of ossification in the skeleton to bathymetry. Examples of hyoid elements remaining partly cartilaginous in adult deep water fishes are Notacanthidae, Melamphaeidae and Ateleopidae.

Ossification may be reduced in order to decrease density. Gas bladders are often reduced or lost in fish below 1000 metres (Marshall, 1960). To avoid energy loss through locomotory efforts to maintain depth, ossification is reduced. It is possible that reduced ossification is also an adaption to lower activity and reduced physical stress from waves and currents. Alternately it may be related to a reduced feed supply. The failure to completely ossify the bones represents the retention of larval characteristics and may be regarded as an adaptation to deepsea existence.

In summary it may be said that branchiostegals and gill membranes respond to the presence of aerial respiratory organs, to small size, to short jaw length and deepsea existence and that gill membrane attachment and the number and form of branchiostegals are interrelated. Some of these factors may act simultaneously. For example, the Kneriidae have an accessory respiratory organ, small size, short jaws and gill openings restricted (they have only three branchiostegals).

SUMMARY AND CONCLUSIONS

1) The branchiostegal series and hyoid arch elements were found to provide sound systematic characters useful in tracing the phylogeny of taxa from levels above the ordinal down to the species level and equal in value to caudal and pelvic rays.

2) The Classes of Gnathostomata may be divided into those that lack rays on the hyoid arch (Pterichthyes and Coccostei) and the remainder that have; those that have rays may be separated into the Teleostomi which may have gular plates, an interhyal and opercular bones, and the Acanthodii and Elasmobranchii which lack these structures.

3) The branchiostegals are derivable from the hyoid rays of the Acanthodii.

4) The lateral and perhaps median gulars, operculum, suboperculum and interoperculum are derivable from expanded branchiostegals.

5) That there is an evolutionary tendency for branchiostegals to decrease is substantiated. Branchiostegals thus agree with Williston's Law. Generally, forms with more branchiostegals are more primitive within a group. Very rarely does the number of branchiostegals increase in a phyletic line.

6) Branchiostegals are divided into four types, a broad, laminar, paddle-shaped <u>spathiform</u>; a narrow, non-laminar, sword-shaped <u>acinaciform</u>, a thread- or string-like <u>filiform</u>; and a rod-like <u>virgaform</u> branchiostegal.

7) An anterior prominence, the <u>clupeoid projection</u>, is found at the base of branchiostegals of clupeoids and derived groups and a jutting angle, the <u>percopsid projection</u> on the anterior base of percopsoids, gadiforms and ophidiiforms.

8) Among other relationships suggested by the branchiostegal series and hyoid arch are:

a) The Hiodontidae are not closely related to the Notopteridae and require placement in a new suborder Hiodontoidei in the Clupeiformes.

b) The Notopteridae, Osteoglossidae, Arapaimidae, †Plethodidae, Pantodontidae and Heterotidae are removed from the Clupeiformes and placed in the enlarged order Mormyriformes.

c) The families Cetomimidae, Barbourisiidae and Rondeletiidae are considered related to the Alepisauroidei and placed in a new suborder, Barbourisoidei, of the Myctophiformes.

d) The †Tselfatoidei belong amongst the primitive Clupeiformes rather than amongst the Beloniformes.

e) The Anabantoidei and Ophicephaloidei are closely related acanthopterygian suborders which should be placed in the same order.

f) The ophidioids are placed in a new order, Ophidiiformes, and associated with the Gadiformes and Ateleopiformes near the Percopsiformes and placed amongst the prepercoid acanthopterygians.

g) The Amblyopsidae are removed from the Cyprindontiformes and placed in the Percopsiformes.

h) Evidence is found for a monophyletic origin of the Pleuronectiformes.

i) The division of the Actinopterygii into three major natural groups is confirmed: I (Chondrostei), II (Holostei) and III (Teleostei), the latter being divisable into the Malacopterygii and the Acanthopterygii. The group Mesichthyes is not substantiated, its members falling into either the Malacopterygii or the Acanthopterygii.

9) The branchiostegal series and hyoid arch were found to provide characters of diagnostic value. Several groups, such as the Mormyriformes, Anguilliformes, Beloniformes, Cyprinodontiformes, Phallostethoidei and Gobiesociformes are characterized by a loss of one or both hypohyals. The Beloniformes lack an interhyal. The Anguilliformes have elongate, slender branchiostegals which curve up around the operculum.

10) Lower numbers of branchiostegals may be associated with:

- a) small size (less than 3 inches or 7.5 cm.)
- b) short jaws - not extending behind a perpendicular through the posterior edge of the eye
- c) gill membranes not separate - either united and free from the isthmus or joined to the isthmus.

11) Numerous branchiostegals are generally retained by filter feeding fishes and by fishes with large jaws (enlarged posteriorly).

12) A low number of branchiostegals may place a restriction upon the posterior enlargement of the jaws.

13) Deepsea life may be accompanied by a reduction in ossification of the branchiostegal series and hyoid arch.

14) A replacement name, †Ichthyotringidae is proposed for the †Rhinellidae (Myctophiformes).

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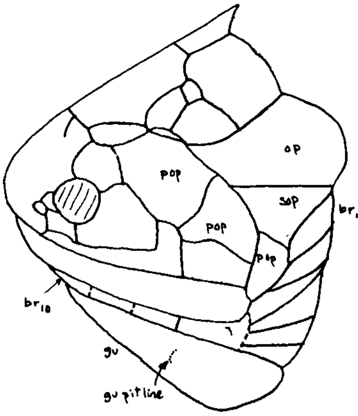
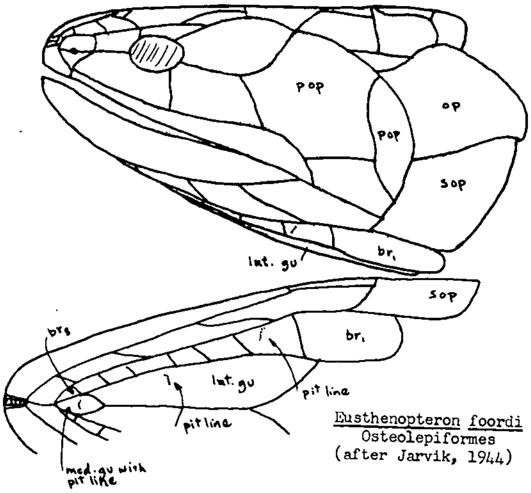
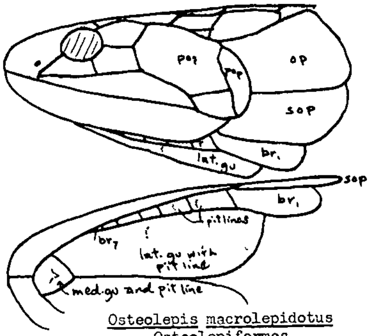


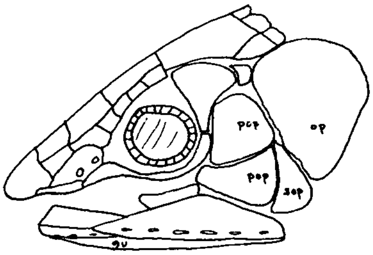
Holoptychius flemingi
Holoptychiformes
(after Stensio, 1947)



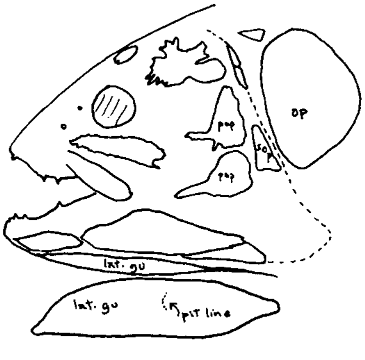
Eusthenopteron foordi
Osteolepiformes
(after Jarvik, 1944)



Osteolepis macrolepidotus
Osteolepiformes
(after Jarvik, 1948)

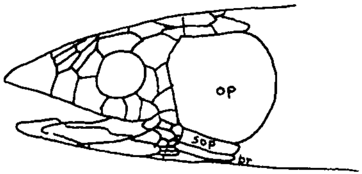


Whiteia - Coelacanthiformes
(after Moy-Thomas, 1937)

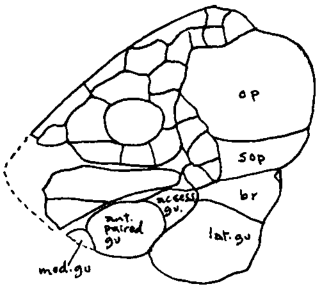


Latimeria chalumnae
Coelacanthiformes
(after Stensio, 1947;
Millot & Anthony, 1958)

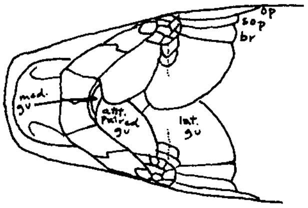
Plate I. Branchiostegal series in the Crossopterygii

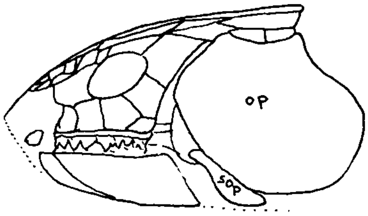


Dipterus valanciennesi
Dipteridae, -iformes
(after Graham-Smith &
Westoll, 1937)

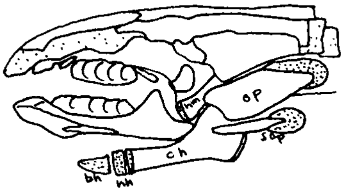


Scaumenacia curta
Scaumenacidae
Phaneropleuriformes
(after Stensio, 1947)





Sagenodus
Ctenodontidae, -iformes
(after Watson & Gill, 1923)



Neoceratodus forsteri
Ceratodidae, -iformes
(after Gregory, 1958)

Lepidosiren paradoxa
Lepidosirenidae, -iformes
(after Holmgren & Stensio,
1936; Bridge, 1898)

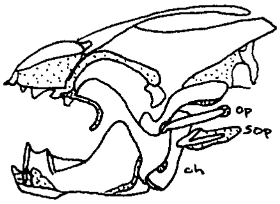
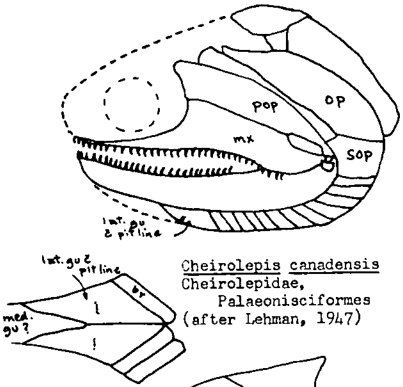
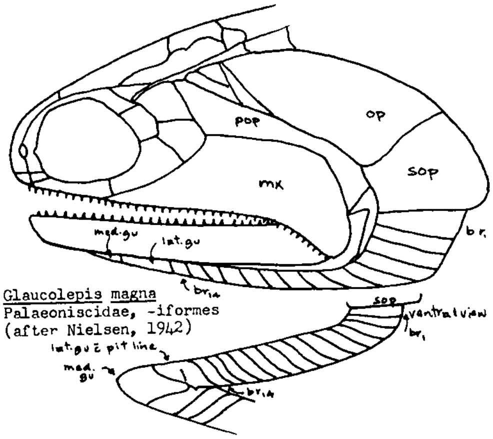


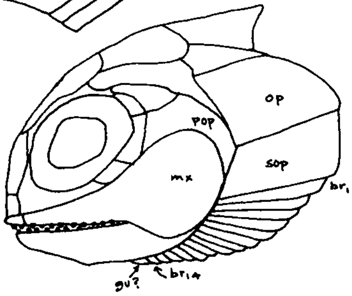
Plate II. Branchiostegal series in the Dipnoi.



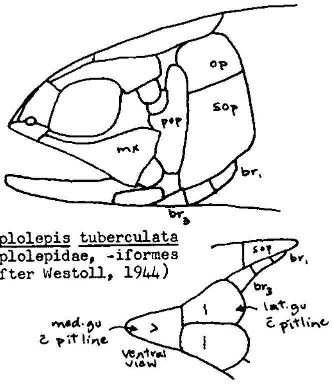
Cheirolepis canadensis
Cheirolepidae,
Palaeonisciformes
(after Lehman, 1947)



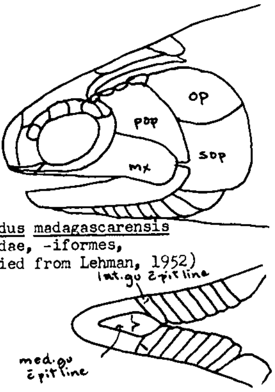
Glaucolepis magna
Palaeoniscidae, -iformes
(after Nielsen, 1942)



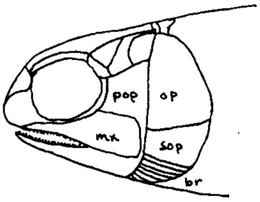
Tarrasius problematicus
Tarrasiidae, -iformes
(after Moy-Thomas, 1934)



Haplolepis tuberculata
Haplolepidae, -iformes
(after Westoll, 1944)

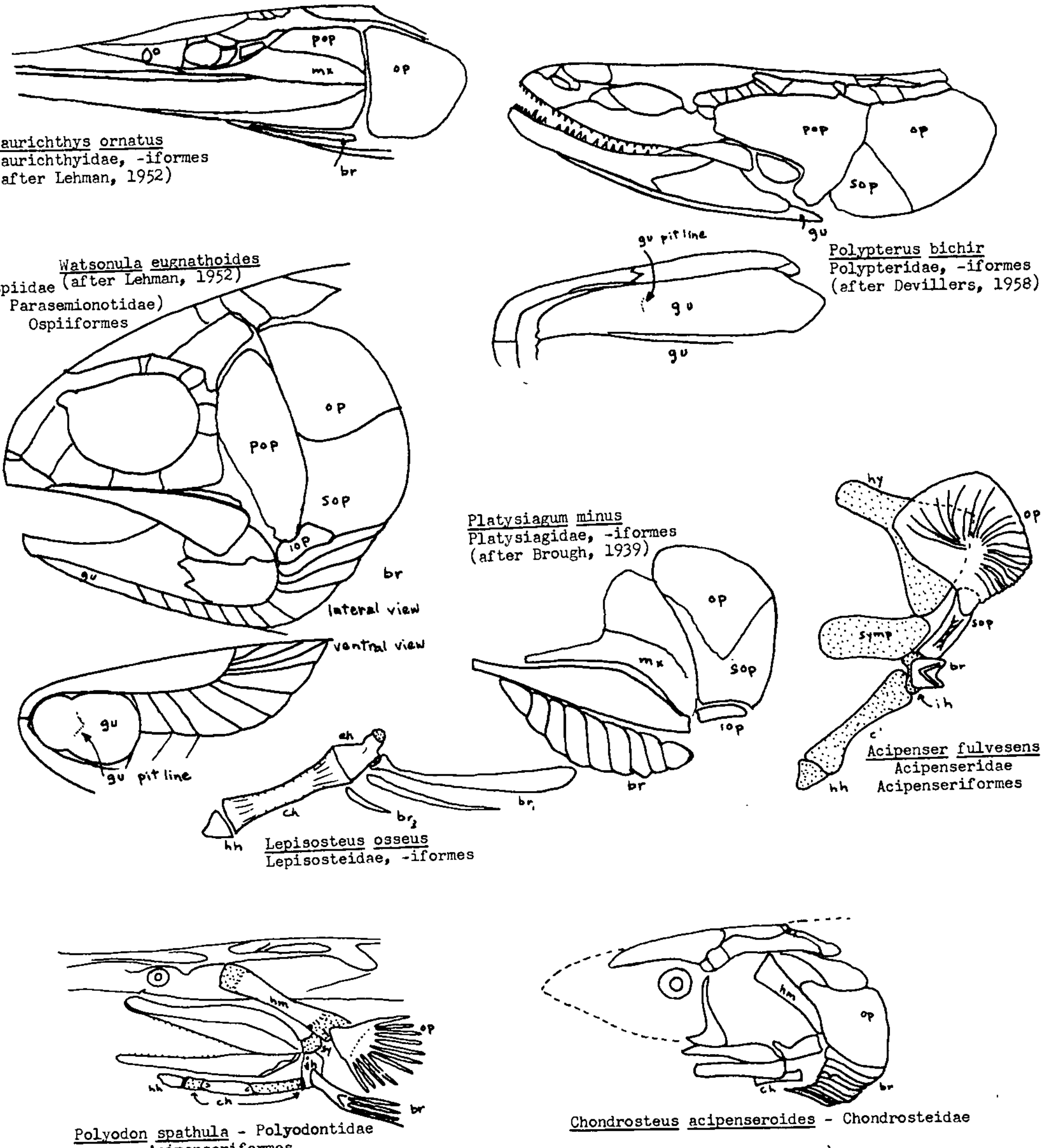


Perleidus madagascarensis
Perleidae, -iformes,
(modified from Lehman, 1952)



Peltopleurus rugosus
Peltopleuridae, -iformes
(after Brough, 1939)

Plate III. Branchiostegal series in the Actinopterygii (Chondrostei)



Saurichthys ornatus
Saurichthyidae, -iformes
(after Lehman, 1952)

Polypterus bichir
Polypteridae, -iformes
(after Devillers, 1958)

Watsonula eugnathoides
(after Lehman, 1952)
Ospiidae
(= Parasemionotidae)
Ospiiformes

Platysiagum minus
Platysiagidae, -iformes
(after Brough, 1939)

Acipenser fulvesens
Acipenseridae
Acipenseriformes

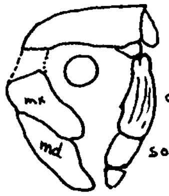
Lepisosteus osseus
Lepisosteidae, -iformes

Polyodon spathula - Polyodontidae
Acipenseriformes
(modified after Bertin, 1958)

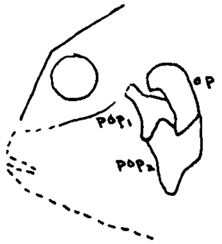
Chondrosteus acipenseroides - Chondrosteidae

(after Woodward, 1895)

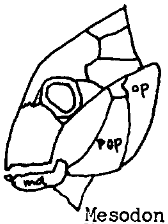
Plate IV. Branchiostegal series in the Actinopterygii (Chondrostei and Holostei) and Brachiopterygii



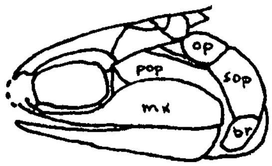
Dorypterus hoffmani
Dorypteridae, -iformes
(after Berg, 1947)



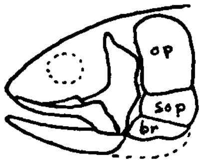
Bobasatrania groenlandica
Bobasatraniidae, -iformes
(after Stensio, 1932)



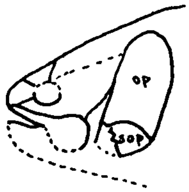
Mesodon macropterus
Gyrodontidae
- Pycnodontiformes
(after Berg, 1947)



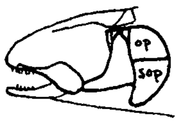
Brookvalia gracilis
Brookvaliidae -
Redfieldiiformes
(after Berg, 1955)



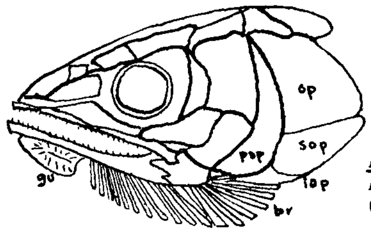
Ptycholepis barbori
Ptycholepidae, -iformes
(after Lehman, 1958)



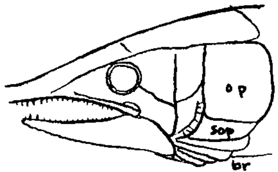
Cephaloxenus macropterus
Cephaloxenidae, -iformes
(after Lehman, 1958)



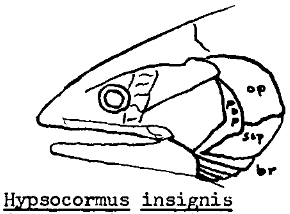
Luganoia lepidosteoides
Luganoidae, -iformes
(after Lehman, 1958)



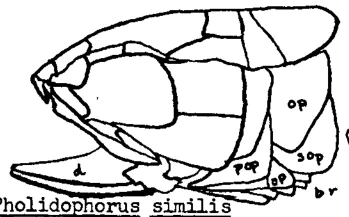
Caturus driani, Furidae
(= Caturidae) Amiiformes
(after Arambourg & Bertin, 1958)



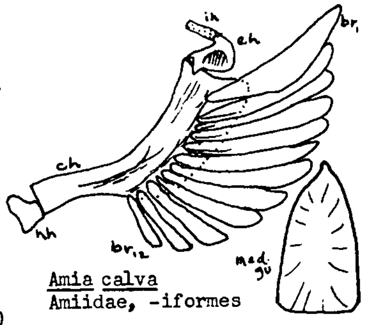
Aspidorhynchus acutirostris
Aspidorhynchidae, -iformes
(after Woodward, 1895)



Hypsocormus insignis
Pachycormidae, -iformes
(after Woodward, 1895)

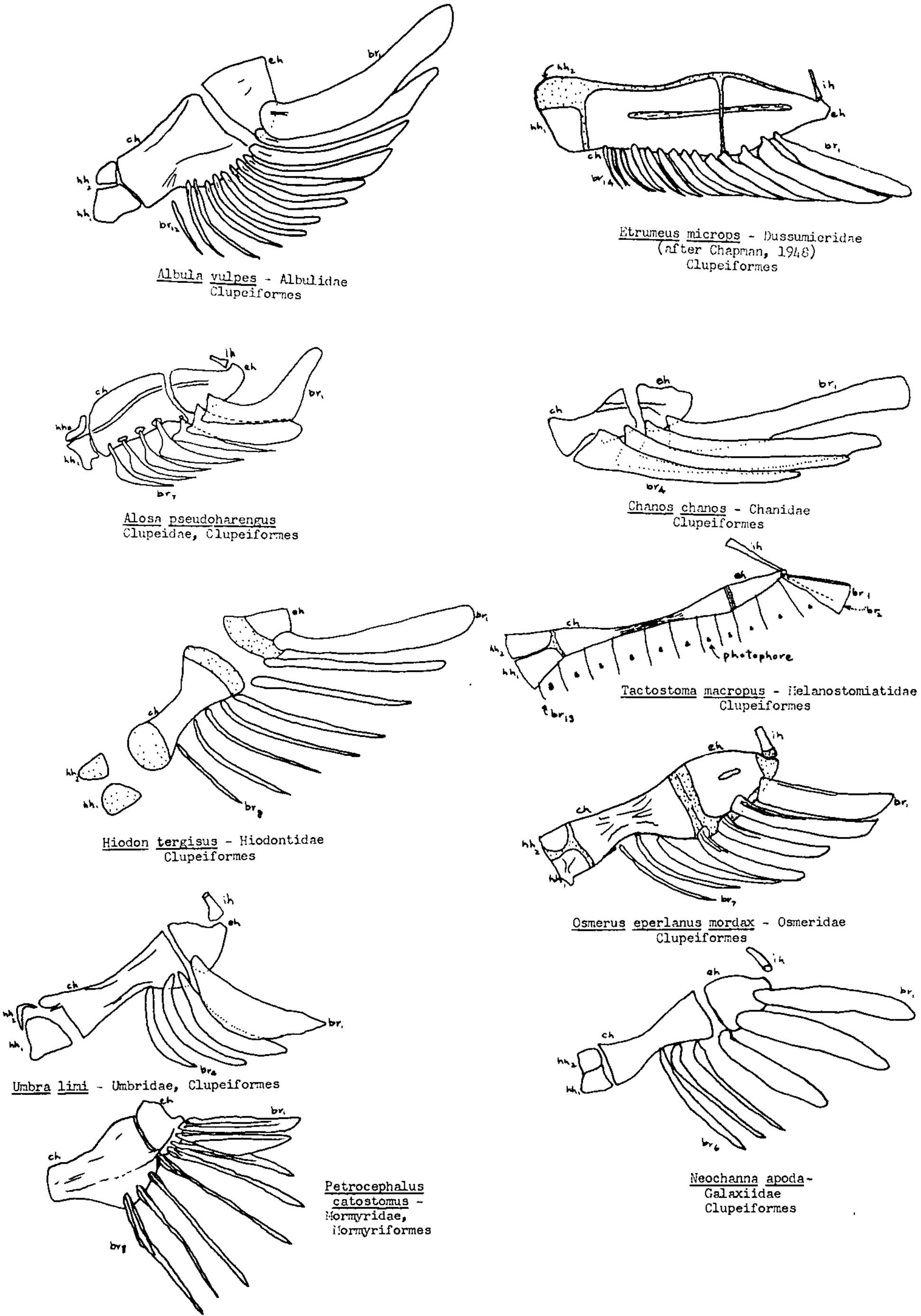


Pholidophorus similis
Pholidophoridae, -iformes
(after Arambourg & Bertin,1958)



Amia calva
Amiidae, -iformes

Plate V. Branchiostegal series in the Actinopterygii (Chondrostei and Holostei)



Albula vulpes - Albulidae
Clupeiformes

Etrumeus microps - Dussumieridae
(after Chapman, 1948)
Clupeiformes

Alosa pseudoharengus
Clupeidae, Clupeiformes

Chanos chanos - Chanidae
Clupeiformes

Tactostoma macropus - Melanostomiatidae
Clupeiformes

Hiodon tergisus - Hiodontidae
Clupeiformes

Osmerus eperlanus mordax - Osmeridae
Clupeiformes

Umbra limi - Umbridae, Clupeiformes

Neochanna apoda -
Galaxiidae
Clupeiformes

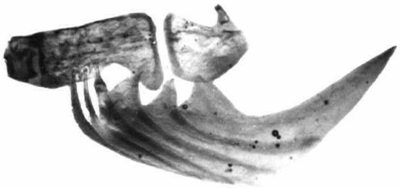
Petrocephalus catostomus -
Mormyridae,
Mormyriformes

Plate VI. Branchiostegal series and hyoid arch in the Actinopterygii (Malacopterygii)

Amia calva (lat.view head)
Amiidae. Amiiformes

Amia calva. Amiidae
Amiiformes

Hiodon tergisus. Hiodontidae
Clupeiformes

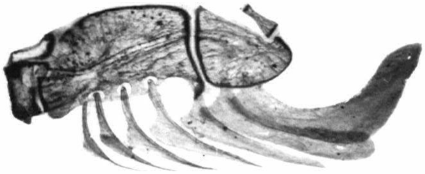


Dorosoma cepedianum Dorosomatidae
Clupeiformes

Gonorhynchus gonorhynchus
Gonorhynchidae. Clupeiformes

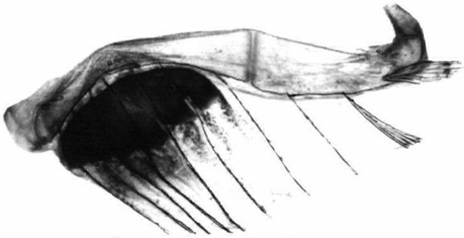
Anchoa hepsetus Engraulidae
Clupeiformes

Osmerus eperlanus mordax
Osmeridae. Clupeiformes



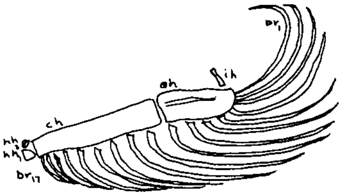
Pomolobus pseudoharengus
Clupeidae. Clupeiformes

Galaxias attenuatus
Galaxiidae. Clupeiformes

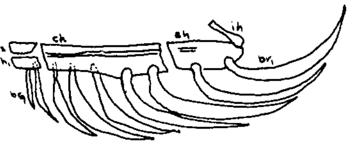


Argyropelecus olfersii
Sternoptychidae. Clupeiformes

Plate VII. Branchiostegal series and hyoid arch in the Actinopterygii (Holostei and Teleostei). (In these and the following photographic plates retouching was used to improve definition).

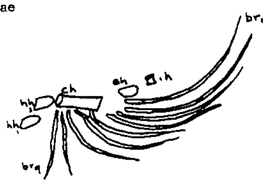


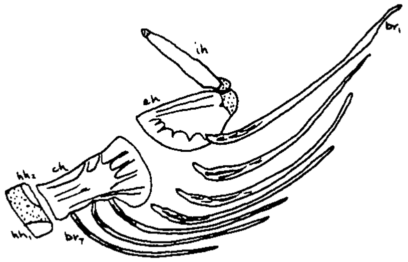
Synodus scituliceps - Synodontidae
Myctophiformes



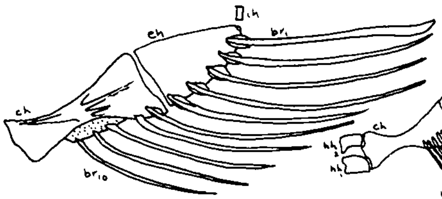
Tarletobeania crenularis - Myctophidae
Myctophiformes

Eutaeniophorus festivus
(after Bertelson & Marshall, 1956)
Eutaeniophoridae, Myctophiformes

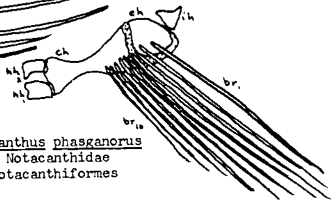




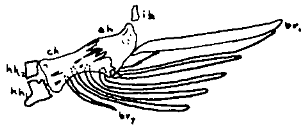
Ateleopus indicus - Ateleopidae
Ateleopiformes



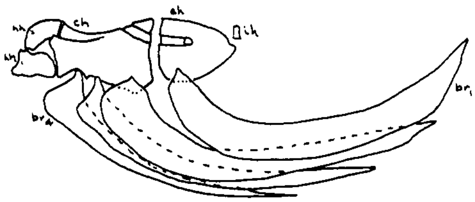
Halosauropsis affinis
Halosauridae
Notacanthiformes



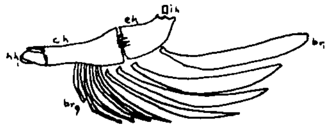
Notacanthus phasganorus
Notacanthidae
Notacanthiformes



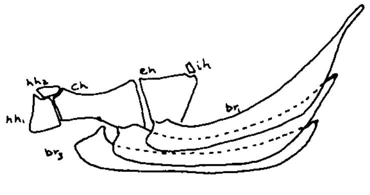
Synodontis woosnami - Mochokidae
Cypriniformes



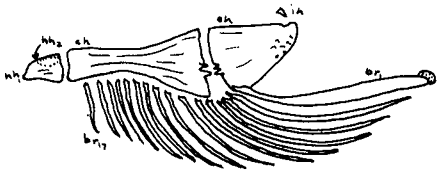
Astyanax fasciatus - Characidae
Cypriniformes



Amphilius platychir - Amphiliidae
Cypriniformes



Notemigonus crysoleucas - Cyprinidae
Cypriniformes



Silurus glanis - Siluridae
Cypriniformes

Ictalurus nebulosus - Ictaluridae
Cypriniformes

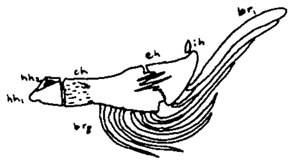
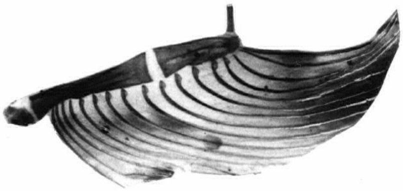


Plate VIII. Branchiostegal series and hyoid arch in the Actinopterygii (Malacopterygii)

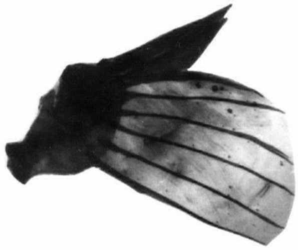


Synodus foetens, Synodontidae
Myctophiformes

Astyanax fasciatus. Characidae
Cypriniformes

Tarletobeania taylori. Myctophidae
Myctophiformes

Notemigonus crysoleucas
Cyprinidae. Cypriniformes

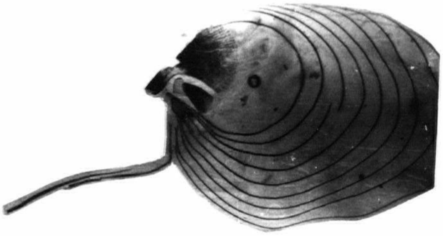


Petrocephalus catostoma. Mormyridae
Mormyriformes

Catostomus commersonii. Catostomidae
Cypriniformes

Gorgasia punctata, Congridae
Anguilliformes

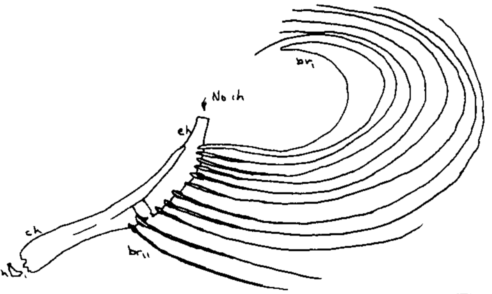
Cobitis taenia. Cobitidae
Cypriniformes



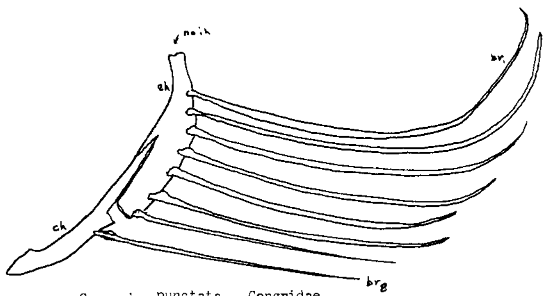
Gymnothorax dovii. Muraenidae
Anguilliformes

Galeichthys felis. Ariidae
Cypriniformes

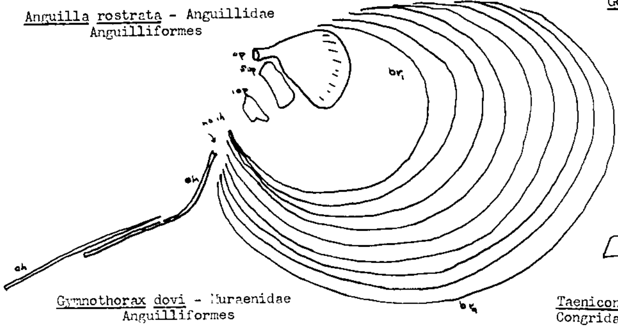
Plate IX. Branchiostegal series and hyoid arch in the Actinopterygii (Malacopterygii)



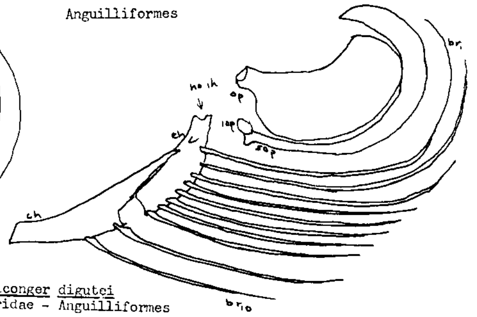
Anguilla rostrata - Anguillidae
Anguilliformes



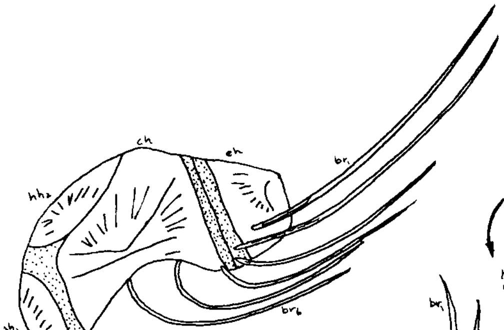
Gorgasia punctata - Congridae
Anguilliformes



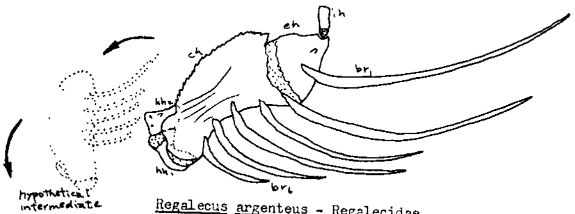
Gymnothorax dovi - Muraenidae
Anguilliformes



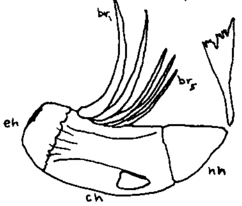
Taeniconger digutei
Congridae - Anguilliformes



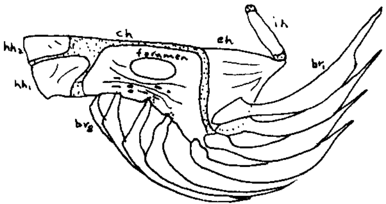
Trachipterus rexsalmonorum
Trachipteridae
Lampridiformes



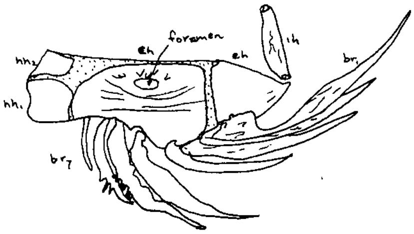
Regalecus argenteus - Regalecidae
Lampridiformes (after Parker, 1890)



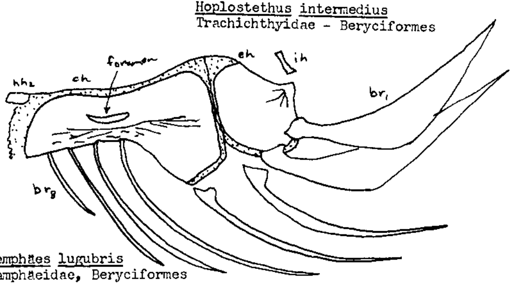
Stylephorus chordatus
Stylephoridae, Lampridiformes
(after Starks, 1908)



Hoplostethus intermedius
Trachichthyidae - Beryciformes

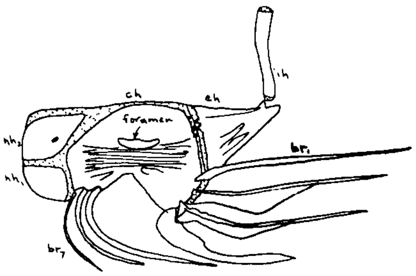


Monocentris japonicus
Monocentridae - Beryciformes

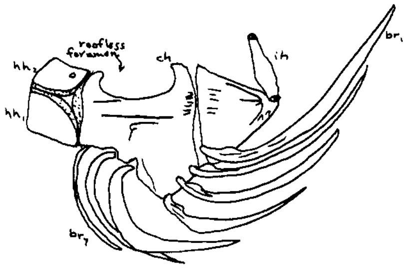


Melamphaes lugubris
Melamphaeidae, Beryciformes

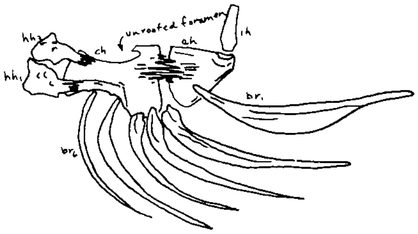
Plate X. Branchiostegal series and hyoid arch in the Actinopterygii (Malacopterygii and Acanthopterygii)



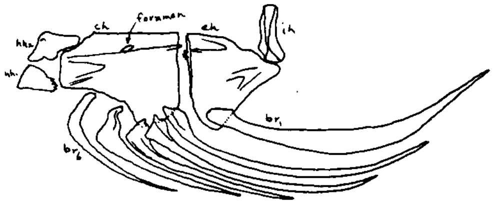
Zeus faber - Zeidae, Zeiformes



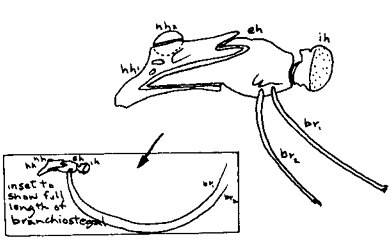
Neocyttus gibbosus, Oreosomatidae
(= Zeidae), Zeiformes



Aphredoderus sayanus gibbosus
Aphredoderidae, Percopsiformes

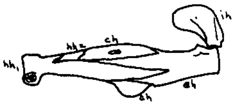


Percopsis omiscomaycus - Percopsidae,
Percopsiformes

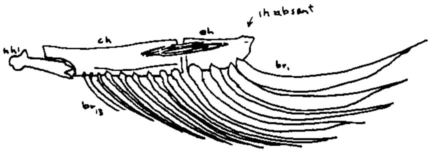


Syngnathus fuscus - Syngnathidae
Syngnathiformes

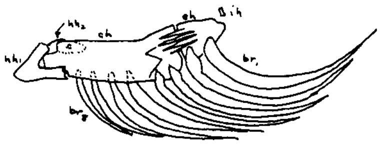
Fistularia petimba - Fistularidae, Syngnathiformes
(after Jungerson, 1910)



Aulostoma coloratum
Aulostomidae, Syngnathiformes
(after Jungerson, 1910)

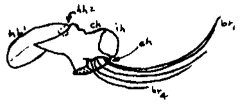


Belone houtuyni - Belonidae, Beloniformes



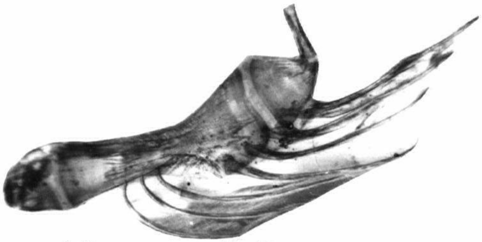
Remora remora - Echeneidae, Echeneiformes

Solenostomus cyanopterus - Solenostomidae
Syngnathiformes (?), (after Jungerson, 1910)



Centriscus
(= Amphisile) strigata Centriscidae
Syngnathiformes (after Jungerson, 1908)

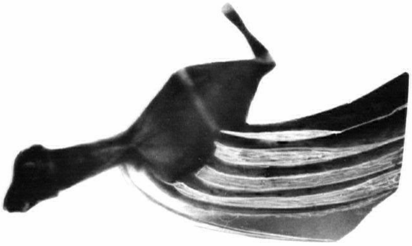
Plate XI. Branchiostegal series and hyoid arch in the Actinopterygii (Malacopterygii and Acanthopyerygii)



Antimora rostrata. Moridae
Gadiformes

Macrourus bairdii. Macrouridae
Gadiformes

Lota lota. Gadidae
Gadiformes

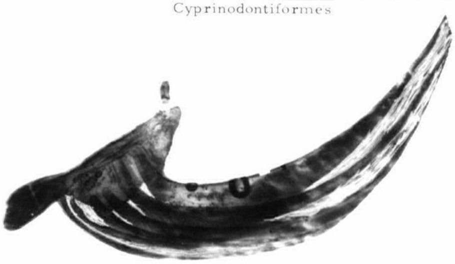


Typhlichthys subterraneus
Amblyopsidae. Percopsiformes

Aphredoderus sayanus gibbosus
Aphredoderidae. Percopsiformes

Neocyttus gibbosus. Oreosomatidae
Zeiformes

Poeciliopsis viriosa. Poeciliidae
Cyprinodontiformes

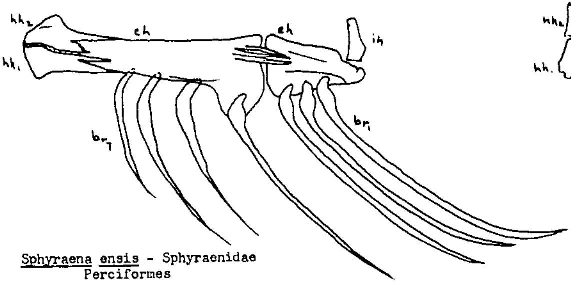


Anableps dowi
Anablepidae. Cyprinodontiformes

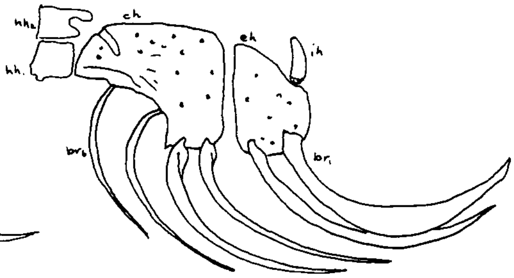
Xenotoca variata. Goodeidae
Cyprinodontiformes

Psettichthys melanostictus
Pleuronectidae. Pleuronectiformes

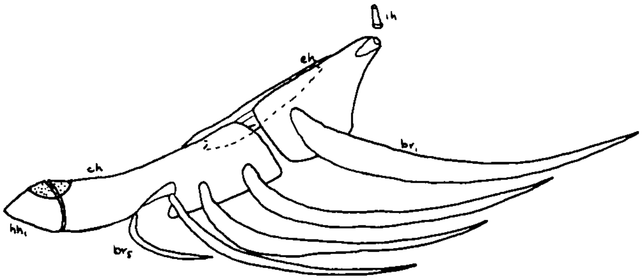
Plate XII. Branchiostegal series and hyoid arch in the Actinopterygii (Acanthopterygii)



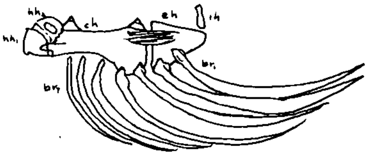
Sphyraena ensis - Sphyraenidae
Perciformes



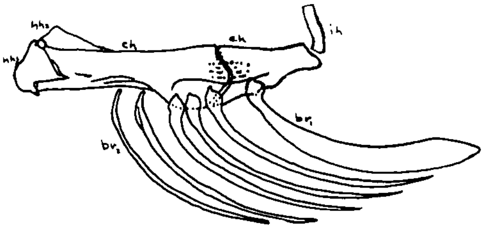
Peprilus palometa - Stromateidae
Perciformes



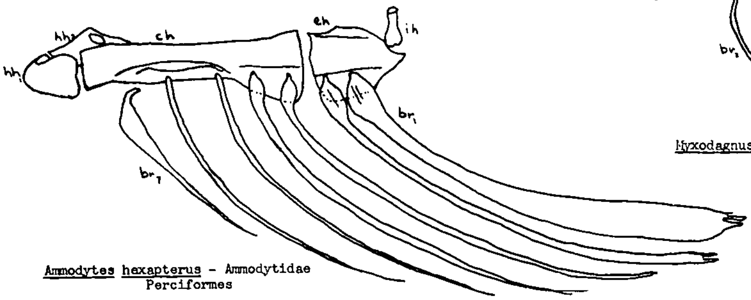
Gulaphallus mirabilis - Phallostethidae
Perciformes



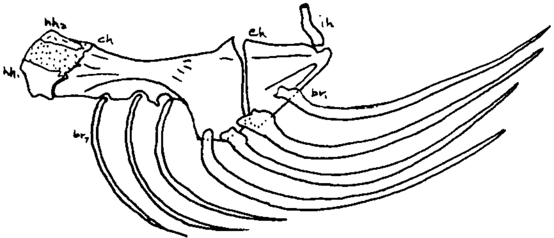
Roccus americanus - Serranidae
Perciformes



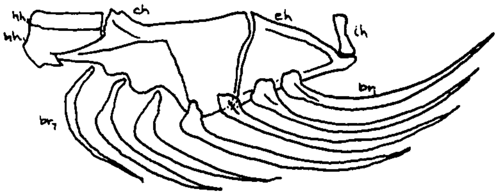
Myxodagnus opercularis - Dactyloscopidae
Perciformes



Ammodytes hexapterus - Ammodytidae
Perciformes

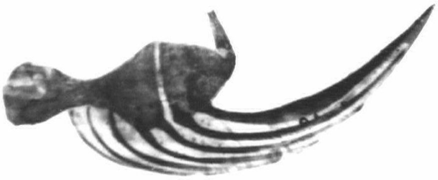


Sebastes marinus - Scorpaenidae
Perciformes



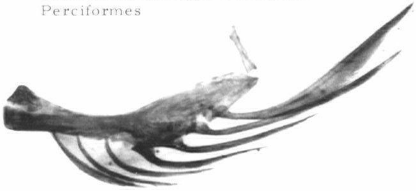
Ogilbia ventralis - Brotulidae
Ophidiiformes

Plate XIII. Branchiostegal series and hyoid arch in the Actinopterygii (Acanthopterygii)

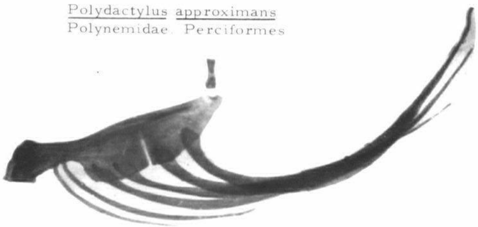


Perca flavescens. Percidae
Perciformes

Trachinotus falcatus. Carangidae
Perciformes



Polydactylus approximans
Polynemidae. Perciformes

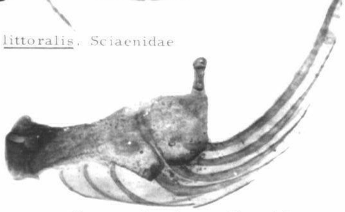


Menidia menidia. Atherinidae
Perciformes

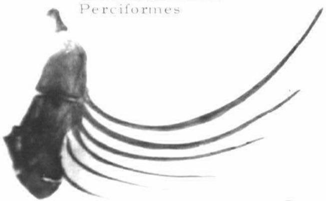
Cymatogaster aggregata
Embiotocidae. Perciformes

Trichodon trichodon. Trichodontidae
Perciformes

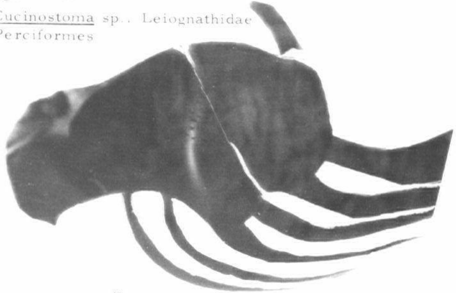
Menticirrhus littoralis. Sciaenidae
Perciformes



Toxotes jaculator. Toxotidae
Perciformes

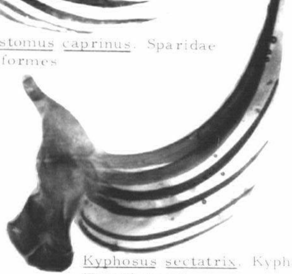


Eucinostoma sp.. Leiognathidae
Perciformes



Peprilus palometta. Stromateidae
Perciformes

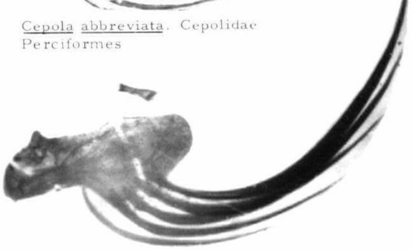
Stenostomus caprinus. Sparidae
Perciformes



Kyphosus sectatrix. Kyphosidae
Perciformes

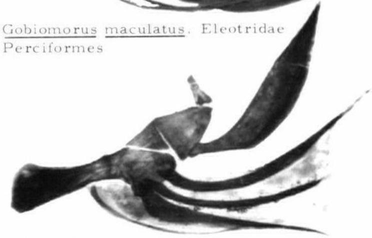
Plate XIV. Branchiostegal series and hyoid arch in the Actinopterygii (Acanthopterygii)

Cepola abbreviata. Cepolidae
Perciformes

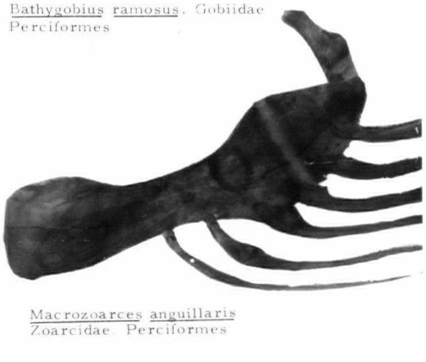


Cichlasoma beani. Cichlidae
Perciformes

Gobiomorus maculatus. Eleotridae
Perciformes



Bathygobius ramosus. Gobiidae
Perciformes



Macrozoarces anguillaris
Zoarcidae. Perciformes

Trematomus bernachii. Nototheniidae
Perciformes

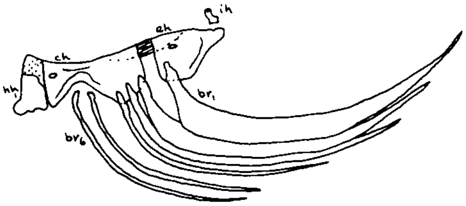
Hexagrammus stelleri. Hexagrammidae
Perciformes

Prionotus carolinus
Triglidae. Perciformes

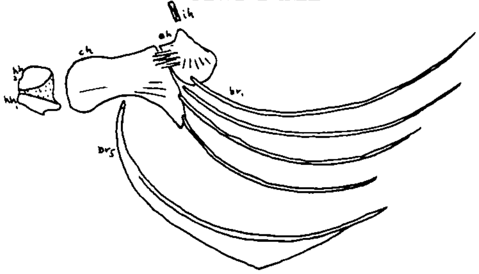
Aspidophoroides monopterygius
Agonidae. Perciformes

Liparis koefoedi
Liparidae. Perciformes

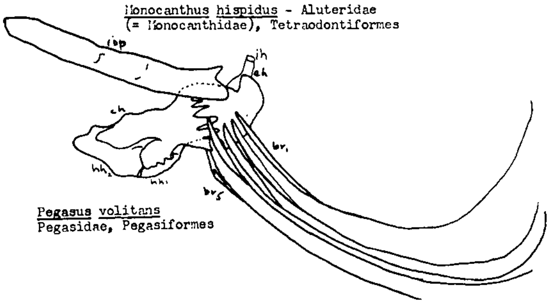
Plate XV. Branchiostegal series and hyoid arch in the Actinopterygii (Acanthopterygii)



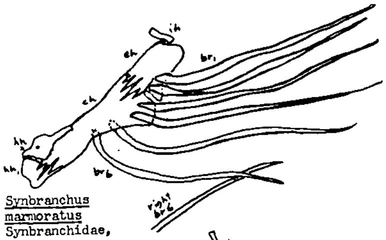
Fundulus diaphanus - Cyprinodontidae, -iformes



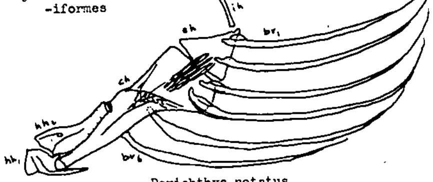
Monocanthus hispidus - Aluteridae
(= Monocanthidae), Tetraodontiformes



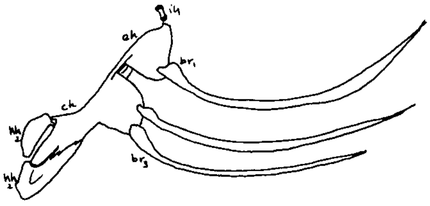
Pegasus volitans
Pegasidae, Pegasiformes



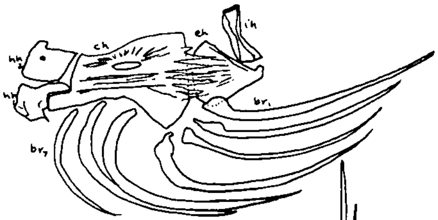
Synbranchus
marmoratus
Synbranchidae,
-iformes



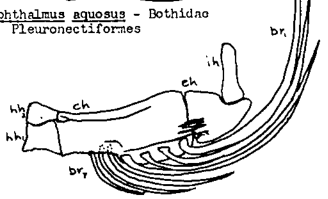
Porichthys notatus
Batrachoididae
Batrachoidiformes



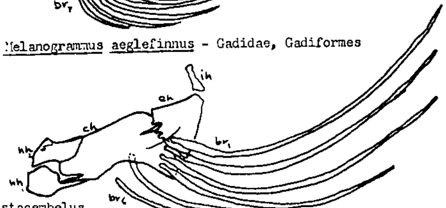
Pungitius pungitius - Gasterosteidae
Gasterosteiformes



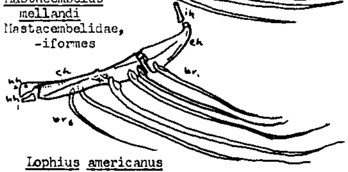
Scophthalmus aquosus - Bothidae
Pleuronectiformes



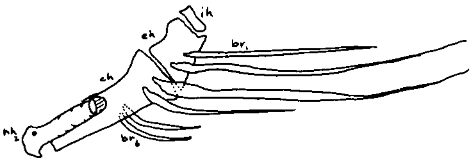
Melanogrammus aeglefinnus - Gadidae, Gadiformes



Mastacembelus
mellandi
Mastacembelidae,
-iformes



Lophius americanus
Lophiidae, -iformes



Gobiesox maeandricus
Gobiesocidae, -iformes

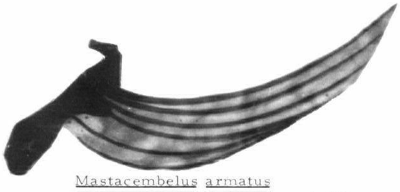
Plate XVI. Branchiostegal series and hyoid arch in the Actinopterygii (Acanthopterygii)

Aulorhynchus flavidum
Aulorhynchidae. Gasterosteiformes

Pungitius pungitius
Gasterosteidae. Gasterosteiformes

Gasterosteus aculeatus
Gasterosteidae. Gasterosteiformes

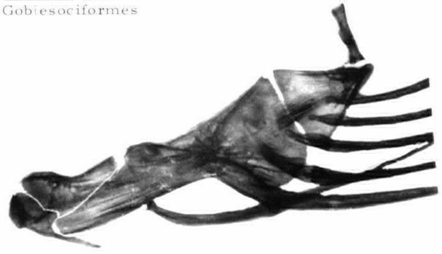
Culaea inconstans. Gasterosteidae
Gasterosteiformes



Mastacembelus armatus
Mastacembelidae. Mastacembeliformes

Synbranchus marmoratus
Synbranchidae, Synbranchiformes

Gobiesox maeandricus. Gobiesocidae
Gobiesociformes



Porichthys notatus. Batrachoididae
Batrachoidiformes

Plate XVII. Branchiostegal series and hyoid arch in the Actinopterygii (Acanthopterygii)

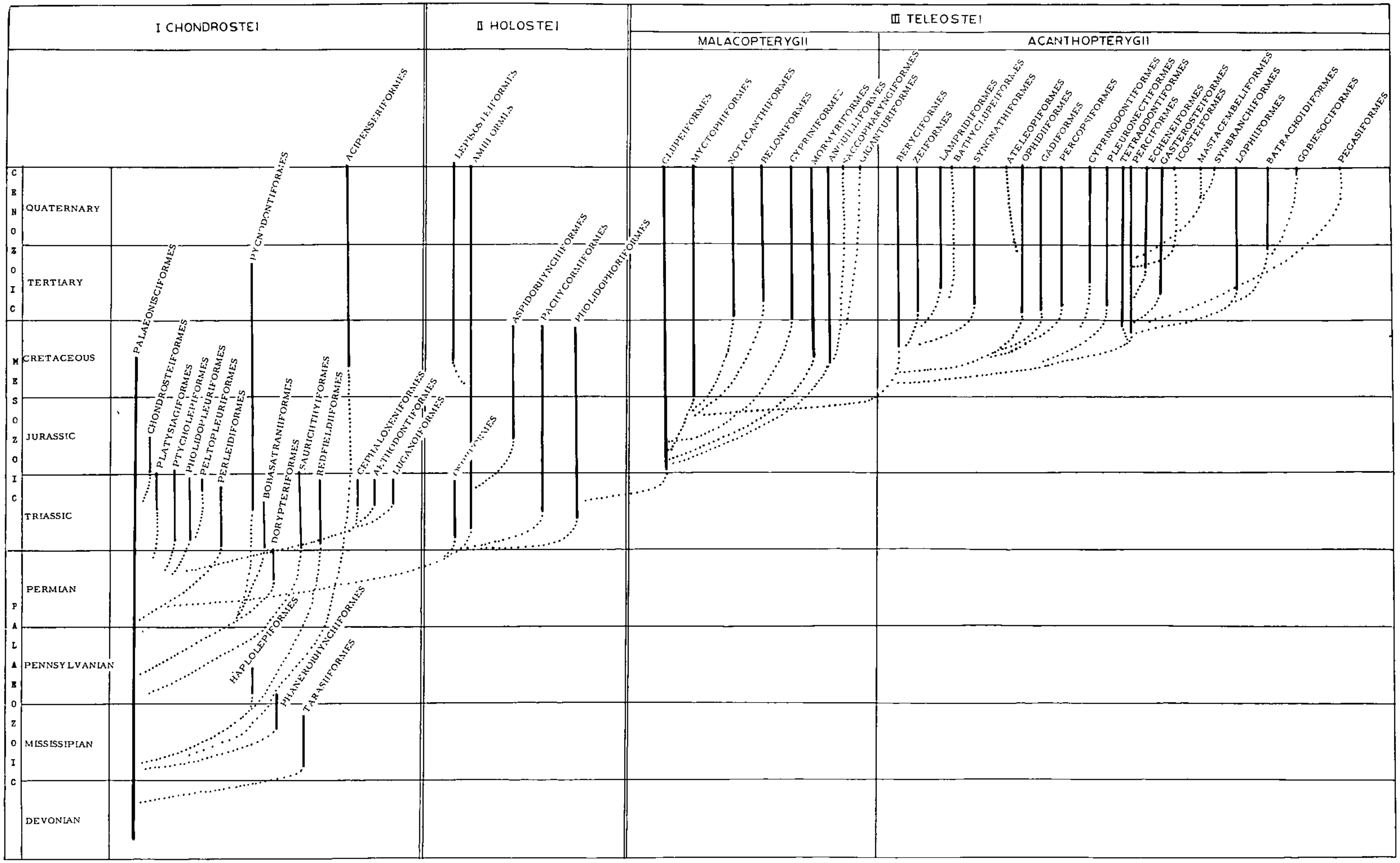


Plate XVIII. Evolutionary relationships of the teleostome fishes. Based on the study of the branchiostegal series and hyoid arch and on other characters. Solid lines represent fossils, dotted lines suggest relationships.